

Christina Wärner

**Ökologie und Biologie
gefährdeter Stromtalpflanzen**

Dissertation



Universität Bremen

Titelbild: Ausschnitt aus einem Gemälde von Max Svabinsky: Morgen an der Elbe - 1921 (URL: <http://www.studgendeutsch.blogspot.com/2007/12/der-tschechische-maler-max-svabinsky.html> [16.10.2009]).

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Fachbereich Biologie/Chemie

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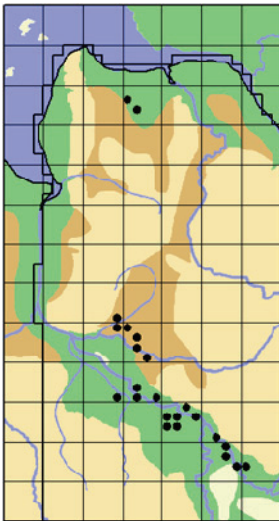
Eigenanteil an englischsprachigen Artikeln

Die in der vorliegenden Dissertation enthaltenen vier englischsprachigen Artikel wurden unter Beteiligung verschiedener Koautoren erstellt. In allen vier Artikeln hat Martin Diekmann zur Ideengebung sowie zur Korrektur der Manuskripte beigetragen. Silke Lehmann hat zum Artikel Wärner et al. 2008 (*Biological Conservation*) einen Teil der Datenerhebung durchgeführt. Walter Durka hat den Artikel Wärner et al. (Eingereicht I) mit genetischen Analysen, deren statistischer Auswertung und der Diskussion dieser Ergebnisse unterstützt. Der Artikel Wärner et al. (Eingereicht II) wurde durch Beiträge zu einzelnen Kapiteln des Manuskriptes von Walter Durka, Erik Welk und Burghard Wittig ergänzt. Ich habe zu allen vier Artikeln die gesamte Feldarbeit oder zumindest den Hauptteil durchgeführt, statistische Analysen durchgeführt sowie die kompletten Manuskripte oder zumindest deren Hauptteil geschrieben.

Das bereits veröffentlichte Manuskript in der Zeitschrift *Biological Conservation* durfte mit der freundlichen Genehmigung von Elsevier in der vorliegenden Dissertation erscheinen.

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Anlass und Ziele



Oben links: Verbreitung von Euphorbia palustris im Weser-Elbe-Gebiet (nach Cordes H, Feder J, Hellberg F, Metzing D, Wittig B (2006) Atlas der Farn- und Blütenpflanzen des Weser-Elbe-Gebietes. Hauschild, Bremen)

Oben rechts: Population von Euphorbia palustris an einem Grabenufer im Einzugsgebiet der Aller (Foto: Christina Wärner).

Unten links: Fragmentierte Flusslandschaft im Bereich der Mündung der Aller in die Weser bei Verden (URL: <http://www.google-earth.de> [25.07.2007]).

Unten rechts: Population von Sanguisorba officinalis auf der Uferbefestigung der Drepte, einem Nebenfluss der Weser (Foto: Christina Wärner).

Allgemeine Einleitung

Im Laufe der Erdgeschichte ist es immer wieder zum natürlichen Aussterben von Arten entweder im Rahmen des evolutiven Prozesses oder durch geologische Katastrophen gekommen. Durch die starke Bevölkerungszunahme in den letzten Jahrhunderten hat das Artensterben allerdings um das hundert- bis tausendfache zugenommen (Lawton und May 1995, Pimm et al. 1995). Habitatverlust und -veränderungen aufgrund der starken Nutzung und Umformung der Erdoberfläche durch den Menschen haben zu dieser drastischen Entwicklung geführt (Vitousek et al. 1997). Der Verlust einer einzigen Art kann bereits gravierende negative Auswirkungen auf die lebensnotwendigen Leistungen eines Ökosystems wie die Bereitstellung sauberen Trinkwassers, sauberer Luft oder fruchtbarer Böden haben (Mooney et al. 1995).

Mitteleuropa gilt als eine der am dichtesten besiedelten Regionen der Erde mit ausgeprägter Verkehrsinfrastruktur und intensiver Landwirtschaft, so dass viele der hier heimischen Arten unter Habitatverlust und -veränderungen leiden. Innerhalb der Gefäßpflanzen-Flora beispielsweise führen die mitteleuropäischen Länder mittlerweile 24 bis 45% ihrer Arten in Roten Listen (z.B. Ludwig und Schnittler 1996, Nikfeld 1999, Kazmierczakowa und Kazimierz 2001, Moser et al. 2002). In einer länderübergreifenden Studie haben Schnittler und Günther (1999) gefährdete Gefäßpflanzen Mitteleuropas zusammengestellt, die einen besonderen Schutz gerade im Hinblick auf ihre globale Stellung beanspruchen. Eine Artengruppe befindet sich innerhalb dieser Aufstellung mit einem über doppelt so hohen Anteil (23%) im Vergleich zu allen übrigen Gefäßpflanzen in einer besonders ernsten Gefährdungssituation auf: die sogenannten Stromtalpflanzen.

Stromtalpflanzen

Stromtalpflanzen sind Arten, die ganz oder überwiegend in ihrem Vorkommen an Stromtäler¹ gebunden sind; dieses besondere Verbreitungsmuster kann jedoch räumlich und/oder zeitlich beschränkt sein (Müller-Stoll et al. 1962, Vent und Benkert 1984, Zacharias und Garve 1996). Viele Arten zeigen nämlich lediglich am Rand ihres Verbrei-

¹ Stromtäler umfassen all die Bereiche der Landschaft, die periodischen Überflutungen ausgesetzt sind oder es ursprünglich einmal waren. Dazu gehören der Fluss selbst, seine Ufer und sein Tal (Forman 1983, Forman und Godron 1986).

tungsgebietes eine Bindung an Stromtäler wie z.B. *Sanguisorba officinalis* oder wechseln im Laufe der Zeit ihr Verbreitungsmuster. Hierzu gehören Arten wie z.B. *Leonurus marrubiastrum*, die vor 100 Jahren noch als Dorfpflanze galt und sich jetzt als Stromtalpflanze verhält (Brandes et al. 2003), oder Neophyten, die sich häufig zunächst entlang der Flusstäler ausbreiten, bevor sie stromferne Gebiete besiedeln.

Das Phänomen der Verbreitung von Pflanzen entlang von Stromtälern wurde erstmals von Ascherson (1859, 1864) beschrieben und der pflanzengeographische Begriff *Stromtalpflanze* später von Loew (1879) eingeführt. Aufgrund des Fehlens eines englischsprachigen Synonyms schlägt Burkart (2001) den Begriff „*river corridor plant*“ für den internationalen Gebrauch vor. Bis heute hat die Wissenschaft allerdings keinen konkreten Beweis für die Mechanismen, denen das Verbreitungsmuster von Stromtalpflanzen unterliegt, liefern können. In früherer Zeit gab es Hypothesen, die entweder auf klimatischen Veränderungen oder auf Migrationsbewegungen basierten (z.B. Schulz 1907, Schalow 1921, Ulbrich 1925, Libbert 1938). Mittlerweile geben wissenschaftliche Beobachtungen Anlass zu der Vermutung, dass neben Hydrochorie entlang der Stromtäler ebenfalls die besonderen Umweltbedingungen der Flusstäler wie Überflutungen, wiederholte Störungen, relativ sommerwarme und -trockene Verhältnisse sowie nährstoffreiche Alluvialböden eine entscheidende Rolle spielen (Burkart 2001). Da sich die Gruppe der Stromtalpflanzen jedoch trotz ihres besonderen gemeinsamen Verbreitungsmusters im Hinblick auf Lebensformen, gewisse Standortansprüche und Strategietypen sehr heterogen verhält, wird es vermutlich keine enggefasste Erklärung für die generierenden Mechanismen geben (Vent und Benkert 1984).

Burkart (2001) zählt heute innerhalb Mitteleuropas 129 Arten zu den Stromtalpflanzen, während Siedentopf (2005) bereits allein für Deutschland eine Liste mit 805 Stromtalarten zusammengestellt hat. Letztere schließt jedoch auch Arten ein, die sich lediglich kleinräumig innerhalb Deutschlands als Stromtalpflanze verhalten. Für das Amt Neuhaus im nordwestdeutschen Raum, einem Teil des Untersuchungsgebietes der vorliegenden Arbeit, werden 84 Arten als Stromtalpflanzen klassifiziert (Zacharias und Garve 1996), von denen sich ein auffallend hoher Anteil von 54% auf der regionalen Roten Liste befindet (Garve 2004). Die Ursachen für diesen hohen Gefährdungsgrad stehen mit großer Wahrscheinlichkeit in direktem Zusammenhang mit der extremen Veränderung der Flusstäler durch den Menschen innerhalb des dichtbesiedelten Europa (vgl. Trockner et al. 2009). Die meisten natürlichen Standorte wurden durch Flussregulierung, Kultivierung der Auen und Intensivierung der Landwirtschaft zerstört. Der Bau

von Deichen hat schließlich zur Abtrennung eines Großteils der Populationen von der natürlichen Flussdynamik geführt. Die natürlichen Standorte von Stromtalpflanzen sind jedoch nicht nur drastisch dezimiert und in ihrer Habitatqualität beeinträchtigt, sondern ebenfalls landschaftlich stark zerschnitten und damit dem Problem der sogenannten Habitatfragmentierung ausgesetzt. Die weitere Entwicklung der Restpopulationen vieler Stromtalpflanzen unter den beschriebenen Bedingungen ist ungewiss.

Habitatfragmentierung

Unter Habitatfragmentierung versteht man die Zerschneidung großer Habitate in kleinere Fragmente, die nicht miteinander verbunden sind. Zu einem gewissen Teil sind die Habitate unserer Landschaft aufgrund natürlicher Faktoren und Prozesse fragmentiert, allerdings hat die anthropogene Habitatfragmentierung die natürliche in den letzten Jahrhunderten stark überlagert, so dass mittlerweile ein Drittel bis die Hälfte der gesamten Erdoberfläche grundlegend verändert ist (Vitousek et al. 1997). Für Pflanzen mit ihrer starken Standortgebundenheit bedeutet dies, dass viele Populationen klein und/oder räumlich voneinander isoliert sind, was eine Reihe von negativen Auswirkungen auf deren Überlebensfähigkeit haben kann (Saunders et al. 1991, Tilman et al. 1994, Hanski und Ovaskainen 2000, Eriksson und Ehrlén 2001, Oostermeijer 2003). Deshalb gilt Habitatfragmentierung als einer der Hauptgründe für den weltweiten Verlust an Biodiversität (Vitousek et al. 1997).

Kleine und teils auch isolierte Populationen sind stärker durch zufällige Ereignisse wie Umweltkatastrophen, standörtliche Fluktuationen, demographische Schwankungen und genetische Drift gefährdet als große und nicht isolierte Populationen (Shaffer 1987, Lande 1993, Kéry et al. 2003). Die Wahrscheinlichkeit, dass eine große Population Fluten, Dürren, Feuer, extreme Wetterereignisse oder Landnutzungswechsel überlebt, ist wesentlich höher als bei kleinen Populationen. Zufällige demographische Schwankungen in kleinen, isolierten Populationen zweihäusiger Arten beispielsweise können das Geschlechterverhältnis aufgrund geringer Individuenzahlen auf 1:0 verschieben und damit die sexuelle Reproduktion der Population verhindern. Dieses Ereignis ist für große Populationen angesichts höherer Individuenzahlen unwahrscheinlich. Die Gefahr des Verlustes genetischer Vielfalt durch genetische Drift ist in kleinen Populationen besonders hoch, gerade dann, wenn der Genfluss zwischen Populationen mittels Vektoren für

Pollen und Diasporen aufgrund von räumlicher Isolation unterbrochen ist (Ellstrand und Elam 1993, Young et al. 1996). Konsequenzen sind häufig Inzucht und damit verbunden die Fixierung und Ansammlung schädlicher Mutationen sowie ein eingeschränktes Potential für evolutionäre Anpassungen an sich ändernde Umweltbedingungen (Lande 1988, Frankham 1996).

Die Störung oder Unterbrechung von biotischen Wechselwirkungen in kleinen und isolierten Populationen, z.B. mit Bestäubern, die diese nicht finden können oder sie nicht für attraktiv halten, kann nicht nur Einschränkungen in der Reproduktion zur Folge haben, sondern auch zu dem Verlust genetischer Diversität durch verminderten Austausch zwischen und innerhalb von Populationen führen (Jennersten 1988, Ågren 1996, Kwak et al. 1998). Schließlich sind fragmentierte Populationen häufig von Randeffekten und verringerter Standortqualität betroffen (Gascon und Lovejoy 1998, Debinsky und Holt 2000).

Die beschriebenen negativen Auswirkungen der Habitatfragmentierung auf Pflanzenpopulationen erhöhen deren Aussterberisiko entweder kurzfristig oder langfristig durch die Verringerung der Fitness² von Individuen und damit der gesamten Population (Lienert 2004). Es wird angenommen, dass die Fitness einer Population immer weiter abnimmt, sobald sie eine gewisse Größe unterschreitet, und dadurch in eine permanente Abwärtsbewegung gerät, die letztendlich zum Aussterben führt (Giplin und Soulé 1986).

Ziel und Gegenstand der Untersuchung

Auch wenn Habitatfragmentierung heutzutage als eine der größten anthropogenen Bedrohungen für das regionale Überleben von Pflanzenarten angesehen wird, gibt es Unterschiede hinsichtlich der Empfindlichkeit verschiedener Arten bzw. Artengruppen

² Im Rahmen der Populationsbiologie versteht man unter dem Begriff Fitness den relativen Erfolg verschiedener Genotypen, ihre Erbinformationen an die nächste Generation weiterzugeben. Da sich dieses Maß von Fitness jedoch schwer ermitteln lässt, wird der Begriff häufig eher allgemein in Form von Überlebensfähigkeit oder Fruchtbarkeit verwendet. Bei Pflanzen beispielsweise werden deshalb vielfach folgende Fitnesskomponenten als Maß verwendet: z.B. vegetative Parameter (Höhe und Ausdehnung der Pflanze, Dimension und Anzahl verschiedener Pflanzenteile), Biomasseproduktion oder reproduktiver Erfolg (Samenquantität, Samenqualität). Nach Silvertown and Charlesworth (2001).

abhängig von ihren Eigenschaften (Henle et al. 2004). Langlebige Arten gelten beispielsweise als weniger negativ von der Habitatfragmentierung betroffen wie kurzlebige Arten (Fischer und Stöcklin 1997, Vellend et al. 2006, Schleuning und Matthies 2009).

Bisher haben sich nur wenige Arbeiten mit Fragmentierungseffekten auf Artgruppenebene auseinandergesetzt (aber siehe z.B. Jacquemyn 2004, Kolb 2005, Aguilar 2006, Honnay und Jacquemyn 2007). Weiterhin gibt es kaum Langzeitstudien, die die Aussterberaten von Pflanzenpopulationen und die diese bedingenden Faktoren untersucht haben (aber siehe Ouborg 1993, Fischer und Stöcklin 1997, Endels et al. 2002, Lienert et al. 2002, Matthies et al. 2004). Dabei sind die Beobachtungen an langlebigen Arten aufgrund ihrer langen Generationszyklen von besonderem Interesse.

Innerhalb der Stromtalpflanzen ist über die Hälfte der Arten ausdauernd (Burkhardt 2001) und durchläuft damit mehr oder weniger lange Generationszyklen. Ob der besonders hohe Gefährdungsgrad dieser Artengruppe auch auf Fragmentierungseffekte zurückgeführt werden kann, ist unklar. Außerdem gibt es einen großen Mangel an ökologischen Untersuchungen insbesondere auf Populationsebene (Burkhardt 2001).

Aus den oben beschriebenen Gründen ist es Ziel der vorliegenden Arbeit, mit Hilfe von Untersuchungen zur Ökologie und Biologie von ausdauernden Stromtalpflanzen auf Populationsebene ihre Reaktion auf Habitatfragmentierung in einem allgemeinen Muster zusammenzufassen, um schließlich konkrete Anweisungen für Managementmaßnahmen zum Schutz dieser gefährdeten Artengruppe geben zu können. Zur Aufklärung der bedingenden Mechanismen für ein mögliches Muster sind ebenfalls weiterführende Untersuchungen auf Einzelartebene erforderlich. Gleichzeitig ist es Ziel, allgemeingültige, über die Stromtalpflanzen hinausgehende Aussagen im Zusammenhang mit der Reaktion von Pflanzen auf Habitatfragmentierung treffen zu können. Folglich bestehen die hauptsächlichen Gegenstände der Untersuchung darin...

...(1) herauszufinden, ob Habitatfragmentierung Auswirkungen auf die Populationssterberaten und/oder Veränderungen der Populationsgröße und damit auf das regionale Überleben von ausdauernden Stromtalpflanzen hat;

...(2) aufzuklären, ob die Reproduktion von ausdauernden Stromtalpflanzen durch Habitatfragmentierung beeinflusst wird;

...(3) die Ursachen für die eingeschränkte Reproduktion der gefährdeten Stromtalart *Euphorbia palustris* in fragmentierten Populationen zu bestimmen, sowie den Einfluss

der Witterung auf mögliche inter-annuelle Variationen der Zusammenhänge zwischen reproduktiver Fitness und ihren Einflussfaktoren zu ermitteln.

...(4) Eigenschaften, Ansprüche und Standortverhalten der typischen Stromtalart *Euphorbia palustris* zu dokumentieren und analysieren.

zu (1) Mit Hilfe von Langzeitdaten (durchschnittlicher Zeitraum von 15 Jahren) werden die Größenentwicklungen von 138 Populationen vier gefährdeter, ausdauernder Stromtalpflanzen untersucht: *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus*. Dabei wird den Fragen nachgegangen, ob kleine und / oder isolierte Populationen höhere Aussterberaten besitzen als große und / oder weniger isolierte, und ob Veränderungen der Größen überlebender Populationen in Zusammenhang mit der früheren Größe, dem Isolationsgrad und den Standorteigenschaften stehen. Weiterhin soll die Erstellung einer Projektionsmatrix Aufschluss über die Entwicklung der untersuchten Populationen in den nächsten Jahrzehnten geben.

zu (2) Anknüpfend an die Ergebnisse zu (1) sollen mögliche Einschränkungen in der Fitness fragmentierter Populationen gefährdeter, ausdauernder Stromtalpflanzen untersucht werden, um so einen denkbaren Mechanismus für höhere Aussterberaten in kleinen Populationen zu belegen. Dazu werden in 58 Populationen der Arten *Euphorbia palustris*, *Lathyrus palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus* die reproduktiven Fitnesskomponenten Samenproduktion, Samengewicht und Keimfähigkeit analysiert. Folgende Fragen sollen beantwortet werden: (i) Ist die Reproduktion in kleinen und/oder isolierten Populationen eingeschränkt? (ii) Welche Rolle spielt die Habitatqualität im Vergleich zur Populationsgröße und zur Isolation der Arten? (iii) Verhalten sich die Arten hinsichtlich der oben untersuchten Beziehungen einheitlich?

zu (3) Zur Erweiterung der Untersuchungen unter (2) wird anhand von 12 Populationen der Art *Euphorbia palustris* sowohl nach den bedingenden Mechanismen für die geringe Reproduktion in kleinen Populationen gesucht als auch die zeitliche Beständigkeit der gefundenen Zusammenhänge überprüft. Im Einzelnen soll ermittelt werden, ob Reproduktion und Populationsgröße mit der genetischen Diversität in Zusammenhang stehen, ob die gefundenen Zusammenhänge zwischen der Reproduktion und den sie beeinflussenden Variablen in drei aufeinanderfolgenden Jahren identisch sind und ob mögli-

che Unterschiede auf unterschiedliche Witterungsbedingungen in den Untersuchungsjahren zurückgeführt werden können.

zu (4) *Euphorbia palustris* ist eine typische Stromtalart, die damit als repräsentativ für viele andere Arten dieser noch wenig untersuchten Gruppe gelten kann. Im Rahmen einer Artmonographie werden Eigenschaften, Ansprüche und Standortverhalten dieser gefährdeten Stromtalpflanze zusammengestellt. Als Grundlage dienen sowohl die einschlägige Literatur als auch eigene Untersuchungen vor allem zu Standortansprüchen, Demographie und Vergesellschaftung. Die Arbeit trägt damit nicht nur zur Entwicklung artspezifischer Schutzmaßnahmen bei.

Die Untersuchungsgegenstände 1 bis 4 entsprechen den Ausführungen in den englischsprachigen Artikeln der Kapitel 3.1 bis 3.4.

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Untersuchungsarten und -gebiet



Oben links: Euphorbia palustris

Mitte: Pseudolysimachion longifolium

Oben rechts: Sanguisorba officinalis

Unten links: Lathyrus palustris

Unten rechts: Senecio paludosus

(Fotos: Christina Wärner)

Auswahl und Beschreibung der untersuchten Arten

Für die geplante Studie wurden fünf Arten ausgewählt, die gemäß Burkart (2001) innerhalb Mitteleuropas als Stromtalpflanzen klassifiziert werden. Da gefährdete Pflanzenarten eher negativ von der Degradierung ihrer Lebensräume betroffen sind als ungefährdete, wurden lediglich Arten der regionalen Roten Liste berücksichtigt: *Euphorbia palustris* L. (Euphorbiaceae), *Lathyrus palustris* L. (Fabaceae), *Pseudolysimachion longifolium* (L.) Opiz (Scrophulariaceae), *Sanguisorba officinalis* L. (Rosaceae), and *Senecio paludosus* L. (Asteraceae). Diese sollten sich im Gebiet zwar im Rückgang befinden aber noch so häufig vorkommen, dass eine ausreichende Anzahl an potentiellen Untersuchungspopulationen zur Verfügung steht (Abb. 1).

Um ein Muster für die Reaktion von ausdauernden Stromtalpflanzen auf Habitatfragmentierung zu finden, das möglichst für alle Arten innerhalb dieser Gruppe gültig ist, müssen die ausgewählten Arten einerseits entsprechende gemeinsame Grundeigenschaften aufweisen und andererseits sollten sie neben diesen eine gewisse Variation innerhalb weiterer Merkmale aufweisen. Gemein ist ihnen - abgesehen von ihren Charakteristika, die sie als Stromtalpflanzen besitzen, wie beispielsweise die Bevorzugung feuchter bis nasser Standorte, die hydrochore Ausbreitung ihrer Samen oder die Lebensform als Hemikryptophyt - dass sie sich über Samen fortpflanzen, aber sich auch vegetativ durch kurze Untergrundrhizome vermehren können, doch nicht klonal sind. Unterschiede weisen sie beispielsweise hinsichtlich des Befruchtungssystems oder der Lebensraumansprüche innerhalb der Flusstäler auf (Tab. 1).

