DIE GEFÄHRDUNG DER KNÄUEL-GLOCKENBLUME *CAMPANULA GLOMERATA* L. IN DEUTSCHLAND

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THE ENDANGERMENT OF THE CLUSTERED BELLFLOWER *CAMPANULA GLOMERATA* L. IN GERMANY

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GUTACHTER:

1. PROF. J. HENSEN (HALLE)
2. PROF. H. BRUELHEIDE (HALLE)
3. PROF. CHR. OBERPRIELER (REGENSBURG)

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INHALTSVERZEICHNIS

KAPITEL I

EINLEITUNG UND FRAGESTELLUNGEN

Aufgrund der Zerstörung, Veränderung und Fragmentierung ihrer Lebensräume sind viele Pflanzen in den letzten Jahrzehnten stark zurückgegangen und kommen heute vor allem in kleinen, isolierten Populationen vor. Derartige Populationen werden durch demographische und genetische Prozesse sowie durch die Störung mutualistischer Beziehungen (z.B. mit Bestäubern) und Umweltschwankungen besonders bedroht (Matthies & Poschlod 2000). Im Zusammenhang mit Landnutzungsänderungen als Ursache für den Rückgang von Pflanzenarten muss die Tatsache, dass in der traditionell genutzten Kulturlandschaft die Besiedlung neu geschaffener Standorte bzw. der Austausch von Individuen zwischen den Populationen unterbunden sein kann, betrachtet werden. Für eine zusammenfassende Analyse der Gefährdung einzelner Pflanzenpopulationen durch zunehmende Fragmentierung und Isolation der Habitate fehlen bisher die Grundlagen (Schmid & Matthies 1994), auch wenn „Risikofaktoren, die aus der Biologie der Art resultieren“ in den „Skalen zur Erfüllung der Kriterien der Einschätzung der Gefährdung“ bei der Erstellung der Roten Liste (Korneck et al. 1996) bereits beachtet worden sind (Poschlod et al. 1999). Die Kenntnisse zu artspezifischen Gefährdungsfaktoren von kleinen, lokal isolierten Populationen seltener Arten, zu den Auswirkungen der Fragmentierung von Lebensräumen auf Pflanzen und zum Flächenbedarf des Naturschutzes sind noch begrenzt. Die in den letzten Jahren entwickelten Ansätze basieren auf einer Weiterentwicklung der Theorie der Inselbiogeographie (MacArthur & Wilson 1967) unter Verwendung populationsbiologischer Methoden, mit denen Prognosen zur Überlebenschance von Arten möglich werden. Solche Prognosen werden als Populationsgefährdungsanalysen (population viability analysis, PVA) bezeichnet.

Eine PVA ist ein komplexes Verfahren, bei dem alle Faktoren betrachtet werden, die das Aussterben einer Art bewirken können (Gilpin & Soulé 1986). Gefährdungsanalysen stellen somit einen Kernbestandteil der Naturschutzforschung und des praktischen Naturschutzes dar (Henle et al. 1999). Um die Basis für allgemein gültige Empfehlungen für den Naturschutz zu verbessern ist es dringend notwendig, zurückgehende und auch stabile Arten populationsbiologisch zu untersuchen (Schmid & Matthies 1994). In absehbarer Zeit wird daher ein Leitfaden zur Erstellung von Gefährdungsanalysen von Nöten sein, um die Ergebnisse vergleichbar und allgemein anwendbar zu machen.

Amler et al. (1999), Poschlod et al. (1999) und Burgmann & Possingham (2000) fassen zusammen, dass Populationsgefährdungsanalysen neben Kenntnissen zur genetischen Variabilität und deren Auswirkung auf demographische Faktoren auch Informationen zum Austausch zwischen Teilpopulationen, Daten über den individuellen Raumanspruch, zu Reproduktion, Mortalität, Wachstum und der Kapazität des Lebensraumes enthalten sollten. Ebenso sollte der Einfluss von Umweltschwankungen auf diese Faktoren bekannt sein. Auch Wechselwirkungen mit weiteren Arten können für eine Einschätzung der Überlebenschancen wesentlich sein. Schließlich müssen auch die vielfältigen Aspekte der Überlebensstrategien von Pflanzen in Populationsgefährdungsanalysen Berücksichtigung finden. Oft werden Gefährdungsanalysen nur mit der Modellierung des Schicksals von Populationen in Verbindung gebracht. Diese Betrachtungsweise beinhaltet jedoch zwei Risiken: zum einen die Gefahr, dass man sich mit dem aktuellen Zustand zufrieden gibt, statt zu versuchen, dem Rückgang einer Art entgegenzuwirken, zum anderen können nur auf Modellierung beruhende Gefährdungsanalysen ohne eine sorgfältige Analyse der Rückgangsursachen an den tatsächlichen Problemen vorbeigehen (Henle et al. 1999). Boyce (1992) empfiehlt für eine Gefährdungsanalyse vordergründig eine Analyse des Ausmaßes des Rückgangs einer Art und der dafür verantwortlichen Ursachen. Erst anschließend kann - mit oder ohne Hilfe von quantitativen Modellen - eine Prognose über die Überlebenschancen erstellt werden.

Eine Pflanzenart, welche auf Grund von Zerstörung, Veränderung und Fragmentierung in Sachsen Anhalt und anderen Bundesländern als gefährdet gilt, ist die Knäuel-Glockenblume *Campanula glomerata* (Sebold et al. 1996, Jedicke 1997, Frank & Neumann 1999, Hardtke & Ihl 2000). Der Rückgang dieser Art bestätigt den Bedarf einer Gefährdungsanalyse und der damit verbundenen Entwicklung von sinnvollen Schutz- und Pflegemaßnahmen. Die derzeitige Bestandssituation von *C. glomerata* erlaubt es, umfangreiche Untersuchungen zur Biologie der Art durchzuführen, ohne die bestehenden Vorkommen wesentlich zu beeinträchtigen.

In der vorliegenden Arbeit zur Gefährdung der Knäuel-Glockenblume in Deutschland sollen zum einen die Gefährdungssituation der Art abgeschätzt und zum anderen, Vorgaben zum Inhalt von Populationsgefährdungsanalysen ausgearbeitet werden um damit zur Optimierung eines für die naturschutzfachliche Bewertung von Pflanzenpopulationen wichtigen Instrumentes beizutragen. Dazu wurden vier Forschungsschwerpunkte ausgearbeitet, in denen das von Amler et al. (1999), Poschlod et al. (1999) und Burgmann & Possingham (2000) zusammengefasste Spektrum des zur Gefährdungsabschätzung von Pflanzen nötigen Wissens beinhaltet ist.

Einen ersten Schwerpunkt bildete die genetische Konstitution der Art. Die Populationsgenetik spielt eine wichtige Rolle bei Schutz und Management bedrohter Arten. Eine hohe genetische Diversität innerhalb von Arten und Einzelpopulationen wird als Vorraussetzung für die Anpassung an variable Umweltbedingungen, für die langfristige Evolutionsfähigkeit einer Art sowie für eine höhere Fitness von Individuen oder Populationen betrachtet. Isolation und geringe Populationsgrößen wirken sich auf Diasporenproduktion, Diasporengewichte, Keimraten und Wüchsigkeit der Pflanzen aus (z.B. Amler et al. 1999, Kery et al. 2000, Jacquemyn et al. 2002, Paschke et al. 2002, Veerger et al 2003, Brys et al. 2004, Hensen & Oberprieler 2005). Kleine Populationsgrößen und hoher Isolationsgrad, d.h. geringer Genfluss, können die genetische Konstitution einer Population folgendermaßen beeinflussen: Einerseits verursacht genetische Drift einen Verlust genetischer Variabilität (Oostermeijer et al. 1996, Richards 2000, Allendorf & Ryman 2002). Kurzfristig kann dies die Anfälligkeit gegenüber Pathogenen erhöhen. Andererseits führt verringerte genetische Variabilität auch vermehrt zu Inzucht. Als Folge von Inzuchtdepression reduziert sich häufig die Vitalität einer Population (z.B. Ellstram & Elam 1993, Kahmen & Poschlod 2000, Frankham et al. 2002, Vergeer et al. 2003). Eine geringere genetische Diversität verringert das Potenzial der evolutionären Anpassung und gefährdet so den Fortbestand einer Population. Durch die Fixierung und Ansammlung leicht schädlicher Mutationen in kleineren Populationen kommt es zu einer Reduktion der Fitness einzelner

Pflanzen (Fischer & Matthies 1998). In Kapitel II „**Is the declining *Campanula glomerata* threatened by genetic factors?”** wurden die genetische Variabilität und deren Auswirkungen auf Populationsgröße und Pflanzenfitness untersucht und Informationen zum genetischen Austausch zwischen den Populationen ausgewertet. Das Ziel dieser Studie war, die Bedeutung der genetischen Konstitution für die Überlebenswahrscheinlichkeit von *C. glomerata* zu eruieren. Folgende Fragestellungen wurden dafür untersucht: Wie verhält es sich mit der genetischen Differenzierung innerhalb der Populationen und im Vergleich untereinander? Besteht zwischen genetischer Differenzierung und geographischer Distanz zwischen den Populationen eine Beziehung? Gibt es Zusammenhänge zwischen genetischer Variation, der Populationsgröße und Fitnessparametern?

Es wird davon ausgegangen, dass neben der genetischen Variabilität und der Populationsgröße auch andere Faktoren wie z.B. die Vegetationszusammensetzung, Bodeneigenschaften, Klima oder Bewirtschaftungsform einen Einfluss auf die Reproduktion von Pflanzenarten haben können (Schmidt & Jensen 2000, Vergeer et al. 2003, Fischer 1996). Die Habitatansprüche bzw. das Maß der Toleranz einer Art gegenüber sich ändernden Umweltbedingungen sind ebenfalls wesentliche, sich auf die Gefährdung einer Population auswirkende Faktoren. Ein weiterer Forschungsschwerpunkt beinhaltet daher Untersuchungen zur Habitatqualität und deren Auswirkung auf Populationsgröße und Fitness von *C. glomerata*. In Kapitel III „**Is habitat quality affecting population size and plant performance in the declining forb *Campanula glomerata*”** wurden Habitatparameter (Bodeneigenschaften, Landnutzung und Vegetation) der Populationsgröße und Fitnessparametern von *C. glomerata* gegenübergestellt. Es sollte die Frage beantwortet werden, ob diese Faktoren einen Einfluss auf die Populationsgröße und die Fitness von *C. glomerata* haben.

Als Hauptursache für den Rückgang der Knäuel-Glockenblume werden sowohl die ausbleibende als auch die intensivierte Form der Landnutzung diskutiert (Frank & Neumann 1999, Hardtke & Ihl 2000). Mit beiden Faktoren ist die Änderung wesentlicher Standortfaktoren verbunden. *C. glomerata* als Festuco-Brometea-Art kommt nach Oberdorfer (2001) vor allem im Mesobromion und im Cirsio-Brachypodion vor. Die meisten Trocken- oder Magerrasen verdanken der Mahd und der Beweidung nicht nur ihre Existenz, sondern erfahren erst durch die Art der Bewirtschaftung das ihnen eigene Artengefüge (Pott 1996), so dass eine ausbleibende bzw. intensivierte Form der Bewirtschaftung nicht nur für die entsprechenden Pflanzengesellschaften, sondern auch für spezielle Pflanzenarten eine Gefährdung darstellt. Dem wichtigen Aspekt der Entwicklung von *C. glomerata* Populationen nach Nutzungsaufgabe wurde in Kapitel IV „**Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use-practices?”** nachgegangen. Hier wurde untersucht, inwieweit sich die Nutzungsaufgabe auf die Entwicklung der Populationsgrößen von *C. glomerata* auswirkt. In einer dreijährigen Studie wurden verschiedene Daten zur Populationsgröße in traditionell genutzten und nicht mehr genutzten Populationen miteinander verglichen.

Im Zusammenhang mit dem Wegfall traditioneller Landnutzung stellten WallisDeVries et al. (2002) fest, dass ausbleibende Beweidung eine Hauptursache für die Umwandlung artenreicher in artenarme Pflanzengesellschaften ist. Da die Aufgabe der traditionellen Landnutzung nicht nur zu verringerter Biodiversität (Balmer & Erhardt 2000, Poschlod & WallisDeVries 2002) sondern auch zur

Änderung von Dominanzverhältnissen führt, ist es wegen des hohen Risikos eines Konkurrenzausschlusses wichtig, auch die Effekte sich ändernder Konkurrenzverhältnisse zu untersuchen (Berendse 1983). Partzsch (2001) beschreibt für die Porphyrkuppenlandschaft des unteren Saaletals einen Umbau ehemals artenreicher Halbtrockenrasen mit *C. glomerata*-Vorkommen in *Festuca rupicola*- oder *Poa angustifolia*-Dominanzbestände durch den Wegfall der traditionellen Bewirtschaftungsweise. In einem Konkurrenzversuch (replacement design) sollte daher untersucht werden, wie die Knäuel-Glockenblume auf die Konkurrenz dieser sich ausbreitender Grasarten reagiert. Mit Hilfe der Ergebnisse aus Kapitel V „**Is *Campanula glomerata* threatened by competition of expanding grasses?”** sollte eingeschätzt werden, wie eine veränderte Konkurrenzsituation das Überleben der Art gefährden kann.

DIE ART *CAMPANULA GLOMERATA*

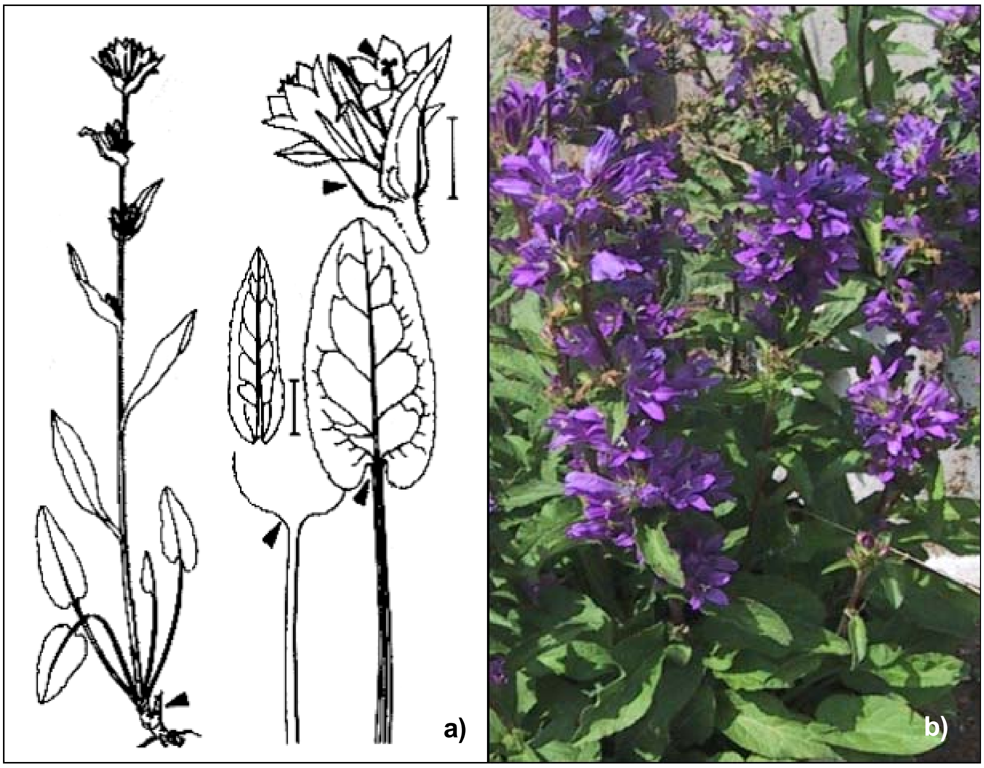

Abbildung I/1: *Campanula glomerata* a) Habitus (Rothmaler 2000), b) Pflanzen im Topfversuch (Photo: Urte Bachmann)

Die Knäuel- oder Büschel-Glockenblume *Campanula glomerata* L. (Abb. I/1) ist eine ausdauernde, etwa 15 bis 70cm hohe Pflanze. Die Grundblätter sind lang gestielt, länglich oval mit herzförmigen Grund, während die Stängelblätter sitzend oder nur kurz gestielt und von ovaler bis schmal linealer Gestalt sind. Die dunkelvioletten Blüten sind in endständigen, oft auch in den Achseln der oberen Stängelblätter sitzenden, am Grunde von verbreiterten Hochblättern gestützten Köpfchen zusammengefasst. Die trichterförmigen Blüten werden 15 bis 30mm lang.

Ein *C. glomerata* Individuum kann bis zu 30 Jahre alt werden (Piskovackova 1980). Als sterile Rosette erscheint die Art vor dem reproduktiven Stadium, aber auch im Ruhe- oder Seneszenz-Stadium. Generative Reproduktion beginnt meist im zweiten Jahr nach der Keimung (Piskovackova 1980). Im Freiland bilden die meisten Rosetten nur einen Blühtrieb. Die Blüte- und Fruchtzeit erstreckt sich von Juni bis September. Die Blüten sind an die Bestäubung durch Insekten, besonders Hymenopteren, angepasst. Die Antheren bilden eine Röhre und entleeren den Pollen noch in der Blütenknospe auf den stark behaarten Griffel. Die Narbenäste sind zu diesem Zeitpunkt noch geschlossen. Am Blütenboden sezerniert ein flacher Drüsenring Nektar. Der wachsende Griffel bürstet den Pollen aus der Röhre heraus und nektarsammelnde Insekten werden mit Pollen eingestäubt. In der nächsten Phase biegen sich die Narbenäste nach unten, so dass die fertile Narbenfläche von Insekten bestäubt werden kann. Selbstbestäubung kann vorkommen, wenn sich die Narbenäste so weit umrollen, dass sie mit ihrem eigenen Pollen in Berührung kommen (Sebold et al. 1996); häufig wurde jedoch Selbststerilität beobachtet (Podlech 1965). Die behaarten, sich am Grunde mit drei Poren öffnenden Kapseln entlassen kleine, rundlich ovale Samen (Hegi 1918). Eine Kapsel kann über 100 Samen enthalten, die vorwiegend durch den Wind verbreitet werden (Emig & Leins 1994, Frank & Klotz 1990). Die vegetative Vermehrung erfolgt über Rhizome (Klotz et al. 2002).

Nach Oberdorfer (2001) kommt *C. glomerata* auf Kalk-Magerrasen oder mageren Wiesen, im Saum lichter Büsche und an Wald- und Wegrändern vor. Die Art bevorzugt sommerwarme, mäßig frische, mehr oder weniger nährstoff- und basenreiche, vorzugsweise kalkhaltige, aber auch mäßig saure Standorte mit humosen, lockeren Lehm- und Lößböden. Ellenberg et al. (2001) bezeichnen die Knäuel-Glockenblume als Halblichtpflanze mit indifferentem Temperaturverhalten, die im Gefälle der Bodenfeuchtigkeit auf trockenen Böden ebenso wie auf mittelfeuchten Böden vorkommen kann. Die kontinentale Art hat in Europa und Sibirien einen submeridional bis borealen Verbreitungsschwerpunkt (Rothmaler 2002). Der deutsche Arealbereich ist Teil des Hauptareals der Art, der Flächenanteil Deutschlands am Gesamtareal beträgt allerdings weniger als 10% (ermittelt und abgeschätzt nach Welk 2001). Nach Partzsch (2001) weist *C. glomerata* eine Bindung zu historisch alten Standorten auf und konnte als Zeiger für langfristige Standorts- und Vegetationsentwicklung unter relativ konstanten Bedingungen (traditionelle Bewirtschaftung) benannt werden.

Die Knäuel-Glockenblume kommt in Sachsen-Anhalt selten bis mäßig häufig vor. Die derzeit rückgängige Bestandssituation wird mit Nutzungsaufgabe und Sukzession begründet (Frank & Neumann 1999). Im Nachbar-Bundesland Sachsen ist in der Bestandsentwicklung ebenfalls ein starker Rückgang zu verzeichnen. Als Gründe dafür werden von Hardtke & Ihl (2000) ebenfalls Aufgabe der Nutzung, aber auch Nutzungsintensivierung, Eutrophierung und zu frühe Mahd- oder Beweidungstermine angegeben. Briemle & Ellenberg (1994) teilten der Knäuel-Glockenblume die Mahdverträglichkeitszahl 5 zu. Das bedeutet, dass die Art mäßig schnittverträglich ist, ein Schnitt jedoch nicht vor Anfang Juli stattfinden sollte. In einem Jahr sollten maximal 2 Schnitte durchgeführt werden. Auch in Baden-Württemberg, wo *C. glomerata* in den Kalkgebieten zwar verbreitet, aber nirgends häufig ist, ist ein Rückgang der Bestände aufgrund von Nutzungsaufgabe oder Intensivierung zu verzeichnen (Sebold et al. 1996). In Schleswig-Holstein und Sachsen hat die Knäuel-Glockenblume den Rote Liste-Status 1 (vom Aussterben bedroht), in Mecklenburg-Vorpommern, in Niedersachsen sowie in Brandenburg gilt sie als stark gefährdet (Rote Liste-Status

2). In Nordrhein-Westfalen, in Thüringen und in Sachsen-Anhalt wird die Bestandssituation als gefährdet (Rote Liste-Status 3) eingeschätzt. In anderen Bundesländern kommt die Art auch vor, wird jedoch nicht als gefährdet angesehen. In der gesamtdeutschen Roten Liste der gefährdeten Pflanzen ist *C. glomerata* nicht aufgeführt. Für die Knäuel-Glockenblume besteht weder in der Bundesartenschutzverordnung, im Washingtoner Artenschutzabkommen, in der Berner Konvention noch im Rahmen der FFH-Richtlinien ein besonderer Schutz (Korneck et al. 1996).

4 UNTERSUCHUNGSGEBIETE

Die Untersuchungen zur Gefährdung von *C. glomerata* wurden in insgesamt 20 Populationen in drei Untersuchungsgebieten in Deutschland durchgeführt (Abb. I/2). Bei der Auswahl der Flächen in der Umgebung von Halle (Sachsen-Anhalt), auf der Schwäbischen Alb (Baden-Württemberg) und in der Nordrheinwestfälischen Kalkeifel (Nordrhein-Westfalen) wurde darauf geachtet, dass sich in jedem Gebiet sowohl ungenutzte als auch in Nutzung befindliche Bestände befanden.

Das Untersuchungsgebiet in der Umgebung von Halle gehört zum Mitteldeutschen Trockengebiet, welches wegen der vorherrschenden Westwinde und der geographischen Lage östlich des Harzes durch relative Niederschlagsarmut gekennzeichnet ist. Das dreißigjährige Jahresmittel (Beobachtungsperiode 1961-1990) für den Niederschlag in diesem Gebiet liegt bei 458mm, die durchschnittliche Jahresmitteltemperatur der Luft beträgt 9,1°C (Wallascheck et al. 1996). Die elf in diesem Gebiet liegenden Populationen kommen auf Löß über Porphyr oder auf Muschelkalk vor und gehören pflanzensoziologisch zum Festuco rupicolae-Brachypodietum pinnati MAHN 1959 emend. oder zum Dauco carotae-Arrhenatheretum elatioris (BR.BL. 1919) GÖRS 1966 (Bestimmung nach Schubert et al. 1995). Die Nutzung der Landschaft bestand historisch überwiegend in der Hutehaltung von Schafen, ist jedoch seit Anfang der neunziger Jahre drastisch zurückgegangen (Dannemann 2000).

Von den sechs Untersuchungsflächen in Baden-Württemberg befinden sich drei auf dem Gelände eines ökologisch wirtschaftenden Bioland-Hofes, zwei in ehemaligen Kalksteinbrüchen und eine im alten Donautal. Mit 700 bis 800mm mittlerem Jahresniederschlag (Beobachtungsperiode 1961-1990, Leibniz-Institut 2003) ist es hier deutlich niederschlagsreicher als auf den Untersuchungsflächen in Sachsen-Anhalt. Beim geologischen Untergrund handelt es sich um Kalk in Form von Zementmergel. Pflanzensoziologisch gehören die Flächen zum Gentiano-Koelerietum pyramidatae KNAPP ex BORNK. 1960, zum Onobrychido-Brometum erecti TH. MÜLL. 1968 oder zum Dauco carotae-Arrhenatheretum elatioris (BR.BL. 1919) GÖRS 1966. In einem der Kalksteinbrüche und im Donautal finden gegenwärtig von den örtlichen Naturschutzvereinen initiierte Pflegemaßnahmen statt.

Die Untersuchungsflächen in der Nordrheinwestfälischen Kalkeifel liegen im Kreis Euskirchen. Das Gebiet gehört zum subatlantischen Klimabereich, der durch unbeständige Wetterlagen mit verhältnismäßig milden Wintern und kühlen Sommern gekennzeichnet ist. Das Jahresmittel der Niederschlagssumme beträgt 600 bis 700mm, das der Lufttemperatur 9,0°C (Leibniz-Institut 2003). Den geologischen Untergrund bildet eine mitteldevonische Kalkmulde. Die Flächen wurden dem

Gentiano-Koelerietum pyramidatae KNAPP ex BORNK. 1960 zugeordnet. Schon seit fränkischer Zeit gab es in diesem Gebiet eine extensive Viehwirtschaft. Neben der Beweidung wurden die Trockenrasen auch gemäht und das Material zur Fütterung genutzt (Pfaffen 1940). Seit 1950 traten jedoch diese Bewirtschaftungsformen der Kalkmagerrasen in den Hintergrund. Im Rahmen des Kulturlandschaftsprogramms von Nordhein-Westfalen wurden die Flächen unter Naturschutz gestellt und werden heute von ortsansässigen Bauern gepflegt.