Lebensraum Flussaue

Natürlicherweise kämen Stromtalpflanzen hauptsächlich in den ursprünglichen Flussauen vor, einer Übergangszone zwischen terrestrischen und aquatischen Bereichen, die sich durch eine hohe Hydro- und Morphodynamik auszeichnet. Aufgrund vielfältiger Landschafts- und Biotopstrukturen wie z.B. Altwässer, Flutrinnen und -mulden, sandige Höhenrücken und reliefierte Ebenen gehören Auen zu den artenreichsten Ökosystemen Europas (Naiman et al. 1993). Heutzutage sind viele Stromtalpflanzen jedoch durch den

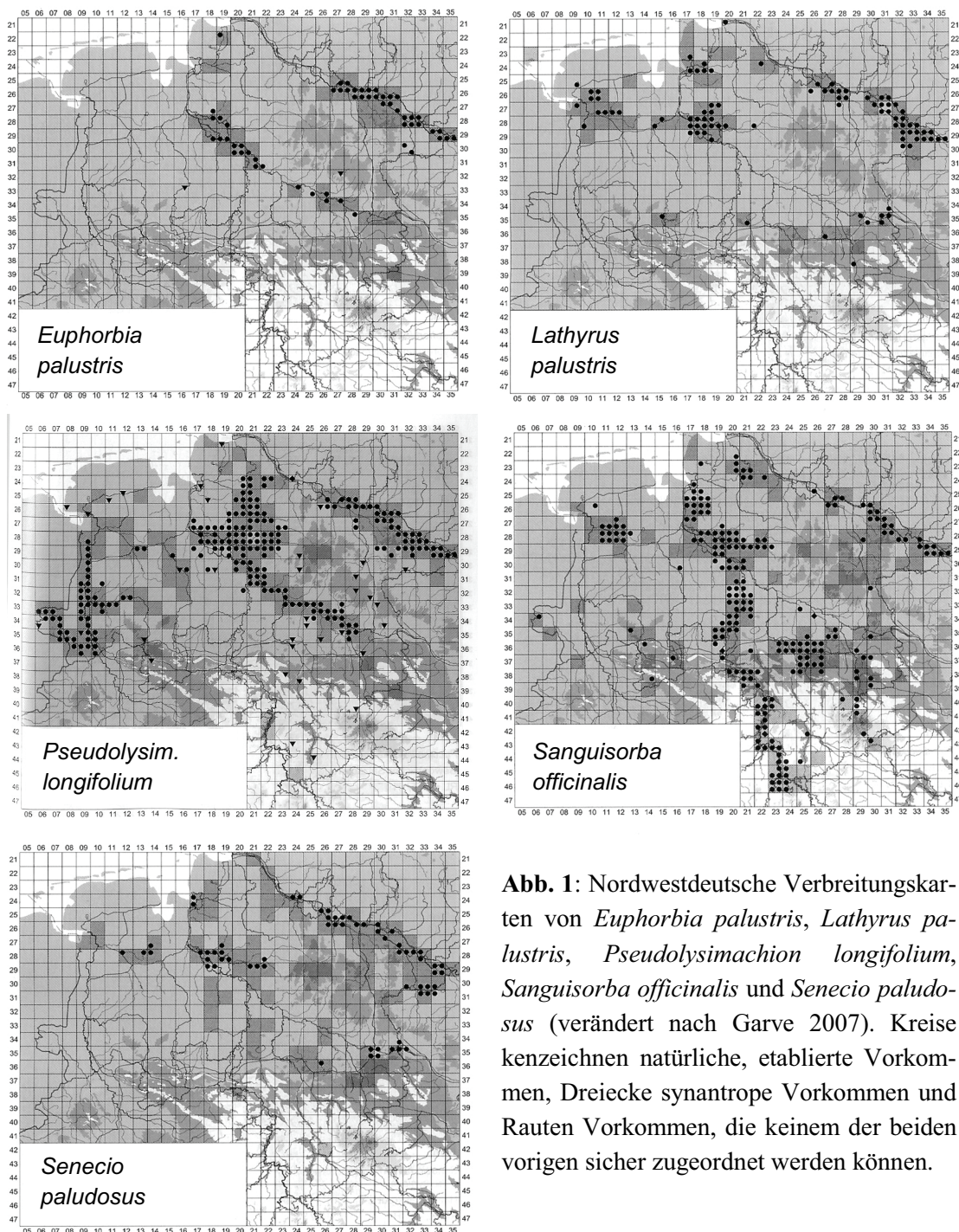


Abb. 1: Nordwestdeutsche Verbreitungskarten von *Euphorbia palustris*, *Lathyrus palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus* (verändert nach Garve 2007). Kreise kennzeichnen natürliche, etablierte Vorkommen, Dreiecke synantrophe Vorkommen und Rauten Vorkommen, die keinem der beiden vorigen sicher zugeordnet werden können.

starken Verbau und die intensive Nutzung der Auen auf Ersatzstandorte wie Grabenränder oder Brachen gedrängt worden.

Die Artengemeinschaften in Flussauen müssen an die besonderen Verhältnisse von Überflutung und teilweise ausgeprägten Trockenphasen angepasst sein (z.B. Ellenberg 1996). Kontinuierliche Nährstoffeinträge durch Ablagerung von Schwebstoffen der

Tab.1: Eigenschaften, Ansprüche und Status der Untersuchungsarten (nach Ellenberg et al. 1991, Oberdorfer 1994, Ludwig und Schnittler 1996, Klotz et al. 2002, Garve 2004 und eigenen Beobachtungen). EZW = Ellenberg-Zeigerwerte (Skala 1-9).

Merkmal	<i>Euphorbia palustris</i>	<i>Lathyrus palustris</i>	<i>Pseudol. longifolium</i>	<i>Sanguis. officinalis</i>	<i>Senecio paludosus</i>
Blühphase	April-Juni	Juni-August	Juni-August	Juni-September	Juli-August
Bestäubung	Insektenbestäubung	Insektenbestäubung	Insekten- und Selbstbestäubung	Insekten- und Selbstbestäubung	Insekten- und Selbstbestäubung
Kompatibilität	selbstinkompatibel	selbstkompatibel	nicht bekannt	nicht bekannt	nicht bekannt
Samenausbreitung	Autochorie, Myrmecochorie, Hydrochorie	Autochorie, Hydrochorie	Anemochorie, Hydrochorie	Anemochorie, Hydrochorie	Anemochorie, Myrmecochorie, Epizoochorie, Hydrochorie
Licht (EZW)	8	8	8	7	7
Temperatur (EZW)	6	6	6	5	6
Feuchte (EZW)	8	8	8	7	9
Feuchtwechsel (EZW)	stark wechselnde Feuchte zeigend	Überschwemmung zeigend	stark wechselnde Feuchte zeigend	keinen Feuchtwechsel zeigend	Überschwemmung zeigend
Reaktion (EZW)	8	8	7	indifferent	indifferent
Areal	Eurasien	Eurasien	Eurasien	Eurasien	Eurasien
Standort	Röhrichte, Bruchwälder, Brachen, Fluss-, Teich-Grabenufer	Feuchtgrünland, Staudenried, Gräben, Großseggenbestände	Feuchtgrünland, Gräben, Sumpfstaudenfluren, Saum von Auengebüsch	Feuchtgrünland, Graben- und Wegränder	Verlandungsgesellschaften, Großseggen- und Röhrichtbestände, Fluss-, Teich-, Grabenufer
Rote Liste Nds.	stark gefährdet	stark gefährdet	gefährdet	gefährdet	stark gefährdet
Rote Liste Deutschland	gefährdet	gefährdet	ungefährdet	ungefährdet	gefährdet

über die Ufer tretenden Flüsse sorgen für eine natürlich hohe Biomasseproduktion. Weiterhin ist der Lebensraum durch höhere Temperaturen und geringere Niederschläge verglichen mit der umgebenden Landschaft gekennzeichnet.

Naturräumliche Bedingungen des Untersuchungsgebietes

Das Untersuchungsgebiet umfasst einen Teil der großen Flusssysteme der Weser und Elbe im Bereich der Nordwestdeutschen Tiefebene (ca. 12960 km²) (Abb. 2). Die untersuchten Populationen befinden sich entlang der Flüsse gemäß der naturräumlichen Gliederung Deutschlands nach Meisel (1959, 1961, 1964) in den Wesermarschen, den Harburger Elbmarschen, der Hamme-Osteniederung, der Wümmeniederung dem Verdener Wesertal und der Unteren Aller-Talsandebene.

Die heutigen Flusssysteme der Weser und Elbe wurden während der Saale-Kaltzeit in Form des Aller-Weser-Urstromtales und des Elbe-Urstromtales angelegt (Meyer 1983). Die häufig breiten Marschgebiete entlang dieser Flüsse stammen von nacheiszeitlichen Ablagerungen durch Meeresspiegelschwankungen sowie klimatisch und jahreszeitlich bedingten Abflussspitzen. Aufgrund des Deichbaus wurde die natürliche Marschbildung allerdings beendet. Die Marsch ist relativ eben, zeigt jedoch wegen ihrer Uferwälle entlang der großen aber auch kleinen Nebenflüsse Niveauunterschiede von bis zu 1,5 m (Behre 2008). Hinter dem durch verstärkte Sedimentablagerungen entstandenen Uferwall, der an Weser und Elbe bis zu 3 km breit ist, ist das niedrigere Sietland gelegen. In diesem Bereich bildeten sich ausgedehnte Niedermoore. Aufgrund der zeitlichen und räumlichen Unterschiede in den Sedimentationsbedingungen zeigen sich sowohl innerhalb des vertikalen als auch des horizontalen Flussmarschenprofils Unterschiede. An der Oberfläche befinden sich neben Niedermoorböden und gelegentlich auch Sanden hauptsächlich fruchtbare Tonböden (Höfle 1976, Behre 1995).

Die ursprüngliche Vegetation entlang der Flüsse im Untersuchungsgebiet wurde von Behre (1983) rekonstruiert: Auf die flussbegleitenden Schlammfluren des Bidention und die Röhrichte (*Phragmites*) folgten auf dem Uferwall galerieartige Auenwälder. Diese wurden zunächst von der Weichholzaue, erst mit Weidengebüsch (*Salicetum triandro-viminalis*) und dann mit Weidenwald (*Salicetum albo-fragilis*), eingeleitet. Die

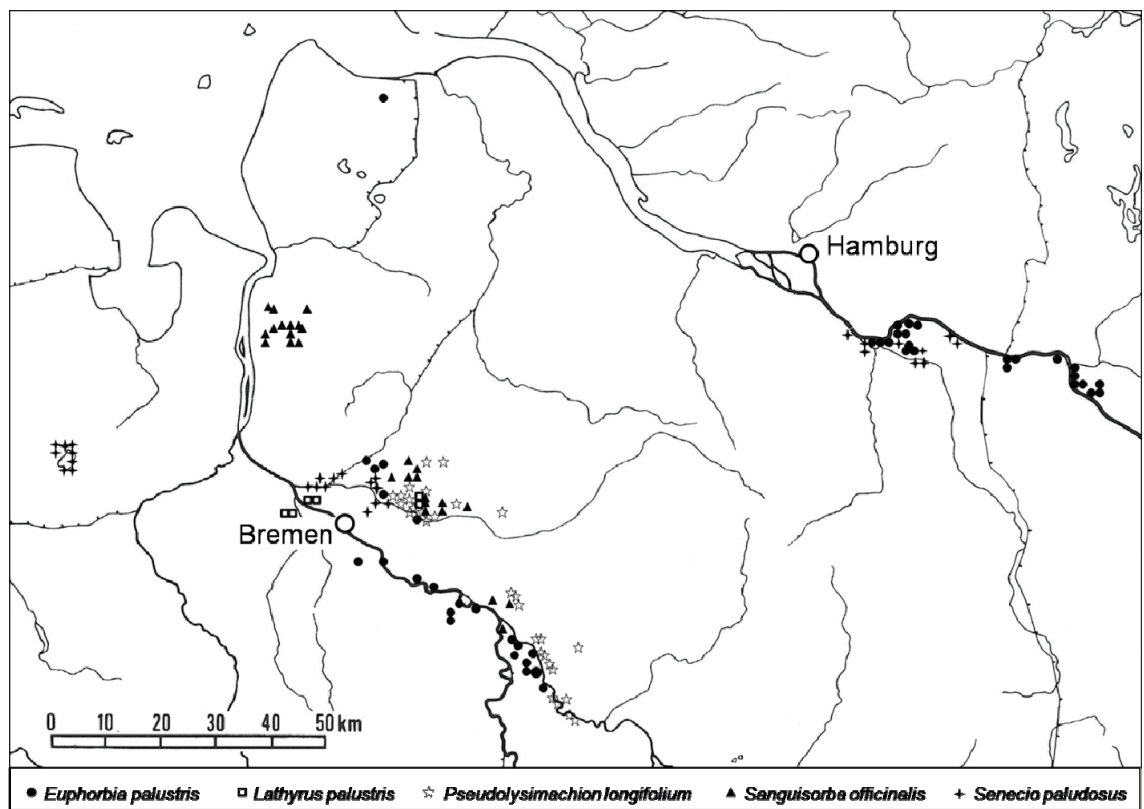


Abb. 2: Untersuchungsgebiet und untersuchte Populationen von *Euphorbia palustris*, *Lathyrus palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus* im Nordwestdeutschen Tiefland. Jedes Symbol (in der Abbildung erklärt) kennzeichnet den Standort einer oder mehrerer Populationen. Karte verändert nach Garve (1994).

ablösende Hartholzaue bestand aus einem Ulmen-Eichen-Eschenwald (Fraxino-Ulmetum), in dem ebenfalls Erlen vorkamen. Die natürliche Vegetation der Sietländer variierte aufgrund mehrerer Vernässungs- und Verlandungsfolgen räumlich und zeitlich stark. Es bestand ein vielfältiges Mosaik aus feuchten bis nassen, nährstoffarmen und -reichen torfbildenden Gesellschaften: Röhrichte, Großseggenrieder, *Filipendula*-beherrschte Hochstaudenfluren, Kleinseggengesellschaften, Erlen- und Birkenbruchwälder sowie Hochmoorgesellschaften.

Das Untersuchungsgebiet ist durch ein atlantisches Klima mit milden Wintern und verhältnismäßig kühlen, regnerischen Sommern gekennzeichnet (Seedorf und Meyer 1992). Die im Untersuchungsgebiet gelegenen Messstationen Bremen und Hamburg

weisen ein Jahresmittel der Lufttemperatur von 8,8°C und 8,6°C sowie einen mittleren Jahresniederschlag von 694 mm und 770 mm auf (URL: <http://www.dwd.de> [31.07.2009]). Die Vegetationsperiode erstreckt sich von etwa Mitte März bis Anfang November über einen Zeitraum von 230 bis 240 Tagen (Seedorf und Meyer 1992).

Veränderungen der Flüsse und ihrer Auen durch den Menschen

Seit dem Einzug der Landwirtschaft und dem Sesshaftwerden des Menschen unterliegen die großen Flüsse Europas und ihre Auen anthropogenen Veränderungen. Die flächenhafte Entwaldung der Einzugsgebiete, ihre landwirtschaftliche Nutzung und Besiedlung hatten schon früh Auswirkungen auf die Flussdynamik und damit auf die Sedimentation und Erosion in den Auen. Die stärksten Eingriffe des Menschen fanden jedoch im 19. und 20. Jahrhundert statt: Verstärkte Kultivierung der Auen, Ausbau der Flüsse für eine bessere Schiffbarkeit, Schutz der Siedlungen und landwirtschaftlichen Flächen vor Hochwasser und die Anlage von Wasserkraftwerken führten zu einer völligen Überprägung der natürlichen Bedingungen. Bis heute sind 88% der ursprünglichen europäischen Auen mit ihren typischen Wäldern verloren gegangen (Hughes 2003) und damit der Großteil natürlicher Retentionsräume sowie der Lebensraum für viele Tiere und Pflanzen. Die Abtrennung der Flüsse von ihren Auen durch Begradigung und das Anlegen von Dämmen und Deichen hat die ökologische Diversität der Flusstäler stark herabgesetzt (Pautou und Decamps 1985).

Besonders die Flüsse des küstennahen Tieflandes, wie die des Untersuchungsgebietes, waren und sind von den genannten Veränderungen aufgrund ihrer Größe sowie der Ausdehnung und geringen Reliefenergie ihrer Auen betroffen (Sommerhäuser und Schuhmacher 2003). Diese Flusstäler boten sich in hohem Maße zur Besiedlung, als Verkehrswege und zur intensiven landwirtschaftlichen Nutzung an. Insbesondere die Unterweser sowie deren Nebenflüsse und Auen gelten als stark verbaut (z.B. Schirmer et al. 1989, Behre 1995, Trockner et al. 2009). Die Unterelbe hingegen zeigt einen relativ geringen Ausbaugrad, jedoch sind 80% ihrer Auen eingedeicht (Dahl und Flade 1994), wovon die meisten der hier untersuchten Populationen betroffen sind. Als Managementziel für das Wesersystem wird die Wiederherstellung natürlicher Flussfunktionen einschließlich der Schaffung von Retentionsflächen gefordert (Trockner et al. 2009). Ähnliche Ziele verfolgt der Naturschutz für das untere Elbesystem mit einer

Wiederentwicklung eines naturnahen Stromästuars durch die Förderung der natürlichen Abfluss- und Morphodynamik in Strom und Aue (Dahl und Flade 1994). Die Umsetzung dieser Ziele würde bestehende Lebensräume der Flusssysteme ökologisch aufwerten und gleichzeitig neue potentielle Standorte schaffen. Für viele Populationen von Stromtalpflanzen würde der Wiederanschluss an die Flussdynamik zu einer enormen Verbesserung der Standortqualität führen sowie den Anschluss an natürliche Wanderungswege durch Hydrochorie bedeuten.

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3.1

Auswirkungen von Habitatfragmentierung auf das Überleben gefährdeter Stromtalpflanzen



Euphorbia palustris, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus* (von links nach rechts; Zeichnungen verändert nach Mossberg B, Stenberg L (2005) *Den nya nordiska Floran*. Wahlström & Widstrand, Stockholm).

River corridor plants in North-western Germany are threatened by small population size

Christina Wärner, Martin Diekmann

(Manuscript)

Abstract

River corridor plants in Central Europe account for an above-average proportion of endangered species. The main objective of this study was to examine the effects of habitat fragmentation and deterioration on the survival and changes in population size of four perennial species over the course of at least ten years. We sampled a total of 138 populations of the endangered *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis*, and *Senecio paludosus* in the Weser and Elbe river systems in North-western Germany.

Overall, 33% of the populations became extinct during the study period. Extinction rates and changes in population size were related to initial population sizes, but not to population isolation and only marginally so to habitat quality (patch size, habitat type, vegetation height, light availability, soil parameters). Large populations (> 100 individuals) had a much higher probability to survive, retain their initial size or increase in size (to > 1.000 individuals) than small populations (< 25 individuals). There was no general decline in population size as only 11% of the populations became smaller while 56% remained unchanged or increased, including small ones, and extinction rates and changes in population size were independent of time. We therefore conclude that the high extinction rates in small populations are best explained by sudden, stochastic short-term environmental events, such as land reclamation, changes in land use, or use of pesticides, rather than by long-term negative effects, for instance of deteriorated habitat quality, genetic deterioration, or disrupted biotic interactions. The construction of a projection matrix, however, predicted that, in 117 years, almost all of the surveyed populations will have become extinct. Since the establishment of new populations in the study area is likely to be very scarce due to the lack of potential habitats, the situation of long-lived river corridor plants will further degrade if no management measures are taken.

Keywords: Endangered species, Extinction rates, Habitat quality, Population isolation, Projection matrix

Introduction

In Central Europe, more than 100 vascular plant species are exclusively or predominantly confined to the basins of large rivers (Burkart 2001). About 23% of these so-called river corridor plants - a proportion nearly twice as high as the average for all Central European vascular plants - have a high conservation priority (Schnittler and Günther 1999). The main reason for the threat of these species may be the destruction and deterioration of their natural habitats along the rivers, caused by the regulation of water courses, land reclamation and agricultural intensification.

River corridor plants form a group of species that are defined only by its peculiar distribution pattern along the large river corridors (Müller-Stoll et al. 1962, Vent and Benkert 1984, Zacharias and Garve 1996). Yet, the group includes species with very different habitat preferences (Korsch 1999), and to date the mechanisms generating this distribution pattern are not well known, although observational studies indicate that the species' ability of water dispersal plays a crucial role. Another factor of importance is the specific environment of river corridors, characterized by regular winter flooding associated with considerable disturbance events, relatively dry and warm conditions during summer, and nutrient-rich alluvial soils (Burkart 2001). At present, however, most populations are completely cut off from the natural river dynamics due to drainage and the construction of dikes, and populations therefore are often small and highly isolated from each other.

Small population size and / or isolation have been identified as having negative effects on plant performance and reproduction. This has been shown for a number of plant species (e.g., Kéry et al. 2000, Jacquemyn et al. 2002, Kolb 2005). Giplin and Soulé (1986) suggested in a general conceptual model that populations that reach a minimum threshold number of individuals may enter into a so-called extinction vortex, a circular process in which ever decreasing plant fitness leads to a decline in population size and eventually to extinction. The increased risk of extinction for small populations is caused by a number of factors. Firstly, small populations may be more sensitive to the effects

of environmental and demographic stochasticity and genetic drift than larger ones (Shaffer 1987, Kéry et al. 2003). Environmental stochasticity, such as habitat destruction or random fluctuations in weather, has been found to be the most important factor for the extinction of fragmented populations (Menges 1992, Lande 1993). Genetic drift in small and isolated populations leads to increased inbreeding and loss of genetic variation (e.g., Ellstrand and Elam 1993, Young et al. 1996). Secondly, the disruption of biotic interactions with pollinators and seed dispersers due to small population size and isolation (Kearns et al. 1998) may also contribute to a genetic deterioration of populations, and pollen limitation may at the same time reduce reproductive success (Jennersten 1988, Ågren 1996, Kwak et al. 1998, Tomimatsu and Ohara 2002, Kolb 2005).

However, there is only little empirical evidence for natural plant populations that small population size and / or increased isolation cause a further decline in population size and eventually lead to extinction. Long-term data on the dynamics of plant populations are required to test this hypothesis, and these are very scarce, only a few studies have compared historical with current population data to investigate extinction rates of plants and the factors causing their local disappearance (Ouborg 1993, Fischer and Stöcklin 1997, Endels et al. 2002, Lienert et al. 2002, Matthies et al. 2004). The monitoring of perennial species is of particular interest, because habitat fragmentation may affect the population turnover of long-lived species less quickly than that of short-lived ones (Fischer and Stöcklin 1997, Vellend et al. 2006, Schleuning and Matthies 2009).

While the precarious state of many river corridor plants in Central Europe is obvious, the factors causing their strong decline are a matter of discussion. In an assessment programme for endangered plants in Lower Saxony, a federal state in North-western Germany where an high proportion (54%) of river corridor plants is endangered (Zacharias and Garve 1996), the location and size of populations has been recorded since the mid 1980s. We used these monitoring data to re-visit 207 populations of four threatened, perennial river corridor plants and to examine the effects of habitat fragmentation and altered environmental conditions on changes in population size over the course of at least 10 years. For the selected species, a previous study had shown that plant fitness was generally negatively affected by small population size and / or isolation, and was also influenced by habitat quality (Winter et al. 2008).

More specifically, we aimed to examine whether small and / or isolated populations were more prone to extinction than large and less isolated ones, and whether the

changes in population size of surviving populations were related to initial population size, isolation and environmental conditions. Our intention was to provide indirect evidence for the negative effects of reduced plant fitness on population survival of long-lived species and to give advice for the conservation of endangered river corridor plants.

Methods

Study area and species

Fieldwork was carried out in 2005 and 2006 in floodplains of the Weser and Elbe river systems in North-western Germany (Fig. 1). In this area, 85 plant species are classified as river corridor plants (Zacharias and Garve 1996). Among the endangered taxa (Garve 2004) that still occur in sufficient numbers of populations four were selected: *Euphorbia palustris* L. (Euphorbiaceae), *Pseudolysimachion longifolium* (L.) Opiz (Scrophulariaceae), *Sanguisorba officinalis* L. (Rosaceae), and *Senecio paludosus* L. (Asteraceae). All species are perennial herbs that reproduce sexually via seeds and vegetatively by means of short underground rhizomes, yet they are considered non-clonal (Klotz et al. 2002). Natural and semi-natural habitats in the study area include wet meadows and the edges of nutrient-rich water bodies. At present, as a result of habitat loss, the species are largely restricted to abandoned grasslands and ditch banks.

Selection and re-visitation of study sites

Within the framework of the assessment programme for endangered plants in North-western Germany, data about the location (marks on a map 1:50 000) and rough estimates of the population sizes (in eight classes: 1, 2-5, 6-25, 26-50, 51-100, 101-1.000, 1.001-10.000, >10.000 flowering individuals) have been collected since 1982. We selected a total of 383 records about the four study species in the study area but only those that referred to population estimates until at least ten years ago in order to take the long life span of the species into account. 176 records had to be omitted from the analysis because of spatial imprecision of the data. In total 207 populations were re-visited during peak flowering of the species. Two observers examined each site for the occurrence of the studied species for up to 2 h. By this extensive search, an overestimation of extinction events, a crucial factor for the calculation of incorrect extinction probabilities of

species (Kéry et al. 2006), was prevented. All species are generally relatively easy to detect in the field owing to their tall stature and conspicuous flowers. If the search remained unsuccessful, we considered the population to have gone extinct. Because the sites of several populations were difficult to access we omitted further populations from the analysis. Finally, a total of 138 populations were included in the data analysis (Table 1).