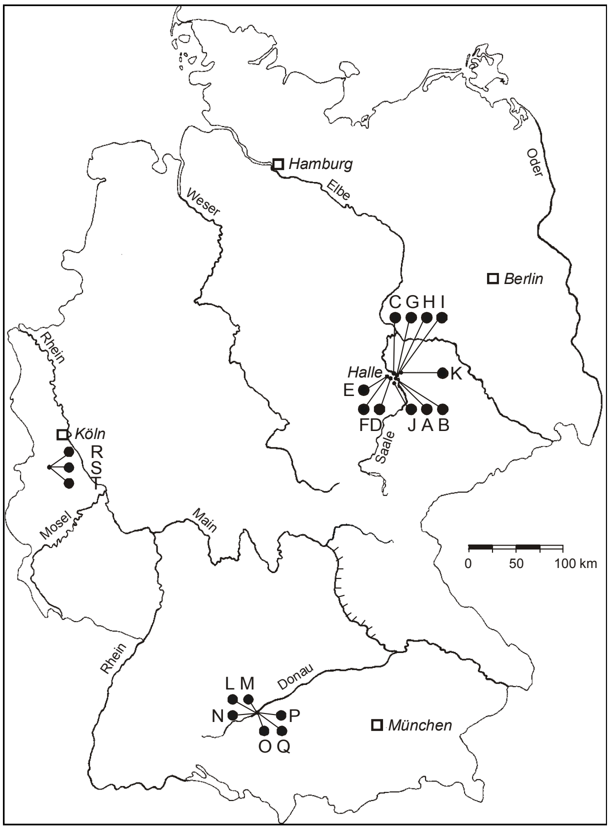

Abbildung I/2: Lage der untersuchten Populationen von *C. glomerata* in Deutschland

LITERATUR

ALLENDORF, F. W. & RYMAN, N. (2002). The Role of Genetics in Population Viability Analysis. In *Population Viability Analysis* (ed. S. R. Beissinger and D. R. McCullough), pp. 50-85. The University of Chicago Press, Chicago.

AMLER, K., HEIDENREICH, A., KÖHLER, G., POETHKE, H.-J. & SAMIETZ, J. (1999). Die Standardisierte Populationsprognose (SPP): eine Anwendung der zoologischen Datenbanken am Beispiel des NSG "Leutratal" (Thüringen). In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 200-212. Ulmer, Stuttgart.

BALMER, O. & ERHARDT, A. (2000). Consequences of succession on extensively grazed grasslands for central european butterfly communities: rethinking conservation practices. *Conservation Biology* **14:** 746-757.

BERENDSE, F. (1983). Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *Journal of Ecology* **71:** 379-390.

BOYCE, M. S. (1992). Population viability analysis. *Annual Review of Ecology and Systematics* **23:** 481-506.

BRIEMLE, G. & ELLENBERG, H. (1994). Zur Mahdverträglichkeit von Grünlandpflanzen. *Natur und Landschaft* **69:**139-147.

BRYS, R., JACQUEMYN, H., ENDELS, P., VAN ROSSUM, F., HERMY, M., TRIEST, L., DE BRUYN, L. & BLUST, G. D. E. (2004). Reduced reproductive success in small populations of the self-incompatible *Primula vulgaris*. *Journal of Ecology* **92:**5-14.

BURGMANN, M. & POSSINGHAM, H. (2000). Population viability analysis for conservation: the good, the bad and the undescribed. In *Genetics, Demography and Viability of Fragmented Populations* (ed. A. G. Young and G. M. Clarke), pp. 96-112. Cambridge University Press, Cambridge.

DANNEMANN, A. (2000). Der Einfluss von Fragmentierung und Populationsgröße auf die genetische Variation und Fitness von seltenen Pflanzenarten am Beispiel von *Biscutella laevigata* (Brassicaceae). doctoral thesis, Philipps-Universität.

ELLENBERG, H., WEBER, H. E., DÜLL, R., WIRTH, V. & WERNER, W. (2001). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* **XVIII**.

ELLSTRAM, N. C. & ELAM, D. R. (1993). Population genetic consequences of small population size: implication for plant conservation. *Ann. Rev. Ecol. Syst.* **24:**217-242.

EMIG, W. & LEINS, P. (1994). Ausbreitungsbiologische Untersuchungen in der Gattung *Campanula* L. I. Vergleichende Windkanalexperimente zur Samenportionierung bei *C. Trachelium* L., *C. sibirica* L. und *C. glomerata* L. *Bot. Jahrb. Syst.* **116:**243-257.

FISCHER, M. (1996). Experimental population biology of the rare Gentianella germanica. Dissertation thesis, Universität Basel.

FISCHER, M. & MATTHIES, D. (1998). RAPD-Variation in relation to population size and plant fitness in the rare plant *Gentianella germanica* (Gentianellaceae). *American Journal of Botany* **85:**811-819.

FRANK, D. & KLOTZ, S. (1990). Biologisch-ökologische Daten zur Flora der DDR. *Wissenschaftliche Beiträge der Martin-Luther-Universität Halle-Wittenberg* **1990/32 (P41)**.

FRANK, D. & NEUMANN, V. (1999). *Bestandssituation der Pflanzen und Tiere Sachsen-Anhalts*. Ulmer, Stuttgart.

FRANKHAM, R., BALLOU, J. D. & BRISCUE, D. A. (2002). *Introduction to conservation genetics*. Cambridge University Press, Cambridge.

GILPIN, M. E. & SOULE, M. E. (1986). Minimum viable populations: processes of species extinction. In *Conservation biology - the science of scarcity and diversity* (ed. M. E. Soulé), pp. 19-34. Sinauer, Sunderland.

HARDTKE, H.-J. & IHL, A. (2000). *Atlas der Farn- und Samenpflanzen Sachsens*. Sächsisches Landesamt für Umwelt und Geologie, Dresden.

HEGI, G. (1918). *Illustrierte Flora von Mitteleuropa Band VI*. Lehmanns, München.

HENLE, K., POSCHLOD, P. & BAHL, A. (1999). Gefährdungsanalysen auf populationsbiologischer Grundlage: Einführung in Konzepte und Begriffe. In *Populationsbiologie in der*

Naturschutzpraxis (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 46-52. Ulmer, Stuttgart.

HENSEN, I. & OBERPRIELER, C. (2005). Effects of population size on genetic diversity and seed production in the rare *Dictamnus albus* (Rutaceae) in Central Germany. *Conservation Genetics* **6:**63-73.

JACQUEMYN, H., BRYS, R. & HERMY, M. (2002). Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. *Oecologia* **130:**617-625.

JEDICKE, E. (1997). *Die Roten Listen. Gefährdete Pflanzen, Tiere, Pflanzengesellschaften und Biotoptypen in Bund und Ländern*. Ulmer, Stuttgart.

KAHMEN, S. & POSCHLOD, P. (2000). Population size, plant performance, and genetic variation in the rare plant *Arnica montana* L. in the Rhön, Germany. *Basic Appl. Ecol.* **1:**43-51.

KERY, M., MATHIES, D. & SPILLMANN, H.-H. (2000). Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *Journal of Ecology* **88:**17-30.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002). BIOLFLOR- Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenr. f. Vegetationskunde* **38:**1-334.

KORNECK, D., SCHNITTLER, M. & VOLLMER, I. (1996). Rote Liste der Farn- und Blütenpflanzen Deutschlands. *Schriftenreihe für Vegetationskunde* **28:**21-187.

LEIBNIZ-INSTITUT. (2003). *Nationalatlas Bunderepublik Deutschland*. Spektrum Akademischer Verlag, Heidelberg, Berlin.

MACARTHUR, R. M. & WILSON, E. O. (1967). *The theory of islands biogeography*. Princeton University Press, Princeton.

MATTHIES, D. & POSCHLOD, P. (2000). The biological flora of Central Europe - aims and concept. *Flora* **195:**116-122.

OBERDORFER, E. (2001). *Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete*. Ulmer, Stuttgart.

OOSTERMEIJER, G., BERHOLZ, A. & POSCHLOD, P. (1996). Genetical aspects of fragmented plant populations. In *Species Survival in Fragmented Landscapes* (ed. J. Settele, C. R. Margules, P. Poschlod and K. Henle), pp. 93-101. Kluwer Academic publishers, Dordrecht.

PARTZSCH, M. (2001). Die Porphyrkuppenlandschaft des unteren Saaletals - Vergleich der Vegetation in Abhängigkeit von Flächengröße und Genese der Prophyrkuppen. *Bot. Jahrb. Syst.* **123:**1-45.

PASCHKE, M., ABS, C. & SCHMID, B. (2002). Relationship between population size, allozyme variation, and plant performance in the narrow endemic *Cochlearia bavarica*. *Conservation Genetics* **3:**131-144.

PFAFFEN, K. H. (1940). Heidevegetation und Ödlandwirtschaft in der Eifel. *Beiträge zur Landeskunde des Rheinlandes* **3**.

PISKOVACKOVA, N. P. (1980). Kolokolcik Skucennyi. In *Biologiceskaja flora Moskovskoj oblasti* (ed. T. A. Rabotnov), pp. 156-169. Moskva universitet, Moskva.

PODLECH, D. (1965). Revision der europäischen und nordafrikanischen Vertreter der Subsect. *Heterophylla* (Wit.) Fed. der Gattung Campanula L. *Feddes Repertorium* **71:**50-187.

POSCHLOD, P., DANNEMANN, A., JACKEL, A.-K. & BONN, S. (1999). Fragmentierung und Isolation von Pflanzenpopulationen - Einführung und Konzepte. In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 336. Ulmer, Stuttgart.

POSCHLOD, P. & WALLISDEVRIES, M. F. (2002). The historical and socioeconomic perspective of calcareous grassland-lessons from the distant and recent past. *Biological Conservation* **104:**361-376.

POTT, R. (1996). Die Entwicklungsgeschichte und Verbreitung xerothermer Vegetationseinheiten in Mitteleuropa unter dem Einfluß des Menschen. *Tuexenia* **16:**337-369.

RICHARDS, C. M. (2000). Genetic and demographic influences on population persistence: gene flow and genetic rescue in *Silene alba*. In *Genetics, Demography and Viability of Fragmented Populations* (ed. A. G. Young and G. M. Clarke), pp. 271-291. University Press, Cambridge.

ROTHMALER, W. (2002). *Exkursionsflora von Deutschland. Gefäßpflanzen: Kritischer Band*. Spektrum, Heidelberg-Berlin.

SCHMID, B. & MATTHIES, D. (1994). Seltenheit und Gefährdung - Populationsbiologische Grundlagen des Artenschutzes. *Naturwissenschaften* **81:**283-292.

SCHMIDT, K. & JENSEN, K. (2000). Genetic structure and AFLP variation of remnant populations in the rare plant *Pedicularis palustris* (Scrophulriaceae) and its relation to population size and reproductive components. *American Journal of Botany* **87:**678-689.

SCHUBERT, R., HILBIG, W. & KLOTZ, S. (1995). *Bestimmungsbuch der Pflanzengesellschaften Deutschlands*. Fischer, Jena.

SEBOLD, O., SEYBOLD, S., PHILIPPI, G. & WÖRZ, A. (1996). *Die Farn- und Blütenpflanzen Baden-Württembergs*. Ulmer, Stuttgart.

VERGEER, P., RENGELINK, R., COPAL, A. & OUBORG, N. J. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91:**18-26.

WALLASCHECK, M., BLISS, P., SCHÖPKE, H. & WITSACK, W. (1996). *Beiträge zur Erfassung der Biodiversität im unteren Saaletal*, Halle/Saale.

WALLISDEVRIES, M. F., POSCHLOD, P. & WILLEMS, J. H. (2002). Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* **104:**265-273.

WELK, E. (2001). *Arealkundliche Analyse und Bewertung der Schutzrelevanz seltener und gefährdeter Gefäßpflanzen Deutschlands*. Dissertation Mathematisch-Naturwissenschaftlich-Technische Fakultät der Martin-Luther-Universität, Halle-Wittenberg.

KAPITEL II

IS THE DECLINING *CAMPANULA GLOMERATA* THREATENED BY GENETIC FACTORS?

BACHMANN, U. & HENSEN, I. (in press). Is the declining *Campanula glomerata* threatened by genetic factors? *Plant Species Biology*

ABSTRACT

Changes in land-use lead to increasing destruction and fragmentation of natural habitats. As a consequence, many plant species become rare. Remnant populations are often too small and too isolated to persist over time, and face a high risk of extinction due to genetic, demographic or environmental problems. As the decline of rare species is always a focal point in plant conservation, the aim of this study was to investigate the relative importance of genetics for the probability of survival of *Campanula glomerata* populations that are not yet rare, but are increasingly on the decline due to land use changes. We studied 20 populations in three regions in Germany (Saxony-Anhalt, Baden-Wuerttemberg, and North-Rhine Westphalia) in order to assess (1) whether there is significant genetic differentiation among and between populations, (2) whether genetic similarity of populations is associated with the geographical distance separating them, and (3) whether there are relationships between genetic variation and either population size and/or fitness parameters. The results show that the genetic structure of *C. glomerata* populations is strongly differentiated on a large, but not on a local scale. As we neither found a correlation between genetic variation and population size parameters, nor one between genetic variation and fitness components such as flower number or seed viability/seed germination, we conclude that so far, *C. glomerata* populations have remained almost unaffected by isolation, inbreeding or genetic drift and are not as yet threatened by genetic factors. We assume that particular life history traits preserve the variability of the populations.

INTRODUCTION

In the last decades changes in land use have caused the alteration and fragmentation of many habitats. Two opposite trends of agricultural management have been experienced: the management of highly-productive areas has intensified, whereas lowly-productive areas have become increasingly more abandoned. As a result, habitat characteristics as well as patterns of interspecific competition have been altered and populations of many plant species have been ever more reduced in size and are more isolated from each other than in the past. Evidence is growing that both small population size and isolation increase the risk of extinction due to genetic, demographic or environmental problems (Oostermeijer 1996, Richards 2000, Allendorf & Ryman 2002, Lowe et al. 2004).

The importance of genetic factors to the risk of extinction is a subject of ongoing controversy (Frankham 2005). The most important genetic factors threatening small and isolated populations are genetic drift (Barrett & Kohn 1991, Young et al. 1996), which reduces genetic variation (Oostermeijer 1996, Lowe et al. 2004, Hensen & Oberprieler 2005), and inbreeding, which leads to an increasing frequency of homozygous genotypes (Oostermeijer 1996) with the possible consequence of inbreeding depression (Lande & Schemske 1985, Ellstram & Elam 1993, Kahmen & Poschlod 2000). Consequently, pronounced genetic differentiation among populations has been reported for an increasing number of rare species (e.g. Cardoso et al. 1998, Ayres & Ryan 1999, Fischer et al. 2000, Hensen et al. 2005, Dittbrenner et al. 2005). One of the main problem is that loss of genetic variation is often associated with reduced reproductive fitness (Oostermeijer et al. 1994, 1998, Ouborg & van Treuren 1995, Fischer & Matthies 1997, 1998, Frankham et al. 2002, Vergeer et al. 2003, Hensen & Wesche in press, Dittbrenner et al. 2005). However, genetic dissimilarity can be counteracted by the immigration of genetic material such as seeds, vegetative parts, or pollen from other populations (Kwak et al. 1998, Frankham 2005).

The main objective of this study was to investigate the relative importance of genetics for the probability of survival of *Campanula glomerata* populations. This long lived perennial is mainly distributed among dry chalk and limestone grasslands. However, it has been ever more restricted to isolated populations, due to the cessation of traditional land use practices and subsequent vegetation changes, and is currently declining in Germany (Frank & Neumann 1999, Hardtke & Ihl 2000). Distribution data provided by Haeupler & Schoenfelder (1989) or Benkert et al. (1996) indicate that in the last 60 years, approximately 10% of populations may have disappeared. Following land use change, in eastern Germany a high percentage of dry grasslands have been converted into those dominated by certain grass species (e.g., *Festuca rupicola, Poa angustifolia*; Passarge 1999, Partzsch 2001). Within the scope of a population viability analysis, a competition experiment revealed that first-year-performance of *C. glomerata* biomass and fitness is indeed negatively affected by the increasing expansion of *Poa angustifolia* (Bachmann et al. 2005). As a decline in the abundance of a plant species as a result of land-use changes is a major focus in plant conservation due to the relationship between loss of genetic variability and reduced reproductive fitness (Fischer et al. 2000, Frankham et al. 2002) and appropriate scientific information is required to design effective conservation plans for any threatened species (Washitani et al. 2005), the present study attempts to elucidate whether genetic factors are affected by decreasing population sizes and isolation of *C. glomerata* populations. With an aim toward examining the importance of genetics to the probability of survival of 20 *C. glomerata* populations distributed in three regions in Germany, we attempted to answer the following questions: 1) Is there any significant genetic differentiation among and within populations of *C. glomerata*? 2) Are levels of genetic similarity correlated to the geographical distances separating them? And 3) Is there a relationship between genetic variation and population size; and is genetic diversity associated with fitness components such as flower number and seed germination?

Study species, study sites, population sizes and fitness components

Campanula glomerata L. is a perennial, continental species, distributed mainly in submeridional to boreal Europe and Siberia (Rothmaler 2002). The average life span of an individual is estimated to be 25 – 30 years. Flowering usually begins in the second year after germination, but sometimes it takes up to 6 years to reach reproductive maturity. Sterile rosettes can be found in the pre-maturity stage, but also in stages of resting or senescence (Piskovackova 1980). Flowering rosettes have stems 5 to 70cm in height, with one to a few flower heads in the leaf axils and at the apical end of the stem. The flowers are strongly protandrous, self-incompatible (Gadella 1964) and insect-pollinated (bees, Rothmaler 2002). Each flower stem produces between 1 and 150 capsules (mean 23.5; n = 1133, data from 20 populations in Germany in 2002) which can contain up to 100 seeds each (Bachmann, unpubl.). Seeds of *C. glomerata* are dispersed by wind but the dispersal efficiency is low (152cm at a windspeed of 10m/s; Emig & Leins 1994). Vegetative propagation occurs by rhizomes (Klotz et al. 2002).

We studied 20 populations distributed in three different regions throughout Germany (figure I/2, page 7, table II/1): 11 populations in the surroundings of Halle/Saale in Saxony-Anhalt (populations A – K), 6 populations at the “Schwäbische Alb” in Baden-Wuerttemberg (populations L – Q) and three populations at the “Nordrheinwestfälische Kalkeifel” in North Rhine-Westphalia (populations R, S, T). A population was defined as a clearly differenciated group of plants separated from their closest conspecifics by either more than 100m, or by natural barriers such as agricultural land or hedgerows. Thus, the geographical distance between two populations ranged from 0.1 to 13.5km within Saxony-Anhalt, from 0.03 to 4.1km within Baden-Wuerttemberg, and from 0.5 to 2km within North-Rhine-Westphalia. Maximum distance between populations was 528km for Saxony-Anhalt and Baden-Wuerttemberg, 509km for Saxony-Anhalt and North-Rhine-Westphalia and 367km for Baden-Wuerttemberg and North-Rhine-Westphalia (table II/3).

Current population size parameters of *C. glomerata* were determined by counting the exact number of sterile rosettes and flowering stems during the flowering period (July and August) in 2002. In order to assess population density/m², numbers were related to their respective occupied areas (for detailed information see Bachmann & Hensen 2006). Data on flower number per stem were collected from all study populations in July 2002 using up to 100 randomly selected plants. Capsules were harvested from 6 to 30 plants, always from the terminal flower head. To determine the germination rate of the seeds, germination was tested on a pooled sample from each population at a temperature of 20°C/10°C (12/12h day/night cycle; n = 5 x 20 seeds) in a climate chamber with a warm white light source. Germination rate was determined after 100 days. The viability of non-germinated seeds was tested using the tetrazolium test (Baskin & Baskin 2001).

RAPD/ISSR analyses

In summer 2002 we collected leaves from 6 to 24 randomly choosen plants of each of the populations (table II/1) and dried them in silica gel. Because differentiation of genets is difficult to assess in the field due to vegetative propagation, where possible we retained a minimum distance between individuals of 1m. DNA was extracted in December 2002 using the protocol described by QIAGEN (2002, DNeasy plant mini kit). An initial screening of 100 RAPD and 22 ISSR primers was performed in order to test amplification, readability and reproducibility. This resulted in the selection of seven RAPD primers from Roth: ACCGCGAAGG (A1), CTGCTGGGAC (B10), AGCGCCATTG (D11), GGGGTGACGA (D13), CCTCTCGACA (J7), AAGCCCGAGG (J10), CCACACTACC (J13); and two ISSR primers from MWG Biotech: CACACACACACACATTA, CTTCTTCTTCTTCTTYTT. RAPD-PCRs were carried out in 10µl reaction volumes containing 6.5µl H_2O, 1µl 1.5mM $MgCl_2$ buffer from Qbiogene, 1µl 2 mM dNTPs from peqlab, 0.1µl 5U/µl Taq polymerase from Qbiogene, 0.6µl 10pmol/µl primer from Roth and 0.8µl 10ng/µl DNA. Polymerase chain reactions were performed in a thermal cycler (“flexigene” from techne) using 384 well plates under the following conditions: initial denaturation at 94°C for 2min, 36 cycles, denaturation at 94°C for 12sec, annealing at 36°C for 45sec, elongation at 72°C for 2min, a final cycle at 72°C for 7min and a final cooling at 4°C. ISSR-PCR reaction mixtures of 13µl contained 6.8µl H_2O, 0.3µl 25mM $MgCl_2$ from Qiagen, 1.05µl 15mM $MgCl_2$ buffer from Qiagen, 0.45µl 2 mM dNTPs from peqlab, 0.6µl 5U/µl Taq polymerase from Qiagen, 0.35µl 50pmol/µl primer from MWG-Biotech, 20µl Q-Solution from Qiagen and 2µl 5ng/µl DNA. ISSR-PCR amplifications were carried out in the same thermal cycler (“flexigene” from techne, 384 plates), programmed as follows: initial denaturation at 95°C for 3min, 36 cycles, denaturation at 94°C for 30sec, annealing at 45.3°C (primer C) or 50°C (primer H) for 2min, elongation at 70°C for 2min 46sec, a final cycle at 70°C for 10min and a final cooling at 6°C. Negative controls and replicates were included to verify repeatability of the results. DNA fragments were separated by electrophoresis in 2% agarose gels with a Tris-acetate-EDTA (TAE) buffer system at 150V for 150min and stained with ethidium bromide. Gels with amplification fragments were visualized and photographed under UV light. All amplifications were repeated twice and only reproducible bands were considered for analysis.

Statistical analysis

The banding patterns were compiled into a 0/1 - matrix (state “0” for absence, “1” for presence of a band) for all scorable bands yielded by the primers used. In accordance to Clausing et al. (2000) and others who found congruent results from RAPD and ISSR matrices, we combined the RAPD and the ISSR data. The software ARLEQUIN (version 2.000, Schneider et al. 2000) was used to assess genetic diversity by dividing the average gene diversity over loci among all members of the population, and by the percentage of polymorphic sites. Variation of banding patterns within and among populations was analyzed with analysis of molecular variance (AMOVA, Excoffier et al. 1992); also using the ARLEQUIN software (version 2.000, Schneider et al. 2000). AMOVA analyses are based on the pairwise Euclidian distances among molecular phenotypes. Populations examined in the AMOVA procedure were split into three groups based on their geographic locations in Germany (Saxony-Anhalt, Baden-Wuerttemberg, North Rhine-Westphalia) and into three groups based on the distances separating them in Saxony-Anhalt (surroundings of Brachwitz, Salzmünde and Teicha). The ARLEQUIN software (version 2.000, Schneider et al. 2000) was also used to assess genetic diversity by dividing the average gene diversity over loci among all members of the population, and by the percentage of polymorphic sites. Pairwise genetic distances (Φ_{ST}) and their corresponding levels of significance among populations were also obtained using this software. From Φ – statistics, gene flow was estimated using the formula $N_em = ¼ (1/\Phi_{ST} - 1)$ (Wright 1951). The Mantel test (Mantel 1967) was used to test whether the matrix of pairwise genetic distances (Φ_{ST}) is correlated with the matrix of geographical distances (ARLEQUIN, version 2.000, Schneider et al. 2000, 1000 permutations). Differences of percentage of polymorphic sites and average gene diversity over loci between regions were analysed using ANOVA. Spearman rank correlations of genetic diversity and either population size parameters and fitness components were carried out with SPSS 12.0.