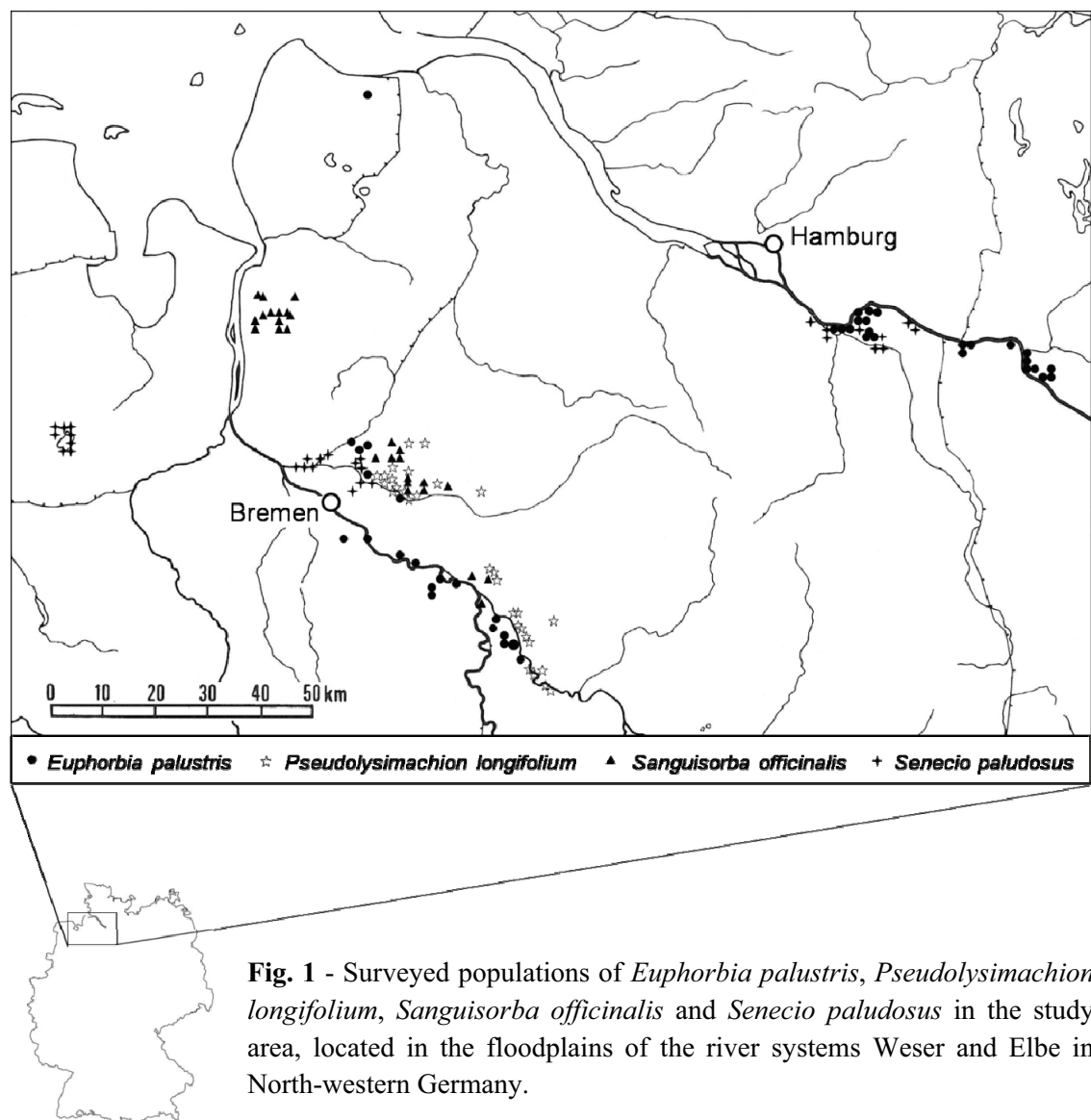


Fig. 1 - Surveyed populations of *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Senecio paludosus* in the study area, located in the floodplains of the river systems Weser and Elbe in North-western Germany.

Population size was determined as the number of flowering plants and assigned to the eight classes previously mentioned. In *E. palustris* and *S. paludosus*, individuals were clearly separated from each other, whereas, in the two other species, individuals in terms of genets were difficult to identify because the shoots form dense clusters that are

impossible to disentangle. Here, each ramet was treated as one individual. The degree of population isolation was defined as the distance to the nearest population determined with the help of detailed topographic maps.

Habitat quality

As it was not possible to locate the exact sites of extinct populations accurately within a few meters, we only selected surviving populations for the acquisition of habitat quality parameters. For 86 populations, patch size (area occupied by a species in m²) and habitat type in six categories ([1] ditch bank, [2] shore of a river or lake, [3] verge, [4] fallow, [5] swamp forest, [6] grassland) were determined. Furthermore, we selected 15 surviving populations in each of the species *Euphorbia*, *Pseudolysimachion* and *Sanguisorba*, which covered a wide range of changes in population sizes, to collect data on additional habitat quality parameters (Table 2). *Senecio* was omitted from this part of the study because only few populations of this species had survived.

In each of these 45 populations, soil samples were collected during a rainless period in July 2006. The samples consisted of five pooled soil cores (100 cm³ down to a depth of 4 cm) taken from below the litter layer. Soil moisture was measured gravimetrically. Prior to chemical analysis, all air-dried samples were passed through a 2-mm-sieve. We determined pH in a solution of 10 g of soil and 25 ml of 0.01M CaCl₂ with a standard glass electrode. Plant available phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were extracted with ammonium lactate. P was measured photometrically by flow injection analysis (FIA) and cations by Atomic Absorption Spectroscopy (AAS) (all expressed in mg per 100 g soil). The contents of carbon (C) and nitrogen (N) were determined to calculate the C/N ratio, using an elemental analyser (EuroEA 3000, HEKA-tech, Germany).

Mean vegetation height of a population was calculated from at least 5 measurements (dependent on the patch size) of the surrounding vegetation. Light intensity was measured as photosynthetic photon flux density (PPFD) of photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{ m}^{-2}$; LI-COR Quantum sensor, USA) at 20 regularly spaced locations directly above the ground on days with overcast sky. Simultaneous measurements were carried out close to each site in the open, to calculate the relative light intensity expressed as $\text{PPFD}_{\text{inside}} / \text{PPFD}_{\text{outside}}$ in percent.

Data analysis

To increase sample size and to enhance the reliability of the statistic results, analyses were performed for data sets including all four study species simultaneously. Data were analysed with a multinomial logistic regression model and a forward selection procedure of variables using the statistical software SAS 9.1.3 (SAS Institute Inc. Cary, NC, USA, 2002 -2003). First, we calculated the transition probability of each initial population size class (ranging from 1 to 6) for the data set of 138 populations (Table 1) to reach another size class from 0 (extinct) to 7 (1.001-10.000 individuals) against the time between surveys. Subsequently, we analysed whether these probabilities were affected also by population isolation (model of data set I) (Table 2). To test for differences between the transition probabilities and for significant effects of the predicting variables, an Exact Likelihood Ratio Chi-Square Test was applied. In a second step, we omitted all extinct populations from the data set, resulting in 86 remaining populations. These served to analyse, apart from the influence of time between surveys and isolation, the impact of patch size and habitat type on the transition probabilities (model of data set II). In a last step, the model was extended to further independent environmental variables (Table 2), which were recorded in a sub-set of 45 populations (model of data set III).

Table 1 - Number of surveyed populations included into the multinomial logistic regression models of data sets I, II, and III for each of the studied species: *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Senecio paludosus*.

Species	Number of populations included in model of		
	Data set I	Data set II	Data set III
<i>Euphorbia palustris</i>	46	34	15
<i>Pseudolysimachion longifolium</i>	31	22	15
<i>Sanguisorba officinalis</i>	27	18	15
<i>Senecio paludosus</i>	34	12	-
Total number of populations	138	86	45

Finally, based on a Leslie matrix (Pielou 1977), a projection matrix was constructed to calculate the prospective development of sizes of all surveyed populations using the statistical program R. For this purpose, the proportion of each initial population size class was entered into the model and related to the calculated transition probabilities.

Predicting variables	Inclusion in model of		
	Data set I	Data set II	Data set III
<i>Time between surveys</i>	×	×	×
<i>Isolation</i>	×	×	×
<i>Patch size</i>		×	×
<i>Habitat type</i>		×	×
<i>Vegetation height [m]</i>			×
<i>Light availability [%]</i>			×
<i>Soil moisture</i>			×
<i>pH</i>			×
<i>carbon</i>			×
<i>nitrogen</i>			×
<i>C/N ratio</i>			×
<i>phosphorus</i>			×
<i>calcium</i>			×
<i>magnesium</i>			×
<i>potassium</i>			×

Table 2 - Explanatory variables included into the multinomial logistic regression models of data sets I, II, and III.

Results

Initial population size classes ranged from 1 (1 individual) to 6 (101-1.000 individuals), while populations at the point of the second survey varied in size between class 0 (extinct) and 7 (1.001-10.000 individuals). Overall, 55% of the current populations included in the data analysis were smaller than 100 flowering individuals, and 33% of the populations had become extinct. The proportion of surviving populations varied among the four species from 88% in *E. palustris* to only 47% in *S. paludosus* (Fig. 2). While 7% of the populations of *S. officinalis* diminished and 44% increased in size, 17% of those of *S. paludosus* decreased in size and only 3% became larger. The proportion of populations keeping their initial size class ranged from 48% in *E. palustris* to 15% in *S. officinalis*.

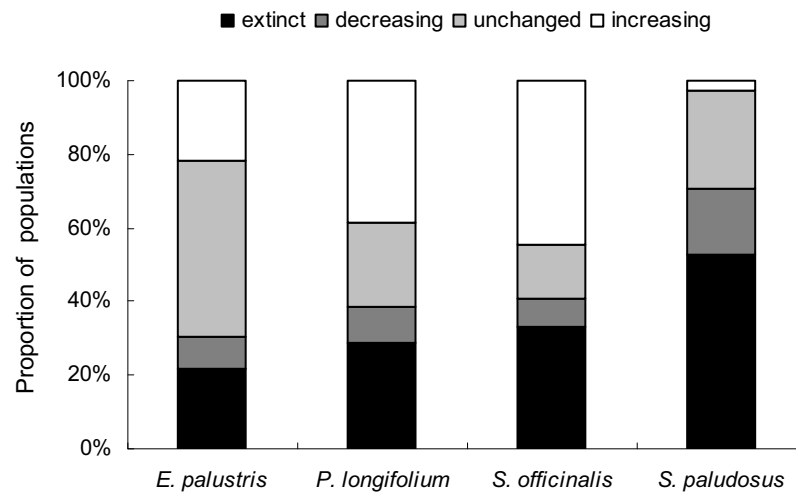


Fig. 2 - Changes in population size (over the course of on average 14.7 years) of all surveyed populations of the four study species *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Senecio paludosus*. The bars reflect the proportions of populations that went extinct, decreased in size, remained unchanged or increased in size.

Pooled over all species, the transition probabilities of reaching another size class varied considerably among the six studied size classes (Fig. 3, Table 3). Large populations (> 100 individuals) had a much higher probability of survival, of staying in their initial size class and of reaching size class 7 than small populations (≤ 25 individuals). Size classes 4 and 5 mostly showed non-significant results, possibly due to low sample sizes (for both $n = 11$). The time between surveys had no effect on the models, therefore the transition probabilities were applied for an average time between surveys of 14.7 years. Including further predictor variables (Table 2) did not or only marginally improve the model. In all three data sets, transition probabilities were not affected by population isolation. Patch size was found to have weak significantly positive effects on the transition probabilities only of the initial population size class 2 in the model of data set 2 ($\chi^2 = 4.26$, $df = 1$, $P = 0.039$). For data set 3, only transition probabilities of initial population size classes 1 and 4 were weakly positively affected by soil moisture ($\chi^2 = 4.25$, $df = 1$, $P = 0.039$; $\chi^2 = 3.99$, $df = 1$, $P = 0.046$).

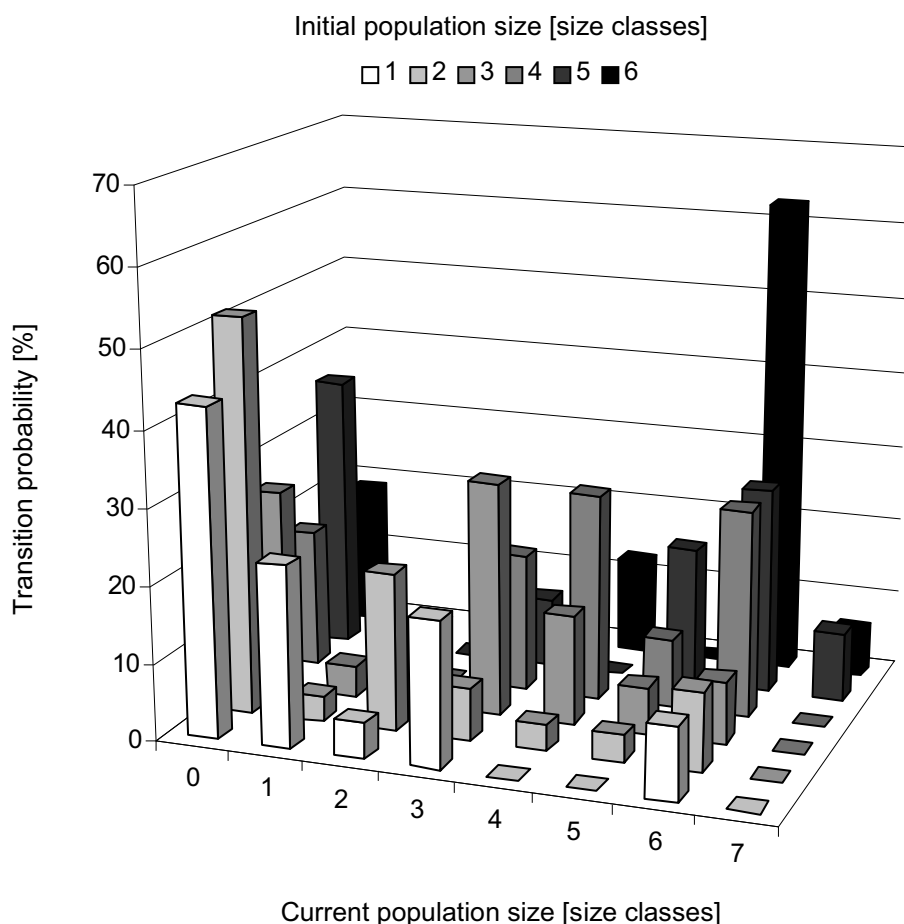


Fig. 3 - Transition probabilities of initial population size classes (1 to 6) to reach another size class from 0 (extinct) to 7 (1.001-10.000 individuals), calculated for populations of *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Senecio paludosus*. Transition probabilities were independent of the time between surveys. Mean time between surveys was 14.7 years.

Table 3 - Results of Exact Likelihood Ratio Chi-Square Tests for differences in the transition probabilities (shown in Fig. 4) within the six studied initial population size classes. P values are given, with significances bolded.

Size class	1	2	3	4	5	6
1	—	0.1539	0.0388	0.0155	0.0591	<0.001
2	—	—	0.0748	0.0516	0.1763	<0.001
3	—	—	—	0.4543	0.0468	<0.001
4	—	—	—	—	0.4998	0.1834
5	—	—	—	—	—	0.1332
6	—	—	—	—	—	—

The construction of a projection matrix for the average time between surveys of 14.7 years resulted in the extinction of 85% of the populations in all six initial size classes after eight time intervals (in about 117 years). 15% of the populations, however, developed into size class seven, but the matrix could not give any information on the fate of these populations because of the lack of populations with initial size class seven in the data set.

Discussion

Small populations of the four studied, endangered, perennial river corridor plants were more prone to become extinct than larger ones. Similar findings were also reported for seven short-lived, threatened plant species in a re-visitation study in northern Germany (Matthies et al. 2004). This result can be explained by various mechanisms. If population sizes are generally in a declining state, possibly due to habitat deterioration, small populations are more likely to become extinct (faster) than large ones (Thomas 1994). Moreover, initial population sizes may have been small because the populations in question occurred in already deteriorated habitats. These explanations, however, were not corroborated by our study because: (i) Mean initial population size was even lower than mean current size of surviving populations (data not shown), which contradicts a general decline in population size, (ii) deteriorated or deteriorating habitat quality cannot in all cases be the reason for small populations to decrease in size or become extinct, since some of them stayed in their initial size class or even developed into larger ones, and (iii) the measured habitat quality parameters had hardly any effect on changes in population size, indicating that habitat quality is no main underlying cause for the extinction process or for the negative growth of a population. Even though the studied river corridor plants possess similar life histories, their responses to environmental conditions may differ, which is why the effects of the measured habitat factors on changes of population size in a composite model of all studied species needs to be interpreted with caution. Still, the relative importance of soil quality on the reproductive success of the four studied species was shown to be much lower than the relative importance of population size (Winter et al. 2008).

A further explanation for the high extinction rates of small populations may be that populations that fall below a certain threshold number of individuals have entered a so-

called extinction vortex, which leads to extinction due to ever-decreasing plant fitness (Gilpin and Soulé 1986). As a consequence, one would expect a high proportion of small populations to decline, which, however, was not the case in our study in which we found only 7% of small populations to diminish, while 20% showed an increase. Moreover, the transition probabilities of reaching another population size class were not affected by the time between surveys. Our results therefore suggest that the increased extinction of small populations is due to short-term rather than long-term effects. More precisely, sudden environmental stochasticity induced by human activity, such as land reclamation, changes in land use, or the application of pesticides, are more important for the increased extinction of small populations than decreasing plant fitness and reduced reproduction. Nevertheless, habitat fragmentation may have considerable negative effects on population survival in the long-term, i.e., over a time span longer than the mean time between surveys of 14.7 years in this study. For example, Eriksson and Ehrlén (2001) demonstrated that fragmented populations of perennials face only a minimal extinction risk during 50 years and this is most likely due to their low population turnover. Accordingly, we did not find population isolation to have any impact on extinction rates and changes in population size, because the negative effects of isolation, for example limited pollinator services and reduced gene flow, will influence the viability of long-lived species only in the long term.

Even though our results show that populations above a threshold size of 100 individuals have a much higher chance of survival, to stay in their initial size class or to reach size class 7 (1.001 - 10.000 individuals), a projection matrix predicted that after 117 years almost all of the surveyed populations would have become extinct. The establishment of new populations is predicted to be very rare, since all the studied species are in a declining state within the study area (Garve 2004). Furthermore, only very few potential new habitats are likely to be colonized, because the change and destruction of the natural landscape by human impact in the study area progresses. The time span of 117 years, however, should be viewed with caution because our projection matrix gives no information about the fate of populations that developed into size class 7 populations. Our findings at least suggest that the studied river corridor plants will further decline in the future.

The variation among the four study species in terms of their proportions of extinct, decreasing, unchanged, and increasing population indicates that these differ in their responses to habitat fragmentation, deterioration, and destruction, possibly due to dif-

ferences in their specific life history traits. These findings are supported by a previous study which showed that the relative importance of population size, isolation, and soil quality for the reproduction of the species varied considerably (Winter et al. 2008). The populations of *E. palustris* had the lowest extinction rates, and a high proportion of them stayed in their initial size classes. However, in a previous study of the demography of this species we found that most populations were static and aged and therefore prone to extinction (Christina Wärner, data not published). Only its very long generation cycle, probably several decades, may enable its survival under sub-optimal environmental conditions for a relatively long time. Compared to the other species studied, *P. longifolium* and *S. officinalis* had relatively high proportions of populations that increased in abundance over time (38 - 44%). A likely explanation is their ability to grow also on pastures and meadows (Klotz et al. 2002), which are more frequent within the study area and provide larger habitat areas for population expansion than most of the habitats of the other species studied. *S. paludosus*, for example, is confined to wet habitat conditions (Ellenberg et al. 1991), and therefore mainly occurs in the vicinity of near-natural rivers and lakes. As these habitats today are even rarer than wet grasslands, fallows and ditch banks, *S. paludosus* may show the highest proportions of extinct (53%) and decreasing (18%) populations.

In summary, small population size was identified as the most probable cause for the high extinction rates of populations of perennial river corridor plants in this study. Small populations are mainly a result of habitat fragmentation caused by extensive river regulation and land reclamation, and this, in turn, can explain the high proportion of endangered river corridor plants. However, there was no evidence for long-term effects of habitat fragmentation on the survival of the species studied, even though a reduced reproductive success in small and / or isolated populations was found in a previous study (Winter et al. 2008), indicating an extinction debt. Contrary to the hypothesis that the drawbacks of small population size act slower in long-lived species (Vellend et al. 2006, Schleuning and Matthies 2009), the small populations of the species in this study were already affected after 15 years and this was most likely due to short-term effects as sudden environmental stochastic events caused by human activities.

Our results predict that river corridor plants are further on the decline in the study area. The restoration of rivers and the creation of retention areas as a result of increasing flooding events due to global warming might, however, provide new suitable habitat areas for these species. On the other hand a colonisation of restored flood plains areas is

unlikely because most species have already disappeared from the regional species pool. The breeding of progeny from seeds for the reintroduction and introduction of species may be therefore a suitable management measure, as recently shown for *E. palustris* (Christina Wärner, data not published). Nevertheless, habitats of extant small populations should be improved and enlarged for enhancing natural population growth and for reducing the risk of extinction.

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3.2

Auswirkungen von Habitatfragmentierung auf die Reproduktion gefährdeter Stromtalpflanzen



Oben: Samen von Euphorbia palustris, Lathyrus palustris, Pseudolysimachion longifolium, Sanguisorba officinalis und Senecio paludosus (von links nach rechts).

Unten links: Fruchtstände von Pseudolysimachion longifolium eingehüllt zum Auffangen reifer Samen am Ufer der Wümme im Einzugsgebiet der Weser.

Unten rechts: Sanguisorba officinalis am Ufer der Drepte, einem Nebenfluss der Weser.

(Fotos: Christina Wärner)

Determinants of reproductive success: A comparative study of five endangered river corridor plants in fragmented habitats

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Abstract

River corridor plants in Central Europe have in recent decades become increasingly rare, caused mainly by habitat destruction and change. The aim of this study was to examine the impact of soil quality, but especially of habitat fragmentation in terms of population size and isolation, on seed production and germination of five selected species, all of which being endangered, perennial herbs: *Euphorbia palustris*, *Lathyrus palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis*, and *Senecio paludosus*. We sampled totally 58 populations in flood plains in the surroundings of Bremen, North-western Germany.

In all five species, there were positive correlations between the number of seeds (total seed mass) and plant height, as well as between germination and seed mass. Seed traits values and / or germination were negatively affected by small population size, in *Euphorbia*, *Lathyrus* and *Pseudolysimachion* additionally by high population isolation. There were also significant effects of soil quality, but these were less consistent across species. The contribution of population size and isolation, compared to soil quality, to the variance explained in the reproductive components was especially high in *Euphorbia* and *Lathyrus*, the only two species depending on insect pollination.

The results indicate that the five species are likely to decline as a consequence of decreased plant fitness in small and / or isolated populations, probably caused by pollen limitation. The studied species may be representative for the group of river corridor plants as a whole that are often restricted to isolated remnants of near-natural flood plain vegetation in a matrix of heavily used agricultural land.

Keywords: Germination, Number of seeds, Population isolation, Population size, Seed predation, Soil quality

Introduction

River corridors are rich in species, but also represent one of the habitat types that are most heavily affected by man. In Central Europe, or parts of it, several plant species are exclusively or predominantly confined to the basins of large rivers: the so-called river corridor plants. As the natural habitats along the rivers have been destroyed and degraded by the regulation of watercourses, land reclamation and agricultural intensification, many of these species have become rare and are now endangered in most parts of Central Europe (e.g., Zacharias and Garve 1996, Schnittler and Günther 1999).

River corridor plants form a group that is defined by its particular distribution pattern, but include species with much different habitat preferences (Korsch 1999). To date, the mechanisms generating this distribution pattern are not well known, although observational studies indicate that the ability of water dispersal plays a crucial role. Another factor of importance is the specific environment of river corridors, characterized by regular flooding, repeated disturbance events, relatively high summer temperatures and nutrient-rich alluvial soils (Burkart 2001). Nowadays, however, most populations of river corridor plants are completely cut off from the dynamics of the river due to drainage and the construction of dikes. While the negative effects of habitat deterioration and habitat loss on river corridor plants are obvious, the impact of habitat fragmentation, generally considered to be one of the most important threats to population viability (Eriksson and Ehrlén 2001, Oostermeijer 2003), is less clear.

Habitat fragmentation is often associated with a decline in population size and increased isolation, affecting plant fitness and population viability (Lienert, 2004). Small populations may be more sensitive to the effects of environmental, demographic and genetic stochasticity than large ones (Shaffer 1987, Kéry et al. 2003), and are therefore expected to face a higher risk of extinction (Matthies et al. 2004). Furthermore, small and isolated populations may suffer from increased inbreeding and loss of genetic variation due to genetic drift (e.g., Ellstrand and Elam 1993, Young et al. 1996). Decreasing plant fitness may eventually lead to a decline in population size and, eventually, to extinction (Gilpin and Soulé 1986; Lamont et al. 1993).

The fitness of plants in small and isolated populations may be reduced also because of the disruption of biotic interactions with pollinators and seed dispersers (Kearns et al. 1998). Small populations are often less attractive to pollinators than larger ones, which may result in pollen limitation and reduced seed set (Jennersten 1988, Ågren 1996,

Kwak et al. 1998, Tomimatsu and Ohara 2002, Waites and Ågren 2004, Kolb 2005). A low inter-population gene flow via pollen or seeds may also contribute to a genetic deterioration of populations. It is important to note that plant fitness is also strongly affected by habitat quality, which has only rarely been addressed in studies on the effects of habitat fragmentation on plant populations (Lamont et al. 1993, Fischer and Matthies 1998a, Oostermeijer et al. 1998, Vergeer et al. 2003, Kolb 2005, Kolb and Lindhorst 2006).