RESULTS

The 276 *C. glomerata* individuals sampled expressed 276 different RAPD/ISSR phenotypes. Length of the DNA fragments varied between 300 and 1150bp. We used 103 bands in the analyses, three of which were monomorphic. The total number of amplified bands per primer varied between 7 and 17. The percentage of polymorphic bands ranged from 29.1% (population P) to 52.4% (population J, table II/1). Gene diversity over loci varied between 0.118 (population T) and 0.162 (population L, table II/1). A strong correlation was noted between both gene diversity values ($r_s = 0.69$, $p < 0.001$). Differences between genetic values among the three regions were not significant. Variation in RAPD banding patterns among groups, among populations within groups, and within populations was highly significant. Molecular variance was found to be the highest (80.1%) within the populations and the lowest (7.8%) between the three regions (table II/2), which left 12.1% of the molecular variance for the division among populations within the different regions. Genetic differentiation within populations was high ($\Phi_{ST} = 0.199$, table II/2), and moderate among regions and among populations within the regions ($\Phi_{CT} = 0.078$, $\Phi_{SC} = 0.131$; table II/2). Gene flow was estimated as $N_em = 1.01$. When only the samples from Saxony-Anhalt (n=11) were considered, genetic differentiation within populations was moderate ($\Phi_{ST} = 0.122$, table II/2). All of the pairwise genetic distances (pairwise Φ_{ST}) values were highly significant ($p < 0.001$). Highest genetic differentiation (pairwise $\Phi_{ST} = 0.318$) was found between population G in Saxony-Anhalt and population N in Baden-Wuerttemberg; and lowest (pairwise $\Phi_{ST} = 0.024$) between populations A and B in Saxony-Anhalt (table II/3). Altogether, geographic and genetic distances among the total of the studied populations correlated significantly (standarized Mantel statistics $r_M = 0.55$; $p < 0.0001$, figure II/1a). However, on the local scale, there was no such correlation (Saxony-Anhalt $r_M = -0.04$; $p = 0.56$, figure II/1b).

In 2002, number of flowering stems varied between 6 and 2381 (table II/1). There were no relationships between both gene diversity values and any of the population size paramaters (e.g. number of flowering stems and percentage of polymorphic loci: $r_s = 0.16$; $p = 0.49$; number of flowering stems and genetic diversity: $r_s = -0.31$; $p = 0.18$). Furthermore, there was no correlation between gene diversity and fitness parameters, such as average number of flowers per stem (percentage of polymorphic loci $r_s = -0.2$, $p = 0.39$; genetic diversity $r_s = 0.1$, $p = 0.68$) and seed germination (percentage of polymorphic loci $r_s = 0.08$, $p = 0.76$; genetic diversity $r_s = -0.13$, $p = 0.59$). Seed germination was highly variable (2 - 69%, table II/1), and non-germinated seeds were always non-viable.

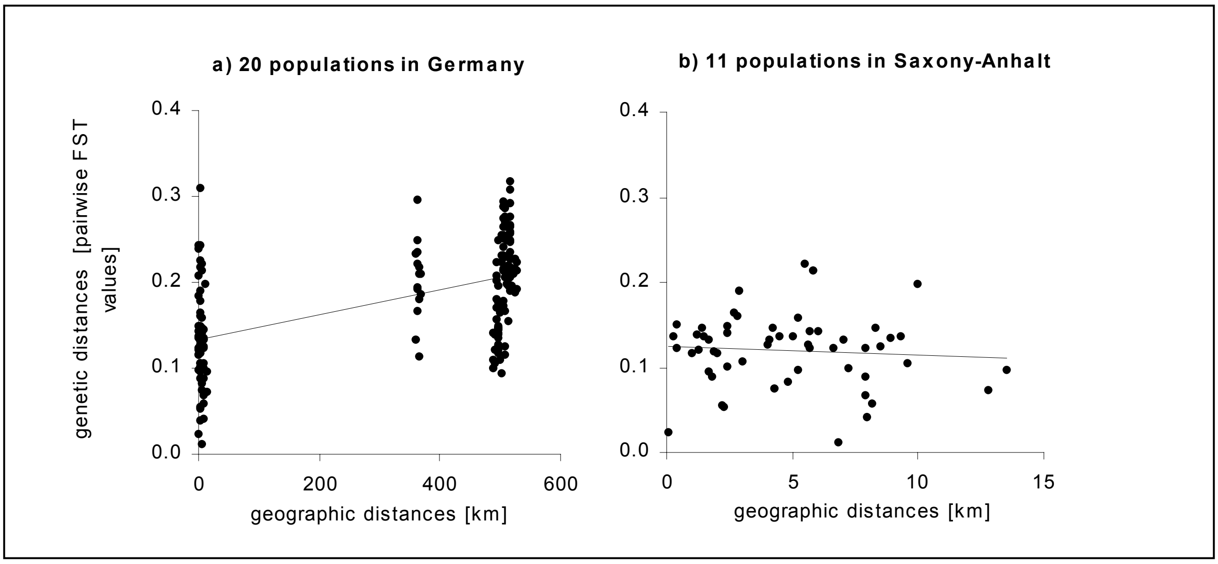

Figure II/1: Relationship between genetic and geographic distances of a) 20 *C. glomerata* populations in Germany and b) 11 populations in Saxony-Anhalt

Table II/1: Genetic diversity, population size and fitness components of the *C. glomerata* populations studied.

		genetic structure		**plant fitness**		**population size**			
population number	sample number	% of polymorphic sites	average gene diversity over loci	germination [%]	average number of flowers per stem	number of flowering stems	number of flowering stems and sterile rosettes	occupied area [m²]	population density [stems and rosettes per m²]
Saxony-Anhalt									
A	24	41.75	0.132	39.0	21.86	1178	1477	600	2.46
B	24	48.54	0.150	8.5	18.48	50	66	4500	0.01
C	24	46.60	0.156	26.7	35.15	83	90	4000	0.02
D	12	39.80	0.152	12.1	44.67	10	10	1	10.00
E	12	32.04	0.112	68.8	21.75	140	151	900	0.17
F	12	37.86	0.147	2.0	12.93	241	301	200	1.50
G	12	42.73	0.142	32.5	36.15	75	98	60	1.63
H	12	44.66	0.151	58.0	26.59	40	55	4	13.75
I	12	38.83	0.137	5.0	31.38	35	41	10	4.10
J	24	52.43	0.149	29.5	20.31	295	299	100	2.99
K	12	38.83	0.150	39.0	52.50	33	33	50	0.66
Baden-Wuerttemberg									
L	12	46.60	0.162	24.0	17.50	14	14	20	0.70
M	12	33.98	0.121	33.0	35.95	106	139	90	1.54
N	6	35.92	0.127	18.0	10.60	6	6	25	0.24
O	12	42.72	0.146	41.0	25.76	414	448	1000	0.45
P	6	29.13	0.135	69.0	35.50	6	17	150	0.11
Q	12	41.75	0.153	26.0	23.51	102	140	1350	0.10
North Rhine-Westphalia									
R	12	40.78	0.133	6.0	9.11	2381	2496	700	3.56
S	12	39.81	0.136	4.0	30.16	143	150	400	0.37
T	12	35.92	0.118	19.0	27.58	150	164	300	0.55

Table II/2: Analysis of molecular variance (AMOVA) for 276 *C. glomerata* individuals, assembled in 20 populations and three regions in Germany (P based on 1000 permutations, upper part) and Analysis of molecular variance (AMOVA) for 180 *C. glomerata* samples, assembled in 11 populations in Saxony-Anhalt (P based on 1000 permutations, lower part).

	d.f.	sum of squares	Variance	% of variation	Φ statistics	P
among 3 regions of Germany	2	147.398	0.709	7.78	$\Phi_{CT} = 0.078$	< 0.0001
among 20 populations within 3 regions of Germany	17	389.169	1.104	12.12	$\Phi_{SC} = 0.131$	< 0.0001
within 20 populations of Germany	262	1912.125	7.298	80.11	$\Phi_{ST} = 0.199$	< 0.0001
among 3 regions of Saxony-Anhalt	2	43.310	0.057	0.68	$\Phi_{CT} = 0.007$	= 0.33
among 11 populations within 3 regions of Saxony-Anhalt	8	192.049	0.974	11.51	$\Phi_{SC} = 0.116$	< 0.0001
within 11 populations of Saxony-Anhalt	169	1257.042	7.438	87.82	$\Phi_{ST} = 0.122$	< 0.0001

Table II/3: Matrix between genetic distances (pairwise Φ_{ST} values; lower left triangle) and geographic distances (km; upper right triangle) among 20 populations of *C. glomerata*. All Φ_{ST} values were highly significant ($p < 0.0001$).

		Saxony-Anhalt											Baden-Wuerttemberg						North Rhine-Westphalia		
		A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**	**T**
Saxony-Anhalt	**A**	-	0.1	2.3	4.0	8.0	6.8	1.8	1.2	1.5	1.4	6.0	515.0	514.0	515.0	505.0	506.0	506.0	496.4	496.9	495.9
	B	0.024	-	2.2	4.1	8.2	7.0	1.7	1.0	1.3	1.7	5.7	515.1	514.6	515.1	505.1	506.1	506.1	496.5	497.0	496.0
	C	0.053	0.055	-	5.2	7.9	7.9	2.4	1.9	2.0	2.4	5.6	528.0	527.5	528.0	525.0	526.0	526.0	496.0	496.5	495.5
	D	0.127	0.132	0.098	-	5.0	2.8	5.8	5.2	5.5	2.9	10.0	509.0	508.5	509.0	506.0	507.0	507.0	493.1	493.6	492.6
	E	0.042	0.058	0.068	0.136	-	4.3	9.6	8.9	9.3	6.6	13.5	513.0	512.5	513.0	510.0	511.0	511.0	488.4	488.9	487.9
	F	0.122	0.133	0.123	0.161	0.075	-	8.5	7.9	8.3	5.7	12.8	504.0	504.5	504.0	501.0	502.0	502.0	491.1	491.6	490.6
	G	0.089	0.096	0.140	0.213	0.105	0.125	-	0.3	0.4	3.0	4.2	516.0	515.5	516.0	506.0	507.0	507.0	497.9	498.4	497.4
	H	0.138	0.116	0.118	0.158	0.134	0.089	0.136	-	0.4	2.4	4.8	515.7	515.2	515.7	505.3	520.4	520.4	497.2	497.7	496.7
	I	0.137	0.121	0.117	0.221	0.136	0.146	0.150	0.123	-	2.7	4.5	516.0	515.0	516.5	506.0	520.8	520.8	497.6	495.1	508.1
	J	0.146	0.133	0.149	0.191	0.123	0.123	0.106	0.101	0.164	-	7.2	515.0	516.5	515.0	505.0	506.0	506.0	495.1	495.6	494.6
	K	0.142	0.143	0.127	0.198	0.097	0.073	0.147	0.083	0.136	0.100	-	516.5	516.0	516.5	517.5	518.5	518.5	508.1	508.6	501.2
Baden-Wuerttemberg	**L**	0.195	0.190	0.192	0.230	0.154	0.173	0.196	0.209	0.217	0.195	0.206	-	0.5	0.5	2.6	3.6	3.6	361.6	361.3	363.0
	M	0.219	0.203	0.213	0.266	0.197	0.255	0.264	0.256	0.258	0.266	0.214	0.143	-	0.5	3.1	4.1	4.1	361.6	361.5	363.0
	N	0.247	0.228	0.224	0.276	0.252	0.295	0.318	0.293	0.307	0.277	0.236	0.243	0.185	-	2.6	3.6	3.6	361.6	361.3	363.0
	O	0.232	0.213	0.215	0.274	0.250	0.254	0.241	0.264	0.216	0.251	0.249	0.136	0.142	0.244	-	1.0	1.0	366.0	365.6	367.3
	P	0.288	0.253	0.228	0.270	0.274	0.224	0.286	0.197	0.209	0.289	0.210	0.226	0.217	0.309	0.240	-	0.03	365.7	365.4	367.1
	Q	0.214	0.178	0.188	0.264	0.198	0.232	0.206	0.227	0.215	0.230	0.216	0.141	0.105	0.178	0.116	0.208	-	365.7	365.4	367.1
North Rhine-West-phalia	**R**	0.148	0.146	0.141	0.224	0.109	0.121	0.176	0.145	0.197	0.170	0.125	0.192	0.221	0.250	0.250	0.180	0.209	-	0.5	1.5
	S	0.117	0.122	0.128	0.202	0.100	0.139	0.110	0.147	0.181	0.140	0.115	0.134	0.166	0.234	0.164	0.218	0.113	0.099	-	2.0
	T	0.146	0.148	0.125	0.208	0.141	0.106	0.149	0.136	0.166	0.157	0.094	0.194	0.236	0.296	0.197	0.209	0.186	0.135	0.039	-

DISCUSSION

We did not find any indication that genetic problems might currently play a major role in the risk of extinction of the *C. glomerata* populations studied. Although our AMOVA-derived Φ_{ST} –value of 0.199 indicates strong genetic differentiation among populations, this value is clearly lower than the mean

Φ_{ST}–value (0.25) of 37 RAPD studies of long-lived perennials reviewed by Nybom & Bartish (2000). Furthermore, our RAPD/ISSR based estimate for gene flow (N_em = 1.01) is high for such a rare species when compared to similar values provided by e.g. Dittbrenner et al. (2005) for *Angelica palustris* (0.34), Fischer & Matthies (1998) for *Gentianella germanica* (0.42) and Hensen & Oberprieler (2005) for *Dictamnus albus* (0.62). Only *Pulsatilla vulgaris*, with a Φ_{ST} of 0.17 and an N_em = 1.22 (Hensen et al. 2005) showed similarly high values as *C. glomerata*. All our individuals sampled expressed individual RAPD/ISSR phenotypes indicating that clonal growth is of low importance in *C. glomerata* reproduction. However, estimates of genetic diversity are astonishingly low, with percentages of polymorphic loci between 29 and 52% and genetic diversity values between 0.12-0.16, compared to genetic values derived from RAPD-based estimates for other rare species such as e.g. *Pulsatilla vulgaris* (65-91% / 0.25-0.38; Hensen et al. 2005), *Dictamnus albus* (40-61% / 0.14-0.25; Hensen & Oberprieler 2005), or *Angelica palustris* (21-61% / 0.11-0.21; Dittbrenner et al. 2005). Despite these data, *C. glomerata* keeps most of its genetic variability within populations (table II/2). Such a result of higher genetic diversity within, rather than among, populations is typical for outcrossing and/or perennial plant species (Hamrick & Godt 1989, 1996, Bartish et al. 1999, Nybom & Bartish 2000). Thus, the high level of genetic diversity within populations of *C. glomerata* is apparently due to particular life history traits that preserve variability such as self-incompatibility and consequent allogamous pollination, production of high seed numbers, vegetative reproduction and a long life span (Loveless & Hamrick 1984).

The genetic differentiation we found among all of the studied populations is correlated to the geographical distance separating them (figure II/1a). This was expected as the three study regions are separated by several hundreds of kilometres. Similar relationships were demonstrated by e.g. Hensen et al. (2005), Ayres & Ryan (1999), Okada & Okada (2002) or Dittbrenner et al. (2005). This trend, however, is not observed when performed within one region (Saxony-Anhalt, figure II/1b), confirming Nybom & Bartish (2000) who pointed out that RAPD-based values for between-population diversity increase with increasing distributional range. Despite these trends, the relationship between genetic and geographic distances are highly variable. In Baden-Wuerttemberg, near distanced populations (30m to 3.6km) were nevertheless highly different in genetic structure (Φ_{ST} of 0.208 to 0.309, table II/3), while in Saxony-Anhalt, two populations of about 14km distance (populations E and K) were genetically closely related (Φ_{ST} = 0.097, table II/3). This fact indicates that the movement of genes may be hampered to a greater extent by natural barriers in the landscape such as unsuitable habitats, streets etc. than by distance alone. Since anemochorously reached seed dispersal distances are limited (Emig & Leins 1996), and seed movement in the fur of grazing animals does not occur anymore, we assume that gene flow by pollen might have considerable impact on the genetic structure of *C. glomerata* populations.

Genetic diversity was not lower in smaller than in larger populations. This finding contradicts the results of various studies on the effects of population size in rare or endangered plant species (e.g. van Treuren et al. 1991, Oostermeijer 1994, Godt et al. 1995, Fischer & Matthies 1997, 1998, Gaudeul et al. 2000, Luijten et al. 2000, Vergeer et al. 2003, Hensen et al. 2005, Hensen & Oberprieler 2005, Dittbrenner et al. 2005, Arzate-Fernandez et al. 2005), but supports the assumption that small *C. glomerata* populations might still not be affected by genetic factors such as genetic drift or inbreeding events. Other endangered species not showing any correlation between genetic variability and population size include *Aster kantonensis* (Maki et al. 1996), *Microseris lanceolata* (Prober et al. 1998), *Succisa pratensis* (Vergeer et al. 2003), *Arnica montana* (Kahmen & Poschlod 2000), *Scabiosa columbaria* (Pluess & Stöcklin 2004a), *Geum reptans* (Pluess & Stöcklin 2004b) and *Juniperus communis* (Oostermeijer & De Knegt 2004). We assume that small populations are survivors from formerly larger populations with relatively high genetic diversity and that population size reduction and isolation are events occuring too recently to have so far affected the genetic diversity of this long-lived perennial. This view is supported by Benkert et al. (1996) who pointed out a significant decrease of *C. glomerata* populations not earlier than from the 1950th onwards; probably due to the halting of grazing. Furthermore, none of our fitness parameters correlated significantly with genetic diversity. This is in line with Kahmen & Poschlod (2000), who also failed to establish such a relationship.

Bachmann & Hensen (2005) observed strong fluctuations in *C. glomerata* populations sizes measured as number of flowering stems and sterile rosettes and supposed that these fluctuations were caused by sprouting and non-sprouting of a subterranean bud bank. The fact that the aboveground structure of a population changes greatly from year to year means that every year there are new possibilities of mating combinations, in turn guaranteeing a strong molecular variance in the sexually generated offspring. A similar hypothesis is made for *Platanthera leucophaea*, an orchid, where plant dormancy patterns and chaotic fluctuations in population size may buffer against stochastic events, especially in small populations (Wallace 2002). We could not find any seedlings of *C. glomerata*, but identifying them in the field is extremely difficult due to the dense grass coverage. However, the fact that all our samples represented genetic individuals, that all viable seeds germinated in our germination experiment, and that sexually generated offspring occurred by chance in a common garden experiment (Bachmann et al. 2005), underlines the high importance of sexual reproduction for the dynamic and survival of *C. glomerata* populations.

Based on the results of this study, *C. glomerata* populations have remained almost unaffected by isolation, inbreeding or genetic drift and seem to be unthreatened by genetic factors as yet. That might be attributed to the longevity and particular life history traits that preserve variability. *C. glomerata* is used as an indicator species for long term constant environmental conditions (Partzsch 2001), so that conservation programs should support the stability of plant communities. Pasturing or manual mowing and biomass extraction can prevent changes in competition in abandoned landscapes, which can in turn have a negative affect on germination and establishment of *C. glomerata* (Bachmann et al. 2005). Any kind of eutrophication and anthropogenic intervention such as planting trees or bushes near populations of *C. glomerata* should be avoided. In order to obtain further information about the causes for the decline of *C. glomerata* populations in Germany, we recommend a monitoring of the 20 populations of this study at intervals of 5 years, including records of demographic and genetic structure.

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REFERENCES

ALLENDORF, F. W. & RYMAN, N. (2002). The Role of Genetics in Population Viability Analysis. In: *Population Viability Analysis* (ed. S. R. Beissinger and D. R. McCullough), The University of Chicago Press, Chicago, pp.50-85.

ARZATE-FERNANDEZ, A., MIWA, M., SHIMADA, T., YONEKURA, T. & OGAWA K. (2005). Genetic diversity of Miyamasukashi-yuri (*Lilium maculatum* Thunb. var. *bukosanense*), an endemic and endangered species at Mount Buko, Saitama, Japan. *Plant Species Biology* **20**:57-65.

AYRES, D. R. & RYAN F. R. (1999). Genetic diversity and structure of the narrow endemic *Wyethia reticulata* and its congener *W. bolanderi* (Asteraceae) using RAPD and allozyme techniques. *American Journal of Botany* **86**:344-353.

BACHMANN, U. & HENSEN I. (2006). Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use practices. *Feddes Repertorium* **117**: 164-171

BACHMANN, U., HENSEN I. & PARTZSCH, M. (2005). Is *Campanula glomerata* threatened by competition of expanding grasses? *Plant Ecology* **180**:257-265.

BARRETT, S. C. H. & KOHN J. R. (1991). Genetic and evolutionary consequences of small population size in plants: Implications for conservation. In *Genetics and conservation* (ed. D. A. Falk and K. E. Holsinger K. E), University Press, Oxford, pp. 3-30

BARTISH, I. V., JEPPSON, N. & NYBOM H. (1999). Population genetic structure in the dioecious pioneer plant species *Hippophae rhamnoides* investigated by random amplified polymorphic DNA (RAPD) markers. *Molecular Ecology* **8**:791-802.

BASKIN, C. C. & BASKIN J. M. (2001). *Seeds - ecology, biogeography, and evolution of dormancy and germination*. Academic press, London.

BENKERT, D., FUKAREK F. & KORSCH H. (1996). *Verbreitungsatlas der Farn- und Blütenpflanzen Ostdeutschlands*. Fischer, Jena.

CARDOSO, M. A., PROVAN J., POWELL W., FERREIRA C. G. & DE OLIVIERA, D. E. (1998). High genetic differentiation among remnant populations of the endangered *Caesalpinia echinata* Lam. (Leguminosae-Caesalpinioideae). *Molecular Ecology* **7**:601-608.

CLAUSING, G., VICKERS, K. & KADEREIT J. W. (2000). Historical biogeography in a linear system: genetic variation of Sea Rocket (*Cakile maritima*) and Sea Hally (*Eryngium maritimum*) along European coasts. *Molecular Ecology* **9**:1823-1833.

DITTBRENNER, A., HENSEN, I. & WESCHE K. (2005). Genetic structure and random amplified polymorphic DNA diversity of the rapidly declining *Angelica palustris* (Apiaceae) in Eastern Germany in relation to population size and seed production. *Plant Species Biology* **20**:191-200.

ELLSTRAM, N. C. & ELAM D. R. (1993). Population genetic consequences of small population size: implication for plant conservation. *Ann. Rev. Ecol. Syst*. **24**:217-242.

EMIG, W. & LEINS P. (1994). Ausbreitungsbiologische Untersuchungen in der Gattung *Campanula* L. I. Vergleichende Windkanalexperimente zur Samenportionierung bei *C. Trachelium* L., *C. sibirica* L. und *C. glomerata* L. *Bot. Jahrb. Syst*. **116**:243-257.

EMIG, W. & LEINS, P. (1996). Ausbreitungsbiologische Untersuchungen in der Gattung *Campanula* L. II. Die Bedeutung der Kapselmorphologie und der Samenausgestaltung für das Ausbreitungsverhalten. *Bot. Jahrb. Syst*. **118**:505-528.

EXCOFFIER, L., SMOUSE P. E. & QUATTRO J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotype: application to human mitochondrial DNA restriction data. *Genetics* **131**:479-491.

FISCHER, M., HUSI, R., PRATI, D., PEINTINGER, M., KLEUNEN, M. & SCHMID, B. (2000). RAPD variation among and within small and large populations of the rare clonal plant *Ranunculus reptans* (Ranunculaceae). *American Journal of Botany* **87**:1128-1137.

FISCHER, M. & MATTHIES, D. (1997). Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). *American Journal of Botany* **84**:1685-1692.

FISCHER, M. & MATTHIES, D. (1998). RAPD-Variation in relation to population size and plant fitness in the rare plant *Gentianella germanica* (Gentianellaceae). *American Journal of Botany* **85**:811-819.

FRANK, D. & NEUMANN, V. (1999). *Bestandssituation der Pflanzen und Tiere Sachsen-Anhalts*. Ulmer, Stuttgart.

FRANKHAM, R. (2005). Genetics and extinction. *Biological Conservation* **126**:131-140.

FRANKHAM, R., BALLOU, J. D. & BRISCUE, D. A. (2002) *Introduction to conservation genetics*. Cambridge University Press, Cambridge.

GADELLA, T. W. J. (1964). Cytotaxonomic studies in the genus *Campanula*. *Wendtia* **11**:1-104.

GAUDEUL, M., TABERLET, P. & TILL-BOTTRAUD, I. (2000). Genetic diversity in an endangered alpine plant, *Eryngium alpinum* L. (Apiaceae), inferred from amplified fragment length polymorphism. *Molecular Ecology* **9**:1625-1637.

GODT, M. J. W., HAMRICK, J. L. M. & BRATTON, S. (1995). Genetic diversity in a threatened wetland species, *Helonias bullata* (Liliaceae). *Conservation Biology* **9**:596-604.

HAEUPLER, H. & SCHOENFELDER, P. (1998). *Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland*. Ulmer, Stuttgart.

HAMRICK, J. L. & GODT, M. J. W. (1989). Allozyme diversity in plant species. In: *Plant Population Genetics, Breeding and Genetic Resources* (ed. A. H. D. Brown, M. T. Clegg, A. L. Kahler and B. S. Weir), Sinauer, Sunderland, pp. 43-63

HAMRICK, J. L. & GODT, M. J. W. (1996). Effects of life history traits on genetic diversity in plant species. *Phil. Trans. Royal Soc. of London Ser. B* **351**:1291-1298.