To protect endangered species it is important to assess the relative importance of different factors for population viability. It is a reasonable assumption that species with different life history traits do not respond to the above-described factors in a uniform way. A recent meta-analysis shows that self-incompatible and rare species are comparatively strongly affected by small population size (Leimu et al. 2006). Here we aim to examine whether the effects of habitat fragmentation can be similarly observed in five river corridor plants showing similar life history attributes, habitats and distribution patterns. River floodplains in north-western Germany offered a suitable study area, as they are exposed to a strong decrease in near-natural habitats and deterioration of habitat quality.

More specifically, we aimed to answer the following questions: (i) Are reproductive success and seed germination reduced in small and / or isolated populations of the studied river corridor plant species? (ii) Compared to the above effects of population size and isolation, what is the importance of habitat quality for the reproductive components of the species? (iii) Are the above effects consistent across species? (iv) Finally, which conclusions can be drawn for the conservation of endangered river corridor plants?

Methods

Study area and species

Fieldwork was carried out in 2005 in floodplains of the Weser and Elbe river systems in North-western Germany. In this area, 85 plant species are classified as river corridor plants (Zacharias and Garve 1996), 54% of which are included in the red list of endangered plant species (Garve 2004). The selection of species was based on the following reasoning: to be included in the study, the species had to occur in the Weser-Elbe region, being present at a minimum number of sites (8 sites) and showing a relatively

large range in population size and isolation (Table 1). We also aimed to select species that are fairly similar in some of their basic life-history traits, in order to examine whether they respond to habitat fragmentation and quality in similar ways. Five species were finally used for this study: *Euphorbia palustris* L. (Euphorbiaceae), *Lathyrus palustris* L. (Fabaceae), *Pseudolysimachion longifolium* (L.) Opiz (Scrophulariaceae), *Sanguisorba officinalis* L. (Rosaceae), and *Senecio paludosus* L. (Asteraceae). All species are perennial herbs that mainly reproduce sexually via seeds, but also form short rhizomes (Klotz et al. 2002). They are either insect-pollinated (*Euphorbia*, *Lathyrus*) or insect-pollinated and self-pollinating (*Pseudolysimachion*, *Sanguisorba*, and *Senecio*). The only species with self-incompatibility is *Euphorbia*. Dispersal modes vary, but considering the species' distribution along river corridors it is likely that seeds of all species at least occasionally may also be dispersed by water. All species are typical indicators for moist to wet soil conditions. Natural habitats in the study area include nutrient-rich lake and river shores, while wet grasslands represent a semi-natural environment. Nowadays, however, the species are largely restricted to abandoned grasslands and ditch banks from which almost all populations were sampled. Up to now, nothing has been known about the effects of population size and isolation on these five species.

Population size and isolation

Based on records of the inventory programme of endangered plants in North-western Germany, we sampled 8-14 populations of each species. For *Euphorbia*, *Lathyrus* and *Senecio*, the material comprised basically all populations in the study area, except those that were not found, could not be reached or occurred in heavily disturbed sites. For *Pseudolysimachion* and *Sanguisorba*, we selected populations to represent as much as variation in population size and isolation as possible. Groups of plants separated by distances of more than 50 m were considered as different populations. Population size was determined as the number of flowering plants during peak flowering. In *Euphorbia* and *Senecio*, individuals were clearly separated from each other, while in the other three species individuals in terms of genets were difficult to identify because the shoots form dense clusters that are impossible to disentangle. Here, each shoot was treated as one individual. Population size was determined either by counting all individuals (in small populations), or by extrapolation based on counts in subsets of the population (in large populations). The degree of population isolation was defined as the distance to the next

population. Apart from determining population size and isolation, we recorded the cover and height of the surrounding vegetation to assess the importance of the abundance of competitors on the reproduction of the studied species.

Table 1 – Number, size (of flowering and all individuals) and isolation of populations of the five studied species *Euphorbia palustris*, *Lathyrus palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Senecio paludosus*. Median values as well as minima and maxima (in parenthesis) are given. Population size refers to the no. of plants (in *Euphorbia* and *Senecio*) or to the number of shoots (in *Lathyrus*, *Pseudolysimachion* and *Sanguisorba*). Isolation is defined as the distance to the nearest population.

Species	No.	Size (flowering)	Population	
			Size (total)	Isolation [m]
<i>Euphorbia palustris</i>	12	31 (3 - 2 128)	38 (7 - 2 841)	2 125 (200 - 62 500)
<i>Lathyrus palustris</i>	8	36 (11 - 753)	101 (22 - 6 320)	100 (50 - 750)
<i>Pseudolys. longifolium</i>	14	58 (14 - 552)	101 (14 - 1 345)	528 (50 - 1 900)
<i>Sanguisorba officinalis</i>	12	104 (29 - 1 074)	Not known	825 (100 - 4 500)
<i>Senecio paludosus</i>	12	13 (1 - 2 089)	13 (1 - 2 089)	300 (50 - 25 500)

Plant traits

In each population we randomly selected and marked 20 (in smaller populations all) flowering individuals. Between May and August 2005 during peak flowering of the species, we recorded a number of reproductive parameters assumed to reflect the fitness of plants. At the time of seed maturity, the number of fruits was counted (except in *Pseudolysimachion*), and randomly selected fruits were collected from each plant. In *Lathyrus* that produces a very low number of seeds, we collected all fruits of the individuals. The number of fruits sampled from each individual differed between species: ≥ 20 in *Euphorbia*, two in *Sanguisorba*, three in *Senecio* and four in *Pseudolysimachion*. In the latter species it was difficult to obtain mature seeds, because these were still unripe when the fruits started to open. We therefore enclosed one inflorescence of each individual with a special fleece before seed maturity.

Fruits and seeds were air-dried and stored in paper bags at room temperature. For each individual, we determined the total number of seeds per fruit and mean seed mass of 40 randomly selected seeds per plant. In *Senecio*, the pappus of the seed was removed prior to weighing. The number of seeds per plant was calculated by multiplying the number of fruits per plant by the number of seeds per fruit, total seed mass by mul-

tiplying the number of seeds per plant by mean seed mass. Many seeds of *Lathyrus* showed signs of predation by insects. The major seed predator was the beetle *Bruchus atomarius*, the presence of which is recognised by a hole in the seed coat. The level of pre-dispersal seed predation of a population was determined as the proportion of seeds damaged by insects.

Soils

Soil samples were collected in all populations during a rainless period in late August and early September. Each sample consisted of seven pooled soil cores (100 cm³ down to a depth of 4 cm) taken from below the litter layer. Soil moisture was measured gravimetrically. Prior to chemical analysis, all air-dried samples were passed through a 2 mm-sieve. We determined pH in a solution of 10 g of soil and 25 ml of 0.01M CaCl₂ with a standard glass electrode. Plant available phosphorus (P) was extracted with ammonium lactate and measured photometrically by flow injection analysis (expressed in mg per 100 g soil). Calcium (Ca), magnesium (Mg) and potassium (K) were also extracted with ammonium lactate and their concentrations measured by Atomic Absorption Spectroscopy. The contents of carbon (C) and nitrogen (N) were determined using an elemental analyzer (EuroEA 3000, HEKA-tech, Germany).

Germination trials

In autumn and winter 2005, 40 ripe seeds (or all seeds if $n < 40$) were randomly selected from each sampled individual for the germination experiment and weighed. In four species (*Euphorbia*, *Lathyrus*, *Sanguisorba*, *Senecio*), pre-treatment of the seeds was required to break dormancy. In *Lathyrus*, peak germination does not occur until three to four years after natural seed shedding, most likely because the seed coat is largely impermeable for water (Hölzel and Otte 2004). To allow moisture penetration, the seed coat was scratched with sandpaper. In the other species the seeds were stratified for eight weeks at 4 °C. All seeds were placed on a double layer of wet filter paper in petri dishes and kept in a growth chamber at a temperature and light regime of 14 h day / 25 °C and 10 h night / 20 °C. We then daily counted the number of germinated seeds (those with an emerged radicle) until no further germination occurred (2-8 weeks after the start of the experiment, depending on the species). The germination rate was calculated for the period (spanning 2-8 days) when the increase in germination was highest

(in all species within the first 14 days after the start of the experiment) and expressed as the slope of the regression of the no. of germinated seeds *vs* time. Total germination was defined as the proportion of the no. of germinated seeds to all seeds used.

Data analysis

To examine whether the reproductive fitness components were affected by population size, population isolation and measures of habitat quality, when simultaneously accounting for varying soil conditions and plant size, stepwise multiple regression with a backward elimination of variables (threshold for exclusion of variables $P = 0.05$) was applied (a forward selection of variables gave the same results). In all species, the values of several soil factors were highly inter-correlated, especially N and C, but also pH and the cations Ca, K and Mg. To avoid multicollinearity and to reduce the number of variables in the multiple regressions, we used only a subset of the soil variables (Table 3). The factors height and cover of the surrounding vegetation were not found to have any effect on seed traits and germination, and therefore not entered into the analysis. The total number of seeds and total seed mass were in all species significantly (or marginally so) positively correlated with plant size, and the same was found to be true for the relation between germination rate / total germination and seed mass. We therefore used the regression residuals of the above relationships as independent variables in the multiple regressions. Plant size refers to plant height (*Euphorbia*, *Sanguisorba*), or to the number of leaves in *Lathyrus*, the mean height of inflorescences in *Pseudolysimachion* and the number of shoots in *Senecio*.

To determine the relative importance of population size & isolation *vs* soil variables for determining reproductive success, partial regression analysis was used (Legendre and Legendre 1998). The single contribution of population size & isolation for a given species and reproductive factor is given by its partial R^2 , computed as the difference between the R^2 of the full (multiple regression) model including all variables and the R^2 of a reduced model containing only the soil variables. Likewise, the variation explained exclusively by the soil variables is calculated by the difference between the R^2 of the full model and the R^2 of the model containing only population size & isolation.

To graphically display the relationship between the number of seeds / total germination and population size, simple linear regressions were applied. For all regression analyses, we log-transformed some of the variables to meet the requirements of normal

data distribution. Population means were used for all statistical analyses, which were carried out in SPSS 15.0 (SPSS, Chicago, USA).

Results

Population sizes varied strongly in all species, the smallest populations having less than ten (in *Senecio* only one) flowering individuals, the largest consisting of more than 500 to 1000 plants. Population isolation differed considerably, ranging from a minimum of 50 to 200 m to a maximum of about 750 m to several km. Population size and isolation were unrelated to each other in all species ($P > 0.1$). The two variables were also unrelated to the soil variables used in the regression analyses.

Seed production and seed mass also varied strongly, both between species and between populations within species (Table 2). Whereas *Lathyrus* showed a low number of seeds per plant (mean 3.1) and some populations almost completely failed to produce any seeds, *Senecio* on average formed more than 100 000 seeds per individual. *Euphorbia* and *Lathyrus* had a relatively high mean seed mass (9.68 and 15.6 mg, respectively), while *Pseudolysimachion* formed tiny seeds of < 0.1 mg. Total germination was equal to or higher than 50% in all species except *Senecio* with only about 19%. The population differences within species were least pronounced in mean seed mass and particularly strong in the number of seeds per plant (capsule).

In *Lathyrus*, total germination was negatively correlated with the proportion of damaged seeds. The level of seed predation tended to increase with increasing population size ($R^2_{adj} = 0.186$, $P = 0.183$, $n = 7$).

Effects of population size and isolation on reproductive success and germination

In all five species, there were effects of either population size and / or population isolation on at least one of the reproductive parameters (Table 3). In all cases except one in which the parameters remained significant in the final models, their effects were consistent, positive for population size and negative for isolation.

Population size was positively related to the number of seeds in *Euphorbia* and *Sanguisorba*, and to the number of seeds per capsule in *Pseudolysimachion*. Congruent results were obtained in the simple linear regressions (Fig. 1). It showed no impact on mean seed mass in the above species, but had a negative effect in *Lathyrus*. In three of

the four species where total seed mass could be estimated, this variable was positively correlated with population size. Positive effects were also observed for total germination in *Senecio* and *Pseudolysimachion* (marginally significant in the simple linear regressions; Fig. 2).

Table 2 – Descriptive statistics of basic reproductive parameters in the five studied species, including the number of seeds per plant (per capsule in *Pseudolysimachion longifolium*), mean seed mass, total seed mass per plant and total germination. Population means, minima and maxima (in parenthesis) are shown.

Species	No. of seeds per plant (capsule)	Mean seed mass [mg]	Total seed mass [mg]	Total germination [%]
<i>Euphorbia</i>	812 (160 - 3 259)	9.68 (5.56 - 13.43)	8 245 (3 197 - 29 653)	78.3 (20.0 - 98.1)
<i>Lathyrus</i>	3.1 (0.1-13.3)	15.6 (12.1 - 21.6)	46.2 (3.1 - 159.8)	71.2 (36.6 - 100)
<i>Pseudolysimachion</i>	9.3 (1.4 - 23.9)	0.06 (0.03 - 0.11)	(not known)	84.9 (51.7 - 99.5)
<i>Sanguisorba</i>	962 (215 - 1 437)	1.83 (0.35 - 2.61)	1.804 (182 - 3 748)	49.3 (3.26 - 83.1)
<i>Senecio</i>	102 953 (9 507 - 691 086)	0.78 (0.60 - 0.90)	122 014 (8 366 - 572 101)	18.5 (0 - 35.6)

The effects of population isolation on the reproductive parameters were generally weaker. Increasing distance to the nearest population was associated with a decrease in the number of seeds per plant in *Lathyrus*. Both mean and total seed mass were unaffected by population isolation. Negative effects on germination rate and total germination were found for *Euphorbia* and on total germination only in *Sanguisorba*.

Effects of soil quality on reproductive fitness parameters

The effects of the edaphic variables on the reproductive parameters were, compared to population size and isolation, somewhat less pronounced. In *Lathyrus*, soil N (highly positively correlated with water content and the concentrations of C and K) had a negative effect on the number of seeds per plant, total seed mass and total germination, but a positive effect on mean seed mass (Table 3). In *Senecio*, N (also reflecting C and water content) had a positive impact on the number of seeds per plant and germination rate in *Senecio*.

Table 3 – Multiple linear regressions (stepwise backward method) of reproductive fitness components on a set of predictive variables (population size, population isolation, variables related to soil quality, in *Lathyrus palustris* also the proportion of damaged seeds) in the five studied species. The values for the total number of seeds, mean seed mass and total seed mass were corrected for plant size, those for germination rate and total germination were corrected for mean seed mass (see methods). Adjusted R^2 values of the final model and standardized regression coefficients (β -values; the signs denote the direction of the relationships) of significant variables are given. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. A “/” indicates that the parameter in question was not used or measured for the species, while empty cells mean that the predictive variable was not significant for the fitness parameter in question.

	<i>Euphorbia</i>	<i>Lathyrus</i>	<i>Pseudolys.</i>	<i>Sanguiso.</i>	<i>Senecio</i>
No. of seeds per plant (in <i>Pseudolysimachion</i> per capsule)					
R^2_{adj} of model	0.476**	0.802**	0.366*	0.534*	0.459**
Population size	0.724**		0.647*	0.902**	
Population isolation		-1.606**			
Soil N		-2.002**			0.713**
Soil C/N ratio				-0.910**	
Mean seed mass					
R^2_{adj} of model	0.000	0.762*	0.000	0.000	0.000
Population size		-0.784*			
Soil N		0.605*			
Total seed mass					
R^2_{adj} of model	0.433*	0.954***	/	0.491*	0.405*
Population size	0.699*	0.798**	/	0.811*	
Soil N		-0.705**	/		
Soil C/N ratio			/	-0.931**	
Soil P			/		-0.678*
Germination rate					
R^2_{adj} of model	0.698**	0.000	0.000	0.000	0.714**
Population isolation	-0.922**				
Soil N					0.447*
Soil Ca	-0.563*				-0.779**
Total germination					
R^2_{adj} of model	0.540**	0.809*	0.407*	0.913***	0.296*
Population size			0.676*		0.600*
Population isolation	-0.769**			-0.603**	
Soil N		-0.568*		0.400**	
Soil P				-0.353*	
Soil Ca				-0.402**	
Proportion of damaged seeds	/	-0.632*	/	/	/

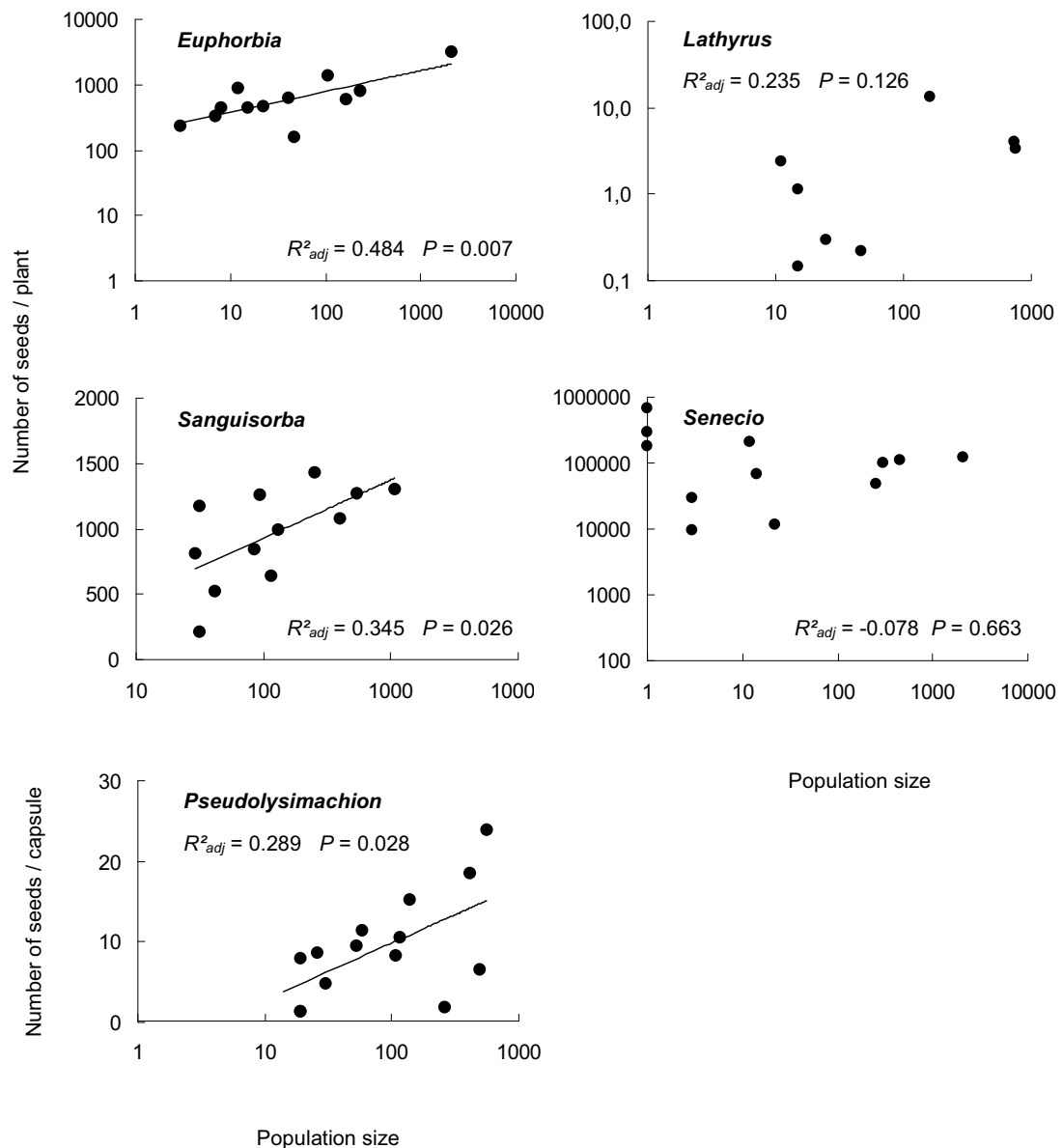


Fig. 1 – Relationship between seed production and population size (number of flowering individuals) in the five studied species. For *Euphorbia palustris*, *Lathyrus palustris*, *Sanguisorba officinalis* and *Senecio paludosus*, the number of seeds per plant is given, for *Pseudolysimachion longifolium* the number of seeds per capsule. Adjusted R^2 values and P values are given. All $n = 12$ except for *Lathyrus* ($n = 8$) and *Pseudolysimachion* ($n = 14$). Depending on the species, one or both axes are log-transformed.

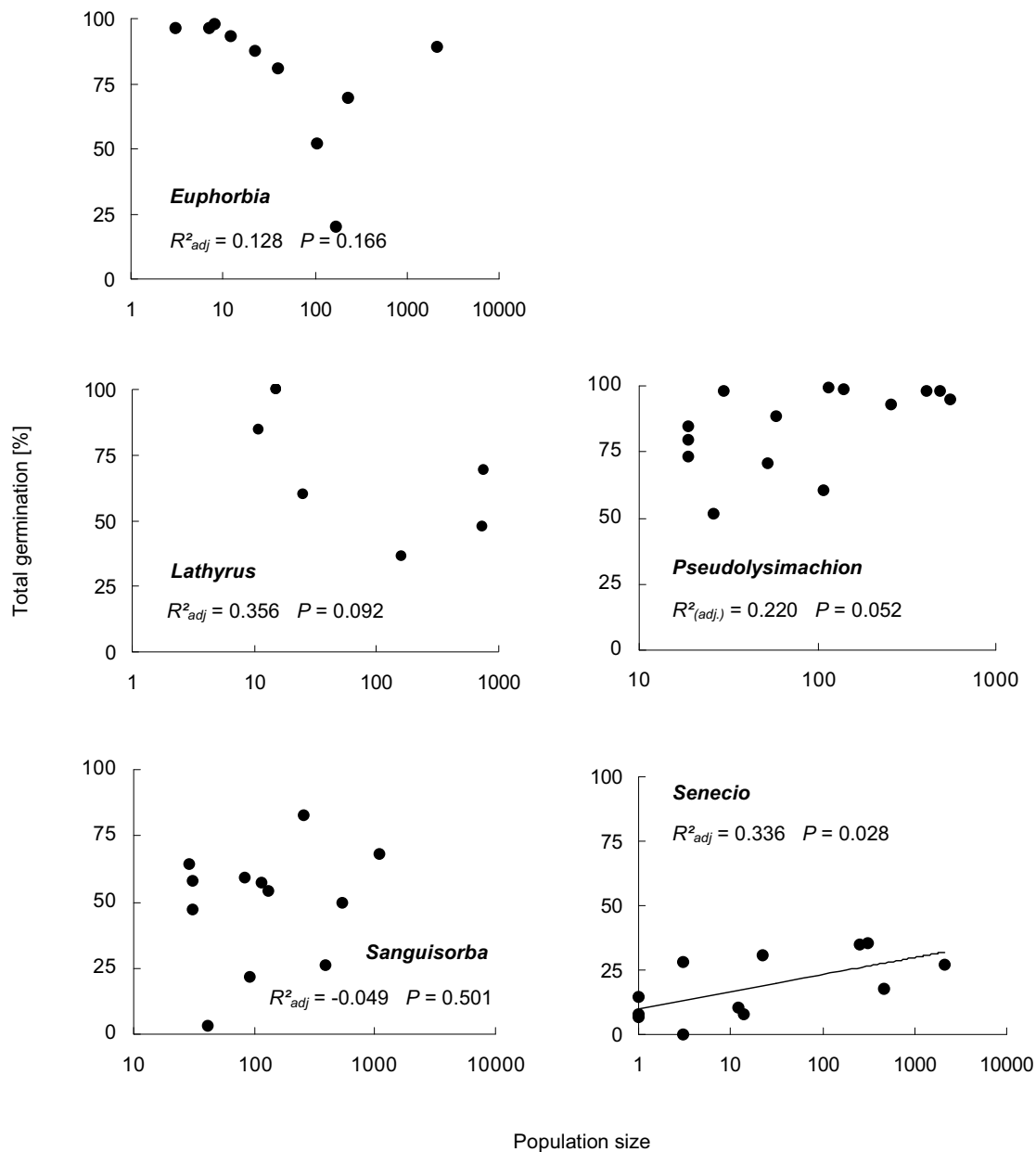


Fig. 2 – Relationship between total germination (proportion of germinated seeds) and population size (number of flowering individuals, axis log-transformed) in *Euphorbia palustris* ($n = 10$), *Lathyrus palustris* ($n = 7$), *Pseudolysimachion longifolium* ($n = 14$), *Sanguisorba officinalis* ($n = 12$) and *Senecio paludosus* ($n = 12$). Adjusted R^2 values and P values are given.