HARDTKE, H.-J. & IHL, A. (2000). *Atlas der Farn- und Samenpflanzen Sachsens*. Sächsisches Landesamt für Umwelt und Geologie, Dresden.

HENSEN, I. & OBERPRIELER, C. (2005). Effects of population size on genetic diversity and seed production in the rare *Dictamnus albus* (Rutaceae) in Central Germany. *Conservation Genetics* **6**:63-73.

HENSEN, I., OBERPRIELER, C. & WESCHE, K. (2005). Genetic structure, Population size, and Seed Production of *Pulsatilla vulgaris* Mill. (Ranunculaceae) in Central Germany. *Flora* **200**:3-14.

HENSEN,I. & WESCHE, K. (in press) Relationships between population size, genetic diversity and fitness components in the rare plant *Dictamnus albus* in Central Germany. *Biodiversity and Conservation*.

KAHMEN, S. & POSCHLOD, P. (2000). Population size, plant performance, and genetic variation in the rare plant *Arnica montana* L. in the Rhön, Germany. *Basic Appl. Ecol*. **1**:43-51.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002). BIOLFLOR-Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenr. f. Vegetationskunde* **38**:1-334.

KWAK, M. M., VELTEROP, O. & VAN ANDEL, J. (1998). Pollen and gene flow in fragmented habitats. *Applied Vegetation Science* **1**:37-54.

LANDE, R. & SCHEMSKE, D. W. (1985). The evolution of self-fertilisation and inbreeding depression in plants. I. Genetic models. *Evolution* **39**:24-40.

LOVELESS, M. D. & HAMRICK, J. L. (1984). Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst*. **15**:65-95.

LOWE, A., HARRIS, S. & ASHTON, P. (2004). *Ecological Genetics: Design, Analysis, and Application*. Blackwell publishing.

LUIJTEN, S. H., DIERICK, A., OOSTERMEIJER, G., RAIJMANN, L. E. L. & DEN NIES, H. C. M. (2000). Population size, genetic variation, and reprodictive success in a rapidly declining, self-incompatible perennial (*Arnica montana*) in The Netherlands. *Conservation Biology* **14**:1776-1787.

MAKI, M., MASUDA, M. & INOUE, K. (1996). Genetic diversity and hierarchical population structure of a rare autotetraploid plant, *Aster kantonensis* (Asteraceae). *American Journal of Botany*, **83,** 296-303.

MANTEL, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**:209-220.

NYBOM, H. & BARTISH, I. V. (2000). Effects of life history traits and sampling strategies on genetic diversity estimates obtained with RAPD markers in plants. *Perspectives in pant Ecology, Evolution and Systematics* **3/2**:93-114.

OKADA, S. & OKADA H. (2000). Genetic diversity and genetic structure of populations of *Ranunculus japonicus* Thunb. (Ranunculaceae). *Plant Species Biology* **17**:59-69.

OOSTERMEIJER, G., VAN`T VEER, R. & DEN NIES J. C. M. (1994). Population structure of the rare, long lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of applied Ecology* **31**:428-438.

OOSTERMEIJER, G. (1996). *Population viability of the rare Gentiana pneumonanthe - the relative importance of demography, genetics and reproductive biology*. doctoral. Amsterdam, Amsterdam.

OOSTERMEIJER, G., LUIJTEN, S. H., KRENOVA, Z. V. & DEN NIES, H. C. M. (1998). Relations between population and habitat characteristics and reproduction of the rare *Gentiana pneumonanthe* L. *Conservation Biology* **12**:1042-1053.

OOSTERMEIJER, G. & DE KNEGT, B. (2004). Genetic population structure of the wind-pollinated, dioecious shrub *Juniperus communis* in fragmented Dutch heathlands. *Plant Species Biology* **19**:175-184.

OUBORG, N. J. & R. VAN TREUREN, R. (1995). Variation in fitness-related characters among small and large populations of *Salvia pratensis*. *Journal of Ecology* **83**:369-380.

PARTZSCH, M. (2001). Die Porphyrkuppenlandschaft des unteren Saaletals - Vergleich der Vegetation in Abhängigkeit von Flächengröße und Genese der Prophyrkuppen. *Bot. Jahrb. Syst.* **123**:1-45.

PASSARGE, H. (1999). *Pflanzengesellschaften Nordostdeutschlands. II. Helocyperosa and Cespitosa.* J. Cramer, Berlin.

PISKOVACKOVA, N. P. (1980). Kolokolcik Skucennyi. In Rabotnov, T. A. (ed). *Biologiceskaja flora Moskovskoj oblasti*. Moskva universitet, Moskva, pp. 156-169

PLUESS, A. R. & STÖCKLIN, J. (2004a). Genetic diversity and fitness in *Scabiosa columbaria* in the Swiss Jura in relation to population size. *Conservation Genetics* **5**:145-156.

PLUESS, A. R. & STÖCKLIN, J. (2004b). Population genetic diversity of the clonal plant *Geum reptans* (Rosaceae) in the Swiss Alps. *American Journal of Botany* **91**:2013-2021.

PROBER, S. M., SPINDLER, L. H. & BROWN, A. H. D. (1998). Conservation of the grassy white box woodlands: Effects of remnant population size on genetic diversity in the allotetraploid herb Microseris lanceolata. *Conservation Biology* **12**:1279-1290.

RICHARDS, C. M. (2000). Genetic and demographic influences on population persistence: gene flow and genetic rescue in *Silene alba*. In *Genetics, Demography and Viability of Fragmented Populations* (ed. A. G. Young and G. M. Clarke), University Press, Cambridge, pp. 271-291

ROTHMALER, W. (2002). *Exkursionsflora von Deutschland. Gefäßpflanzen: Kritischer Band*. Spektrum, Heidelberg-Berlin.

SCHNEIDER, S., ROESSELI, D. & EXCOFFIER, L. (2000). *ARLEQUIN ver 2.000: A software for population genetics data analysis*. University of Geneva, Switzerland.

VAN TREUREN, R., BIJLSMA, R., VAN DELDEN, W. & OUBORG, N. J. (1991). Genetic differentiation in *Salvia pratensis* and *Scabiosa columbaria* in relation to population size. *Heredity* **66**:181-189.

VERGEER, P., RENGELINK, R., COPAL, A. & OUBORG, N. J. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91**:18-26.

WALLACE, L. E. (2002). Examining the effects of fragmentation on genetic variation in *Platanthera leucophaea* (Orchidaceae): Inferences from allozyme and random amplified polymorphic DNA markers. *Plant Species Biology* **17**:37-49.

WASHITANI, I., ISHIHAMA, F., MATSUMURA, C., NAGAI, M., NISHIHIRO, J. & NISHIHIRO, M. A. (2005). Conservation ecology of *Primula sieboldii*: Synthesis of information toward the prediction of the genetic/demographic fate of a population. *Plant Species Biology* **20**:3-15.

WRIGHT, S. (1951). The genetical structure of populations. *Annual Eugen*. **15**:323-354.

YOUNG, A., BOYLE, T. & BROWN, T. (1996). The population genetic consequences of habitat fragmentation for plants. *Trends in ecology and evolution* **11**:413-418.

KAPITEL III

IS HABITAT QUALITY AFFECTING POPULATION SIZE AND PLANT PERFORMANCE IN THE DECLINING FORB *CAMPANULA GLOMERATA*?

BACHMANN, U. & HENSEN, I. (submitted to *Plant Species Biology*)

ABSTRACT

In Central Germany, many species are known to decline due to the abandoning of traditional land-use practices, and one such species is *Campanula glomerata*. Besides leading to fragmentation and isolation of natural habitats, changes in land-use alter habitat characteristics that might influence plant performance. In the present study we analysed the effects of habitat related parameters such as vegetation cover, land-use, and soil conditions on *C. glomerata* population size and plant performance. Neither land-use nor soil conditions affected population size or plant performance. Height of flowering stems was positively related to flower number and seed weight and was found to correlate positively with vegetation cover. We conclude that *C. glomerata* is able to tolerate higher vegetation cover. However, as the positive influence of increasing vegetation cover on plant performance might be counteracted by hampered establishment, management should focus on the creation of open sites for seed germination.

INTRODUCTION

Land-use change alters the structure, composition and dynamics of ecosystems, as well as the survival of plant populations (Donohue et al. 2000). As a result, habitat characteristics as well as patterns of interspecific competition have been changed and populations of many plant species have been ever more reduced in size and have become more isolated from each other than in the past. Evidence is growing that both small population size and isolation increase the risk of extinction due to genetic, demographic and/or environmental problems (Oostermeijer 1996, Allendorf & Ryman 2002, Lowe et al. 2004). As the decline of rare species is always a focal point in plant conservation, the evaluation of the relative importance of several interacting factors on their survival is essential (e.g. Menges 1990, Oostermeijer 1996). Thus, many studies have been analysing the interacting effects of genetic variation and population size on the performance of several rare plant species (van Treuren et al. 1991, Godt et al. 1995, Fischer & Matthies 1998, Gaudeul et al. 2000, Luijten et al. 2000, Dittbrenner et al. 2005, Hensen & Oberprieler 2005, Hensen et al. 2005). However, combined effects of environmental stress, genetic variation and population size on plant performance have, as yet, been addressed by only a few authors (Fischer 1996, Vergeer et al. 2003a, Vergeer et al. 2003b).

The results of several studies imply that, apart from molecular variance or population size, habitat related factors such as vegetation composition, standing crop, C:N ratio and soil pH (Schmidt & Jensen 2000), as well as climate, surrounding vegetation and management practice (Fischer 1996) do have impacts on the variation of reproductive components. Vegetation structure is known to affect the most important phases in the demography of plant species: germination, seedling establishment and flowering (Hegland et al. 2001). In addition, NH_4 and NO_3 concentrations in the soil (Vergeer et al. 2003a) and the amount of shading (Eisto et al. 2000) may also affect population size and performance in certain plant species. For conservation purposes it is important to assess how, and to what extent, habitat quality interacts with genetic and demographic processes and how these interactions affect population persistence and performance (Vergeer et al. 2003a).

Campanula glomerata, a long-lived perennial, has been increasingly more restricted to isolated populations due to the cessation of traditional land-use practices with subsequent vegetation changes, or the intensification of agriculture, and is currently declining in Germany (Frank & Neumann 1999, Hardtke & Ihl 2000). Within the scope of a population viability analysis, previous studies revealed neither a correlation between genetic variation and population size parameters, nor one between genetic variation and fitness components such as flower number or seed germination (Bachmann & Hensen, in press). However, first-year performance of *C. glomerata* biomass and fitness was shown to be negatively affected by the increasing expansion of *Poa angustifolia* (Bachmann et al. 2005). This result and additional field observations support the assumption that *C. glomerata* performance depends in part on the structure of the surrounding vegetation. Therefore, the aim of the present study was to analyse the effects of the habitat parameters vegetation cover, land-use and soil conditions on population size and plant performance in *C. glomerata*.

METHODS

Study species

Campanula glomerata L. is a perennial, insect pollinated forb distributed mainly in submeridional to boreal Europe and Siberia (Rothmaler 2002). The average life span of an individual is estimated to be 25 – 30 years. Flowering usually begins in the second year after germination, but sometimes it takes up to 6 years to reach reproductive maturity. Sterile rosettes can be found in the pre-maturity stage, but also in stages of resting or senescence (Piskovackova 1980). Most rosettes produce only one flowering stem, 5 to 70cm in height, with one to a few flower heads in the leaf axils and at the apikal end of the stem. A flower head consists of one or more purplish blue, protandrous single flowers. Each *C. glomerata* capsule can contain up to 100 seeds (Bachmann, unpubl.), which are dispersed by wind (Emig & Leins 1994). Vegetative propagation occurs by rhizomes (Klotz et al. 2002).

Study sites and data collection

We studied 20 populations in three different regions in Germany (figure I/2, page 7): 11 populations in the surroundings of Halle/Saale in Saxony-Anhalt (populations A – K); 6 populations in the "Schwäbische Alb" in Baden-Wuerttemberg (populations L – Q); and three populations in the

“Nordrheinwestfälische Kalkeifel” in North Rhine-Westphalia (populations R, S, T). A population was defined as a clearly differentiated group of plants separated from their closest con-specific by either more than 100m or by natural barriers such as agricultural stretches or hedgerows. In every region we randomly selected populations for investigation that were either part of a traditionally used landscape or of a landscape where land-use had been abandoned at least 10 years previous. In total, we studied 10 *C. glomerata* populations in pastured or mowed grasslands (pasturing or mowing occurred always after sampling) and 10 in abandoned grasslands (for more details see Bachmann & Hensen 2006). Populations were found either on loess over porphyry or calcareous rock within the following mesoxerophytic grassland communities: Festuco rupicolae-Brachypodietum pinnati MAHN 1959 emend (nomenclature according to Schubert et al. 1995), Gentiano-Koelerietum pyramidatae KNAPP 1942 ex BORNK. 1960, Dauco carotae-Arrhenatheretum elatioris (BR.BL. 1919) GÖRS 1966, and Onobrychido-Brometum erecti TH. MÜLL. 1968.

Population sizes of *C. glomerata* were determined by counting the exact number of flowering stems during the flowering period (July or August) in 2002. In August 2002 we randomly selected at most 100 flowering stems of *C. glomerata* in each population and measured height and counted flowers. Capsules were harvested from 4 to, where possible, 30 randomly selected plants from the terminal flower head. Seeds were drystored in paper bags under ambient laboratory conditions (20°C). In December 2002, seeds were weighted in a batch of 100. Germination was tested on a pooled sample from each population at a temperature of 20°C/10°C (12/12h day/night cycle; n = 5 x 20 seeds) in a climate chamber with a warm white light source and ceased after 100 days when germination was at zero. The viability of ungerminated seeds was tested using the tetrazolium test (Baskin & Baskin 2001). Vegetation cover was estimated three times in each population in an area measuring 4m² at the soil surface, and in layers at 10, 20, 30, 40, 50 and 60cm above the ground. Populations were found in all exposures. Soil depth was estimated by driving a rod into the ground (20 times per study site). Soil samples were taken in July 2002. For each population we took 10 randomised samples from 0 - 20cm in depth. The mixed soil samples were analysed for pH-value (20g soil in 50ml H_2O; SenTix 21, WTW, Germany); plant available content of monovalent (K^+, Na^+) and bivalent (Ca^{2+}, Mg^{2+}) cations (NH_4Cl-extraction followed by atomic absorption spectrometry, Flame AAS Vario 6 Analytik Jena, Germany); total C and N (Dumas method; CN Analyser Vario EL, Elementar, Germany); and conductivity (Cond 315i, WTW Germany). All data refer to dry (105°C) fine soil (particle size < 2mm).

Statistical Analyses

Statistical Analyses were performed using SPSS 10.0.5. (1999). Correlations between *C. glomerata* performance parameters (Table III/1) were calculated using Pearson’s R. We used stepwise multiple regression analyses to create models with population size (number of fertile *C. glomerata* stems) and plant performance parameters (average height of flowering stems and germination) as dependent variables. Habitat parameters, including pH-value, conductivity, content of K^+, Na^+, Ca^{2+} and Mg^{2+}, C/N, soil depth, exposition, land-use, vegetation cover at ground level and 10cm, 20cm, 30cm, 40cm, 50cm and 60cm above ground, were used as predictor variables. Land-use was defined as “0” = no land-use and “1” = land-use. Percentages were arcsine transformed; data on conductivity, content of

K^+, Na^+, Ca^{2+} and Mg^{2+} and C/N were log transformed. Exposure was termed as divergence from north.

RESULTS

Parameters of population size and plant performance are listed in table III/1, habitat parameters are specified in table III/2. As the average height of flowering stems significantly correlated to average number of flowers per stem (Pearson R = 0.635, P = 0.003) and to average seed weight (Pearson R = 0.64, P = 0.002), the multiple regression analysis was performed with only the plant performance parameters "height of flowering stems" and "germination" (equated to seed viability, table III/1). The model showed that out of 17 tested habitat quality parameters (table III/2), only vegetation cover at 20cm above ground significantly affected plant performance ("height of flowering stems", table III/3). We found no effects of habitat quality parameters on population size.

Table III/1: Population sizes and plant performance parameters of 20 *C. glomerata* populations in Germany. As all viable seeds germinated, germination can be equated with seed viability.

population	number of fertile stems	average height of flowering stems [cm]	average number of flowers per stem	germination [%]	average seed weight [mg]
A	1178	29.6	21.9	39	0.11
B	50	23.1	18.5	9	0.08
C	83	28.4	35.2	27	0.1
D	10	32.9	44.7	12	0.12
E	140	30.7	21.8	69	0.17
F	241	24.8	12.9	2	0.13
G	75	38.0	36.1	33	0.15
H	40	14.5	26.6	58	0.09
I	35	31.1	31.4	5	0.13
J	295	25.3	20.3	30	0.14
K	33	71.7	52.5	39	0.18
L	14	32.5	17.5	24	0.15
M	106	48.6	35.9	33	0.16
N	6	30.0	10.6	18	0.13
O	414	41.8	25.8	41	0.13
P	6	47.8	35.5	69	0.17
Q	102	31.2	23.5	26	0.14
R	2381	28.9	9.1	6	0.15
S	143	44.8	30.2	4	0.17
T	150	30.5	27.6	19	0.18

Table III/3: Results of stepwise multiple regression analyses.

	average length of flowering stems	
F	29.432	
Significance	< 0.000	
adjusted R^2	0.599	
predictor variable	Beta	P
vegetation cover 20cm above ground level	0.788	< 0.000

Table III/2: Parameters of habitat quality (plant community: 1 = Festuco rupicolae-Brachypodietum pinnati, 2 = Dauco carotae-Arrhenatheretum elatioris, 3 = Gentiano-Koelerietum pyramidatae, 4 = Onobrychido-Brometum erecti, land-use: 0 = no land-use, 1 = land-use).

population	plant community	land use	vegetation cover at ground [%]	vegetation cover ... above ground [%]						soil depth [cm]	pH-value	conductivity [µscm]	K [mg/kg]	Mg [mg/kg]	Ca [mg/kg]	Na [mg/kg]	C/N	exposition
				10cm	20cm	30cm	40cm	50cm	60cm									
A	1	1	95	70	25	7	3	1	1	27	7.1	279	247	176	2020	29	9.7	SO
B	1	1	100	65	25	6	1	0	0	30	6.1	220	177	179	2125	33	9.8	N
C	1	0	90	30	10	5	0	0	0	23	7.5	238	167	146	2040	26	8.4	NW
D	1	0	95	30	15	5	0	0	0	19	7.3	388	401	183	2380	30	16.2	SW
E	1	0	100	60	15	5	0	0	0	30	7.3	452	461	498	2340	33	13.9	W
F	1	0	95	30	5	2	0	0	0	30	7.7	298	221	103	2220	32	16.1	W
G	1	0	100	100	80	10	3	0	0	30	7.4	243	192	114	1956	30	9.6	N
H	1	0	100	40	20	3	0	0	0	30	7.4	272	139	105	1696	31	10.2	N
I	1	0	100	90	40	10	5	0	0	21	6.6	240	273	182	2040	30	7.6	N
J	1	1	75	45	25	2	0	0	0	18	7.5	378	205	102	2670	31	11.7	NW
K	2	0	100	100	100	50	20	10	5	30	7.3	252	213	76	1894	27	8.5	NO
L	3	1	90	90	50	5	2	2	0	15	7.6	322	151	71	2780	30	17.0	SO
M	2	1	95	100	100	80	40	20	10	5	7.5	303	105	82	2120	26	21.1	O
N	3	1	95	100	75	25	5	2	0	15	7.4	367	134	90	3240	26	17.0	SO
O	4	1	100	100	75	40	5	2	2	30	7.4	273	184	119	2640	28	9.0	N
P	3	0	100	100	80	10	5	2	0	15	7.4	422	219	83	3220	29	11.7	S
Q	3	1	100	40	30	10	5	2	0	18	7.4	477	249	91	3200	27	12.9	S
R	3	1	100	60	10	5	0	0	0	10	7.7	305	256	618	1620	26	17.6	SO
S	3	0	100	100	100	90	50	5	0	10	7.6	419	353	784	1980	26	11.4	S
T	3	1	100	100	80	10	5	0	0	9	7.6	464	303	770	1826	26	14.0	SO

DISCUSSION

Our data revealed that the cover realised by surrounding vegetation significantly affects the average height of flowering *C. glomerata* stems. This performance parameter was significantly correlated to average number of flowers per stem and average seed weight. Thus, *C. glomerata* grows and reproduces better, the denser the surrounding vegetation. These results suggest a positive influence of greater resource availability on plant performance, although we did not establish a relationship between vegetation cover and any of the other habitat related parameters. Another possible explanation for better performance in dense vegetation are different neighbour effects of the dominating grass species: *C. glomerata* might grow better in the vicinity of *Arrhenatherum elatius* - which builds up stands with the highest vegetation density - than surrounded by other dominating grassland species such as *Brachypodium pinnatum* or *Koeleria pyramidata*. Distinct responses of *C. glomerata* to the presence of either *Poa angustifolia* or *Festuca rupicola* have already been demonstrated by Bachmann et al. (2005) and accounted for by the grasses growth form (long subterranean branched stolons versus tussock growth form). Indeed, Bobbinks & Willems (1987) emphasised the negative effects exerted on biodiversity by the increasing dominance of the rhizomatous graminoid, *Brachypodium pinnatum*. However, as Hegland et al. (2001) found population structures of *Salvia pratensis* strongly correlated to the surrounding vegetation, our results should be discussed in the context of other stages in the reproductive cycle of *C. glomerata*. In an earlier study, dense vegetation cover was shown to negatively affect germination and establishment of sown *C. glomerata* seeds, probably due to a limitation of light and space (Bachmann et al. 2005). Thus, germination and establishment of *C. glomerata* may be hampered by a closed vegetation cover, which is in accordance with data from Jutila & Grace (2002) and Williams et al. (2002), who found similar responses in other grassland species.

We found no effects of other habitat related parameters such as soil conditions on population size and plant performance in *C. glomerata*. This was surprising as deteriorating habitat quality has been suggested as a causative factor of reduced plant performance by several authors (Dueck & Elderson 1992, Pegtel 1994, Oostermeijer et al. 1998). Habitat parameters, such as standing crop, C:N ratio or soil pH, do have an impact on the variation of reproductive components of *Pedicularis palustris* (Schmidt & Jensen 2000). Nutrient-poor habitats appeared to support larger populations of *Succisa pratensis* (Vergeer et al. 2003a), and the population size of *Campanula cervicaria* was negatively related to the amount of shade (Eisto et al. 2000). Lindborg et al. (2005) found a tendency for population sizes to get smaller along a successional gradient where habitats become more unfavourable, and the age structure of *Gentiana pneumonanthe* - with a decreasing proportion of generative individuals - becomes increasingly unbalanced as the vegetation structure closes (Oostermeijer et al. 1994).

Our model also showed that there was no effect of land-use on population size and plant performance in *C. glomerata*. This is in accordance with a three year study revealing that populations in used and in abandoned landscapes did not differ in any of the size parameters we determined (Bachmann & Hensen 2006). Different authors attribute the decline of *C. glomerata* to the abandonment of traditional land-use practices as well as the intensification of agriculture (e.g. Sebold et al. 1996, Frank & Neumann 1999, Hardtke & Ihl 2000). Our results give rise to the suspicion that loss of habitat, rather than the abandonment of traditional land-use practices, might be the main factor for the observed decline of population numbers and sizes.

The results of our study imply that altered habitat quality due to cessation of traditional land-use practices might not directly affect population sizes and plant performance of *C. glomerata* that is able to tolerate higher vegetation cover without limitation of pollination and seed quality in certain grassland communities. However, the positive influence of increasing vegetation cover on plant performance might be counteracted by hampered seedling establishment. Thus, to ensure persistence of the populations, management practices should include the creation of open sites for seed germination and establishment.

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REFERENCES

ALLENDORF, F. W. & RYMAN, N. (2002). The Role of Genetics in Population Viability Analysis. In *Population Viability Analysis* (ed. S. R. Beissinger and D. R. McCullough), pp. 50-85. Chicago: The University of Chicago Press.

BACHMANN, U. & HENSEN, I. (2006). Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use practices. *Feddes Repertorium* **117***:*164-171.

BACHMANN, U. & HENSEN, I. (in press). Is the declining *Campanula glomerata* threatened by genetic factors? *Plant Species Biology*.

BACHMANN, U. HENSEN, I., & PARTZSCH, M. (2005). Is *Campanula glomerata* threatened by competition of expanding grasses? *Plant Ecology* **180:**257-265.

BASKIN, C. C. & BASKIN, J. M. (2001). *Seeds - ecology, biogeography, and evolution of dormancy and germination*. London: Academic press.

BOBBINK, R. & WILLEMS, J. H. (1987). Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: A threat to a species-rich ecosystem. *Biological Conservation* **40:**301-314.

DITTBRENNER, A., HENSEN, I. & WESCHE, K. (2005). Genetic structure and random amplified polymorphic DNA diversity of the rapidly declining *Angelica palustris* (Apiaceae) in Eastern Germany in relation to population size and seed production. *Plant Species Biology* **20:**191-200.

DONOHUE, K. FOSTER, D. R., & MOTZKIN, G. (2000). Effects of the past and the present on species distribution: land-use history and demography of wintergreen. *Journal of Ecology* **88:**303-316.

DUECK, T. A. & ELDERSON, J. (1992). Influence of NH_3 and SO_2 on the growth and competitive ability of *Arnica montana* L. and *Viola canina* L. *New Phtologist* **122:**507-514.

EISTO, A.-K., KUITUNEN, M., LAMMI, A., SAARI, V., SUHONEN, J., SYRJÄSUO, S. & TIKKA, P. M. (2000). Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. *Conservation Biology* **14:**1413-1421.

EMIG, W. & LEINS, P. (1994). Ausbreitungsbiologische Untersuchungen in der Gattung Campanula L. I. Vergleichende Windkanalexperimente zur Samenportionierung bei *C. Trachelium* L., *C. sibirica* L. und *C. glomerata* L. *Bot. Jahrb. Syst.* **116:**243-257.

FISCHER, M. (1996). Experimental population biology of the rare *Gentianella germanica*, *Philosophisch-Naturwissenschaftliche Fakultät*. Basel: Universität Basel.

FISCHER, M. & MATTHIES, D. (1998). RAPD-Variation in relation to population size and plant fitness in the rare plant *Gentianella germanica* (Gentianellaceae). *American Journal of Botany* **85:**811-819.

FRANK, D. & NEUMANN, V. (1999). *Bestandssituation der Pflanzen und Tiere Sachsen-Anhalts*. Stuttgart: Ulmer.

GAUDEUL, M., TABERLET, P. & TILL-BOTTRAUD, I. (2000). Genetic diversity in an endangered alpine plant, *Eryngium alpinum* L. (Apiaceae), inferred from amplified fragment length polymorphism. *Molecular Ecology* **9:**1625-1637.

GODT, M. J. W., MHAMRICK, J. L. & BRATTON, S. (1995). Genetic diversity in a threatened wetland species, *Helonias bullata* (Liliaceae). *Conservation Biology* **9:**596-604.

HARDTKE, H.-J. & IHL, A. (2000). *Atlas der Farn- und Samenpflanzen Sachsens*. Dresden: Sächsisches Landesamt für Umwelt und Geologie.

HEGLAND, S. J., VAN LEEUWEN, M. & OOSTERMEIJER, G. (2001). Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *Journal of applied Ecology* **38:**1277-1289.

HENSEN, I. & OBERPRIELER, C. (2005). Effects of population size on genetic diversity and seed production in the rare *Dictamnus albus* (Rutaceae) in Central Germany. *Conservation Genetics* **6:**63-73.

HENSEN, I., OBERPRIELER, C. & WESCHE, K. (2005). Genetic structure, Population size, and Seed Production of *Pulsatilla vulgaris* Mill. (Ranunculaceae) in Central Germany. *Flora* **200:**3-14.

JUTILA, H. M. & GRACE, J. B. (2002). Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *Journal of Ecology* **90:**291-302.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002). BIOLFLOR- Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenr. f. Vegetationskunde* **38:**1-334.

LINDBORG, R., COUSINS, S. A. O. & ERIKSSON, O. (2005). Plant species response to land-use change - *Campanula rotundifolia, Primula veris* and *Rhinathus minor*. *Ecography* **28:**29-36.

LOWE, A., HARRIS, S. & ASHTON, P. (2004). *Ecological Genetics: Design, Analysis, and Application*: Blackwell publishing.

LUIJTEN, S. H., DIERICK, A., OOSTERMEIJER, G., RAIJMANN, L. E. L. & DEN NIES, H. C. M. (2000). Population size, genetic Variation, and reproductive succes in a rapidly declining, self-incompatible perennial (*Arnica montana*) in The Netherlands. *Conservation Biology* **14:**1776-1787.

MENGES, E. S. (1990). Population viability analysis for an endangered Plant. *Conservation Biology* **4:**52-62.

OOSTERMEIJER, G. (1996). Population viability of the rare *Gentiana pneumonanthe* - the relative importance of demography, genetics and reproductive biology, *Universität*. Amsterdam: Amsterdam.

OOSTERMEIJER, G., LUIJTEN, S. H., KRENOVA, Z. V. & DEN NIES, H. C. M. (1998). Relations between population and habitat characteristics and reproduction of the rare *Gentiana pneumonanthe* L. *Conservation Biology* **12:**1042-1053.

OOSTERMEIJER, G., VAN`T VEER, R. & DEN NIJS, J. C. M. (1994). Population structure of the rare, long lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology* **31:**428-438.

PEGTEL, D. M. (1994). Habitat characteristics and the effect of various nutrient solutions on the growth and mineral nutrition of *Arnica montana* L. grown on a natural soil. *Vegetatio* **114:**109-121.

PISKOVACKOVA, N. P. (1980). Kolokolcik Skucennyi. In T. A. Rabotnov (Ed.), *Biologiceskaja flora Moskovskoj oblasti* (pp. 156-169). Moskva: Moskva universitet.

ROTHMALER, W. (2002). *Exkursionsflora von Deutschland. Gefäßpflanzen: Kritischer Band*. Heidelberg-Berlin: Spektrum.

SCHMIDT, K. & JENSEN, K. (2000). Genetic structure and AFLP variation of remnant populations in the rare plant *Pedicularis palustris* (Scrophulriaceae) and its relation to population size and reproductive components. *American Journal of Botany* **87:**678-689.

SCHUBERT, R., HILBIG, W. & KLOTZ, S. (1995). *Bestimmungsbuch der Pflanzengesellschaften Deutschlands*. Jena: Fischer.

SEBOLD, O., SEYBOLD, S., PHILIPPI, G. & WÖRZ, A. (1996). *Die Farn- und Blütenpflanzen Baden-Württembergs*. Stuttgart: Ulmer.

VAN TREUREN, R., BIJLSMA, R., VAN DELDEN, W. & OUBORG, N. J. (1991). Genetic differentiation in *Salvia pratensis* and *Scabiosa columbaria* in relation to population size. *Heredity* **66:**181-189.

VERGEER, P., RENGELINK, R., COPAL, A. & OUBORG, N. J. (2003a). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91:**18-26.

VERGEER, P., RENGELINK, R., OUBORG, N. J. & ROELOFS, J. M. G. (2003b). Effects of population size and genetic variation of *Succisa pratensis* to eutrophication and acidification. *Journal of Ecology* **91:**600-609.

WILLIAMS, M. I., SCHUMAN, G. E., HILD, A. L. & VICKLUND, L. E. (2002). Wyoming Big Sagebrush Density: Effects of seeding rates and grass competition. *Restoration Ecology* **10:**385-391.

KAPITEL IV

ARE POPULATION SIZES OF *CAMPANULA GLOMERATA* ON THE DECLINE FOLLOWING THE ABANDONMENT OF TRADITIONAL LAND-USE PRACTICES?

BACHMANN, U. & HENSEN, I. (2006). Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use practices? *Feddes Repertorium* **117**:164-171

ABSTRACT

In Central Germany, many species are known to decline due to the abandonment of traditional land use practices, among them *Campanula glomerata*. Within the scope of a population viability analysis for this species we monitored the development of several population size parameters such as total number of stems, number of flowering stems, population density and the area occupied by a population, all in landscapes defined by traditional land use practices as well as in landscapes where land use has been halted. However, over a time span of three years we did not detect any constant tendency for decreasing sizes of populations of *C. glomerata* on disused land compared to those on traditionally used land. Populations in used and abandoned landscapes were characterized by a high variability and fluctuation of size, and did not differ in any of the size parameters we determined. Further studies should include the monitoring of the age state structure of populations as important to facilitate a meaningful comparison of *C. glomerata* populations in abandoned and traditionally used landscapes.

INTRODUCTION

The monitoring of population sizes is indispensable to the effective design of conservation programs aimed at maintaining rare plant species, as their associated dynamics serve as predictions of the degree to which a certain plant species may be, or become, endangered (Fischer & Stöcklin 1997). Decreasing population sizes serve as warning signals because small populations may thereby suffer from a decrease in genetic diversity, due to inbreeding and reduced gene flow, resulting in a compromise of plant fitness and competition ability, which in turn increases the risk of local extinction (Pluess & Stöcklin 2004).

In Saxony-Anhalt, 14% of all vascular plant species are classified as being endangered (red list category 3) and 9% as being critically endangered (red list category 2, Jedicke 1997). These estimates indicate that local populations are decreasing in size and may consequently be threatened by further risks. One of these species is *Campanula glomerata*, a long lived perennial that is often found on historically old grasslands and is an indicator of long-term constant environmental conditions (Partzsch 2001). According to Hardtke & Ihl (2000), Frank & Neumann (1999) and Korneck et al. (1996), the abandonment of traditional land-use practices is the main reason for the current decline. Cessation of grazing is thought to be the primary factor behind the conversion of species-rich, semi-natural grasslands into species-poor communities (WallisDeVries et al. 2002). Consequently, a high percentage of dry grasslands in eastern Germany have been converted into those dominated by several grasses following political reunification (Passarge 1999, Partzsch 2001). Bachmann et al. (2005) demonstrated experimentally that an increasing dominance of certain grass species in dry grassland communities negatively affects the biomass production and fitness parameters of *C. glomerata*. For these reasons, we expected to observe a significant decrease in sizes of *C. glomerata* populations on abandoned sites compared to populations that are still subjected to low-intensity types of agricultural land-use such as grazing or mowing. Within the scope of a population viability analysis, we monitored the development of several population size parameters in 20 *C. glomerata* populations found on still traditionally used landscapes and on abandoned landscapes of central and southern Germany over a period of three consecutive years.

METHODS

STUDY SPECIES AND SITES

Campanula glomerata L. is a perennial, insect pollinated herb distributed mainly in submeridional to boreal Europe and Siberia (Rothmaler 2002). The average life span of an individual is estimated to be 25 – 30 years. Flowering usually begins in the second year after germination, but the pre-flowering stage may take up to 6 years. Sterile rosettes are characteristic for this stage, but also for periods of resting or senescence (Piskovackova 1980). Most rosettes produce only one flowering stem, 5 to 70 cm in height, with one to a few flower heads in the leaf axils and at the apikal end of the stem. A flower head consists of one or more purplish blue, protandrous single flowers. Each capsule can contain up to 100 seeds (Bachmann, unpubl.). Because vegetative propagation occurs by rhizome pleiokorms (Klotz et al. 2002), differentiation of single individuals is difficult.

We studied 20 populations in three different regions in Germany: 11 populations in the surroundings of Halle/Saale in Saxony-Anhalt; 6 populations at the “Schwäbische Alb” in Baden-Wuerttemberg; and three populations at the “Nordrheinwestfälische Kalkeifel” in North Rhine-Westphalia. In every region we randomly selected populations for monitoring that were either part of a traditionally used landscape or of a landscape where land use had been given up at least 10 years previous (figure IV/1). In total we studied 10 *C. glomerata* populations in pastured or mowed grasslands and 10 in abandoned grasslands. A population was defined as a clearly differentiated group of plants separated from their closest con-specific by more than 100m or by natural barriers such as agricultural stretches or hedgerows.

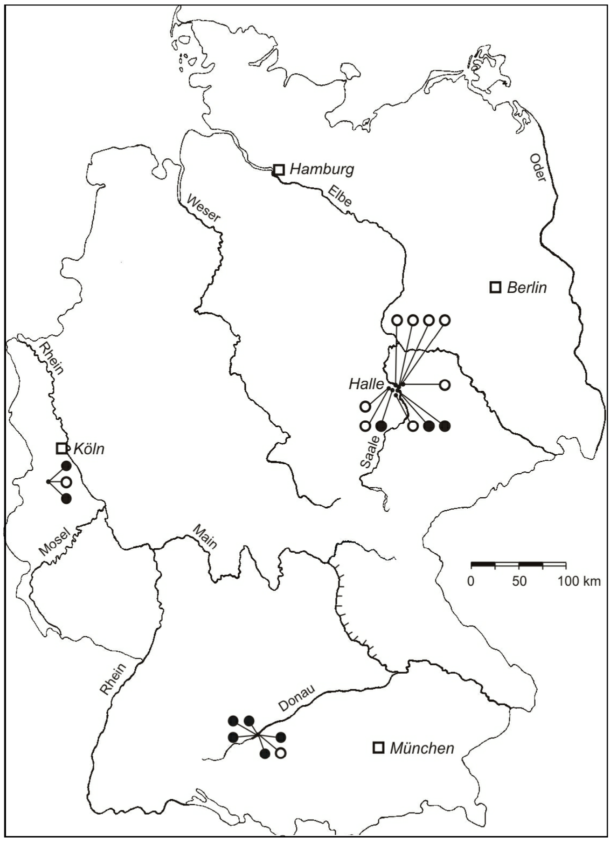

Figure IV/1: Map of Germany showing the locations of studied populations of *C. glomerata* (filled circles = traditional used landscapes, unfilled circles = landscapes where land-use was given up for at least 10 years).

Determination of population sizes

Population sizes of *C. glomerata* were determined by counting the exact number of sterile rosettes and flowering stems during the flowering period (July or August) in 2002, 2003 and 2004. In order to assess population density, these numbers were correlated to their respective occupied areas. In 2004, we were not able to revisit the sites in Baden-Wuerttemberg. According to Stöcklin et al. (1999), populations were considered to be stable when the difference from the previous year's size was < 10%.

Statistical analyses

Statistical analyses were performed using SPSS 10.0.5. (1999). For the comparison of size parameters of used and abandoned populations data was tested for normal distribution (Kolmogorov-Smirnov-test) and equal variance (Levene-test); percentages were arcsin-transformed before statistical analysis. Normal distributed data was compared using the T-test and non parametric data using the Mann-Whitney-U-test.

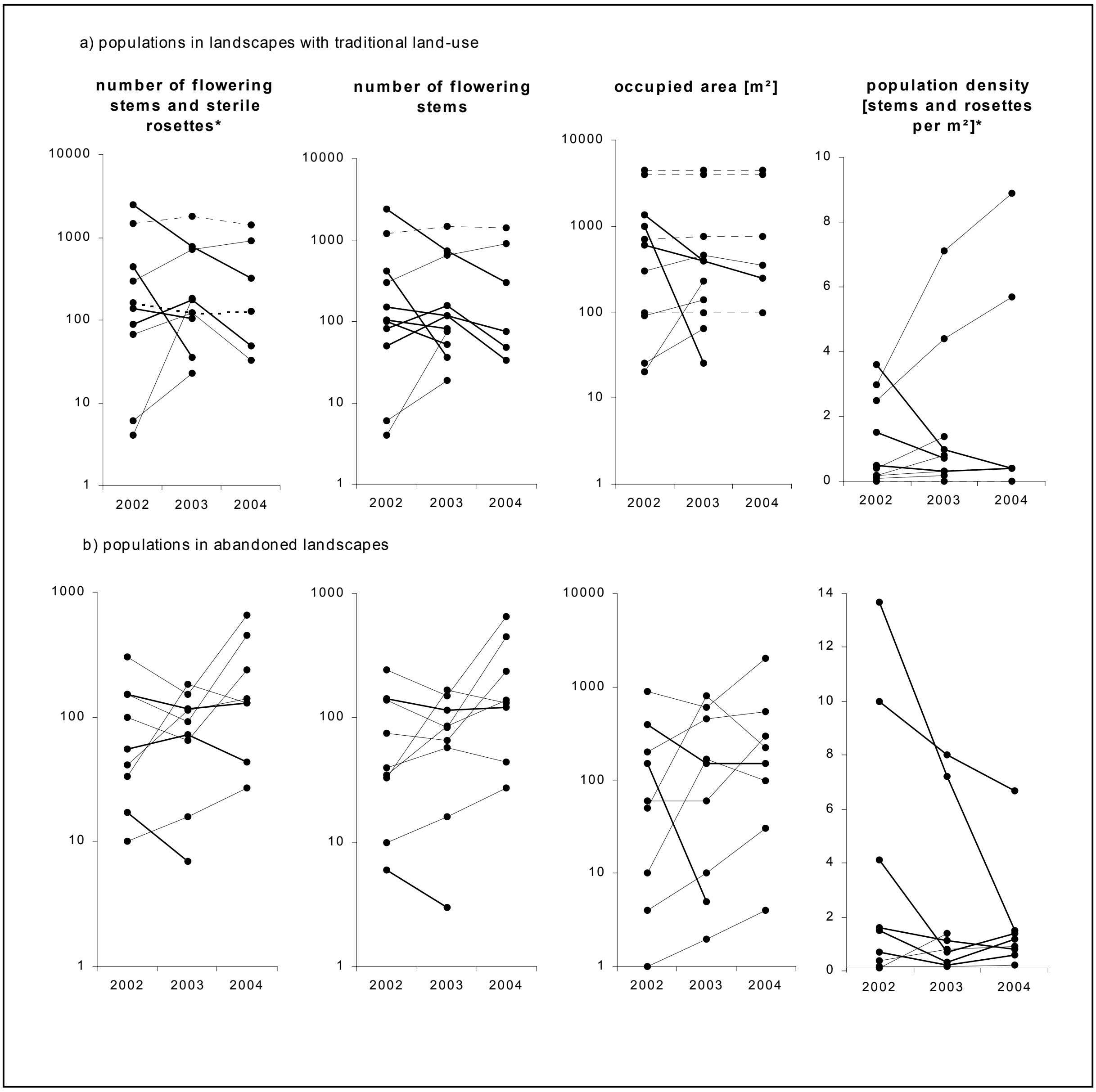

Figure IV/2: Fluctuations of population size parameters in 20 *C. glomerata* populations in Germany in a) landscapes with traditional land-use and b) in abandoned landscapes (boldface lines = decreasing, fine lines = increasing and broken lines = non changing population sizes from 2002 to 2004, in Baden-Wuerttemberg from 2002 to 2003, * two data sets overlay each other in a)

Size parameters of *C. glomerata* populations varied widely over the study period (figure IV/2). In 2002, the smallest populations, with only 4 to 6 flowering stems and sterile rosettes as well as the population with the highest number of individuals (2496), were among those still subjected to agricultural use. However, the largest population of 2002 showed the strongest decrease in population size by 2004 when only 323 stems and rosettes were assessed (figure IV/2). Between 2002 and 2004 a threefold increase in the number of fertile stems and sterile rosettes was observed in populations on used as well as abandoned grasslands. Most populations were characterized by a high number of flowering stems in all of the years (figure IV/2). In 2004, we were not able to find any sterile rosettes in several populations under varying land-use conditions. Considering the development of the number of flowering stems from 2002 to 2004, 66% of the populations in traditionally used landscapes decreased in size, whereas in abandoned landscapes only 13% decreased. There were also high variations in the size of the area occupied by a population that increased from 2002 to 2004 in most of the cases in abandoned landscapes while population density decreased. This tendency was more balanced in the populations on traditionally used grasslands. The highest population density was 13.7 flowering stems and rosettes per m² in a population of an abandoned landscape in 2002. However, two years later we recorded only 1.47 shoots per m² in the same population.

Populations on used grasslands were no larger than those on unused grasslands, and vice-versa. There were no significant differences between any of the studied size parameters of populations on used grasslands and unused grasslands, and the decreases or increases of population sizes were not significantly more pronounced on abandoned grasslands than they were on used grasslands.

Discussion

The results of our monitoring show that, land-use conditions aside, populations of *C. glomerata* are characterized by high variability and fluctuations in all of the size parameters we assessed: total number of stems (flowering and sterile); number of flowering stems; population density; and the area occupied by a population. In traditionally used stands most of the populations decreased in size, whereas in abandoned landscapes most of the populations showed an increase. As our study only encompassed three consecutive years, we do not know whether these fluctuations are random events or if they indicate long-term trends. However, we were not able to detect any constant tendency for decreasing sizes in abandoned grassland populations of *C. glomerata* in the studied time span.

The observed large fluctuations in population size parameters are in line with the observations of various authors. According to Eisto et al. (2000), populations of the perennial *C. cervicaria* persist even through a temporary loss of fertile plants. Menges (1990) described varying demographic parameters for the herbaceous perennial *Pedicularis furbishiae* over a period of three consecutive years. Strong fluctuations in population size were also observed for the perennials *Biscutella laevigata* (three years; Dannemann 2000), *Angelica palustris* (three years; Dittbrenner et al. 2005), *Primula farinosa* (three years; Hambler & Dixon 2003, 6-12 years; Peintinger 1990), several orchid species (*Orchis morio* and *O. coriophora* 17 years; Peintinger 1990, *Ophrys sphegodes* 10 years; Hutchings 1987, *Epipactis tallosii* 10 years; Mered'a 2002), and the annual *Eichhornia paniculata* (7 years; Husband & Barrett 1998).

There are several explanations for the observed changes in population sizes, as they can be influenced by several factors including plant performance and reproduction, climatic conditions, predators as well as land-use by man. According to Pimm (1991), fluctuations of population sizes are often stochastic: whereas demographic stochasticity is caused by random variation in individual fitness and produces random fluctuations in mean fitness or population growth, environmental stochasticity affects the fitness of all individuals in a population in the same fashion (Lande 2002). The fluctuations in population size we recorded for *C. glomerata* may be most likely caused by life cycle parameters, as individuals undergo different life cycle stages (Piskovackova 1980). As *C. glomerata* is a hemicryptophyte characterized by a 5 to 10cm deep rhizome (Kutschera & Lichtenegger 1992), we assume that the subterranean rhizome pleiokorm - a system of shoots which protrudes from the main root and subsists for several years - is implicated in the super-terranean population size fluctuations (Klotz et al. 2002).

Eisto et al. (2000) report that populations of *C. cervicaria* recover either from sterile rosettes or from a subterranean seed bank - but the latter have been shown to occur sparsely or in patches (Often 1999). We did not find any seedlings of *C. glomerata*, but may have missed them as identifying seedlings in the field is difficult. In a common garden experiment a lot of seedlings developed from seeds without any special treatment. As flowering can begin in the second year after germination, increasing population sizes may indeed be caused by newly recruited individuals. However, fluctuations in the number of flowering stems that are easily countable indicates that changing population sizes are not an artefact. Reasons for fluctuating population sizes may include local environmental variation or human disturbance (Heschel & Paige 1995, Husband & Barrett 1998), succession (Eisto et al. 2000), or different land use practices (Taylor & Rumsey 2003). Additionally, year-to-year variation of climatic parameters may be an important driving factor in community dynamics. Long-term data on community composition often show dramatic fluctuations in the abundance of individual species, with peaks in abundance sometimes being related to peaks in climatic variables such as temperature or precipitation (Herben et al. 2003). For example, a fluctuation in the population size of the biennial *Angelica palustris* was related to precipitation in June (Dittbrenner et al. 2005), and climatic parameters were also related to fluctuations in population sizes of *Gentianella ciliata, G. germanica* (Dierschke 1986) and *Scabiosa columbaria* (Runge 1963).

In our study, used grassland and disused grassland populations of *C. glomerata* did not differ in population size parameters over the study duration of three years. The history of some of the 20 populations showed a more or less constant development of population sizes: Some populations at the “Schwäbische Alb” in Baden-Wuerttemberg have been grazed since 1975 and there is no explicit increase or decrease observable (Mammel, pers. com.). It therefore appears that there is no detectable effect of increasing dominance of grasses and changing community composition - due to abandonment of traditional land-use practices - on the size parameters of *C. glomerata* populations. Visual observations of Partzsch (pers. com.) confirm this finding: three populations in the surroundings of Halle in Saxony-Anhalt have not visibly decreased or increased since 1992 (when land-use was abandoned). In contrast to the results of our study, Reinhammer et al. (2002) found differences in the development of *Pseudorchis albida* in a managed (mowed) and an unmanaged grassland plot. In the mowed plot, the number of new individuals appearing annually was quite large and stable, whereas in the unmanaged plot no new individuals occurred in the last two years of the five year study. Like *C. glomerata*, *Pseudorchis albida* can be ubiquitously present quite a long time after the cessation of traditional grassland management, but it tends to become “senile” (Reinhammer et al. 2002), which means that the share of young plants and seedlings is low in unmanaged sites compared to managed ones. Oostermeijer et al. (1994) reported the same tendency in a demographic study on *Gentiana pneumonanthe* following the abandonment of traditional land-use practices. As we failed to demonstrate demographic differentiations we recommend that, in addition to counting flowering individuals, monitoring should include a further assessment of the age stage structure of populations as this might be correlated to management practices (Hegland et al. 2001).

In several studies on threatened plant species plant performance or genetic variation were correlated with population size, but in most cases only data from one year were considered (e.g. Prober et al. 1998, Fischer & Matthies 1998, Jacquemyn et al. 2002, Vergeer et al. 2003, Hensen et al. 2005, Hensen & Oberprieler 2005). Apparently, population size was assumed to be a stable, non fluctuating parameter. As our data provide evidence to the contrary, such correlations may bias the results. We therefore recommend that such correlations are only be performed when it is known that population size has remained more or less constant during the preceding few years.

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REFERENCES

BACHMANN, U., HENSEN, I. & PARTZSCH, M. (2005). Is *Campanula glomerata* threatened by competition of expanding grasses? *Plant Ecology* **180**: 257-265.