Soil P remained only twice in the final models: it was negatively related to total seed mass in *Senecio* and to total germination in *Sanguisorba*. The soil C/N ratio showed negative effects on the number of seeds per plant and total seed mass in *Sanguisorba*. Finally, soil Ca (in all species highly correlated with K and Mg) was found to be sig-

nificant for either germination rate or total germination in *Euphorbia*, *Sanguisorba* and *Senecio*.

The contributions of population size and isolation vs soil quality for the variation explained in the reproductive components were largely consistent with the above results (Table 4). In *Euphorbia*, population size and isolation explained more of the variation in seed production and similar amounts of variation in germination compared to the soil variables. Also in *Lathyrus*, population size and isolation contributed generally more to reproductive success. In contrast, the soil variables were found to be more important in the other three species, especially in *Sanguisorba* and *Senecio*.

Discussion

We found negative effects of small population size on reproductive variables in all species, supporting the results of studies on various other plant species (e.g., Fischer and Matthies 1998a, Kéry et al. 2000, Luijten et al. 2000, Jacquemyn et al. 2002, Vergeer et al. 2003, Brys et al. 2004, Kolb 2005). Negative effects of large isolation were found in some of the species (*Euphorbia*, *Lathyrus* and *Sanguisorba*), again consistent with the literature (Steffan-Dewenter and Tschamntke 1999). Soil factors also contributed to the variation in reproductive components, but in a less consistent way compared to population size and isolation.

The reduced reproductive success of plants in small and / or isolated populations is most likely due to pollen limitation (Ågren 1996, Colling et al. 2004, Aguilar et al. 2006), possibly also to genetic deterioration (Fischer and Matthies 1998b, Lienert et al. 2002, Luijten et al. 2002, Vergeer et al. 2003). Plants in small populations are often less attractive to pollinators and thus have lower visitation frequencies, resulting in pollen limitation and reduced seed set (Sih and Baltus 1987, Jennersten 1988). This may be an explanation for the positive relationship between population size and the number of seeds / total seed mass found in four of the five species. Furthermore, spatial isolation of populations may reduce pollinator services as the different patches may be out of the foraging range of pollinators (Kearns et al. 1998). As self-incompatibility can lower seed production in small populations due to the absence of compatible mates, species with such a breeding system are most prone to the negative effects of habitat fragmentation, as recently shown by Aguilar et al. (2006). Accordingly, in the self-incompatible

Table 4 – Results of partial regression analyses showing the amount of variation (R^2) that can be attributed exclusively to the variable groups (1) population size and isolation, and (2) soil variables. Full models for the respective variable groups were used, i.e. not only the significant variables obtained in Table 3. The R^2 of the variable group explaining more of the variation in a given reproductive component is bolded. “/” indicates that the parameter in question was not used or measured for the species.

Species	Determinant	No. of seeds per plant		Mean seed mass [mg]		Total seed mass [mg]		Germination rate		Total germination [%]	
		Population size & isolation	Soil variables	Population size & isolation	Soil variables	Population size & isolation	Soil variables	Population size & isolation	Soil variables	Population size & isolation	Soil variables
<i>Euphorbia</i>		0.283	0.064	0.258	0.377	0.364	0	0.293	0.370	0.294	0.219
<i>Lathyrus</i>		0.103	0.233	0.266	0.146	0.125	0.034	0.280	0.216	0.297	0.098
<i>Pseudolysimachion</i>		0.341	0.256	0.159	0.818	/	/	0.058	0.109	0.161	0.318
<i>Sanguisorba</i>		0.307	0.603	0.203	0.733	0.401	0.733	0.229	0.625	0.228	0.381
<i>Senecio</i>		0.058	0.382	0.087	0.068	0.101	0.425	0.055	0.725	0.208	0.129

Euphorbia, the impact of population size and isolation on seed production variables was stronger than in the four other species.

In *Lathyrus*, pre-dispersal seed predation tended to increase with increasing population size, which may partly counterbalance the negative effect of small population size on seed production. The absence of the seed predator *Bruchus atomarius* from small populations may result from the unattractiveness of small patches of *Lathyrus* for the insect. This result suggests that habitat fragmentation may not only disrupt mutualistic but also antagonistic interactions, such as between plants and their seed predators. For *Scorzonera humilis* it was shown that not only seed production increased with increasing population size, but also the levels of seed predation and infestation by a pathogenic fungus, which compensated the negative effects of declining population size (Colling and Matthies 2004). Similar effects of habitat fragmentation on antagonistic interactions and reproduction were also reported for *Gerbera aurantiaca* (Johnson et al. 2004) and *Lathyrus vernus* (Östergård and Ehrlén 2005).

We used seed mass and germination as measures for offspring fitness, which may be influenced by maternal and / or genetic effects. Environmental stress on maternal plants may be carried over to the progeny, especially in the first stages of their development (Roach and Wulff 1987). Furthermore, plant fitness in small populations may be reduced due to the loss of genetic variation or inbreeding depression (e.g., Fischer and Matthies 1998b, Lienert et al. 2002). Only in *Lathyrus*, however, seed mass parameters were affected by variables related to habitat fragmentation: mean seed mass was significantly higher in small populations than in large populations, while total seed mass increased with population size, a pattern similar to those reported by Kéry et al. (2000) and Jacquemyn et al. (2002). These findings indicate that a reduction in seed number may result in greater resource availability per seed and, hence, in larger seed size, because seeds compete for maternal resources (Matthies 1990, Venable 1992, Oostermeijer et al. 1995). If, however, enough resources are available to the plants in large populations to allocate energy to the seeds also when many seeds are produced, average seed mass is not reduced, while total seed mass increases, such as in *Euphorbia*, *Lathyrus* and *Sanguisorba*. In all studied species, seed mass strongly affected germination, and except in *Pseudolysimachion*, germination was also related to measures of soil quality; both results suggest large maternal carry-over effects.

Although seeds of *Lathyrus* damaged by seed predation were rejected prior to the germination trials, the level of seed predation had a strong negative effect on total germination. A likely explanation is that at least some affected seeds had no external signs of damage by predation and were therefore included in the experiment. If the proportion of these seeds is in turn correlated with the level of seed predation, increased seed predation would indeed result in reduced total germination. Accordingly, Honek and Martinkova (2005) found a negative relationship between total germination and the level of seed damage by larvae in *Taraxacum officinale*.

Germination was negatively affected by increased isolation in *Euphorbia* and *Sanguisorba*, indicating inbreeding depression due to deficient gene flow (e.g., via pollen or seeds between populations). Unfortunately, we do not possess sufficient historical data on the population sizes and structures to assess whether the populations have been small and/or isolated long enough to experience genetic deterioration in spite of their long generation cycle.

Reduced total seed mass in small populations, as observed in *Euphorbia*, *Lathyrus* and *Sanguisorba*, may lead to negative population growth rates in the short term, and

eventually to the extinction of populations in the long term. Venable (1992), however, showed that a low seed production may be compensated by an increased offspring fitness. In our study, such a pattern may only apply to *Lathyrus*, where seeds of small populations were heavier and their total germination was higher.

In addition to the consequences of population size and population isolation the reproductive success of plant populations may also be affected by environmental conditions (e.g., Vergeer et al. 2003). The results of this study suggest that soil quality has a species-specific impact on seed traits and germination. In *Senecio*, soil N, C and moisture (highly positively inter-correlated) had positive effects on seed production and germination rate, which is consistent with the species' ecological preference for very wet sites (Ellenberg indicator value for moisture: 9). In *Lathyrus*, seed production and total germination were negatively related to the complex-gradient of soil N, C, Ca, K and water content, again consistent with the ecological optimum of the species at low-fertility sites (Ellenberg N values of 3). The significant relations between reproductive parameters and soil variables found in *Sanguisorba* are difficult to interpret.

Conclusions

Pollen limitation was identified as a key process for the decline in reproductive success in small and / or isolated populations of the five studied species. This reduced reproduction may eventually lower also the viability of the populations since the long-term persistence of these river corridor plants depends on sexual reproduction.

If our study species are representative for many more river corridor plants, decreasing population size and increasing isolation may be major threats to this group of species as a whole and one reason for the high proportion of threatened species in this group. However, these effects are not uniform among species, but, as our results suggest, may depend on the species' life history traits, for example their mating system. Finding general response patterns of plants to habitat fragmentation on the basis of their traits should be subject to future research as it might give valuable insights for a successful conservation and management of habitats and species.

Increasing population sizes and improving connectivity between populations should be included in a conservation plan for river corridor plants. Unfortunately, most of the studied populations are situated in the agricultural landscape along drainage ditches or

in abandoned grasslands outside nature reserves, occupying relatively small areas. The matrix between these areas usually is fairly hostile or unsuitable for the species in question. In addition, long-distance dispersal of seeds is hampered as it depends on water transport (seeds of *Senecio* are also dispersed by wind), while most populations are no longer connected to a river. A further problem is the abandonment of land use, resulting in a closure of the vegetation and an increased thickness of the litter layer. Both processes reduce the number of microsites for seedling establishment which might explain why, in most populations, no recruitment was observed (data not shown). The conservation management of river corridor plants should aim at restoring suitable habitats for the species, but also at re-introducing the species into restored flood plains, for example by means of the transplantation of mature plants or the transfer of seed material to ecologically intact and suitable habitats.

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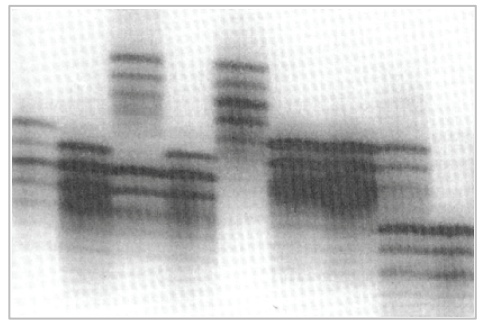
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3.3

Variierende Einflüsse auf die Reproduktion der Stromtalart *Euphorbia palustris* in fragmentierten Populationen



Oben links: Fruchtstand von Euphorbia palustris (Foto: Christina Wärner).

Oben rechts: Variation von Mikrosatelliten bei einem Wombat (Bild verändert nach Allendorf FW, Luikart G (2008) Conservation and the genetics of populations. Blackwell, Malden).

Unten links: Keimungsexperiment. Petrischalen mit Samen von Euphorbia palustris in einem Klimaschrank (Foto: Christina Wärner).

Unten rechts: Massenbestand von Euphorbia palustris auf einer Grünlandbrache mit Grabenstruktur in der Nähe des Elbeufers im Landkreis Harburg (Foto: Christina Wärner).

**Weather conditions determine the inter-annual variation
in the relationships between reproductive success, population size,
genetic variation and habitat quality in *Euphorbia palustris* L.**

Christina Wärner, Walter Durka, Martin Diekmann

(Submitted)

Abstract

We studied the reproductive success of 12 German populations of the rare perennial *Euphorbia palustris* in relation to population size, genetic variation and habitat quality over three years (2005-2007). The aim of the study was to examine the inter-annual variation in the relationships between these parameters and to analyze whether these could be attributed to differences in weather conditions (temperature, sunshine duration, precipitation).

The number of alleles, but not allelic richness, was positively correlated with population size, and allelic richness decreased with increasing scores of the first axis of a PCA, reflecting a gradient in soil conditions, especially moisture, N and C contents. The number of seeds differed significantly between years (2005 > 2006 > 2007). In some, but not all years, seed production was reduced in small and genetically less diverse populations and was negatively related to PCA axis 1. Mean seed mass and germination were not or only weakly affected by the explanatory variables studied. The differences in seed production across sites between years were strongly affected by soil quality, but not by population size or allelic richness.

Our results suggest that weather conditions that differ strongly from the long-term mean, particularly in terms of excessive or relatively low precipitation, alter the order of significance of predictors for reproductive fitness of *E. palustris*. Hence, when weather conditions are favourable, population size has a significant positive impact on seed production, probably due to pollen limitation in small populations, while genetic variation and soil quality do not play a significant role. The two latter variables, in contrast, gain importance for reproductive success when weather conditions are unfavourable. In con-

clusion, studies on the impact of habitat fragmentation on the fitness of plant populations should preferably be based on surveys conducted over several consecutive years.

Keywords: Germination, Habitat fragmentation, Seed mass, Seed production, Soil quality

Introduction

Habitat fragmentation, frequently creating small and isolated populations, is considered to be one of the greatest threats to plant population viability (Eriksson and Ehrlén 2001, Oostermeijer 2003), and many studies have examined the relationships between population size, genetic variation and reproductive success (e.g., Fischer and Matthies 1998, Luitjen et al. 2000, Vergeer et al. 2003). The basic assumption is generally that the reproduction of small populations is reduced due to (i) increased levels of inbreeding, a loss of genetic variation through, for example, random genetic drift and founder effects, and (ii) pollen limitation and / or the loss of compatible mates in self-incompatible species. Low reproduction of small populations may lead to a further decline in population size and genetic variation, and, eventually, to extinction (Gilpin and Soulé 1986, Lamont et al. 1993). A meta-analysis showed that the relationships between population size, genetic variation and plant fitness are generally positive (Leimu et al. 2006). Pollination seems to be a crucial factor for plant reproductive success, as it is negatively affected by habitat fragmentation and thus may be the most proximate cause of reduced reproduction in fragmented plant populations (Aguilar et al. 2006).

Despite this general pattern, some studies yielded contrasting results. For example, in fragmented populations of *Lycochrysum albicans* (Costin et al. 2001) and *Heliconia acuminata* (Bruna and Kress 2002), reproductive success was not reduced compared to non-fragmented populations. In *Gentianella austriaca* (Greimler and Dobeš 2000), *Antirrhinum charidemi* and *A. valentinum* (Mateu-Andrés and Segarra-Marague 2000), and *Iris haynei* and *I. atrofusca* (Arafeh et al. 2002), no relationship between population size and genetic diversity could be found. Furthermore, in *Parnassia palustris* (Bonnin et al. 2002), reproductive success was unrelated to genetic diversity. One explanation for these deviating results may be that populations have not been small sufficiently long to experience genetic deterioration and the associated negative effects on reproductive

success (see Greimler and Dobeš 2000; Costin et al. 2001). Another reason may be found in specific life history traits of the studied species in terms of, for example, their longevity, breeding system and dispersal syndrome. In general, the negative effects of small population size on genetic variation and plant fitness appear to be less detrimental in self-compatible species (Leimu et al. 2006). In some species, the reduced reproductive success of small populations may also be counterbalanced by the absence of antagonistic interactions in these populations (e.g., Colling and Matthies 2004).

A further reason for the lack of effects of population size and genetic diversity on plant fitness may be the overriding importance of habitat quality. Given the widely acknowledged relationship between biodiversity loss and habitat destruction, it is likely that also remnant plant populations are affected by environmental conditions, especially light availability and soil quality. In populations of *Gentiana pneumonanthe*, for example, both habitat characteristics and population size had an impact on reproductive fitness, while the level of heterozygosity did not show any significant effect (Oostermeijer et al. 1998). In *Succisa pratensis*, population size was strongly influenced by habitat quality, and a reduction in plant fitness was better explained by genetic effects and habitat deterioration than by population size alone (Vergeer et al. 2003). Effects of both habitat fragmentation and habitat quality were also shown for other herb species (Winter et al. 2008, Tsaliki and Diekmann 2009).

If populations are simultaneously affected by their population size, genetic constitution and habitat quality, the proportional contribution of these factors to total fitness is expected not to be stable over time, but to differ between years, mainly because of the inter-annual variation in weather conditions. The latter affect various aspects of plant performance, for example aboveground biomass (Dunnett et al. 1998), mortality and the number of flowers per plant (Rose et al. 1998), and the number of seeds per plant (Abrahamson and Layne 2003). However, even though data from several years on the effects of habitat fragmentation would shed light on the temporal variation in the contribution of the above factors to plant fitness, only few studies have extended over more than one growing season (but see Alexandersson and Ågren 1996, Morgan 1998, Yates et al. 2007, Rabasa et al. 2009).

In a previous, one-year study of the perennial herb *Euphorbia palustris*, we found its reproductive success to be strongly affected by population size and less so by habitat quality (Winter et al. 2008). Here, we present new data on the genetics of populations and examine the relationships between reproductive success and the three predictors

population size, genetic variation and habitat quality over three successive growing periods. We seek to answer the following main questions: (i) Is genetic diversity related to population size, and does it affect reproductive success? (ii) Are the relationships between reproductive fitness and its predictors consistent across years? And (iii) can the inter-annual differences in the studied relationships be attributed to the differences in weather conditions between years?

Methods

Study species, area and populations

Euphorbia palustris L. is a long-lived perennial forming one to several annual shoots and reaching a height of up to 1.80 m. Most shoots produce flowers that are arranged in several compound umbels. The species mainly reproduces sexually via seeds, but also forms short rhizomes (Klotz et al. 2002). *E. palustris* is self-incompatible (W.D., unpublished data), the female flowers are protogynous and thus depend on cross-pollination by insects to produce intact seeds. Each fruit (capsule) normally contains three seeds that are pre-dominantly self-dispersed, but may also be transported by water. *E. palustris* can be found from eastern Spain in the West to East Asia in the East and reaches as far north as South Scandinavia. It is considered as a so-called river corridor plant, a species that is exclusively or predominantly confined to the basins of large rivers (Burkart 2001). Natural habitats include nutrient-rich backwaters and river banks, while wet grasslands form the most important semi-natural environment. Already in the post-glacial period, local extinction and migration events resulted in a rather fragmented distribution of the species (Hegi 1975). During the last 100 years the natural habitats along the rivers were largely destroyed or degraded by the regulation of watercourses, land reclamation and agricultural intensification, and this has resulted in a further fragmentation of populations. Today, the plant is endangered in many parts of Central Europe (Ludwig and Schnittler 1996, Nikfeld 1999, Moser et al. 2002).

In 2005, 2006 and 2007, we conducted field studies in 12 populations of *E. palustris* in floodplains of the Weser and Elbe river systems in North-Western Germany (Table 1). The populations were selected based on records of the inventory program for endangered plant species for that area. The study basically comprises all populations in the region, except those that could not be found or reached, or consisted of only one

individual. All sampled populations occurred in typical habitats of the species, at ditch banks, in swamp forests and fallows. The distances between populations ranged from 1.3 to 108 km (mean = 44.9 km). In 2005, Population size was determined as the number of flowering plants during peak flowering by counting all individuals. Only in the largest population, the estimates were based on counts in sub-sets of the population followed by extrapolation. As changes of population size in 2006 and 2007 compared to 2005 were only marginal, this parameter was not determined again.

Climatic data for the study area was available from the German meteorological service (Deutscher Wetterdienst; URL: <http://www.dwd.de>) and recorded for the weather station next to the populations, Bremen Airport. For all years we recorded the climatic parameters precipitation, air temperature and sunshine hours. For the two latter mainly the values for the months from March till July were considered important, as these describe the period most relevant to the growth and seed production of the species. As the soils accumulate the water from rainfall continuously we calculated the cumulative amount of precipitation for the whole vegetation cycle of *E. palustris* from August of the preceding year (the beginning of the resting period of the species) till July (time of seed maturity) of the study season.

Plant traits

In 2005, we randomly selected and marked 20 (in smaller populations all) flowering individuals in each population. These individuals were also used for records in the two following years. Between the end of May and the beginning of June, corresponding to the peak flowering period of the species, we counted the number of inflorescences and the number of secondary umbels. At the time of seed maturity, the number of capsules was counted, and 20 (or all) randomly selected capsules were collected from each plant. The capsules were air-dried and stored in paper bags at room temperature.

For each individual, we determined the total number of seeds and mean seed mass of 40 randomly selected seeds per plant. The number of seeds per plant was calculated by multiplying the number of capsules per plant by the number of seeds per capsules. In 2007, most populations produced only few or no intact seeds, therefore seed mass parameters were not calculated for this year. Both in 2005 and 2006, there were two populations with hardly any seed production for which therefore no seed mass data was available.

Table 1 – Summary of studied populations, including the type of habitat in which the population was found, population size (number of flowering individuals in 2005), number of individuals sampled for the genetic analysis, expected heterozygosity, the number of alleles, allelic richness and the inbreeding coefficient.

Population	Habitat type	Population size (flowering)	No. of individuals sampled	Expected Heterozygosity (H_e)	Number of alleles (A)	Allelic richness (A_r)	Inbreeding coefficient (F_{is})
<i>Viehland</i>	Swamp forest	3	3	0.611	2.4	2.43	-0.364
<i>Wahnebergen</i>	Ditch bank	7	7	0.658	4.6	3.13	-0.116
<i>Ahnebergen</i>	Ditch bank	8	7	0.660	4.0	2.99	-0.052
<i>Tietjenshütte</i>	Fallow	12	12	0.325	2.0	1.77	-0.137
<i>Beppen</i>	Ditch bank	15	12	0.611	4.4	2.90	0.065
<i>Ahsen</i>	Swamp forest	22	21	0.713	4.9	3.15	0.140
<i>Feldhausen</i>	Fallow	40	24	0.778	7.3	3.66	0.058
<i>Verden</i>	Fallow	47	25	0.632	4.1	2.80	0.174
<i>Ihlienworth</i>	Swamp forest	105	26	0.609	5.3	2.83	-0.083
<i>Westen</i>	Fallow	166	25	0.738	5.3	3.34	0.043
<i>Cliverswerder</i>	Fallow	230	24	0.706	6.9	3.25	0.043
<i>Lassrönne</i>	Fallow	2128	22	0.642	6.9	3.22	0.070

Genetic variation

Leaf material was sampled from 25 randomly selected plants per population, or from all plants in smaller populations. DNA was extracted using the DNeasy extraction kit (QIAGEN). Samples were genotyped at seven microsatellite loci as described previously (W.D., submitted). We quantified genetic variability within populations on the allelic level as the mean number of alleles across loci (A) and as allelic richness (A_r), a measure of allelic diversity that corrects for sample size (minimum sample size = 3) and as mean gene diversity (H_e) across loci using the program Fstat v. 2.9.3 (Goudet 1995). Because the sample sizes were low for some populations with few individuals, we only used A_r in the correlation analyses. Tests for Hardy-Weinberg-equilibrium performed in those populations that were analysed for at least 20 individuals showed that three out of seven populations deviated from HWE, most probably due to null alleles at loci Ep75 and Ep29 (Table 1). Population differentiation was assessed with F -statistics using Weir and Cockerham (1984) estimators calculated with Fstat. Because microsatellites are highly polymorphic, measures of population differentiation may be biased downward. We therefore used Hedrick's (2005) method to standardize estimates of population differentiation: $F_{ST}' = F_{ST} / F_{STmax}$. For estimation of F_{STmax} data was recorded as such that each population had a unique set of alleles, keeping the original allele frequencies with the program RecodeData (Meirmans 2006). We tested for isolation by distance with a Mantel test (2000 randomizations) of the relation between genetic distance (F_{ST}) and geographic distance using Fstat.

Environmental conditions

In each year, soil samples were taken in all populations during a rainless period in August. Each sample consisted of seven pooled soil cores (100 cm³ down to a depth of 4 cm) taken from below the litter layer. Soil moisture was measured gravimetrically. Prior to chemical analysis, all air-dried samples were passed through a 2 mm-sieve. We determined pH in a solution of 10 g of soil and 25 ml of 0.01M CaCl₂ with a standard glass electrode. Plant available phosphorus (P) was extracted with ammonium lactate and measured photometrically by flow injection analysis. Calcium (Ca), magnesium (Mg) and potassium (K) were also extracted with ammonium lactate and their concentrations measured by Atomic Absorption Spectroscopy. The contents of carbon (C) and

nitrogen (N) were determined using an elemental analyzer (EuroEA 3000, HEKA-tech, Germany).

Apart from soil quality, we also recorded the cover and height of the vegetation surrounding the target plants to assess any competitive effects of other species on the reproduction of *Euphorbia*. In addition, relative light intensity was determined as photosynthetic photon flux density (PPFD) of photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$; LI-COR Quantum Sensor). On overcast days, we measured the light values at 20 different locations across each population, simultaneously recording a reference value outside of the population in the open. The measurements were averaged and expressed as $\text{PPFD}_{\text{population}} / \text{PPFD}_{\text{open}}$ in percent.