DANNEMANN, A. (2000). Der Einfluss von Fragmentierung und Populationsgröße auf die genetische Variation und Fitness von seltenen Pflanzenarten am Beispiel von *Biscutella laevigata* (Brassicaceae). *Dissertationes Botanicae* **330**

DIERSCHKE, H. (1986). Untersuchungen zur Populationsdynamik der *Gentianella*-Arten in einem Enzian-Zwenken-Kalkmagerrasen. *Natur und Heimat* **3**:73-81.

DITTBRENNER, A., M. PARTZSCH & HENSEN, I. (2005). Beiträge zur Populationsbiologie und Vergesellschaftung von *Angelica palustris* (BESSER) HOFFM. *Hercynia N.F.* **38:**59-88

EISTO, A.-K., KUITUNEN, M., LAMMI, A., SAARI, V., SUHONEN, J., SYRJÄSUO, S. & TIKKA, P.M. (2000). Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. *Conservation Biology* **14**:1413-1421.

FISCHER, M. & STÖCKLIN, J. (1997). Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-85. *Conservation Biology* **11**:727-737.

FISCHER, M. & MATTHIES, D. (1998). RAPD-Variation in relation to population size and plant fitness in the rare plant *Gentianella germanica* (Gentianellaceae). American Journal of Botany 85:1685-1692.

FRANK, D. & NEUMANN, V. (1999). Bestandssituation der Pflanzen und Tiere Sachsen-Anhalts. - Ulmer, Stuttgart.

HAMBLER, D. J. & DIXON J.M. (2003). Biological Flora of the British Isles. Primula farinosa L. Journal of Ecology 91:694-705.

HARDTKE, H.-J. & IHL, A. (2000). Atlas der Farn- und Samenpflanzen Sachsens. - Sächsisches Landesamt für Umwelt und Geologie, Dresden.

HEGLAND, S.J., VAN LEEUWEN, M. & OOSTERMEIJER, J.G.B. (2001). Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *J. Applied Ecology* **38**: 1277-1289.

HENSEN, I., OBERPRIELER, C. & WESCHE, K. (2005). Genetic structure, Population size, and Seed Production of *Pulsatilla vulgaris* Mill. (Ranunculaceae) in Central Germany. *Flora* **200**:3-14.

HENSEN, I. & OBERPRIELER, C. (2005). Effects of population size on genetic diversity and seed production in the rare *Dictamnus albus* (Rutaceae) in Central Germany. *Conservation Genetics* **6**:63-73.

HERBEN, T., KRAHULEC, F., HADINCOVA, V., PECHÁCKOVÁ, S. & WILDOVÁ, R. (2003). Year-to-year variation in plant competition in a mountain grassland. *Journal of Ecology* **91**:103-113.

HESCHEL, M. S. & PAIGE, K.N. (1995). Inbreeding despression, environmental stress, and population size variationin Scarlet Gilia (*Ipomopsis aggregata*). *Conservation Biology* **9**:126-133.

HUSBAND, B. C. & BARRETT, S.C.H. (1998). Spatial and temporal variation in population size of *Eichhornia paniculata* in ephemeral habitats: implications for metapopulation dynamics. *Journal of Ecology* **86**:1021-1031.

HUTCHINGS, M. J. (1987). The population biology of the early Spiorder Orchid, *Ophrys sphegodes* Mill. I. A demographic study from 1975 to 1984. *Journal of Ecology* **75**:711-727.

JACQUEMYN, H., BRYS, R. & HERMY, M. (2002). Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. *Oecologia* **130**:617-625.

JEDICKE, E. (1997). Die Roten Listen. *Gefährdete Pflanzen, Tiere, Pflanzengesellschaften und Biotoptypen in Bund und Ländern.* - Ulmer, Stuttgart.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002). BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenr. f. Vegetationskunde* **38**:1-334.

KORNECK, D., SCHNITTLER, M. & VOLLMER, I. (1996). Rote Liste der Farn- und Blütenpflanzen Deutschlands. *Schriftenreihe für Vegetationskunde* **28**:21-187.

KUTSCHERA, L. & LICHTENEGGER, E. (1992). *Wurzelatlas Mitteleuropäischer Grünlandpflanzen Band 2 Teil 1.* - Fischer, Jena.

LANDE, R. (2002). Incorporating Stochasticity in Population Viability Analysis. In *Population Viability Analysis* (ed. S. R. Beissinger and D. R. McCullough), pp.18-40. University of Chicago Press, Chicago.

MENGES, E. S. (1990). Population viability analysis for an endangered Plant. *Conservation Biology* **4**:52-62.

MERED'A JR., P. (2002). Morphometric and population-biological study of the species *Epipactis tallosii* (Orchidaceae) on the site in the Ilavská Kotlina Basin (Western Slovakia). *Acta Facultatis Rerum Naturalium Universitatis Comenianae Botanica* **41**:23-29

OFTEN, A. (1999). *Campanula cervicaria*: seed arresting mechanism and seed pools in winter stander and soil. *Flora* **194**:103-112.

OOSTERMEIJER, G., VAN`T VEER, R. & DEN NIJS, J.C.M. (1994). Population structure of the rare, long lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of applied Ecology* **31**:428-438.

PARTZSCH, M. (2001). Die Porphyrkuppenlandschaft des unteren Saaletals - Vergleich der Vegetation in Abhängigkeit von Flächengröße und Genese der Prophyrkuppen. *Bot. Jahrb. Syst.* **123**:1-45.

PASSARGE, H. (1999). *Pflanzengesellschaften Nordostdeutschlands. II. Helocyperosa and Cespitosa*. Berlin.

PEINTINGER, M. (1990). Bestandsschwankungen bei seltenen Pflanzenarten in Pfeifengraswiesen des westlichen Bodenseegebietes. *Carolinea* **48**:69-84.

PIMM, S. L. (1991). *The balance of nature? Ecological issues in the conservation of species and communities.* Universtiy of Chicago press, Chicago.

PISKOVACKOVA, N. P. (1980). Kolokolcik Skucennyi: 156-169 In: T. A. RABOTNOV (ed.), *Biologiceskaja flora Moskovskoj oblasti*. Moskva universitet, Moskva.

PLUESS, A. R. & STÖCKLIN, J. (2004). Genetic diversity and fitness in Scabiosa columbaria in the Swiss Jura in relation to population size. *Conservation Genetics* **5**:145-156.

PROBER, S. M., SPINDLER, L.H. & BROWN, A.H.D. (1998). Conservation of the grassy white box woodlands: Effects of remnant population size on genetic diversity in the allotetraploid herb *Microseris lanceolata*. *Conservation Biology* **12**:1279-1290.

REINHAMMER, L.-G., OLSSON, E.G.A. & SORMELAND, E. (2002). Conservation biology of an endangered grassland plant species, *Pseudorchis albida*, with some references to the closely related alpine *P. straminea* (Orchidaceae). *Botanical Journal of the Linnean Society* **139**:47-66.

ROTHMALER, W. (2002). *Exkursionsflora von Deutschland. Gefäßpflanzen: Kritischer Band 4*, 9. Aufl. Heidelberg-Berlin.

RUNGE, F. (1963). Die Artmächtigkeitsschwankungen in einem Nordwestdeutschen Enzian-Zwenkenrasen. *Vegetatio* **11**:237-240.

STÖCKLIN, J., MEIER, V.G. & RYF, M. (1999). Populationsgrösse und Gefährdung von Magerwiesen-Pflanzen im Nordschweizer Jura. *Bauhinia* **13**:61-68.

TAYLOR, K. & RUMSEY, F.J. (2003). Biological Flora of the British Isles. *Bartsia alpina* L. *Journal of Ecology* **91**:908-921.

VERGEER, P., RENGELINK, R., COPAL, A. & OUBORG, N.J. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91**:18-26.

WALLISDEVRIES, M. F., POSCHLOD, P.& WILLEMS, J.H. (2002). Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* **104**:265-273.

KAPITEL V

IS *CAMPANULA GLOMERATA* THREATENED BY COMPETITION OF EXPANDING GRASSES?

BACHMANN, U., HENSEN, I. & PARTZSCH, M. (2005). Is *Campanula glomerata* threatened by competition of expanding grasses? *Plant Ecology* **180**: 257-265

ABSTRACT

In East Germany, a high percentage of species-rich, semi-natural dry grasslands has been converted into species-poor communities dominated either by *Poa angustifolia* or *Festuca rupicola*. The disappearance of low-intensity types of agricultural land-use such as mowing and grazing has been the cause for the decline of many grassland species, as lack of biomass extraction leads to a new situation in competition. Here we evaluate the performance of the rare forb *Campanula glomerata* in competition with *P. angustifolia* and *F. rupicola* using a replacement design experiment. *C. glomerata* responded to the presence of these grass species in contrasting ways: whereas the presence of *P. angustifolia* had a negative effect on *C. glomerata* biomass and fitness, the presence of *F. rupicola* affected the forb in a positive way. The results of an additional sowing experiment revealed that the germination and establishment rates of *C. glomerata* decrease in accordance with increasing density of *P. angustifolia.* Thus the response of this rare forb varies among neighbour species.

INTRODUCTION

Land use change alters the structure, composition and dynamics of ecosystems, as well as the survival of plant populations (Donohue et al. 2000). Since agriculture started in Central Europe, man has been developing many different land use practices, in turn creating new habitat types, which often bring about the fragmentation and loss of others (Ellenberg 1988, Poschlod & WallisDeVries 2002, Römermann et al. 2005). In the last few decades, two opposite trends of agricultural management have been observed: the management of highly-productive areas has intensified, whereas less-productive areas are being abandoned.

Abandonment of traditional land-use practices has resulted in the decline of many species from unproductive sites (Thomas & Morris 1995, Oostermeijer 1996, Frank & Neumann 1999, Holsinger 2000). These species suffer from shading and from competition by plants that invade habitats following abandonment (Armesto & Picket 1985, Zobel 1992). The decline of rare species is always a focal point in plant conservation, so the evaluation of the relative importance of several interacting factors is essential (e.g. Menges 1990, Oostermeijer 1996). Besides genetic diversity and demographic uncertainties, the impact of changing environmental conditions is the main factor that may particularly influence population dynamics as well as species composition in a plant community (Poschlod et al. 1999, Burgmann & Possingham 2000, Poschlod & WallisDeVries 2002). As the abandonment of traditional land use practices leads not only to a decrease in biodiversity (Balmer & Erhardt 2000, Poschlod & WallisDeVries 2002), but also to a change in the dominance balances of species, the study of competitive effects on rare plant species is essential because of the high risk of competitive exclusion (Berendse 1983).

The halting of grazing is thought to be the main factor behind the conversion of species-rich, semi-natural grasslands into species-poor communities (WallisDeVries et al. 2002). In eastern Germany, a high percentage of dry grasslands has been converted into those dominated by *Poa angustifolia* (Passage 1999, Partzsch 2001) - a vegetation type that did not occur in former times and has been described only recently (Partzsch 2000, 2001, Partzsch et al. 2003). Stands dominated by *Festuca rupicola* have also increased on abandoned grasslands, but this compositional shift seems to happen more slowly (Partzsch et al. 2003). These findings give cause for concern as Willems (1987) showed that increasing dominance of grass species negatively influences biodiversity. In addition, competition with grasses has been shown to reduce measures of plant fitness in several species (Guerrant 1992, Gordon & Rice 1993, Carlsen et al. 2000).

Our aim is to analyse the impact of the loss of traditional land use practices and subsequent vegetation changes on the performance of the rare forb *Campanula glomerata*. This long-lived perennial is often found in historically old grasslands and is used as an indicator species for long-term constant environmental conditions (Partzsch 2001). According to the Red Data Lists of Germany (Korneck et al. 1996), *C. glomerata* is currently in decline (Frank & Neumann 1999, Hardtke & Ihl 2000), and we expect it to be negatively affected by the expansion of *F. rupicola* and *P. angustifolia*. We hypothesized that growth and fitness of *C. glomerata* decrease with increasing competition from *F. rupicola* and *P. angustifolia*. The growth, fertility, and survival of *C. glomerata* were studied in a greenhouse competition experiment in combination with the two aforementioned grass species. In order to investigate whether germination and establishment of subsequent *C. glomerata* generations is affected by vegetation density, an additional greenhouse and field experiment were carried out.

METHODS

Study Species

Campanula glomerata L. (Clustered Bellflower) is a perennial, insect pollinated, continental species, distributed mainly in submeridional to boreal Europe and Siberia (Rothmaler 2002) in chalk and limestone grasslands and in open woodlands. Vegetative propagation occurs by rhizomes (Klotz et al. 2002).

Festuca rupicola Heuff. is a perennial tussock grass without stolons occuring in the submeridional and temperate Europe and West Asia (Rothmaler 2002), in dry grasslands, open forests, roadsides and on embankments (Conert et al. 2000).

The perennial grass *Poa angustifolia* L. occurs from meridional to boreal Eurasia (Conert et al. 2000, Rothmaler 2002) in dry grasslands, open forests, roadsites, embankments, walls and rock debris. It is characterized by the formation of small, dense tufts with numerous renewal buds and long subterranean branched stolons.

Competition Experiment

We used a replacement design wherein the proportion of species within mixtures was varied maintaining a constant density throughout (De Wit 1960). In March 2002, seeds of *C. glomerata* (source: Botanical Garden Regensburg), *F. rupicola* and *P. angustifolia* (source: Botanical Garden Halle) were sown into plastic pots on a compost sand mixture (2:3, pH value 7.0) and cultivated in an unheated greenhouse. In June, the young plants were transferred to pots (9 plants each, diameter 22cm, height 19cm) filled with the same compost sand mixture. Treatments included pure *P. angustifolia* (P9, number equals number of plants), *P. angustifolia* and *C. glomerata* (P6C3, P3C6), pure *F. rupicola* (F9), *F. rupicola* and *C. glomerata* F6C3, F3C6 and pure *C. glomerata* C9. Individuals were planted in three lines with three plants each, with the species with the lower abundance in the middle. Distances between individual plants and lines within a pot were kept constant. Each combination was replicated four times. The pots were located randomly; positions were changed every two weeks. Pots were equally supplied with water. In September 2002, the pots were moved outdoors (open cold frames in the area of the Botanical Garden Halle) and, subsequently, the survival rate per pot was determined monthly.

In June 2003, we measured the length of the fruit-bearing stems of *C. glomerata* as well as the number of flowering shoots and the number of single flowers per individual. Capsules were harvested just before opening in order to determine the number and size of seeds. Ten capsules per pot were chosen, five of them randomly from a terminal flowering head, and the other five from flowering heads in a position two heads below the terminal head. A Delta-T Image Analysis System (Delta-T Devices LTD) was used for counting and measuring length and width of seeds. To determine whether competition influences the germination rate of *C. glomerata* seeds, germination was tested on one pooled sample from each of the combinations described above at a temperature of 20°C/10°C (12/12 hour day/night cycle; n = 5 x 20 seeds) in a climate chamber with a warm white light source. Germination rate was determined after 100 days. The viability of ungerminated seeds was tested using the tetrazolium test (Baskin & Baskin 2001).

At the end of June 2003, plants were cut at ground level, dried at 80°C and weighed to determine aboveground biomass. Belowground biomass was not assessed. The level of competition was estimated by calculating the Relative Neighbour Effect (RNE, Markham and Chanway 1996): RNE = $(P_{-N} - P_{+N})/x$ where P is the performance of plants in the presence (+N) and absence (-N) of neighbours, x is P_{-N} when P_{-N} is greater than P_{+N} and P_{+N} when P_{+N} is greater than P_{-N}. The index ranges from –1 to 1 with negative values indicating facilitation and positive values indicating competition. We used biomass per individual as a measure of plant performance.

Sowing Experiment

For the greenhouse experiment *P. angustifolia* seeds were sown into a compost sand mixture (2:3, pH value 7.0) in April 2002. After 30 days, nine seedlings each were planted into ten plastic pots (10 x 10cm). During the following year, the grass plants of half of the pots were clipped every 2 months, approximately 2cm above ground level, whereas the other half remained unclipped. Another 5 pots were filled with composted soil as a control.

For an accompanying field experiment we choosed a *F. rupicola* community on a porphyry outcrop (Lettin, Saxony Anhalt) where *C. glomerata* occurs naturally, but was absent from our study plots. Fifteen 10 x 10cm plots were permanently marked and treated as described above: the vegetation of 5 plots each was either clipped, remained unclipped, or was completely removed. At five similar sites we arranged three plots of each treatment closely together; distances between the sites were 1m.

In April 2003, 20 seeds of *C. glomerata* were sown into each of the 15 pots in the greenhouse and in the 15 plots in the field. In the greenhouse, the pots were randomly placed and watered equally. Germination and establishment of *C. glomerata* was observed until December 2003.

An additional germination experiment of 10 x 20 *C. glomerata* seeds was carried out to determine the impact of darkness on germination, as it would arise from increasing vegetation density. For this experiment, five of the ten replicates (20 seeds each) were wrapped in aluminium foil to avoid light penetration. The experiment was ended after 100 days. The viability of ungerminated seeds was tested using the tetrazolium test (Baskin and Baskin 2001).

Statistical Analyses

Statistical analyses were performed using SPSS 10.0.5. (1999) and GraphPad Prism 3.0 (1999). Data was tested for normal distribution (Kolmogorov-Smirnov-test) and equal variance (Levene test). According to these results, multiple comparisons were done with parametric (ANOVA and Tukey´s post hoc test) or nonparametric tests (Kruskal-Wallis (H)-test followed by a post hoc Dunn´s test). Two sets of data were compared using a t-test. Percentages were arcsine transformed.

RESULTS

Competition Experiment

C. glomerata mass increased with increasing proportion of *Festuca rupicola* (figure V/1a), but decreased with increasing *P. angustifolia* (figure V/1b). Consequently, the mean RNE values of *C. glomerata* were negative in combination with *F. rupicola,* and positive in combination with *P. angustifolia* (figure V/2a). Survival of *C. glomerata* was not affected by either of the two grass species.

C. glomerata developed almost twice as many flowering shoots and flowers and about 30% more seeds per capsule when grown with *Festuca rupicola* than when grown with *P. angustifolia* (figures V/2b–d). Compared to the *Campanula* monoculture, the number of flowering shoots and the number of single flowers per *C. glomerata* individual increased with increasing proportions of *F. rupicola* and decreased with increasing proportions of *P. angustifolia* (figures V/2b and V/2c). There was no influence of *F. rupicola* on seed number per capsule for *C. glomerata,* whereas in combination with *P. angustifolia*, seed production per *C. glomerata* individual decreased significantly compared to the monoculture (figure V/2d). Length of fertile stems, seed size, and seed germination of *C. glomerata* was not affected by growing among either of the two grass species (figures V/2e-h). We also observed that capsules of *C. glomerata* ripened later in combination with *P. angustifolia,* and found a higher amount of immature seeds than with among *F. rupicola* (Bachmann unpubl.). Seed germination rate was 39% in the monoculture of *C. glomerata* and increased with decreasing frequency of *C. glomerata* in both mixtures (not significant, figure V/2h). The tetrazolium test showed that all viable seeds germinated.

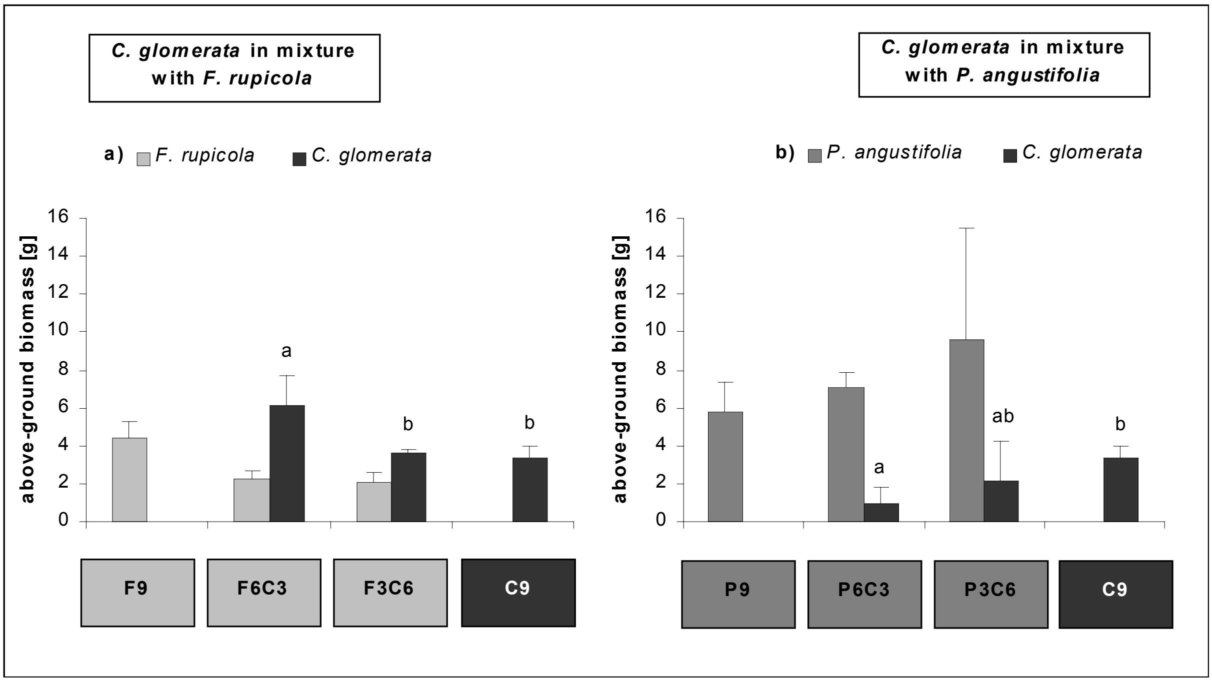

Figure V/1: Biomass per individual in the competition experiment (mean and SD, different letters mean significant differences between mixtures): a) in mixture with *F. rupicola* (Kruskal-Wallis (H)- test, n = 4, p < 0.05) and b) in mixture with *P. angustifolia* (ANOVA, n = 4, p < 0.05)

Sowing Experiment

In the greenhouse experiment, the density of *P. angustifolia* vegetation cover had a significant influence on germination and establishment of *C. glomerata*. While an average of 3.4 seedlings (from 20 seeds) survived over 180 days in the pots without grass vegetation, only a mean of 0.4 established themselves permanently in the clipped *P. angustifolia* pots and none in the unclipped ones (table V/1). From the 17th observation day on, the number of seedlings in the control pots was significantly higher than in the unclipped ones ($p < 0.05$).

No seeds germinated in the corresponding field experiment.

Germination rate of *C. glomerata* seeds was significantly lower in darkness (4%) than in light (21%; t-test, n = 5, $p < 0.05$). All viable seeds germinated in light, whereas in darkness only 18% of all viable seeds germinated.

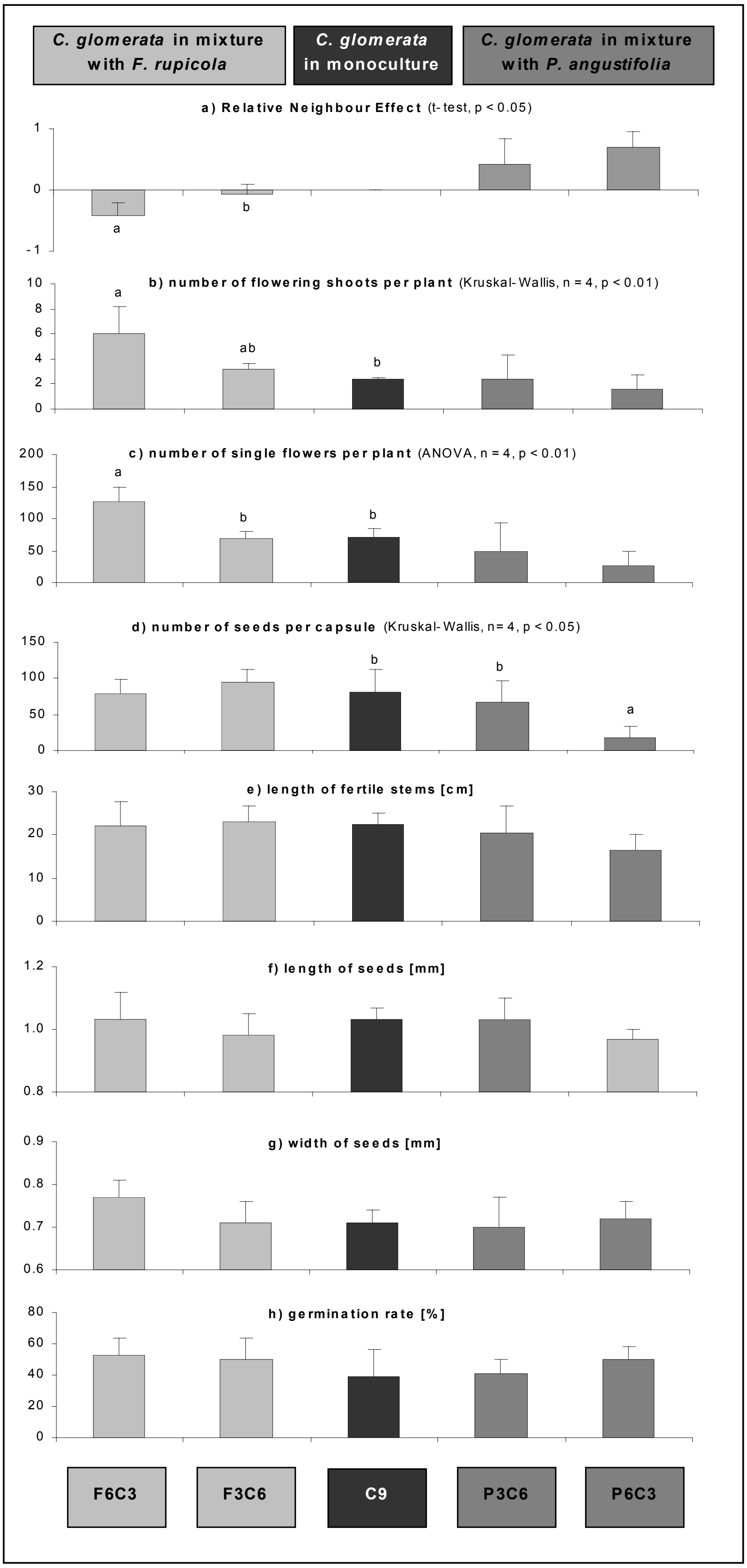

Figure V/2: RNE (a) and response of fitness parameters of *C. glomerata* (b-h) in the competition experiment (mean and SD, different letters mean significant differences). We tested mixtures for each grass species separately.

Table V/1: Mean number of established *C. glomerata* seedlings in the greenhouse experiment (ANOVA, n = 5). Different letters mean significant differences.

time after sowing [days]	unclipped	without vegetation	clipped	p
6	0.0	0.0	0.0	n.s.
9	0.0	2.2	0.0	n.s.
17	0.2^{a}	7.2^{b}	0.8^{b}	$p < 0.01$
31	0.4^{a}	8.6^{b}	0.4^{a}	$p < 0.05$
45	0.2^{a}	6.0^{b}	0.4^{a}	$p < 0.05$
54	0.0^{a}	5.4^{b}	0.6^{a}	$p < 0.05$
79	0.0^{a}	5.6^{b}	0.8^{ab}	$p < 0.01$
172	0.0^{a}	3.4^{b}	0.4^{ab}	$p < 0.05$

DISCUSSION

In semi-natural habitats of Central Germany, *C. glomerata* is associated with *F. rupicola* and *P. angustifolia* in the same grassland community; the Festuco-Brachypodietum (Mahn 1959). Our results suggest that *C. glomerata* may be affected by the increasing dominance of these grass species as a consequence of the current abandonment of traditional land-use in many grassland areas of eastern Germany.

However, in contrast to our expectations, only the presence of *P. angustifolia* had a negative effect on first-year-performance of *C. glomerata*, whereas the presence of *F. rupicola* affected biomass development and several fitness parameters in a positive way. The latter data corresponds to Ridenour & Callaway (2003) who found that above-ground biomass of *Centaurea maculosa* was almost four times higher among *Festuca idahoensis* than in monoculture. Differences in neighbour effects on plant performance were also described by Gerry & Wilson (1995), who reported on significant interactions between species identity and competition, and by Rebele (2000), who demonstrated distinct responses of *Solidago canadensis* when grown among either *Tanacetum vulgare* or *Calamagrostis epigejos.*

Several authors suggested that the competitive ability of a plant species is related to growth height, aboveground biomass, and relative growth rate (for examples see Pywell et al. 2003). In accordance, we assume that the positive or negative effect of the two grass species on *C. glomerata* can be explained by differences in their growth form: whereas *P. angustifolia* develops 2-3 nodes at the base of each stem and is characterized by 2mm wide leaves, the 2-3 leaves of *F. rupicola* are clearly narrower (< 1mm). Thus, *F. rupicola* forms dense tussocks whereas *P. angustifolia* develops branched, subterranean shoots of up to 30cm in length (Conert et al. 2000). This indicates a more efficient growth rate which was confirmed by our experiment - as *P. angustifolia* produces more biomass in monoculture than monocultures of *C. glomerata* or *F. rupicola* and, after cutting, grew back faster than *F. rupicola* (second flowering already 3 weeks after cutting, Bachmann unpubl. data). In accordance, Frank & Klotz (1990) characterized *P. angustifolia* as a strong competitor (C-strategist) and *F. rupicola* and *C. glomerata* as intermediate CS-strategists (stress tolerant competitors). The dense growth of *P. angustifolia* might lead to increased shading of neighbour plants in contrast to the compact growth of *F. rupicola*. Perry & Galatowitsch (2004) demonstrated that total biomass of *Carex hystericinia* and *Phalaris arundinacea* was reduced by experimental shading*.* The effective clonal spread of *P. angustifolia* will probably affect *C. glomerata* even more in the following years, as Pywell et al. (2003) pointed out that the ability of vegetative growth becomes an increasingly important determinant of success with time in restored grassland communities.

In addition to biomass development, several *C. glomerata* fitness parameters responded in a contrasting way to grass competition. Competitive effects, in terms of decreasing fertile stem length or flower number, were also reported by Whigham (1984) for *Ipomoea hederacea*, who suggest that competition for nutrients was important. Reduced seed number has been demonstrated to be the result of interspecific competition in other cases, e.g. *Bouteloua gracilis, Buchloë dactyloides* (Aguiar et al. 2001) and *Erodium cicutarium* (Inouye et al. 1980). In contrast, seed size (length and width) as well as germination rate of *C. glomerata* was not affected by competition. Following Roach & Wulff (1987), we expected that seed size and germination might be determined to a high degree by maternal effects while seed number might be more significantly influenced by environmental factors such as light and nutrient availability, and thus by competition. These findings are in accordance with Whigham (1984) who reported that the presence of other plants significantly affected all biomass and number variables of *Ipomoea hederacea* except fruit mass. Inheritability of seed size was reported by Stanton (1984) and Thompson (1984) while Lee & Bazzaz (1980) found the seed weight of *Abutilon theophrasti* to be twice as high at lower rather than higher plant densities in a competition experiment. Plant height of *C. glomerata* was not significantly affected by the two grass species in our study. But in a further study we found a significant relationship between increasing plant height of *C. glomerata* and increasing cover of surrounding vegetation (Bachmann unpubl.). In a similar approach, Lowe et al. (2003) demonstrated a suppression of plant height for *Bromus tectorum* and *Bouteloua gracilis* due to increasing number of *B. tectorum* individuals.

The results of the sowing experiment confirmed our expectation that a dense vegetation cover of *P. angustifolia* affects germination and establishment of *C. glomerata*, probably due to limitation of light and space*.* This is in accordance with e.g. Eliason & Allen (1997), Brown & Bugg (2001), Jutila & Grace (2002) and Williams et al. (2002), all of whom demonstrated that living biomass and litter strongly inhibits seed germination and seedling survival of numerous plant species. Grace (1999) characterized the suppression of germination by the established vegetation cover as a cryptic form of competition. The fact that *C. glomerata* completely failed to establish under field conditions emphasises the results of other studies compiled by Pywell et al. (2003), which demonstrated poor performance of *C. glomerata* seeds sown in field experiments, probably due to drought stress. Pywell et al. (2003) found large differences in performance indices for establishment and persistence of grassland species in restored grassland communities, but grasses consistently out-performed forbs: Four years after sowing, the performance index of *Poa pratensis* was higher than that of *Festuca ovina*, but both indices were higher than that of *C. glomerata*, which was one of the species with the poorest performance.

Our study only encompassed first-year performance of *C. glomerata* and the associated grass-species. The replacement series experiment will be continued, as competitive superiority of one species over another is only evident in long-term experiments (Rebele 2000). In addition, although replacement designs are useful tools for studying effects of land-use change on the interactions of plants with other species (Sackville Hamilton 1994), they do not fully reflect the very complex conditions in the field (Gibson 2002). As with many other biological factors, competitive effects are highly dynamic (Peltzer & Köchy 2001) and may change due to changing or fluctuating climatic conditions from year to year. Greenlee & Callaway (1996) demonstrated that interactions between bunchgrasses and rare mustard (*Lesquerella carinata*) switched from facilitation to competition when a dry and hot year was followed by a wet and cool year. In addition, the results of Herben et al. (2003) indicated that year-to-year variation of climatic parameters has the potential to affect species co-existence and richness and can be an important driving factor in community dynamics. Nevertheless, our results give cause for concern as the increasing dominance of certain grass species in dry grassland communities of eastern Germany may increasingly threaten *C. glomerata*.

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REFERENCES

AGUIAR, M. R., LAUENROTH, W. K. & PETERS, D. P. (2001). Intensity of intra- and interspecific competition in coexisting shortgrass species. *Journal of Ecology* **89**:40-47.

ARMESTO, J. J. & PICKETT, S. T. A. (1985). Experiments on disturbance in old field plant communities: Impact on species richness and abundance. *Ecology* **66**:230-240.

BALMER, O. & ERHARDT, A. (2000). Consequences of succession on extensively grazed grasslands for central european butterfly communities: rethinking conservation practices. *Conservation Biology* **14**:746-757.

BASKIN, C. C. & BASKIN, J. M. (2001). *Seeds - ecology, biogeography, and evolution of dormancy and germination*. Academic press, London.

BERENDSE, F. (1983). Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *Journal of Ecology* **71**:379-390.

BROWN, C. S. & BUGG, R. L. (2001). Effects of established perennial grasses on introduction of native forbs in California. *Restoration Ecology* **9**:38-48.

BURGMANN, M. & POSSINGHAM, H. (2000). Population viability analysis for conservation: the good, the bad and the undescribed. In *Genetics, Demography and Viability of Fragmented Populations (ed.* A. G. Young and G. M. Clarke), pp.96-112. Cambridge University Press, Cambridge.

CARLSEN, T.M., MENKE, J.W. & PAVLIK, B.M. (2000). Reducing Competitive Suppression of a Rare Annual Forb by Restoring Native California Perennial Grasslands. *Restoration Ecology* **8**:18-29.

CONERT, H. J., JÄGER, E. J., KADEREIT, J. W., SCHULTZE-MOTEL, W., WEBER, H. E. & WAGENITZ, G. (2000). *Hegi, G. Illustrierte Flora von Mitteleuropa*. Parey, Berlin.

DE WIT, C. T. (1960). On competition. *Verslagen van Landbouwkundige Onderzoekingen* **66**:1-82.

DONOHUE, K., FOSTER, D. R. & MOTZKIN, G. (2000). Effects of the past and the present on species distribution: land-use history and demography of wintergreen. *Journal of Ecology* **88**:303-316.

ELLENBERG, H. (1988). *Vegetation Ecology of Central Europe*. Cambridge University Press.

ELIASON, S. A. & ALLEN, E. B. (1997). Exotic grass competition in supressing native shrubland re-establishment. *Restoration Ecology* **5**:245-255.

FRANK, D. & KLOTZ, S. (1990). Biologisch-ökologische Daten zur Flora der DDR. *Wissenschaftliche Beiträge der Martin-Luther-Universität Halle-Wittenberg* **1990/32 (P41)**.

FRANK, D. & NEUMANN, V. (1999). *Bestandssituation der Pflanzen und Tiere Sachsen-Anhalts*. Ulmer, Stuttgart.

GERRY, A. K. & WILSON, S. D. (1995). The influence of initial size on the competitive responses of six plant species. *Ecology* **76**:272-279.

GIBSON, D. J. (2002). *Methods in comparative plant population ecology*. University Press, Oxford.

GORDON, D.R. & RICE, K.J. (1993). Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* **74**:68-82.

GRACE, J. B. (1999). The factors controlling species density in herbaceous plant communities: an assesment. *Perspectives in Plant Ecology, Evolution and Systematics* **2**:1-28.

GREENLEE, J. T. & CALLAWAY, R. M. (1996). Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist* **148**:386-396.

GUERRANT, E.O. (1992). Genetic and demographic considerations in the sampling and reintroduction of rare plants. In *Conservation Biology: the theory and practice of nature conservation, preservation, and management (*ed. P.L. Fiedler and S. K. Jain), pp. 321-344. Chapmann and Hill, New York.

HARDTKE, H.-J. & IHL, A. (2000). *Atlas der Farn- und Samenpflanzen Sachsens*. Sächsisches Landesamt für Umwelt und Geologie, Dresden.

HERBEN, T., KRAHULEC, F., HADINCOVÁ, V., PECHÁCKOVÁ, S. & WILDOVÁ, R. (2003). Year-to-Year variation in plant competition in a mountain grassland. *Journal of Ecology* **91**:103-113.

HOLSINGER, K. E. (2000). Demography and extinction in small populations. In *Genetics, Demography and Viability of fragmented populations (*ed. A. G. Young and G. M. Clarke), pp. 55-74. University Press, Cambridge.

INOUYE, R. S., BYERS, G. S. & BROWN, J. H. (1980). Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* **61**:1344-1351.

JUTILA, H. M. & GRACE, J. B. (2002). Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *Journal of Ecology* **90**:291-302.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002). BIOLFLOR- Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenr. f. Vegetationskunde* **38**:1-334.

KORNECK, D., SCHNITTLER, M. & VOLLMER, I. (1996). Rote Liste der Farn- und Blütenpflanzen Deutschlands. *Schriftenreihe für Vegetationskunde* **28**:21-187.

LEE, T. D. & BAZZAZ, F. A. (1980). Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *Journal of Ecology* **68**:813-821.

LOWE, P. N., LAUENROTH, W. K., & BURKE, I. C. (2003). Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. *Plant Ecology* **167**:247-254.

MARKHAM, J. H. & CHANWAY, C. P. (1996). Measuring Plant Neighbour Effects. *Functional Ecology* **10**:548-549.

MENGES, E. S. (1990). Population viability analysis for an endangered Plant. *Conservation Biology* **4**:52-62.

OOSTERMEIJER, G. (1996). *Population viability of the rare Gentiana pneumonanthe - the relative importance of demography, genetics and reproductive biology*. doctoral. Amsterdam, Amsterdam.

PARTZSCH, M. (2000). Die Porphyrkuppenlandschaft des unteren Saaletals - Strukturwandel ihrer Vegetation in den letzten vier Jahrzehnten. *Tuexenia* **20**:153-187.

PARTZSCH, M. (2001). Die Porphyrkuppenlandschaft des unteren Saaletals - Vergleich der Vegetation in Abhängigkeit von Flächengröße und Genese der Porphyrkuppen. *Bot. Jahrb. Syst.* **123**:1-45.

PARTZSCH, M., SCHERF, W. & HENSEN, I. (2003). Die Porphyrkuppenlandschaft des unteren Saaletals - Vegetationsdynamische Untersuchungen auf kleinflächigen Kuppen unterschiedlicher Entstehungszeit. *Tuexenia* **23**:227-255.

PASSAGE, H. (1999). *Pflanzengesellschaften Nordostdeutschlands*. II. Helocyperosa and Cespitosa. J. Cramer, Berlin.

PELTZER, D. A. & KÖCHY, M. (2001). Competitive effects of grasses and woody plants in mixed grass prairie. *Journal of Ecology* **89**:519-527.

PERRY, L. G. & GALATOWITSCH, S. M. (2004). The influence of light availability on competition between *Phalaris arundinacea* and a native wetland sedge. *Plant Ecology* **170**:73-81.

POSCHLOD, P. & WALLISDEVRIES, M. F. (2002). The historical and socioeconomic perspective of calcareous grasslands-lessons from the distant and recent past. *Biological Conservation* **104**: 361-376.

POSCHLOD, P., DANNEMANN, A., JACKEL, A.-K. & BONN, S. (1999). Fragmentierung und Isolation von Pflanzenpopulationen - Einführung und Konzepte. In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 336. Ulmer, Stuttgart.

PYWELL, R. F., BULLOCK, J. M., ROY, D. B., WARMAN, L., WALKER, K. J. & ROTHERY, P. (2003). Plant traits as predictors of performance in ecological restauration. *Journal of applied Ecology* **40**:65-77.

REBELE, F. (2000). Competition and coexistence of rhizomatous perennial plants along a nutrient gradient. *Plant Ecology* **147**:77-94.

RIDENOUR, W. L. & CALLAWAY, R. M. (2003). Root herbivores, pathogenic fungi, and competition between *Centaurea maculosa* and *Festuca idahoensis*. *Plant Ecology* **169**:167-170.

ROACH, D. A. & WULFF, R. D. (1987). Maternal effects in plants. *Ann. Rev. Ecol. Syst*. **18**:209-235.

RÖMERMANN, C., DUTOIT, T., POSCHLOD, P. & BUISSON, E. (2005). Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. *Biological Conservation* **121**:21-33.

ROTHMALER, W. (2002*). Exkursionsflora von Deutschland*. Gefäßpflanzen: Kritischer Band. Spektrum, Heidelberg-Berlin.

SACKVILLE HAMILTON, N. R. (1994). Replacement and additive designs for plant competition studies. *Journal of Applied Ecology* **31**:599-603.

STANTON, M. L. (1984). Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *Am. J. Bot.* **71**:1090-1098.

THOMAS, J. A. & MORRIS, M. G. (1995). Rates and patterns of extinction among British invertebrates. In *Extinction Rates* (ed. J. H. Lawton and R. M. May), pp. 111-130. University Press, Oxford.

THOMPSON, J. N. (1984). Variation among individual seed masses in *Lomatium grayi* (Umbelliferae) under controlled conditions: Magnitude and partioning of variance. *Ecology* **65**:626-631.

WALLISDEVRIES, M.F., POSCHLOD, P. & WILLEMS, J.H. (2002). Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* **104**:265-273.

WHIGHAM, D. F. (1984). The effect of competition and nutrient availability on the growth and reproduction of *Ipomoea hederacea* in an abandoned old field. *Journal of Ecology* **72**:721-730.

WILLEMS, J. H. (1987). Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to species-rich ecosystem. *Biological Conservation* **40**:301-314.

WILLIAMS, M. I., SCHUMAN, G. E., HILD, A. L. & VICKLUND, L. E. (2002). Wyoming Big Sagebrush Density: Effects of seeding rates and grass competition. *Restoration Ecology* **10**:385-391.

ZOBEL, M. (1992). Plant species coexistence: the role of historical, evolutionary and ecological factors. *Oikos* **65**:314-320.

KAPITEL VI

ZUSAMMENFASSUNG

„Populationsgefährdungsanalysen stellen ein Instrumentarium dar, Wissen und Nichtwissen so zu strukturieren, dass wir das verfügbare Wissen optimal nutzen: Einerseits, um die Überlebenswahrscheinlichkeit von Populationen unter bestimmten Rahmenbedingungen möglichst gut vorhersagen und vergleichen zu können und andererseits, um Wissenslücken aufzudecken, die eine verlässliche Einschätzung erschweren oder unmöglich machen und daher Anlass für zielgerichtete Untersuchungen sein sollten“ (Henle et al. 1999). In der vorliegenden Arbeit wurde versucht, die allgemeine Konstitution von *C. glomerata* zu erfassen und auf dieser Basis die Überlebenswahrscheinlichkeit einzuschätzen und Empfehlungen für den weiteren Umgang mit dieser Art zu geben. Um die Gefährdungssituation der Knäuel-Glockenblume in Deutschland zu beschreiben, wurden in 20 Populationen Untersuchungen mit verschiedenen Zielsetzungen durchgeführt.

In Kapitel II “**Is the declining *Campanula glomerata* threatened by genetic factors?”** wurde festgestellt, dass die genetische Konstitution der Bestände bisher kein Gefährdungsrisiko darstellt. Die Ergebnisse zeigten, dass die genetische Struktur der 20 Populationen stark differenziert ist. Die hohe genetische Diversität innerhalb der *C. glomerata* Populationen wurde auf spezielle Merkmale dieser Pflanze, wie z.B. Selbstinkompabilität, allogame Bestäubung, Produktion einer großen Anzahl Samen, vegetative Reproduktion oder auch die lange Lebenszeit der Art zurückgeführt. Die Tatsachen, dass alle getesteten Pflanzen genetisch verschiedene Individuen repräsentierten, dass im Keimversuch alle lebensfähigen Samen aufliefen und dass sich im Freilandexperiment eine große Anzahl Jungpflanzen aus Samen entwickelten, unterstreichen die Bedeutung der sexuellen Reproduktion für die Dynamik und das Weiterbestehen von *C. glomerata* Populationen. Deutschlandweit betrachtet korrelieren die genetische Diversität und die geographischen Entfernungen der Populationen miteinander. Auf lokaler Ebene ergibt sich dieser Zusammenhang nicht mehr. Diese Tatsache wurde als Hinweis darauf gedeutet, dass nicht nur große Entfernungen die Verbreitung von genetischem Material unterbinden, sondern auch z.B. ungeeignete Habitate, Straßen oder Heckensäume als natürliche Barrieren in Frage kommen. Weder zwischen der genetischen Diversität und der Populationsgröße noch zwischen der genetischen Diversität und der Fitness der Pflanzen wurden signifikante Zusammenhänge festgestellt. Das lässt vermuten, dass kleine *C. glomerata* Populationen bisher nicht von Isolation, genetischer Drift und Inzuchtereignissen betroffen sind.

Viele Autoren veröffentlichen Studien, in denen die genetische Variation der Populationsgröße oder der Fitness von Pflanzen gegenübergestellt wird (Prober et al. 1998, Fischer & Matthies 1998, Jacquemyn et al. 2002, Vergeer et al. 2003, Hensen et al. 2005, Hensen & Oberprieler 2005). In den meisten Fällen handelt es sich dabei jedoch um die Momentaufnahme eines Jahres, jegliche mögliche Fluktuationen, wie sie z.B. von Menges (1990), Dannemann (2000), Eisto et al. (2000), Hambler & Dixon (2003) und Dittbrenner et al. (2005) und auch in Kapitel IV gezeigt wurden, bleiben dabei

unbeachtet. Auch in Kapitel II wurden nur die Werte eines Jahres ausgewertet. Doch mit dem Wissen um große Fluktuationen wurde aus den Ergebnissen geschlussfolgert, dass die untersuchten Populationen für die Momentaufnahme bisher von Isolation, Inzucht oder genetischer Drift nicht betroffen sind. Es ist jedoch dringend notwendig, diese Schlussfolgerung mit weiteren Analysen zu bestätigen.

Da die genetische Diversität in der vorliegenden Studie nicht im Zusammenhang mit der Populationsgröße und der Fitness der Pflanzen steht, wurde in Kapitel III „**Is habitat quality affecting population size and plant performance in the declining forb *Campanula glomerata*?“** untersucht, ob die Habitatqualität einen Einfluss auf diese Faktoren ausübt. Dabei zeigte die Länge der fertilen Triebe eine signifikante Beziehung zur Höhe der umgebenden Vegetation: Je dichter die Vegetation 20cm über dem Erdboden, desto länger die fertilen Triebe von *C. glomerata*. Die Länge der fertilen Triebe korreliert signifikant mit der Anzahl der Blüten pro Trieb und dem mittleren Samengewicht. Daraus wurde geschlussfolgert, dass die Art auch mit zunehmender Dichte der Vegetation, womit nach Ausbleiben traditioneller Landnutzung zu rechnen ist, in der Lage ist, mit entsprechender Anzahl hoch gelagerter Blüten ausreichend Insekten anzulocken, so dass Bestäubung und Samenansatz gewährleistet sind. Die Größe von *C. glomerata* Populationen zeigte keine Abhängigkeit von der Habitatqualität. Auch hier ist zu beachten, dass es sich um eine Momentaufnahme handelt und die in Kapitel IV beschriebenen Fluktuationen durchaus von Habitateigenschaften verursacht sein können, die in der vorliegenden Studie noch unbeachtet blieben (z.B. Klima).

Die Ergebnisse dieser Untersuchung warfen die Frage auf, wie es nach Aufgabe der Nutzung zum in der Literatur beschriebenen Rückgang der Art kommt. Dazu wurden in Kapitel IV „**Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use-practices?”** verschiedene Populationsgrößenparameter in nach wie vor landwirtschaftlich genutzten Gebieten und auf Flächen, die seit mindestens 10 Jahren von der Nutzung ausgenommen sind, miteinander verglichen. In einem Zeitraum von drei Jahren wurde kein Rückgang der Populationsgröße in von der Nutzung ausgenommenen Gebieten beobachtet. Bewirtschaftete und unbewirtschaftete Populationen unterschieden sich nicht in ihren Größen und waren durch starke Fluktuationen in der Gesamtzahl der Triebe, der Anzahl der fertilen Triebe, der von der Population eingenommenen Fläche sowie der Populationsdichte gekennzeichnet. Es wurden keine Hinweise gefunden, dass *C. glomerata* Populationen in von der Nutzung ausgenommenen Beständen stärker vom Rückgang betroffen sind als noch in Nutzung befindliche. Daher wird vermutet, dass kurzfristig nicht die Aufgabe traditioneller Landnutzung, wie von Frank & Neumann (1999) und Hardtke & Ihl (2000) beschrieben, sondern Habitatverlust durch Zerstörung oder Umnutzung die eigentliche Ursache für den stetigen Rückgang der Art ist. Die beobachteten starken Fluktuationen bei allen aufgenommenen Populationsgrößen-Parametern machen eine Weiterführung dieses Untersuchungsansatzes für mehrere Jahre dringend notwendig.