Germination trials

In February 2006 and 2007, 40 ripe seeds (or all seeds if $n < 40$) collected in the previous year were randomly selected from each sampled individual for the germination experiments, and weighed. The germination ability of seeds in 2007 and of two populations in 2005 and 2006 was not analyzed due to low seed production. To break dormancy, the seeds were stratified for eight weeks at 4 °C. All seeds were placed on a double layer of wet filter paper in Petri dishes and kept in a growth chamber at a temperature and light regime of 14 h/day at 25 °C and 10 h/night at 20 °C. We daily counted the number of germinated seeds (those with a developed radicula) until no further germination occurred about three weeks after the start of the experiment. The germination rate was calculated for the period when the increase in germination was highest, i.e., within the first three days after the start of the experiment, and expressed as the slope of the regression of the number of germinated seeds on time. Total germination was defined as the proportion of the number of germinated seeds to all seeds used.

Data analysis

Some of the variables used for the statistical analysis were log-transformed to achieve normality and homogeneity of variances. First, we analyzed the relationship across sites between the values of environmental variables for different years, using Pearson correlation. Then we examined whether the measured values were higher or lower in particular years, applying paired t-test.

To avoid multi-collinearity and to reduce the number of environmental variables in the regressions, a principal component analysis was carried out on the soil variables to construct a composite measure of soil quality. The relationship between the measured values and the (varimax rotated) PCA scores was examined by means of the rotated component loadings.

The relationships between population size, allelic richness and habitat quality were analyzed by simple linear regression. To examine whether the reproductive fitness components were affected by any of the above factors, both simple linear regression and stepwise multiple regression with a backward elimination of variables (threshold for exclusion of variables $P = 0.05$) were applied. As estimates of population size and genetic variability were only available for two years and one year, respectively, we could not carry out a more sophisticated nested GLM analysis. The multiple procedure did not result in statistically significant predictors that were not also found to be significant in the simple regressions, and no interaction effects between variables were detected. In the following, we therefore give the results only of the simple regressions that have the advantage to be more suitable for graphical presentation. The factors height and cover of the surrounding vegetation did not appear to have any effect on population size, allelic richness and reproduction, and were therefore excluded from the analysis.

To test whether the variation in seed production across years were affected by population size, allelic richness, relative light availability or soil quality, reflecting also the different weather conditions of the study years, we used a general linear model (GLM, type III sums of squares). The differences in the number of seeds per plant between years (05/06, 06/07, 05/07) were entered as dependent variables into the model, with the above factors as covariates. As the light values and PCA scores of soil variables were highly inter-correlated between the three study seasons (see Results) only the values of 2005 were used for this model. All statistical analyses were carried out on population means using SPSS 15.0 (SPSS, Chicago, USA).

Results

Weather conditions and habitat quality

The weather conditions varied considerably between years. In 2005, temperature, precipitation and sunshine duration were all close to the long-term mean (Fig. 1). In 2006,

July was extremely hot and sunny. The spring in 2007 was very mild, and April was exceptionally sunny and almost rainless. In May 2007, on the other hand, precipitation was nearly twice as high as the long-term mean for that month. The calculation of the cumulative amount of precipitation for the whole vegetation cycle of the species shows that 2006, unlike 2005, was exceptionally dry, whereas 2007 had unusually high rainfall values.

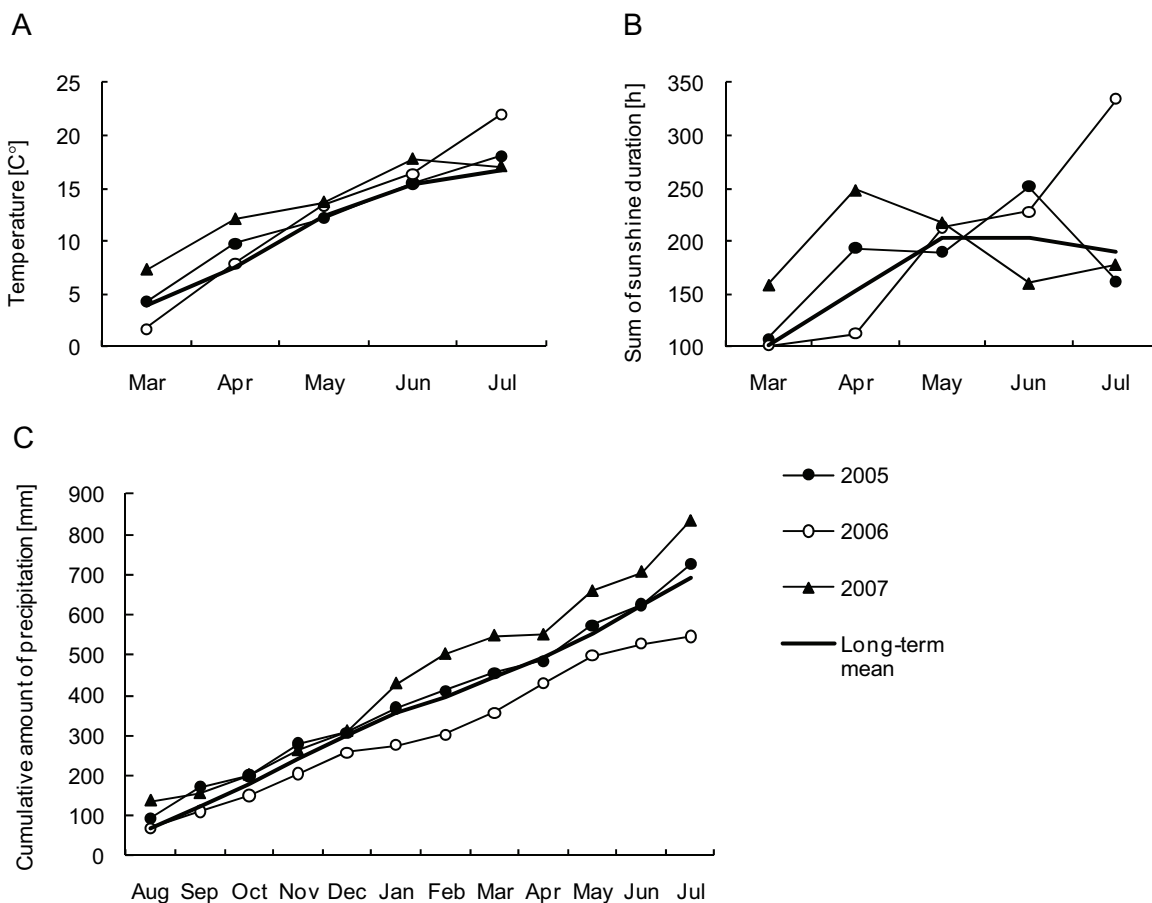


Fig. 1 – Monthly temperature values (a) and the monthly sum of sunshine hours (b) in the study area from March till July (the period assumed to be important for growth and seed production of *Euphorbia palustris*) in 2005, 2006 and 2007. In addition, the cumulative amount of precipitation (c) from August of the preceding year (the month in which the resting period of *E. palustris* starts) till July (time of seed maturity of the species) is given for the three years. The long-term means are also indicated. Data was obtained from the German Meteorological Service (URL: <http://www.dwd.de>) for the weather station Bremen Airport.

Habitat quality differed considerably between the years. Consistent with the cumulative amount of precipitation (Fig. 1), soil moisture was lower in 2006 than in 2005 and 2007

(05 vs 06 – $T = 7.24$, $P < 0.001$, 06 vs 07 – $T = -3.75$, $P = 0.003$). In 2006, the contents of phosphate, magnesium and calcium were lower than in 2005 and 2007 (P: 05 vs 06 – $T = 3.94$, $P = 0.002$, 06 vs 07 – $T = -7.20$, $P < 0.001$; Mg: 05 vs 06 – $T = 3.79$, $P = 0.003$, 06 vs 07 – $T = -3.80$, $P = 0.003$; Ca: 05 vs 06 – $T = 4.02$, $P = 0.002$, 06 vs 07 – $T = -4.48$, $P = 0.001$). The contents of nitrogen and carbon in 2007 were higher than those in the previous years (N: 05 vs 07 – $T = -5.04$, $P < 0.001$, 06 vs 07 – $T = -3.30$, $P = 0.007$; C: 05 vs 07 – $T = -7.12$, $P < 0.001$, 06 vs 07 – $T = -2.68$, $P = 0.021$). In 2005, the C/N ratio was lower than in the two following years (05 vs 06 – $T = -3.47$, $P = 0.005$, 05 vs 07 – $T = -3.05$, $P = 0.011$).

In spite of these inter-annual differences, all values of environmental variables (with one exception) were highly correlated across sites between the three years (Table 2), indicating stable differences in environmental conditions over time between sites. This is also reflected in the PCA analyses calculated separately for the three years (Table 3; Pearson correlation of scores between years: in all cases $P < 0.001$). In each of the years, the three PCA axes together accounted for at least 87% of the total variation. PCA axis 1 was in all years highly correlated with soil moisture, nitrogen and carbon. PCA 2 axis was associated with pH and P, and PCA axis 3 with K. Other soil variables showed varying relationships with the PCA axes between the years.

Variable	2005 vs 2006	2005 vs 2007	2006 vs 2007
<i>Light availability</i>	0.599*	0.624*	0.702*
<i>Soil moisture</i>	0.946***	0.961***	0.891***
<i>pH</i>	0.913***	0.908***	0.883***
<i>carbon</i>	0.961***	0.985***	0.966***
<i>nitrogen</i>	0.958***	0.987***	0.965***
<i>C/N ratio</i>	0.537	0.701*	0.910***
<i>phosphorus</i>	0.935***	0.902***	0.956***
<i>calcium</i>	0.872***	0.861***	0.893***
<i>magnesium</i>	0.977***	0.957***	0.939***
<i>potassium</i>	0.945***	0.942***	0.881***

Table 2 - Relationship between the values of environmental variables measured in different years (2005, 2006, 2007; $n = 12$). Pearson correlation coefficients and significance probabilities are given; * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$.

Population size and genetic variation

The populations selected for this study in 2005 differed strongly in size, ranging from three to 2.128 flowering individuals (Table 1). Population size was neither related to

Table 3 - Principal component loadings of soil variables measured in 2005, 2006 and 2007 (varimax rotation). Loadings given in boldface indicate the axis with the highest correlation between original values and principal component scores for a particular year.

Variables	2005			2006			2007		
	PCA axis 1	PCA axis 2	PCA axis 3	PCA axis 1	PCA axis 2	PCA axis 3	PCA axis 1	PCA axis 2	PCA axis 3
<i>Soil moisture</i>	0.930	-0.056	0.220	0.955	-0.192	-0.018	0.850	-0.279	0.261
<i>pH</i>	0.015	0.924	-0.190	-0.113	0.951	-0.030	0.011	0.936	-0.026
<i>nitrogen</i>	0.907	-0.151	0.358	0.950	-0.253	0.141	0.927	-0.327	-0.003
<i>carbon</i>	0.931	-0.169	0.299	0.945	-0.301	0.033	0.922	-0.343	0.102
<i>C/N ratio</i>	0.814	-0.187	-0.149	-0.012	-0.349	-0.804	0.229	-0.223	0.880
<i>phosphorus</i>	-0.265	0.867	-0.068	-0.355	0.863	-0.004	-0.271	0.904	-0.028
<i>calcium</i>	0.476	0.017	0.793	0.764	0.472	0.401	0.929	0.278	-0.072
<i>magnesium</i>	0.722	0.399	0.411	0.605	-0.052	0.709	0.852	-0.023	-0.363
<i>potassium</i>	0.050	-0.317	0.890	0.019	-0.361	0.847	0.481	-0.311	-0.739
Variance explained by rotated components	4.037 (44.9%)	1.954 (21.7%)	1.918 (21.3%)	3.796 (42.2%)	2.318 (25.8%)	2.049 (22.8%)	4.377 (48.6%)	2.221 (24.7%)	1.537 (17.1%)

soil conditions as reflected in the PCA axes nor to light availability (Fig. 3 for the relationships with PCA axis 1 and light; all $P > 0.2$).

Across 208 individuals genotyped in 12 populations we found a total of 101 alleles in 7 microsatellite loci, ranging from 10 alleles at locus Ep18 to 19 alleles at locus Ep05. Expected heterozygosity ranged from $H_e = 0.325$ to 0.778 (mean 0.640) indicating high genetic diversity in all but one population, and was thus not related to population size ($R^2_{\text{adj}} = 0.000$, $P = 0.403$). The average number of alleles ranged from $A = 2.0$ to 7.3 (mean 4.8) and was strongly positively affected by population size ($R^2_{\text{adj}} = 0.495$, $P = 0.006$). Allelic richness ranged from $A_{r(3)} = 1.77$ to 3.66 (mean 2.96), and was not significantly related to population size (Fig. 2). In all three years, there was a negative relationship between allelic richness and PCA axis 1 (Fig. 3), but no correlation with PCA axes 2 and 3 ($P > 0.5$, data not

shown). In 2007, allelic richness was marginally positively related to light availability.

Populations were strongly differentiated as indicated by an overall F_{ST} of 0.228 (SE = 0.026) and standardised F_{ST}' of 0.667. Pairwise F_{ST} values between populations ranged from 0.103 to 0.435 and were all highly significant except those with population Viehland, which had a very low population size, rendering significance testing impossible despite strong differentiation. Population differentiation was not correlated to geographic distance ($r = -0.196$, $P = 0.116$). Thus, overall the patterns of genetic differentiation indicated substantial genetic drift and lack of gene flow among populations.

Reproductive success

Seed production varied significantly between years: The mean number of seeds per plant decreased from 812 in 2005 to 302 in 2006 and 198 in 2007 (05 vs 06 – $T = 3.58$, $P = 0.004$, 05 vs 07 – $T = 3.84$, $P = 0.003$, 06 vs 07 – $T = 2.34$, $P = 0.039$). Mean seed mass and total germination, determined only in 2005 and 2006, did not differ significantly between the two years (mean seed mass: 9.68 mg in 2005 vs 9.44 mg in 2006 – $T = -0.38$, $P = 0.717$; total germination 78,3% in 2005 vs 72,1% in 2006 – $T = 0.28$, $P = 0.790$).

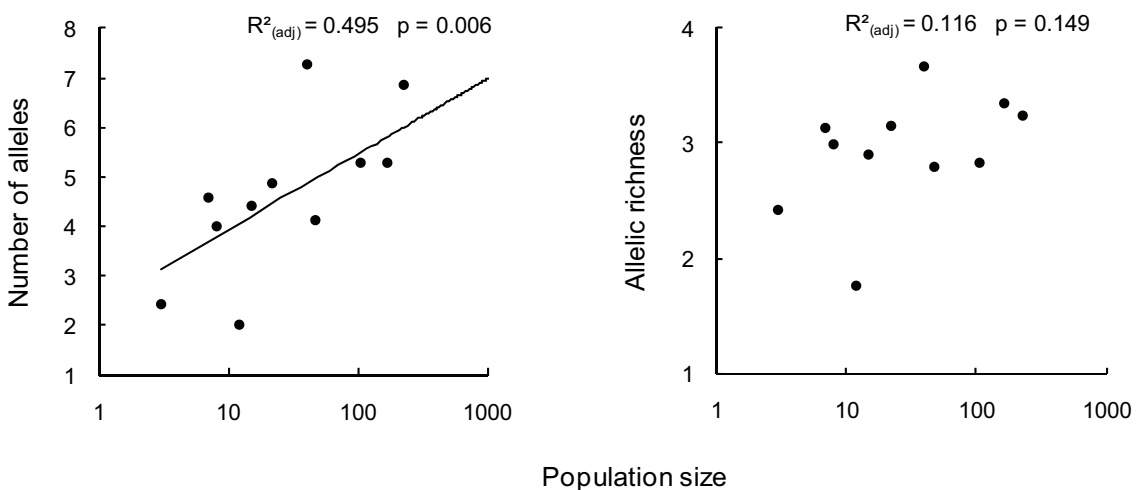


Fig. 2 – Relationship between the number of alleles / allelic richness and population size (number of flowering individuals log-transformed) for the year 2005 ($n = 12$).

We found several significant relationships between reproductive variables and population size, allelic richness and habitat quality, but these were not consistent across the three study years (Fig. 4 for the relationships with seed production). In 2005 and 2006,

but not in 2007, seed production was positively correlated with population size, whereas it increased with increasing allelic richness only in 2006. A significant effect of soil conditions (PCA axis 1) on the number of seeds was only observed in 2006 and 2007. Light availability had a marginally significant effect on seed production in 2007, but not in the previous years. The relationships between total seed mass (the product of the number of seeds per plant and mean seed mass) and its predictors were almost identical to those of seed production (data not shown). The differences in seed production across sites between years were strongly affected by soil quality, but not by population size or allelic richness (PCA axis 1 and 2) (Tab. 4).

Mean seed mass and total germination (and likewise germination rate) were not or only weakly affected by the predictors studied. In 2006, total germination tended to be negatively influenced by population size ($R^2_{\text{adj}} = -0.333$, $P = 0.061$) and allelic richness ($R^2_{\text{adj}} = -0.255$, $P = 0.095$). In 2006, mean seed mass was negatively correlated with PCA axis 3 ($R^2_{\text{adj}} = -0.648$, $P = 0.005$).

Discussion

Genetic diversity

We found some evidence that genetic diversity plays an important role in a system of interactions with population size, reproductive success and habitat quality for the viability of *Euphorbia palustris*, similar to what has been observed in the perennial *Succisa pratensis* (Vergeer et al. 2003). The strong negative relationship between allelic richness and soil moisture, nitrogen and carbon content (reflected in PCA axis 1) may possibly be explained by the following scenario, assuming that present habitat conditions are largely representative of past habitat conditions: At particular sites the soil conditions (especially the high soil water content) may have been so unfavourable to *Euphorbia* that the plants had a reduced ability to reproduce and survive environmental stochastic events, for example changes in land use, eutrophication etc. (cf. Oostermeijer 2003). Then, the populations in question may have gone through a bottleneck and recovered from a few surviving individuals with a reduced gene pool. This interpretation is supported by a model developed by Picó et al. (2009) that illustrates that population persistence at unfavourable sites is, for example, more prone to the negative effects of inbreeding.

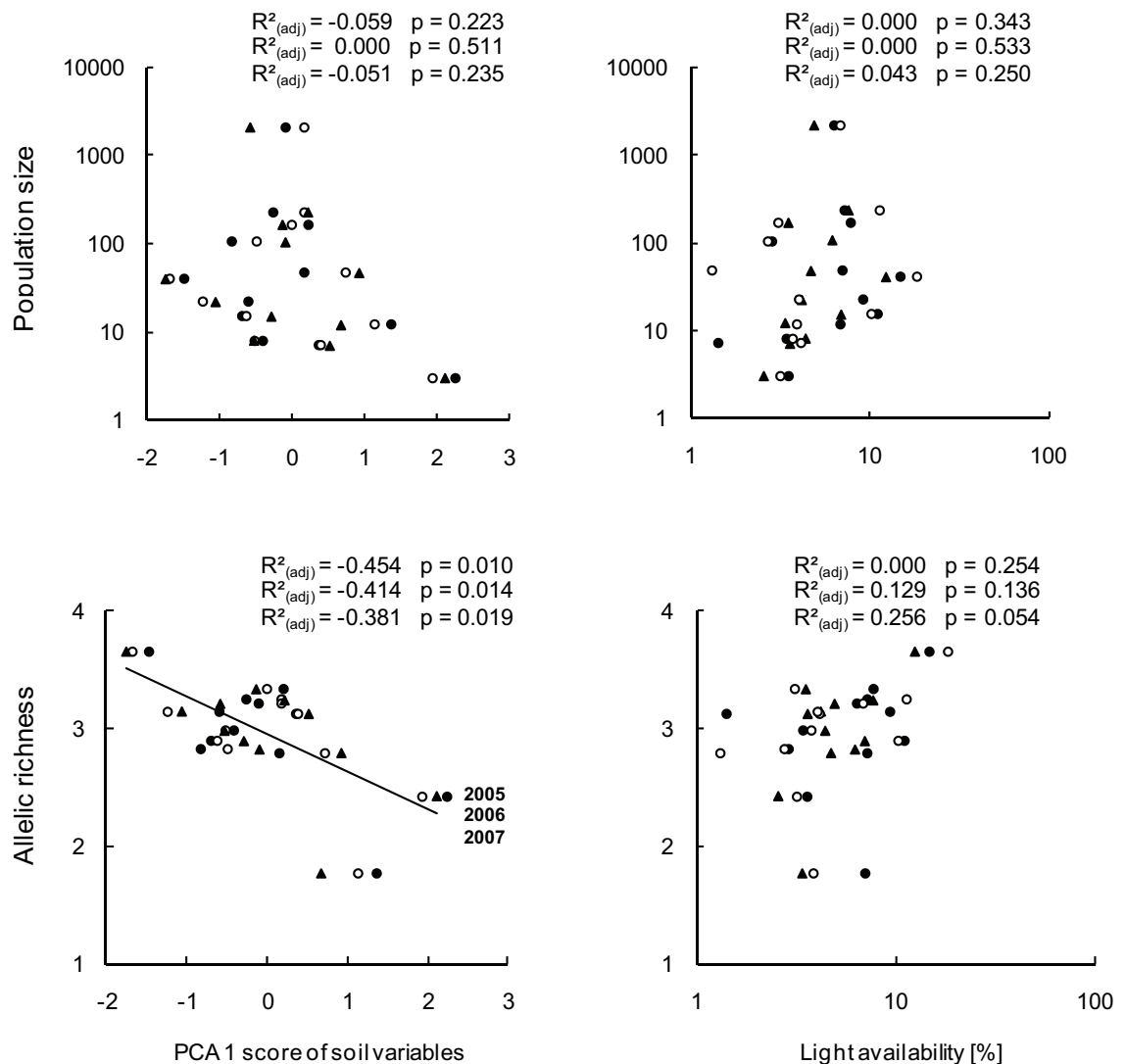


Fig. 3 – Relationship between population size (number of flowering individuals, log-transformed) and PCA score 1 (reflecting the main variation in soil conditions; upper left). between allelic richness and PCA score 1 (lower left). between population size and light availability (log-transformed; upper right). and between allelic richness and light availability (lower right) ($n = 12$). Symbols for 2005 - filled circles, 2006 - open circles, 2007 - crosses. Linear regression lines are shown only if $P < 0.05$. The adjusted R^2 values and significance probabilities are given. The order of the statistics corresponds to the study seasons 2005, 2006 and 2007.

Furthermore, increased inbreeding and loss of genetic variation in small populations can be caused by genetic drift (Ellstrand and Elam 1993, Young et al. 1996). In our study, reduced population size clearly led to genetic drift which reduced total allelic variation at the population level as indicated by the lower mean numbers of alleles (A) in smaller populations. However, on the individual level, and taking into account sample size, however, this effect is hardly visible as both allelic richness (A_{r3}) and expected hetero-

zygosity (H_e) were maintained at high levels in most populations, even if population size was very small. Numerous studies have reported a positive relationship between population size and genetic variation (Leimu et al. 2006), however, exceptions from this rule are not uncommon (Greimler and Dobeš 2000, Leimu and Mutikainen 2005, Medrano and Herrera 2008). Long-lived outcrossers such as *E. palustris*, are less prone to the negative effects of reduced population size. The effect of genetic drift depends on the number of generations passed (Hartl and Clark 1989) and only few generations ago *E. palustris* populations may have been much larger. Most importantly, however, is the effect of the mating system, which can account for the maintenance of genetic variation at the individual level. Self-incompatibility will minimize the effect of genetic drift because close inbreeding is prohibited leading to high levels of individual heterozygosity in the next generation. Thus the genetic deterioration in small populations and at sites with sub-optimal environmental conditions is still in an early phase, and the negative effects on the population level are only marginal. This interpretation is supported by the fact that population size was not related to habitat quality. Genetic deterioration, however, may be strong enough to impair plant fitness in terms of seed production, depending on weather conditions during the vegetation period (see below).

Reproductive success and its relationship to population size and habitat quality

Population size effects on reproduction were observed in two of the study years, which points at the importance of pollination by insects. Pollinators are less attracted by small populations, if they manage to locate them at all. This will lower visitation rates, consequently affect pollination and finally seed setting (Sih and Baltus 1987; Jennersten 1988). This, compared to genetic deterioration, may be the most likely proximate cause for the positive relationship between the number of seeds and population size, as *E. palustris* is self-incompatible and seed production depends on insect pollination. The higher susceptibility of self-incompatible plants to habitat fragmentation caused by the dependence on pollinator mutualism was recently shown by Aguilar et al. (2006). Lack of compatible genotypes may then decrease reproductive success in small populations of *E. palustris* even further.

Seed production was negatively affected by high soil moisture and high contents of nitrogen and carbon (PCA axis 1) in two out of three years. This is in contrast to the perception that *E. palustris* prefers moist to wet sites and has a broad tolerance of vary-

ing levels of soil nutrients (Ellenberg et al. 1991). However, the species is dependent on a certain summer drought (Hejný 1960, Burkhardt 2001), and the amount of plant-available nutrients, especially of nitrogen that is limited in soils with too high or too low soil moisture, generally affects seed production.

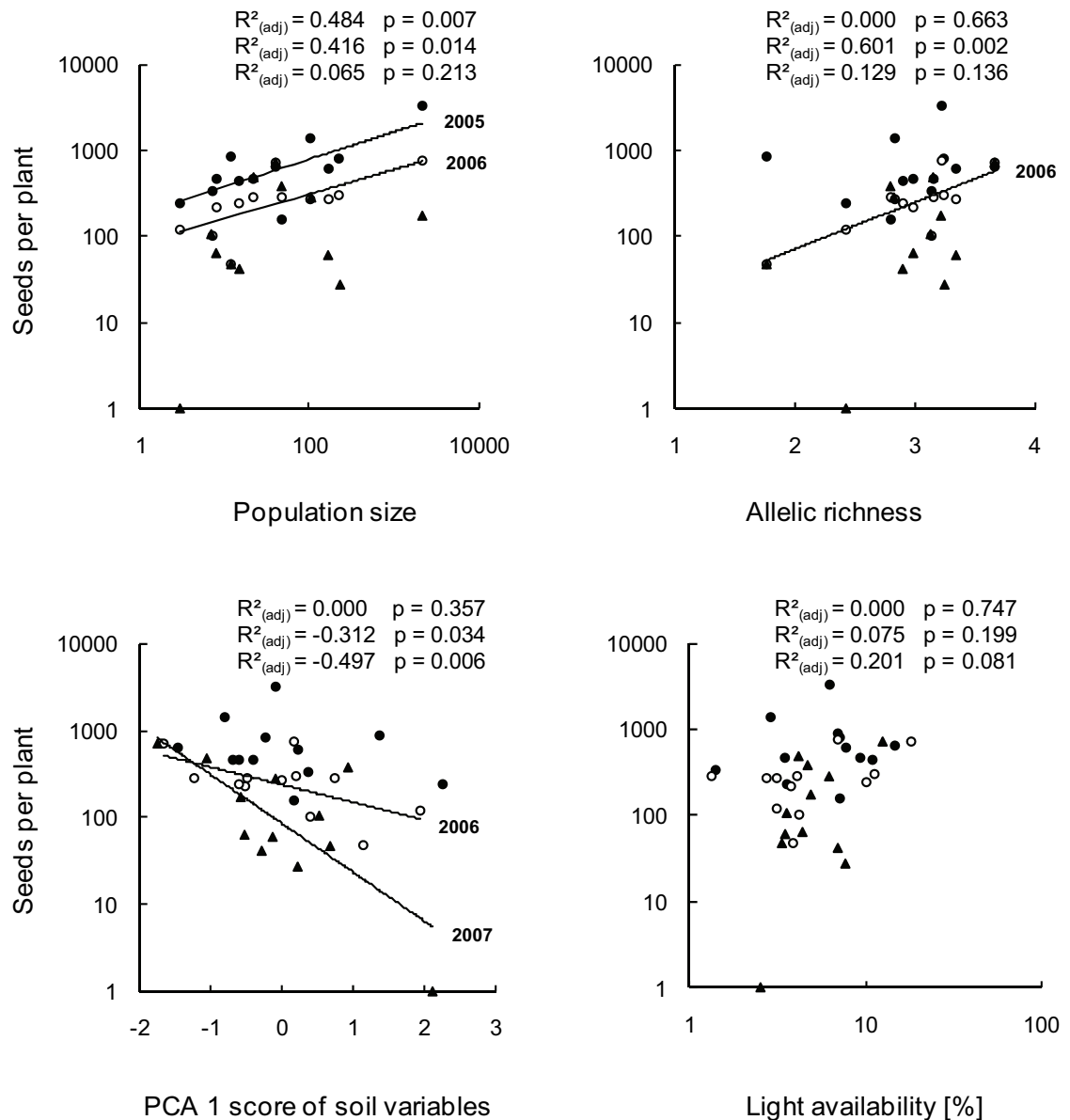


Fig. 4 – Relationship between the response variables seed production (number of seeds per plant, log-transformed, $n = 12$), and the explanatory variables population size (number of flowering individuals, log-transformed; upper left), allelic richness (upper right), PCA score 1 (lower left) and light availability (log-transformed; lower right). Symbols for 2005 - filled circles, 2006 - open circles, 2007 - crosses. Other details as in Fig. 3.

Contrary to the expectation that all measured reproductive parameters would be reduced in small populations, we found a tendency towards higher germination ability in small and genetically less diverse populations. These results suggest that large and genetically diverse populations invest more resources in the number of seeds than in seed quality. This interpretation is supported by the fact that total germination decreased with an increasing number of seeds produced (data not shown). Furthermore, mean seed mass was strongly positively affected by phosphorus and magnesium contents and negatively by the C/N ratio of parental sites (PCA axis 3). These findings are in accordance with the results of several other studies demonstrating that the parental resource status affects the fitness of offspring, and indicates a trade-off between the number of seeds and seed size or weight (see, e.g., Veneable 1992 and references cited therein).

Influence of weather conditions on the inter-annual differences in the relationships between reproductive success and its predictors

Several studies have shown that weather conditions during the growing season may strongly influence the reproduction of plants (e.g., Abrahamson and Layne 2003, Pfeifer et al. 2006, Prieto et al. 2008). In *E. palustris*, seed production was lower in the study years 2006 and 2007 than in 2005, most likely due to unfavourable weather conditions in these years. In 2006, seed production decreased by more than 60% compared to 2005, a year when weather conditions were almost congruent with the long-term mean, probably caused by high temperatures, high insulation and relatively low rainfall. In 2007, seed production was even lower than in 2006, possibly because the extreme rainfall in May had destroyed the flowers and reduced the activity of pollinators. This is in accordance with results from McCall and Primack (1992) showing that insect visitation rates in plant communities were affected by weather conditions.

	<i>df</i>	<i>F</i>
<i>Population size</i>	1	0.18
<i>Allelic richness</i> (A_{r3})	1	0.50
<i>Light availability</i>	1	0.00
<i>PCA axis 1</i>	1	10.57**
<i>PCA axis 2</i>	1	11.53**
<i>PCA axis 3</i>	1	2.77
<i>Years of difference</i>	2	3.38*
Error	27	—

Table 4 - General linear model of the effects of a set of covariates on the difference in seed production between years (05/06. 06/07. 05/07). PCA axes reflect soil quality. F-values and significance probabilities (* - $P < 0.05$. ** - $P < 0.01$) are given.

Extreme weather conditions throughout the growing season have considerable effects on soil quality, and this in turn may affect plant fitness. Sardans and Peñuelas (2007), for example, demonstrated that drought led to a diminished plant uptake of mineral nutrients, affecting plant fitness negatively. In accordance, the close negative relationship between seed production and PCA axis 1, basically reflecting a gradient in soil moisture that is affected by precipitation, in *E. palustris* shows the importance of weather conditions also in this species. This effect may also have caused the inter-annual variation in the relationships between the reproductive variables and population size, allelic richness, and habitat quality. Only in 2006 and 2007 when weather conditions differed considerably from the long-term mean, environmental conditions affected the reproduction: seed production was negatively related to soil moisture, nitrogen and carbon contents (PCA axis 1) and positively related to light availability (only weakly so in 2007). In 2005, weather conditions appeared to be optimal for seed production, and this variable was only affected by small population size, possibly due to pollinator limitation (see above). This result indicates that small population size, if weather conditions are at an average or optimum, is the most important reason for reduced reproductive success of *E. palustris*. Habitat quality and genetic diversity, on the other hand, are more important for the fitness of the species under deviant or sub-optimal weather conditions, as genetic variation influences a population's ability to respond to changes in its environment (Lande 1988, Frankham 1996). Accordingly, in 2006 altered habitat quality and genetic deterioration had, in addition to small population size, negative effects on seed production, too. In 2007, weather conditions may have been so determinant for seed production that the latter was only affected by altered habitat quality. Owing to the extreme rainfall in May, the pollinator activity in this year was probably low (see above) in all populations so that small population size had no effect on seed production.

In summary, precipitation and its influence on soil moisture appears to be the most important predictor for reproductive success and generates inter-annual differences in the relationships between fitness and population size, genetic variability and habitat conditions. Precipitation that deviates considerably from the long-term mean was also found to be the crucial factor for the fitness and reproductive success of plants in several other studies (Rose et al. 1998, Abrahamson and Layne 2003, Sardans and Peñuelas 2007, Prieto et al. 2008). Importantly, our findings support the notion that a single-year study may not be sufficient to provide a realistic view on the relative contributions of

population size, genetic diversity and habitat quality on the fitness of plant populations (Hobbs and Yates 2003, Rabasa et al. 2009).

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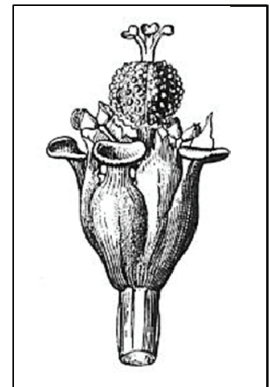
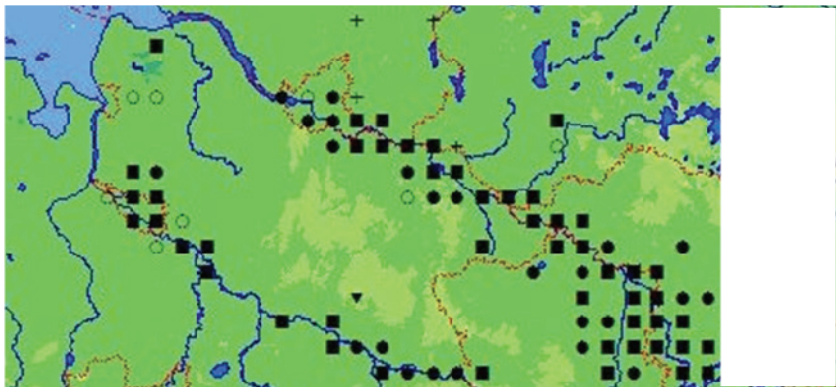
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3.4

Artmonographie der Stromtalpflanze

Euphorbia palustris L.



Oben links: Verbreitung von Euphorbia palustris entlang der Flusstäler von Weser und Elbe im Norddeutschen Raum. Karte verändert nach dem Bundesamt für Naturschutz, Netzwerk Phytodiversität Deutschland [NetPhyD].

Oben rechts: Cyathium von Euphorbia palustris. Zeichnung verändert nach Hegi G (1975) Illustrierte Flora von Mitteleuropa. 3. Teil Linaceae - Violaceae. Paul Parey, Hamburg, Berlin.

Unten links: Habitus von Euphorbia palustris. (Foto: Christina Wärner).

Unten rechts: Trugdöldchen von Euphorbia palustris mit 7 Cyathien. (Foto: Katrin Nüssel).

Biological flora of Central Europe: *Euphorbia palustris* L.

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(Submitted)

Abstract

Euphorbia palustris L. (Euphorbiaceae) is a tall perennial pleiocorm hemicryptophyte, native to Europe and small parts of adjacent Western Asia. It is considered a so-called river corridor plant that is exclusively or predominantly confined to the basins of large rivers. As most natural habitats along European rivers have been destroyed and the remaining habitats fragmented and degraded by the regulation of watercourses, land reclamation, and agricultural intensification, *E. palustris* is now endangered in several parts of Central Europe. To enhance its conservation, to give scientific advice for its management and to supplement the scarce information available from the literature, this paper reviews the species' taxonomy, morphology, distribution, habitat requirements, life cycle, population biology, and genetics as well as the conservation status across its distribution range.

Keywords: Distribution range, Endangered species, Habitat requirements, Plant communities, Reproduction, River corridor plant

Introduction

“*Euphorbia*, which Rudbeck called *Tithymalus maximus Oelandicus*, grew abundantly here in the middle of the field close to a little brook, Fällbäcken, although we had never seen it wild in Sweden before; it grew as shrubs a few ells tall; the stem perishes each year; the leaves are alternate, lanceolate, obtuse and entire. ...We saw this plant later on during the day here and there in the meadows on the *alvar*-land.” (Linné 1745).

This citation from Linné's journey to Öland and Gotland is probably the first scientific description of the biology and ecology of *Euphorbia palustris* L., a nowadays rare and, in several parts of Central Europe, endangered species. This article deals with the tax-

onomy, morphology, distribution, habitat requirements, life cycle, population biology, and genetics of this species, following the outline for the Biological Flora of Central Europe (Matthies and Poschlod 2000). To provide a comprehensive overview of the species we used already published information as well as unpublished data and personal observations of the ecology of the species conducted in the years 2005, 2006, and 2007 in 12 populations located along the Weser and Elbe river systems in North-western Germany. Unless otherwise stated, data given without a published literature source refer to these investigations. Most quantitative information in the sections “Morphology” and “Reproduction” is based on our own measurements in the above populations, where also data on environmental conditions were gathered (chapters “Habitat” and “Response to abiotic factors”). Additional information was obtained while compiling and analyzing data regarding the geographical distribution of the species. Information given in the section “Germination” is based on germination experiments conducted at the University of Bremen. Studies of the demography of *E. palustris* were conducted in three relatively large populations and form the basis for the chapters “Life cycle”, “Spatial distribution of plants within populations” and “Herbivores and pathogens”. Finally, genetic information provided in the section “Genetic data” is derived from own microsatellite analyses. We hope that this detailed monograph of *Euphorbia palustris* leads to a better understanding of the species’ ecology and the causes behind its severe decline in many parts of Europe.

Taxonomy and morphology

Taxonomy

Euphorbia palustris L., Spec. Plant. I: 462 (1753) (Euphorbiaceae) – Sumpf-Wolfsmilch, marsh spurge.

Homotypic synonyms: *Tithymalus palustris* (L.) Garsault, Fig. Pl. Méd.: 592 (1764), – *Galarhoeus palustris* (L.) Haw., Syn. Pl. Succ.: 145 (1812)

Heterotypic synonyms: *Euphorbia nuda* Velenovsky, Fl. Bulg.: 506-507 (1891) – *Euphorbia velenovsky* Bornm., Bot. Jb. 66: 117 (1933), nom. illeg. – *Euphorbia sauliana* Boreau ex Boiss., DC. Prodr. XV/2: 1266 (1866).

The genus *Euphorbia* belongs to one of the largest dicotyledonous families, the Euphorbiaceae, which includes 300 genera and 8,000 species (Webster 1987) occurring in all parts of the world except the arctic regions, and having its distribution centre in the tropics. Because of its tremendous morphological diversity, encompassing broad-leaved trees in the tropical rainforest, succulents in arid ecosystems, perennial herbs mainly in Europe, annual weeds, and even a *Salvinia*-like water plant (*Phyllanthus fluitans* Benth.), the taxonomy of the family is still disputed (Webster 1987).

Euphorbia is a large genus of over 2,000 species of almost cosmopolitan terrestrial distribution, which is sub-divided into many subgenera and sections (Govaerts et al. 2000). While the genus is very rich in species in subtropical, semi-arid areas, particularly in Africa, much less species reach out to cooler regions, such as the European and West Asian temperate to boreal zones (Kuzmanov 1964). The subgenus *Esula* Pers. consists of about 500 species and is a native Eurasian group (Park, 1998). Within this group, the section *Tulocarpa* (Raf.) Prokh. (sect. *Tithymalus* (Scop.) Boiss. subsect. *Galarrhaei* Boiss.) includes tall perennial herbs and small shrubs, predominantly distributed in sub-meridional and temperate Eurasia. *E. palustris* belongs to the subsection *Lutescentes* Prokh. (ser. *Lutescentes* (Prokh.) Radcliffe-Smith). Its closest relatives are *Euphorbia soongarica* Boiss., *E. lamprocarpa* Prokh. and *E. aristata* Prokh. (Baikov, pers. comm.). Govaerts (Catalogue of Life 2007) included these species into a broader concept of *E. palustris*. While the morphological and ecological similarity of *E. lamprocarpa* and *E. aristata* to *E. soongorica* was already advocated by Lipsky (1897), there is a marked difference between *E. palustris* and *E. soongorica* with regard to their habitat preferences. The latter occurs in temporarily moist, open habitats of sub-continental (mountain) steppe regions, whereas *E. palustris* is strongly tied to seasonally wet riparian habitats in lowland river corridor ecosystems. Therefore, the placement of the species in a separate Series *Soongaricae* Baikov (Baikov 2003a, 2003b, 2007) seems justified (also see World Checklist 2009). Accordingly, Meusel et al. (1978) described *E. palustris* as a lowland species within a group of mountain steppe plants of Western Asia. Molecular-genetic studies on the phylogenetic relationships of *E. palustris*, however, are lacking.

Morphology

Euphorbia palustris is a perennial herb resembling a small willow bush in its habit (Fig. 1). Flowering plants reach a height of 70-180 cm (120 cm on average). They have a central woody rhizome in form of a beet with innovation buds and stem axes that develop adventitious roots (Rauh 1937; Fig. 2). New shoots grow either directly after hibernation or during the growing season, forming a tussock. We found an average stem axis diameter of 5 cm, and the stem axis may reach a belowground length of more than 1 m (Hejný 1960). *E. palustris* is a typical pleiocorm species with relatively short horizontal stem axes that, after several years, can form independent shoots. These shoots grow separate but always within short distance from the main root stock

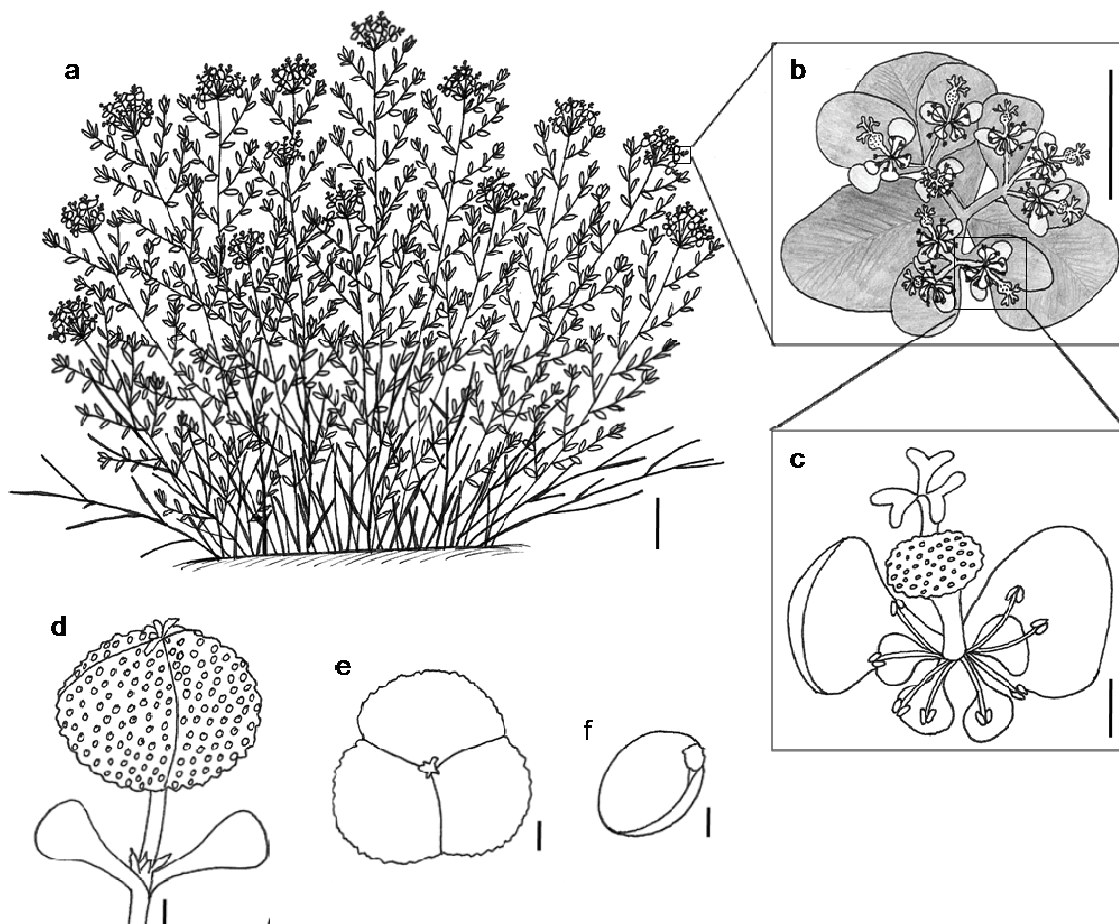


Fig. 1 - *Euphorbia palustris*. (a) habit (scale bar: 10 cm), (b) detail of one main ray of the pseudumbel (scale bar: 1 cm), (c) detail of cyanthium (scale bar: 1 mm), (d) detail of fruit (scale bar: 1 mm), (e) fruit, view from above (scale bar: 1 mm), (f) seed (scale bar: 1 mm). Drawings by K. Nüssel.

(Krumbiegel 2002). Afterwards the plant splits into several individuals and the main rootstock normally withers. Thus, the species has the ability to propagate vegetatively.

Erect shoots normally emerge from the main rootstock. Young flowering individuals may consist of one shoot only while large adults can form up to 120 shoots. The stem has an average diameter of 17 mm (max: 22 mm) at the basis. It is hollow, glabrous, bluishly pruinose and often with a reddish touch at the base. The upper parts of the flowering shoots are branched and, at fruiting time, sterile branches overtop the terminal inflorescences. Shoots do not possess any stomata (von Kirchner et al. 1908).

The sessile leaves are numerous and alternately arranged at the stem and its branches. They are of a bluish green colour, soft, glabrous and have a water repellent surface (Neinhuis and Barthlott 1997).

Leaf shape ranges from lanceolate to oblong-lanceolate and from blunt to acuminate. The leaves have a narrow cartilaginous light margin that is entire or very soft serrate. The anomocytic stomata are arranged at the underside of the leaf solely (von Kirchner et al. 1908) and count 210 per mm² on average (Sehgal and Paliwal 1974). Stem leaves are on average 9.2 cm long and 2.0 cm wide, while branch leaves are smaller with an average length of 4.6 cm and width of 1.2 cm. Average leaf size is 616 mm² with a mean mass of 29.9 mg (average dry matter content of 323.8 mg/g), resulting in an average specific leaf area of 20.43 mm²/mg (Kleyer et al. 2008).

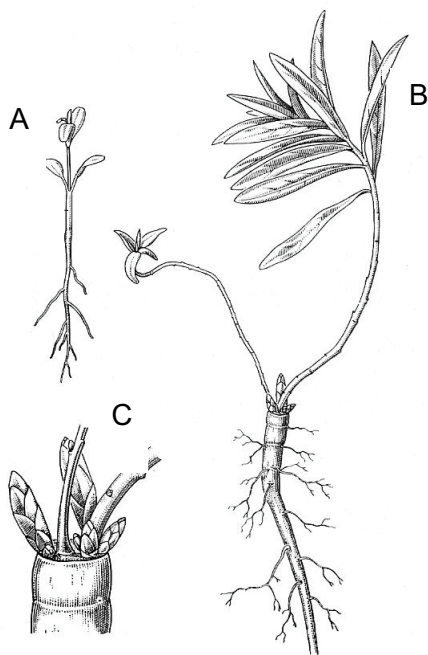


Fig. 2 - *Euphorbia palustris*. (A) seedling, (B) one year-old plant, (C) top of the beet of a one year-old plant. Modified from Rauh (1937).

The inflorescence is a pseudoumbel with 12 main rays on average: these first branch three- to fivefold and subsequently threefold, each final branch carrying a terminal cyathium, the typical pseudanthium of the Euphorbioideae. The latter consists of a bundle of highly reduced unisexual flowers with only one female flower in the centre and four surrounding male flowers. The female flower has a petiolate ovary and a style with a three-part stigma, the male flower carries two filaments. Four wax-yellow nectar

glands are arranged around the male flowers and the entire cyathium is coated by two yellow bracts. Occasionally, a single cyathium without bracts is situated in the middle of the second level of the pseudoumbel. Two bracts protrude from the base of the second level of the pseudoumbel and two to four bracts grow at the basis of each main ray. The central cyathium within the synflorescence contains staminate flowers but mostly lacks the pistillate flower. Thus, *E. palustris* is functionally andromonoecious like many other species of the genus (Narbona et al. 2002).

Capsules are erect and three-loculate, each loculus containing one seed; correspondingly, each fruit normally carries three seeds. The capsules are round-shaped, short-warty and 5 to 6 mm long and wide (Hegi 1975). The grey-brown-black ovate to roundish seeds have a smooth and slightly shiny surface with a pale convex caruncle of 1 x 1.3 mm. For seed size, see Reproduction.