Da bei ausbleibender Nutzung mit Verschiebungen der Artenzusammensetzung und geänderten Konkurrenzverhältnissen zu rechnen ist, sollte auch die Reaktion der an langfristige Standorts- und Vegetationsentwicklung unter relativ konstanten Bedingungen angepassten Art *C. glomerata* (Partzsch 2001) auf zunehmende Konkurrenz am Beispiel zweier Grasarten untersucht werden. In Kapitel V „**Is *Campanula glomerata* threatened by competition of expanding**

grasses?" zeigte sich in einem experimentell angelegten Konkurrenzversuch, dass die Konkurrenz von *Poa angustifolia* im ersten Jahr die Biomasseproduktion und die Fitness der Knäuel-Glockenblume negativ beeinflusst, während von *Festuca rupicola* keine Konkurrenz für *C. glomerata* ausgeht. Da kompetitive Überlegenheit aber erst in Langzeitversuchen offensichtlich wird (Rebele 2000), können diese Aussagen zwar auf einen Trend hinweisen, diesen aber nicht als endgültig belegen. Eine Fortführung dieses Experiments ist unbedingt erforderlich, um vorhersagen zu können, inwieweit die zunehmende Dominanz verschiedener Gräser nach Nutzungsaufgabe das Fortbestehen von *C. glomerata* beeinflusst. Als Ursache für diese Effekte wurde die unterschiedliche Wuchsform der Gräser (ein weit verzweigtes, unterirdisches Ausläufersystem oder dichte Horste) vermutet. Außerdem wurde nachgewiesen, dass Keimung und Etablierung von *C. glomerata* mit zunehmender Grasdichte behindert werden. So konnte zwar in Kapitel III und IV nachgewiesen werden, dass die generative Reproduktion in dichter Vegetation bzw. nach Aufgabe der traditionellen Bewirtschaftung nicht reduziert ist. Doch da in dichten Beständen die Keimung und Etablierung von Jungpflanzen beeinträchtigt ist, muss davon ausgegangen werden, dass die Entwicklung solcher Populationen stagniert.

Eine Modellierung der Überlebenswahrscheinlichkeit mit mathematischen Modellen erwies sich auf Grund einer biologischen Eigenschaft der Knäuel-Glockenblume im Rahmen dieser Studie als unmöglich: Die vegetative Vermehrung über Rhizome (Klotz et al. 2002) verhindert die Ansprache einzelner Individuen im Gelände. So konnte keine genaue Anzahl der Individuen pro Population, welche als Grundlage für Modellierungen benötigt wird, sondern immer nur die Anzahl fertiler oder steriler Triebe, ermittelt werden (vergleiche Menges 1991, Münzbergova & Ehrlen 2005).

Es zeigte sich, dass die von Amler et al. (1999), Poschlod et al. (1999) und Burgmann & Possingham (2000) zusammengefassten Inhalte von Populationsgefährdungsanalysen (siehe Einleitung) ausreichend und in einem Untersuchungszeitraum von drei Jahren auch erfassbar sind. Drei Untersuchungsjahre sollten jedoch für die Abschätzung der Gefährdung einer mehrjährigen Pflanzenart das Minimum sein.

Abschließend lässt sich zusammenfassen, dass die allgemeine Konstitution der Knäuel-Glockenblume in den untersuchten Populationen gut ist, so dass von einer akuten Gefährdung nicht auszugehen ist. Es erwies sich als sinnvoll, genetische, demographische, standortkundliche und experimentelle Untersuchungen in einer Gefährdungsanalyse miteinander zu verbinden. Für weitere Arbeiten wird zusätzlich empfohlen, Daten zur Altersstruktur der Populationen zu erfassen. Aussagen zur Gefährdung einer Art, die auf Zusammenhängen zwischen genetischen und demographischen Daten eines Untersuchungsjahres beruhen, sollten bei mehrjährigen Arten unbedingt in einem Folgejahr auf ihre Gültigkeit überprüft werden. Für den weiteren Umgang mit *C. glomerata* wird ein Monitoring der Populationen in Intervallen von fünf Jahren empfohlen, um den Zeitpunkt erfassen zu können, wann ein naturschutzfachliches Eingreifen zum Erhalt der Art notwendig sein wird. Die Förderung des Erhalts stabiler Pflanzengesellschaften sowie die Unterbindung von Eutrophierung oder Zerstörung bestehender Habitate muss bis dahin als die wichtigste Schutzmaßnahme für diese Art betrachtet werden.

SCHLUSSFOLGERUNGEN UND AUSBLICK

Gefährdungssituation von *C. glomerata* in Deutschland und sich daraus ableitende Maßnahmen:

- *C. glomerata* ist momentan von Isolation, Inzucht oder genetischer Drift nicht beeinträchtigt, da Langlebigkeit und verschiedene Merkmale die Erhaltung der Variabilität der Populationen unterstützen. Die sexuelle Reproduktion spielt eine bedeutende Rolle für die Dynamik und das Weiterbestehen von *C. glomerata* Populationen

- Im Vergleich zu in Nutzung befindlichen *C. glomerata* Populationen wurde in ungenutzten Populationen keine negative Entwicklung von Populationsgröße und Fitness der Pflanzen festgestellt. Es wird vermutet, dass kurzfristig nicht die Aufgabe traditioneller Landnutzung, sondern Habitatverlust durch Zerstörung oder Umnutzung die eigentliche Ursache für den stetigen Rückgang der Art ist.

- Nach Nutzungsaufgabe ist bei zunehmender Dominanz von *Poa angustifolia* mit einer Beeinträchtigung von Biomasseentwicklung und Fitness von *C. glomerata* zu rechnen, während mit einer solchen bei zunehmendem Auftreten von *Festuca rupicola* nicht zu rechnen ist. Bei der Einschätzung der Gefährdung einzelner *C. glomerata* Populationen müssen daher unbedingt die Dominanzverhältnisse der umgebenden Arten beachtet werden.

- Der im Rahmen dieser Arbeit angelegte Konkurrenzversuch mit zwei verschieden Grasarten und *C. glomerata* sollte über einen längeren Zeitraum fortgeführt werden, damit die Einflüsse zunehmender Konkurrenz dieser Gräser auf das Bestehen der Knäuel-Glockenblume auch langfristig eingeschätzt und in die Gefährdungsanalyse aufgenommen werden können.

- *C. glomerata* zeigt eine Abhängigkeit von der Habitatqualität in der Form, dass in dichter, hoher Vegetation die Blühtriebe entsprechend länger sind. Bestäubung und Samenansatz werden dadurch gewährleistet, jedoch ist die Etablierung von Jungpflanzen in dichter Vegetation beeinträchtigt. In diesem Zusammenhang muss bei Pflegemaßnahmen besonderes Augenmerk auf Populationen in dichten Pflanzengesellschaften gerichtet werden, da es in diesen als Erstes zum Verlust genetischer Variabilität durch die ausbleibende Etablierung neuer Individuen kommen kann.

- Schutzprogramme für *C. glomerata* sollten sich nicht nur speziell auf diese Art konzentrieren, sondern vielmehr den Erhalt stabiler Pflanzengesellschaften fördern. Traditionelle Bewirtschaftung (Beweidung) oder Mahd mit anschließender Biomasseentfernung sind dazu geeignet. Jegliche Art von Eutrophierung, Zerstörung und anthropogenen Eingriffen wie z.B. das Pflanzen von Bäumen und Sträuchern muss in entsprechenden Habitaten unterbunden werden.

- Für die in der vorliegenden Arbeit untersuchten Flächen besteht bezüglich der Gefährdung von *C. glomerata* kein dringender Handlungsbedarf. Es wird jedoch ein Monitoring der Populationen in Intervallen von fünf Jahren empfohlen, welches demographische Aufnahmen und Untersuchungen zur genetischen Diversität beinhalten sollte, um Wissenslücken zu schließen und den Fortbestand der Populationen wissenschaftlich zu begleiten. Nur so kann der Zeitpunkt festgestellt werden, zu dem ein naturschutzfachliches Eingreifen zum Erhalt der Art notwendig sein wird. Außerdem wird empfohlen, für jede Population verlässliche Klimadaten aufzunehmen, da diese als Ursache für die Fluktuationen bei den Populationsgrößen in Frage kommen.

Richtlinien für Inhalte von Gefährdungsanalysen

- Populationsdaten: Neben verschiedenen Populationsgrößenparametern (Anzahl der fertilen und sterilen Individuen/Triebe, Dichte) ist es empfehlenswert, auch Daten zur Altersstruktur der Populationen aufzunehmen. Auf Grund von jährlichen Fluktuationen empfiehlt sich für Untersuchungen zur Einschätzung der Gefährdung mehrjähriger Arten ein Untersuchungszeitraum von mindestens drei, besser jedoch fünf Jahren. Für die statistische Absicherung der Ergebnisse erwiesen sich zwanzig Populationen als ausreichend.

- Pflanzendaten: Als Fitnessparameter einer Pflanze sollten alle Parameter aufgenommen werden, die Aufschluss über das reproduktive Verhalten der Art geben können. Dazu gehören die Anzahl der fertilen Triebe, die Anzahl der Blüten pro Trieb/Individuum, die Anzahl der pro Blüte gebildeten Samen und die Keimfähigkeit der Samen. In Abhängigkeit von der Populationsgröße wird ein Minimum von 20 zu erfassenden Trieben bzw. Individuen empfohlen. Als weiterer wichtiger Punkt muss festgestellt werden, ob im Freiland Keimung und Etablierung von Jungpflanzen stattfinden kann.

- Genetische Daten: Aus den molekularbiologischen Untersuchungen sollten Aussagen zur genetischen Struktur, zur Differenzierung innerhalb und zwischen den Populationen bzw. Regionen, zum Zusammenhang zwischen genetischer Differenzierung und geographischer Entfernung sowie zum Genfluss hervorgehen. Daraus kann abgeleitet werden, ob die Populationen von Isolation, Inzucht oder genetischer Drift beeinflusst sind. Auch hier werden pro Population mindestens 20 zu untersuchende Proben empfohlen.

- Standortdaten: Wichtige und ohne großen Aufwand zu erfassende Parameter sind das Untergrundgestein, der Bodentyp und die Bodenart sowie die Pflanzengesellschaft. Von diesen Daten lassen sich Aussagen zur Bodenchemie, zum Wasserhaushalt und über die Zeigerwerte (Ellenberg et al., 2001) auch Aussagen zu den Licht- und Temperaturverhältnissen, zur Bodenfeuchtigkeit, zum Kalk- und Stickstoffgehalt sowie zum Chloridgehalt des Bodens machen. Bei entsprechenden Möglichkeiten werden genauere

Untersuchungen des Boden-pH-Wertes und der Stickstoffversorgung der Pflanzen empfohlen, da gerade diese auf die Fitnessparameter wirken kann. Für die Keimung und Etablierung können die Licht- bzw. Deckungsverhältnisse in verschiedenen Vegetationsschichten von Bedeutung sein. Diese können auf abgesteckten Untersuchungsflächen mit Hilfe eines Zollstockes relativ einfach geschätzt werden (am besten nur von einer Person). Klimadaten sind im günstigsten Fall auf jeder Untersuchungsfläche separat aufzunehmen, können aber auch bei den örtlichen Klimastationen erfragt werden.

- Aussagen zur Gefährdung einer Art, die auf Zusammenhängen zwischen genetischen und demographischen Daten eines Untersuchungsjahres beruhen, sollten bei mehrjährigen Arten unbedingt in einem Folgejahr auf ihre Gültigkeit überprüft werden.

- Da auf Grund unterschiedlicher morphologischer Eigenschaften der Pflanzen oder verschiedener finanzieller und praktischer Vorraussetzungen eines Projektes mit Abweichungen und Kompromissen beim Umfang der Untersuchungen im Rahmen einer Gefährdungsanalyse gerechnet werden muss, bietet sich als Alternative zur Vorgabe durchzuführender Methoden ein auszufüllender Fragenkatalog an. Um die Gefährdung einer Pflanzenart mit diesem Hilfsmittel erfassen zu können, sollten folgende Fragen beantwortet werden:

1. Gibt es Hinweise, dass die Populationen von Isolation, Inzucht oder genetischer Drift beeinflusst werden?
2. Besteht zwischen den Populationen die Möglichkeit zum Austausch von genetischem Material (z.B. Pollen, Samen)?
3. Sind die Populationsgrößenparameter über Jahre gesehen stabil oder durch Fluktuationen gekennzeichnet?
4. Gibt es Zusammenhänge zwischen der Populationsgröße und Habitateigenschaften (Boden, Klima, Nutzung, Konkurrenz mit anderen Arten)?
5. Steht die Fitness der Pflanzen in Zusammenhang mit der Populationsgröße, der genetischen Diversität oder mit Habitateigenschaften (Boden, Klima, Nutzung, Konkurrenz mit anderen Arten)?
6. Welche Rolle spielt die generative, welche die vegetative Reproduktion?
7. Gibt es besondere Überlebensstrategien, die den Erhalt der Art trotz ungünstiger Verhältnisse unterstützen können?
8. Gibt es artspezifische Gefährdungsfaktoren (Fraßfeinde, Parasiten u.ä.)?

LITERATUR

AMLER, K., HEIDENREICH, A., KÖHLER, G., POETHKE, H.-J. & SAMIETZ, J. (1999). Die Standardisierte Populationsprognose (SPP): eine Anwendung der zoologischen Datenbanken am Beispiel des NSG "Leutratal" (Thüringen). In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 200-212. Ulmer, Stuttgart.

BURGMANN, M. & POSSINGHAM, H. (2000). Population viability analysis for conservation: the good, the bad and the undescribed. In *Genetics, Demography and Viability of Fragmented Populations* (ed. A. G. Young and G. M. Clarke), pp. 96-112. Cambridge University Press, Cambridge.

DANNEMANN, A. (2000). Der Einfluss von Fragmentierung und Populationsgröße auf die genetische Variation und Fitness von seltenen Pflanzenarten am Beispiel von *Biscutella laevigata* (Brassicaceae). doctoral thesis, Philipps-Universität.

DITTBRENNER, A., HENSEN, I. & WESCHE, K. (2005). Genetic structure and random amplified polymorphic DNA diversity of the rapidly declining *Angelica palustris* (Apiaceae) in Eastern Germany in relation to population size and seed production. *Plant Species Biology* **20**:191-200.

EISTO, A.-K., KUITUNEN, M., LAMMI, A., SAARI, V., SUHONEN, J., SYRJÄSUO, S. & TIKKA, P. M. (2000). Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. *Conservation Biology* **14**:1413-1421.

ELLENBERG, H., WEBER, H. E., DÜLL, R., WIRTH, V. & WERNER, W. (2001). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* XVIII.

FISCHER, M. & MATTHIES, D. (1998). RAPD-Variation in relation to population size and plant fitness in the rare plant *Gentianella germanica* (Gentianellaceae). *American Journal of Botany* **85**:1685-1692.

FRANK, D. & NEUMANN, V. (1999). *Bestandssituation der Pflanzen und Tiere Sachsen-Anhalts*. Ulmer, Stuttgart.

HAMBLER, D. J. & DIXON, J. M. (2003). Biological Flora of the British Isles. *Primula farinosa* L. *Journal of Ecology* **91**:694-705.

HARDTKE, H.-J. & IHL, A. (2000). *Atlas der Farn- und Samenpflanzen Sachsens*. Sächsisches Landesamt für Umwelt und Geologie, Dresden.

HENLE, K., POSCHLOD, P. & BAHL, A. (1999). Gefährdungsanalysen auf populationsbiologischer Grundlage: Einführung in Konzepte und Begriffe. In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 46-52. Ulmer, Stuttgart.

HENSEN, I. & OBERPRIELER, C. (2005). Effects of population size on genetic diversity and seed production in the rare *Dictamnus albus* (Rutaceae) in Central Germany. *Conservation Genetics* **6**:63-73.

HENSEN, I., OBERPRIELER, C. & WESCHE, K. (2005). Genetic structure, Population size, and Seed Production of *Pulsatilla vulgaris* Mill. (Ranunculaceae) in Central Germany. *Flora* **200**:3-14.

JACQUEMYN, H., BRYS, R. & HERMY, M. (2002). Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. *Oecologia* **130**:617-625.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002). BIOLFLOR- Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenr. f. Vegetationskunde* **38**:1-334.

MENGES, E. S. (1990). Population viability analysis for an endangered Plant. *Conservation Biology* **4**:52-62.

MENGES, E. S. (1991). The application of minimum viable theory to plants. In *Genetics and conservation* (ed. D. A. Falk and K. E. Holsinger), pp. 450-461. Oxford University Press, New York.

MÜNZBERGOVA, Z. & EHRLEN, J. (2005). How best to collect demographic data for population viability analysis models. *Journal of applied Ecology* **42**:1115-1120.

PARTZSCH, M. (2001). Die Porphyrkuppenlandschaft des unteren Saaletals - Vergleich der Vegetation in Abhängigkeit von Flächengröße und Genese der Prophyrkuppen. *Bot. Jahrb. Syst.* **123**:1-45.

POSCHLOD, P., DANNEMANN, A., JACKEL, A.-K. & BONN, S. (1999). Fragmentierung und Isolation von Pflanzenpopulationen - Einführung und Konzepte. In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, K. Henle, G. Kaule, P. Poschlod and J. Settele), pp. 336. Ulmer, Stuttgart.

PROBER, S. M., SPINDLER, L. H. & BROWN, A. H. D. (1998). Conservation of the grassy white box woodlands: Effects of remnant population size on genetic diversity in the allotetraploid herb *Microseris lanceolata*. *Conservation Biology* **12**:1279-1290.

REBELE, F. (2000). Competition and coexistence of rhizomatous perennial plants along a nutrient gradient. *Plant Ecology* **147**:77-94.

VERGEER, P., RENGELINK, R., COPAL, A. & OUBORG, N. J. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91**:18-26.

Kapitel VII

ERKLÄRUNG ÜBER DEN PERSÖNLICHEN ANTEIL AN DEN PUBLIKATIONEN

Da es sich um eine kumulative Dissertation mit Co-Autorenschaften handelt, ist im Folgenden mein Eigenanteil an den Publikationen aufgelistet:

KAPITEL II: **BACHMANN, U. & HENSEN, I. (in press). Is the declining *Campanula glomerata* threatened by genetic factors? *Plant Species Biology***

- Auswahl der Untersuchungsgebiete: 100%
- Bestimmung der Populationsgrößen: 100%
- Durchführung der Keimversuche: 100%
- Durchführung der RAPD/ISSR-Analysen: 100%
- Datenanalyse und Statistische Auswertung: 95%
- Schriftliche Umsetzung: 90%

Kapitel III: **BACHMANN, U. & HENSEN, I. (submitted) Is habitat quality affecting population size and plant performance in the declining forb *Campanula glomerata*? *Plant Species Biology***

- Auswahl der Untersuchungsgebiete: 100%
- Bestimmung der Populationsgrößen: 100%
- Durchführung der Keimversuche: 100%
- Bestimmung der Vegetationsdichte: 100%
- Analyse der Bodenparameter: 95%
- Datenanalyse und Statistische Auswertung: 100%
- Schriftliche Umsetzung: 90%

Kapitel IV: **BACHMANN, U. & HENSEN, I. (2006). Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use practices? *Feddes Repertorium* 117:164-171**

- Auswahl der Untersuchungsgebiete: 100%
- Bestimmung der Populationsgrößen: 100%
- Datenanalyse und Statistische Auswertung: 100%
- Schriftliche Umsetzung: 90%

Kapitel V: **BACHMANN, U., HENSEN, I. & PARTZSCH, M. (2005). Is *Campanula glomerata* threatened by competition of expanding grasses? Plant *Ecology* 180: 257-265**

- Aufzucht und Pflege der Pflanzen: 100%
- Ernte, Vermessen und Biomassebestimmung der Pflanzen: 100%
- Durchführung der Keimversuche: 100%
- Datenanalyse und Statistische Auswertung: 100%
- Schriftliche Umsetzung: 80%

Status der Co-Autoren:

Prof. Dr. rer. nat. habil. Isabell Hensen, Professorin für Pflanzenökologie am Institut für Geobotanik und Botanischer Garten der Martin-Luther-Universität Halle-Wittenberg, Betreuerin

Dr. rer. nat. Monika Partzsch, wissenschaftliche Mitarbeiterin am Institut für Geobotanik und Botanischer Garten der Martin-Luther-Universität Halle-Wittenberg

Bestätigung des betreuenden Hochschullehrers

Prof. Dr. Isabell Hensen

CURRICULUM VITAE

Name: Urte Jördis Bachmann, geb. Heinze
Geburtsdatum: 20. 01. 1975
Geburtsort: Halle/Saale

AUSBILDUNG

August 1990 - Juli 1993	Thomas-Müntzer-Gymnasium Halle/Saale, **Abitur**
1994 bis 2001	Biologiestudium **an der Martin-Luther-Universität Halle-Wittenberg** Hauptfach: Botanik 1. Nebenfach: Zoologie 2. Nebenfach: Bodenkunde 3. Nebenfach: Naturschutz Diplomarbeit zum Thema: „*Calamagrostis epigejos* (L.) ROTH - zur Strategie einer sehr erfolgreichen Art“

BERUFLICHER WERDEGANG

Sommersemester 2001	Lehrauftrag an der Martin-Luther-Universität Halle-Wittenberg -**Pflanzenbestimmungsübungen** (Geologen/Geografen) -**Biologisches Grundpraktikum „Faule Ort“** (Biologen)
April 2001 - Mai 2001	**Kartierung von Weichholzaue-Beständen** zwischen Magdeburg und Arneburg für SALIX - Assoziation freiberuflicher Biologen
Juni 2001	**Wissenschaftliche Hilfskraft mit Hochschulabschluss** an der Martin-Luther-Universität Halle-Wittenberg Fachbereich Biologie Institut für Zoologie Projektleiter: Dr. W.-R. Große Erstellung von Vegetationsaufnahmen im Rahmen einer zoologischen Promotionsarbeit
Juli 2001 – September 2001	**Gutachtertätigkeit**, Erstellung eines Gutachtens zur Auswirkung von Grundwasserstandsänderungen auf den Baumbestand der Saale-Aue südlich von Halle

Oktober 2001 – September 2003	**Promotionsstipendium** im Rahmen der Graduiertenförderung des Landes Sachsen-Anhalt, Arbeitstitel: „Wie erfasst man die Gefährdung von Pflanzen - Konzept einer Gefährdungsanalyse für *Campanula glomerata*“
Wintersemester 2001/2002	Lehrauftrag an der Martin-Luther-Universität Halle-Wittenberg -**Botanisches Grundpraktikum** (Geowissenschaftler, Agrarwissenschaftler, Biologen)
Sommersemester 2002	Lehrauftrag an der Martin-Luther-Universität Halle-Wittenberg -**Praktikum „Entwicklungszyklen der Pflanzen“** (Biologen) -**Botanische Exkursion „Dölauer Heide“** (Biologen) -**Biologisches Grundpraktikum „Faule Ort“** (Biologen)
Sommersemester 2003	Lehrauftrag an der Martin-Luther-Universität Halle-Wittenberg -**Botanische Exkursion „Dölauer Heide**“ (Biologen) -**Ökologisches Grundpraktikum** (Biologen)
Oktober 2003 – September 2004	**Förderung der Promotion** durch die Professor Dr. Zerweck-/Cassella- Stiftung Frankfurt und die Herbert Quandt-Stiftung der VARTA-AG Hannover

PUBLIKATIONSLISTE

BACHMANN, U. & HENSEN, I. (in press). Is the declining *Campanula glomerata* threatened by genetic factors? *Plant Species Biology*

BACHMANN, U. & HENSEN, I. (submitted) Is habitat quality affecting population size and plant performance in the declining forb *Campanula glomerata*? *Plant Species Biology*

BACHMANN, U., HENSEN, I. & PARTZSCH, M. (2005). Is *Campanula glomerata* threatened by competition of expanding grasses? *Plant Ecology* **180**: 257-265

BACHMANN, U. & HENSEN, I. (2006). Are population sizes of *Campanula glomerata* on the decline following the abandonment of traditional land-use practices? *Feddes Repertorium* **117**:164-171

GRÜTTNER, A. & **BACHMANN, U.** (2006). Resource allocation to sexual and clonal reproduction in a consolidation strategist. (submitted)

GRÜTTNER, A. & **HEINZE, U.** (2003). *Calamagrostis epigejos* (L.) ROTH: Bestandsstruktur, Gesamtbiomasse und Biomasseverteilung an unterschiedlichen Standorten. - *Hercynia N. F.* **36**:235-259.

GRÜTTNER, A. & **HEINZE, U.** (2003). Welche Bedeutung hat die sexuelle Reproduktion für den Erfolg der Art *Calamagrostis epigejos* (L.) ROTH? - *Feddes Repertorium* **114**/ 3-4:240-256.

EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst habe. Es wurden keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und diese auch als solche kenntlich gemacht.
Ich habe noch keinen Doktorgrad erworben oder mich in der Vergangenheit darum bemüht.

Halle/Saale, den

Urte Bachmann

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