Distribution and habitat requirements

Geographical distribution

Euphorbia palustris is a rather rare species, particularly so in Central Europe. The native geographical distribution ranges from northern Spain in the Southwest to South Scandinavia in the Northwest and from northwest Kazakhstan in the Northeast to the southeast of Turkey in the Southeast (Fig. 3). Also Western Siberia and the Altai mountains are sometimes listed as distribution areas of the species (e.g., Gel'tman 1996), but these western Asian range parts concern several closely related species considered to belong to *E. palustris* by Ledebour (1833). The species is recorded from all European countries except the United Kingdom, Ireland, Belgium, Iceland, Lithuania, Portugal and Malta (Tutin 1964, van Rompaey and Delvosalle 1979, Greuter et al. 1986, Tzvelev 2006). Doubtful and inconsistent observations were reported from Corsica, Balearic Islands, Southern Catalonia, Central Spain, Crimea, North-eastern Turkey, Middle Ural, and Upper Tobol Valley (maps in Hegi 1924, Polatschek 1971, Hultén and Fries 1986). The highest densities of *E. palustris* are supposedly to be found in Hungary, Croatia, Serbia, the Ukraine, and in the steppe and forest-steppe regions of southeastern European Russia; thus, the Pannonian to Pontic floristic regions represent the range centre of the species, and the general distribution can be described as submeridional to north

temperate within the continentality regions (1) 3 to 7 (9) in Europe (Westasia) (Meusel et al. 1978).

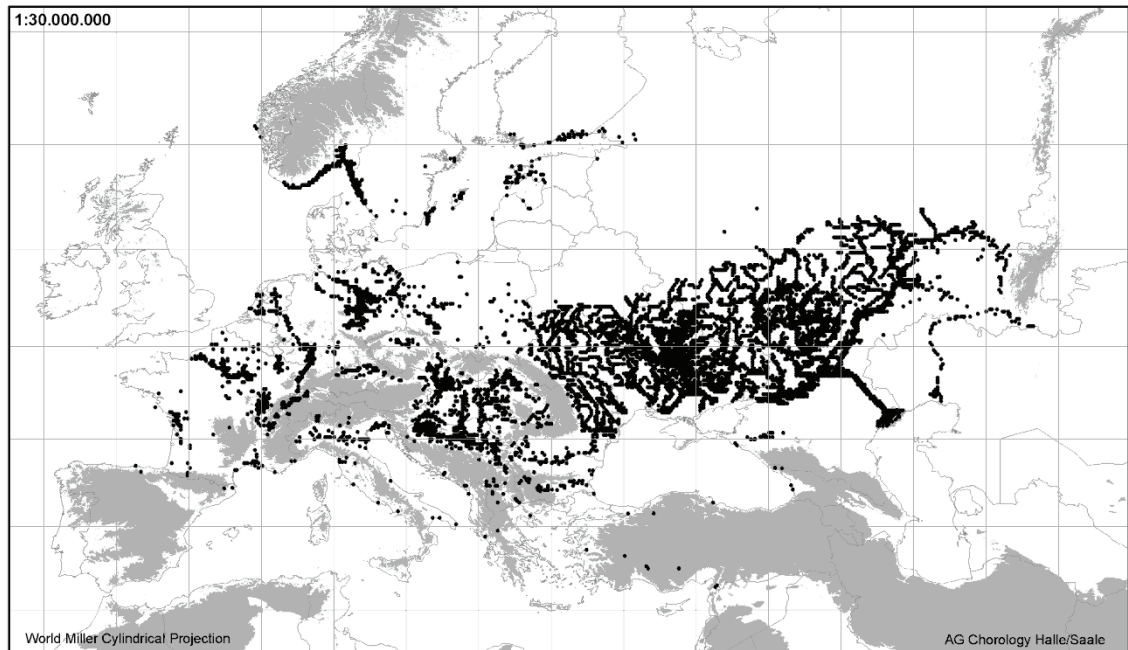


Fig. 3 - Global distribution of *Euphorbia palustris*.

The species is predominantly confined to the lowland basins of large rivers and its tributaries (90% of occurrences between ca. 10 m and 300 m asl.) (Figs. 3 and 4). In Central Europe, several other plant species share a similar distribution pattern and are therefore called river corridor plants (Loew 1879, Burkart, 2001). However, the mechanisms generating this pattern are diverse and not well understood (Burkart 2001). In the Central European range parts the distribution of *E. palustris* along the rivers is usually rather irregular and erratic, and it has been hypothesized to be not predominantly caused by present-day or relatively recent changes in climatic or edaphic conditions, but most likely by extinction and recolonization events during post-glacial times (Schulz 1899), assuming that the populations spread out along the rivers in warmer periods, but became extinct at unfavorable sites in colder periods. The re-colonization of Central Europe probably originated from refugia in areas of the highest density of the species: the flood plains of the Danube were colonized from Hungary, the river Rhine from France, and the rest of the area along the meltwater streamways (furrows of the glacial valleys) from Russia (Schulz 1899). Strictly regressive processes seem to have acted in Southern Europe. Here, the isolated occurrences in coastal wetlands and on lakeshores of the Medi-

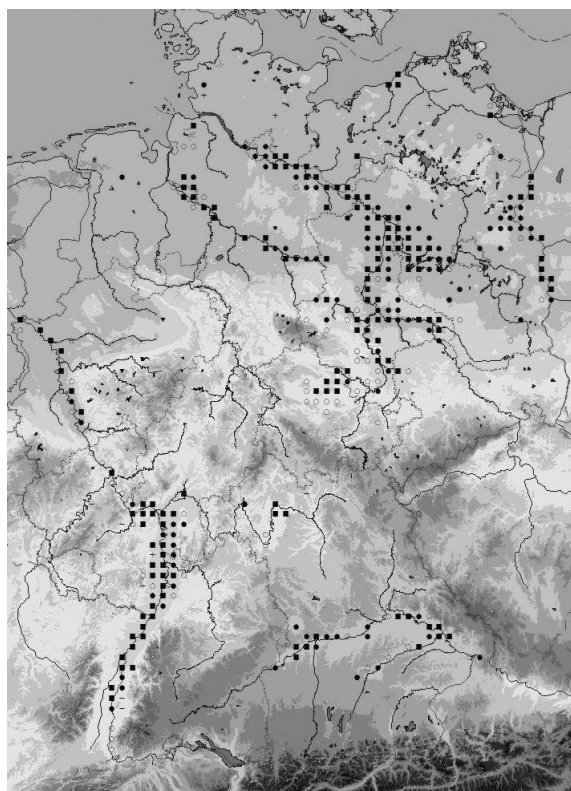


Fig. 4 - Distribution of *Euphorbia palustris* in Germany, showing the species' restriction to river corridors. Symbols: open circles - reports not being confirmed after 1950; full circles - reports after 1950, but before 1981; squares - reports since 1981; triangles - synanthropic occurrences; and crosses – populations extinct. The distribution map was made available by the Bundesamt für Naturschutz, Netzwerk Phytodiversität Deutschland [NetPhyD].

interglacial deposits (Kreftenheye Formation) in the Netherlands (van der Ham et al. 2008). Present-day occurrences in open swamp forests of the Colchic region in western Georgia probably offer climatic conditions that are similar to those present in many parts of Europe during the Late Tertiary (Denk et al. 2001).

Habitat

River corridor plants such as *Euphorbia palustris* prefer flood plain habitats in the lowlands with summer-warm conditions and winterly inundations in Central to Western Europe, or springtime floods in Eastern Europe (Hejný 1960, Burkhardt 2001). The

terranean area may be old, relic populations that represent remains of a formerly wider and more continuous distribution in moister climate periods of the Pleistocene or Pliocene. Scattered occurrences in wetlands are often supposed to originate from ornithochorous dispersal by waterfowl, however, the seed characteristics of *E. palustris* does not make this explanation very likely. Since all the above hypotheses remain highly speculative, phylogeographic investigations using molecular markers are urgently needed for a better understanding of the distribution pattern of the species.

E. palustris was identified in middle Pliocene (Late Brunssumian) browncoal sediments in Northern Germany (van der Burgh and Zetter 1989), in late Pliocene (Akchagylia deposits) in the Kama River paleovalley in southeastern Udmurtia (Pisareva 2006), and in Eemian (Ipswichian)

Table 1 - Soil conditions in 12 *Euphorbia palustris* populations in North-western Germany. In 2005, 2006 and 2007, mixed soil samples were collected from all populations during a rainless period in August. Population means, minima and maxima are given for each of the years studied.

Soil factor	2005			2006			2007		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Moisture in summer [%]	32.6	12.8	55.5	23.3	1.9	49.0	33.0	11.7	67.5
pH	4.6	4.0	5.4	4.7	4.1	5.4	4.7	4.2	5.4
Total nitrogen [%]	6.5	1.2	21.8	7.4	2.7	27.8	8.8	1.6	33.5
Total carbon [%]	0.6	0.1	1.5	0.6	0.1	1.9	0.7	0.1	2.3
C/N ratio	11.3	9.8	14.5	12.5	10.9	14.5	12.1	10.7	14.4
Pphosphorus content [mg/100 g]	5.2	1.4	14.4	2.3	0.5	5.5	5.2	0.9	10.2
Potassium content [mg/100 g]	19.8	6.6	38.3	21.5	6.9	49.1	20.6	9.0	36.2
Magnesium content [mg/100 g]	29.2	5.3	50.6	25.8	3.8	42.5	31.1	6.8	53.7
Calcium content [mg/100 g]	357.1	36.2	629.0	190.7	25.8	356.4	274.3	57.2	511.3

species mainly occurs along the shores of rivers, backwaters and lakes, in swamp forests and wet grasslands (e.g., Hejný 1960, Tutin 1964, Horvat et al. 1974, Shishkin 1974, Davis 1982, Pignatti 1982, Seibald et al. 1992, Adler et al. 1994, Oberdorfer 1994, Tuba, 1995, Lauber and Wagner 1996, Schmeil and Fitschen 1996, Godreau et al. 1999, Matuszkiewicz 2002, Muller 2002, Hagyo 2003, Tzvelev 2006). In Central Europe, it is nowadays frequently restricted to ditch banks, field edges and abandoned grasslands (Oberdorfer 1994), as a result of the deterioration of natural habitats due to the regulation of watercourses, land reclamation and agricultural intensification. Today, most populations in this region are cut off from the natural river dynamics and thereby from winter inundation. In Southern Scandinavia, however, the habitat preferences of the species are different, as it nearly exclusively occupies the shores of the Baltic Sea (Fig. 3; Nordhagen 1939/40, Gillner 1960, von Schantz and Hackman 1983). *E. palustris* tolerates low concentrations of salt (Frank and Klotz 1990, Ellenberg et al. 1991, Oberdorfer 1994), and it occurs under saline conditions also in

inland salt marshes in Hungary (Hagyó 2003), at the shores of the brackish Lago di Burano in Italy (Angiolini et al. 2002), and in many of the habitats in the Lower Volga valley where the mean salt content in 32 plots was about 1% (Golub and Mirkin 1986).

E. palustris mostly grows on calcareous, humous or peaty mud and clayey soils with stagnant moist to alternately wet and drier conditions (Sebald et al. 1992, Oberdorfer 1994). It is highly tolerant of varying nutrient regimes (Frank and Klotz 1990; Table 1), and although the species is described as an indicator for alkaline soils (Frank and Klotz 1990, Ellenberg et al. 1991, Sebald et al. 1992, Oberdorfer 1994), in North-western Germany it mainly occurs on slightly acidic sites (pH 4,13 – 5,24) (Table 1). *E. palustris* is classified as a light-demanding species (Frank and Klotz 1990, Ellenberg et al. 1991, Oberdorfer 1994), but can grow also under more shady conditions, for example in swamp forests or in closed reed beds. The regional classification of *E. palustris* as a somewhat thermophilous species (Frank and Klotz 1990, Ellenberg et al. 1991) corresponds to its natural distribution pattern along the large flood plains providing warmer conditions than the surrounding regions.

Communities

In Central Europe, *E. palustris* is by most authors considered as a characteristic species of the *Veronico longifoliae*-*Euphorbietum palustris* as part of the alliance *Filipendulion* within the order *Molinietalia* and the class *Molinio-Arrhenatheretea* (Oberdorfer 1983, 2001). This association is confined to river corridors and characterized mainly by tall herbs such as the eponymous *Euphorbia* and *Pseudolysimachion* (*Veronica*) *longifolium*. Other authors (e.g., Berg et al. 2004) proposed to assign the association to the alliance *Senecion fluviatilis* within the order *Convolvuletalia*, while Dierschke (1996) stressed its floristic affinity to the class *Phragmitetea*. As *E. palustris* occurs also in other communities such as *Phragmites* reeds, the fringe of willow shrubs and abandoned meadows (Sebald et al. 1992, Oberdorfer 2001), the syntaxonomical affiliation of the species remains unclear.

To obtain a clearer view of the community ecology of the species, we compiled all phytosociological relevés with *E. palustris* from Central and northern Europe that were available to us. The data set is summarized in Table 2 showing a list of the most frequent species associated with *E. palustris* and their constancy values in four different geographic regions. One result emerging from this table is that, in general, the most

frequent companions of the target species belong to the class Phragmitetea (*Phragmites australis*, *Lysimachia vulgaris*, *Iris pseudacorus*, *Phalaris arundinacea*, *Carex acutiformis*, etc.), followed by taxa typical for Filipendulion and Calystegietalia (*Lythrum salicaria*, *Calystegia sepium*, *Stachys palustris*, *Thalictrum flavum*, *Filipendula ulmaria*). Typical Molinio-Arrhenatheretea grassland species, including *Vicia cracca*, *Sanguisorba officinalis*, *Alopecurus pratensis* and *Caltha palustris*, are clearly less frequent. This observation supports the opinion that the Veronico longifoliae-Euphorbietum palustris might be treated as part of the class Phragmitetea (according to Berg et al. 2004 including the syntaxa Filipendulion and Senecion) rather than Molinio-Arrhenatheretea. However, Table 2 also shows that there is a strong geographic differentiation, which is also supported by a TWINSpan classification (results not shown). Whereas most German and the Dutch sample plots (columns 1 and 2) correspond to the above-given description, the composition of Marsh Spurge communities at the species' northern range margin and in the south-eastern part of Central Europe differs. Here, several of the elements of reeds and tall-herb communities are less prominent, and some Phragmitetea species with high frequencies especially in the Netherlands (e.g., *Calamagrostis canescens*, *Lysimachia thyrsiflora* and *Typha latifolia*) are almost completely lacking. In eastern Central Europe (including data from Eastern Austria, Czechia and Hungary), *E. palustris* is often associated with species that are characteristic for wet meadows assigned to the alliances Cnidion and Molinion, such as *Cnidium dubium*, *Allium angulosum* and *Gratiola officinalis*, and *Serratula tinctoria* and *Iris spuria*, respectively. In Scandinavia and in the Baltic area in Germany, as already pointed out, *E. palustris* is largely confined to coastal sites. This is also reflected in Table 2 in which relevés from S Norway, SW Sweden and NE Germany are summarized in column 3: most of the differential species possess a weak, but distinct salt tolerance (Ellenberg et al. 1991) and are characteristic elements of marine drift lines (alliance Agropyro-Rumicion) and other tidal habitats, for example *Elymus repens*, *Angelica archangelica* ssp. *archangelica*, *Potentilla anserina*, *Festuca rubra*, *Atriplex* sp., *Bolboschoenus maritimus*, *Sonchus arvensis* ssp. *uliginosus* and *S. palustris* (Nordhagen 1940, Dahl and Hadac 1941, Gillner 1960, Rehbein and Berg 1999). The coastal distribution is especially striking in Bohuslän in SW Sweden, where *E. palustris* assembles with *Beta vulgaris* ssp. *maritima*, *Crambe maritima*, *Ligusticum scoticum*, *Glaucium flavum* and *Mertensia maritima* on boulder and shingle shores (Rydin et al. 1999).

Table 2 - Constancy table of the most frequent plant species in 472 sample plots with *Euphorbia palustris* in Central and Northern Europe compiled from literature data. The four columns show the relative frequencies (in %) of the species in different sub-regions. Species are clustered into groups, which are ordered according to their presence in, first, the geographic sub-regions, and, second, in different phytosociological syntaxa. C - character species, D - differential species.

Region	Germany [except Baltic sea area]	Netherlands	Eastern Central Europe	N Europe & Baltic sea area in Germany
No. of sample plots	146	196	93	37
<i>Euphorbia palustris</i>	100	100	100	100
Western Central Europe				
<i>Calamagrostis canescens</i> D Phragmitetea	14	57	0	5
<i>Lysimachia thyrsiflora</i> C Phragmitetea	0	40	5	0
<i>Typha latifolia</i> C Phragmitetea	0	41	1	0
<i>Cirsium palustre</i> C Molinietalia	3	34	6	0
<i>Thelypteris palustris</i>	0	35	8	0
<i>Carex paniculata</i> C Phragmitetea	0	33	0	0
<i>Angelica sylvestris</i> ssp. <i>sylvestris</i> Molinietalia	0	28	0	3
<i>Potentilla palustris</i> D Phragmitetea	0	28	0	0
<i>Ventenata dubia</i>	0	27	2	0
<i>Juncus subnodulosus</i>	1	24	1	0
<i>Persicaria amphibia</i>	18	10	6	0
<i>Dryopteris cristata</i>	0	21	0	0
<i>Viola palustris</i>	0	19	0	0
Eastern Central Europe				
<i>Lysimachia nummularia</i>	3	8	32	0
<i>Serratula tinctoria</i> D Molinion	2	0	29	11
<i>Iris spuria</i> C Molinion	0	0	29	0
<i>Potentilla reptans</i> D Cnidion	12	4	20	0
<i>Cnidium dubium</i> C Cnidion	1	0	18	0
<i>Galium verum</i> D Molinion	2	0	17	5
<i>Molinia arundinacea</i> D Molinion	0	0	16	0
<i>Allium angulosum</i> C Cnidion	3	0	14	0
<i>Leucojum aestivum</i>	1	1	12	0
<i>Alisma plantago-aquatica</i> D Phragmitetea	0	3	12	0

Region	Germany [except Baltic sea area]	Netherlands	Eastern Central Europe	N Europe & Baltic sea area in Germany
No. of sample plots	146	196	93	37
<i>Gratiola officinalis</i> C Cnidion	0	0	10	0
<i>Viola elatior</i> C Cnidion	0	0	10	0
<i>Trifolium medium</i>	0	0	10	0
N Europe & NE Germany				
<i>Elymus repens</i>	12	3	3	51
<i>Angelica archangelica</i> ssp. <i>archangelica</i>	0	0	0	46
<i>Potentilla anserina</i>	1	2	10	43
<i>Festuca rubra</i>	1	3	5	38
<i>Sonchus palustris</i> C Convolvuletalia	0	11	0	32
<i>Sonchus arvensis</i>	1	0	1	29
<i>Rumex crispus</i>	3	3	6	24
<i>Galeopsis tetrahit</i>	1	7	0	24
<i>Galeopsis bifida</i>	1	7	0	22
<i>Atriplex littoralis</i>	0	0	0	19
<i>Agrostis gigantea</i>	4	1	4	16
<i>Oenanthe lachenalii</i>	0	0	0	16
<i>Aster tripolium</i>	0	0	0	16
<i>Bolboschoenus maritimus</i>	1	0	0	14
<i>Artemisia vulgaris</i>	0	1	0	14
<i>Atriplex prostrata</i>	3	0	0	11
<i>Tripleurospermum perforatum</i>	0	0	0	11
Molinietalia				
<i>Caltha palustris</i> C Calthion	3	27	15	0
<i>Lathyrus palustris</i>	8	12	10	5
<i>Silene flos-cuculi</i>	1	9	11	8
<i>Epilobium palustre</i>	2	16	1	3
<i>Myosotis scorpioides</i>	2	8	12	0
<i>Molinia caerulea</i>	1	9	5	5
<i>Juncus effusus</i>	1	6	2	11
<i>Succisa pratensis</i> D Molinion	2	5	11	0
<i>Inula salicina</i> C Molinion	5	1	10	0

Region	Germany [except Baltic sea area]	Netherlands	Eastern Central Europe	N Europe & Baltic sea area in Germany
No. of sample plots	146	196	93	37
Molinio-Arrhenatheretea				
<i>Vicia cracca</i>	26	8	24	46
<i>Sanguisorba officinalis</i>	15	5	24	0
<i>Alopecurus pratensis</i>	17	6	20	0
<i>Poa pratensis</i> agg.	5	1	15	19
<i>Cardamine pratensis</i>	1	25	11	0
<i>Lathyrus pratensis</i>	9	1	17	8
<i>Ranunculus acris</i>	0	3	18	5
<i>Galium album</i>	5	2	4	14
<i>Achillea millefolium</i>	1	2	9	11
<i>Holcus lanatus</i>	1	14	2	5
<i>Rumex acetosa</i>	2	11	8	0
<i>Festuca pratensis</i>	0	1	10	8
<i>Prunella vulgaris</i>	0	5	13	0
Convolvuletalia & Filipendulion				
<i>Lythrum salicaria</i>	41	68	54	5
<i>Calystegia sepium</i>	41	72	26	48
<i>Stachys palustris</i>	27	33	33	8
<i>Thalictrum flavum</i>	23	25	22	5
<i>Filipendula ulmaria</i>	25	32	8	5
<i>Eupatorium cannabinum</i>	1	31	8	24
<i>Valeriana officinalis</i>	12	1	15	8
<i>Pseudolysimachion longifolium</i>	17	1	12	0
Phragmitetea				
<i>Phragmites australis</i>	53	85	34	73
<i>Lysimachia vulgaris</i>	60	47	49	14
<i>Iris pseudacorus</i>	44	65	30	24
<i>Phalaris arundinacea</i>	67	28	28	16
<i>Galium palustre</i>	23	46	51	19
<i>Carex acutiformis</i>	20	38	18	16
<i>Carex riparia</i>	16	12	28	22
<i>Carex acuta</i>	28	14	22	0

Region	Germany [except Baltic sea area]	Netherlands	Eastern Central Europe	N Europe & Baltic sea area in Germany
No. of sample plots	146	196	93	37
<i>Peucedanum palustre</i>	0	49	1	16
<i>Carex elata</i>	8	42	13	0
<i>Lycopus europaeus</i>	2	26	22	3
<i>Poa palustris</i>	10	8	24	0
<i>Carex disticha</i>	16	8	9	3
<i>Glyceria maxima</i>	13	9	12	0
<i>Sium latifolium</i>	2	8	12	11
<i>Scutellaria galericulata</i>	5	16	3	3
<i>Rumex hydrolapathum</i>	2	4	15	8
<i>Rorippa amphibia</i>	4	4	10	0
<i>Oenanthe aquatica</i>	1	2	10	0
Others				
<i>Symphytum officinale</i>	49	31	41	3
<i>Urtica dioica</i>	36	22	28	27
<i>Rubus caesius</i>	37	7	30	5
<i>Mentha aquatica</i>	4	28	14	35
<i>Cirsium arvense</i>	26	7	15	24
<i>Galium aparine</i>	16	13	10	22
<i>Poa trivialis</i>	12	28	9	11
<i>Solanum dulcamara</i>	11	18	15	11
<i>Glechoma hederacea</i>	23	6	10	3
<i>Ranunculus repens</i>	7	5	34	8
<i>Deschampsia cespitosa</i>	8	4	28	3

However, *E. palustris* shows a different community ecology on the Swedish island of Öland: here, under continental climatic conditions, the species grows in wet meadows and along mires on calcareous soils characterized by a strongly fluctuating water table, sites with a high ecological and floristic affinity with the SE European communities.

The literature from other parts of Europe is in agreement with the community affiliation of *E. palustris* as depicted from the synoptic table. In Western France, the species accompanies communities of the *Phragmites australis*, *Magno-Caricion elatae*, *Molinietalia caeruleae*, *Molinio-Holoschoenion* and *Convolvulion sepium* (Lombard and

Arnal 2001). It is also reported from managed alluvial grasslands corresponding to the Senecioni-Brometum, but today shows a higher abundance in abandoned grasslands with *Filipendula ulmaria*, *Althaea officinalis* and *Thalictrum flavum* (Muller 2002).

On the Balcan peninsula, *E. palustris* exhibits a broader habitat spectrum. The species occurs in sedge swamps (e.g., *Caricetum elatae*, *Caricetum gracilis*, *Caricetum ripariae*, *Carici-Menyanthetum*), reeds (*Phragmitetum*), willow shrubs and open alluvial forests and their mantle communities (*Salicetum albo-triandrae*, *Populetum nigro-albae*, *Leucojo-Fraxinetum*, *Euphorbio palustris-Crataegetum nigrae*, *Filipendulion ulmariae*, *Filipendulo-Petasition*) as well as grasslands (*Bromo-Cynosuretum cristati*, *Agrostio-Beckmannion*, *Deschampsietum cespitosae*, *Ventenato-Trifolietum pallidi*, *Molinietum arundinaceae*) (Horvat et al. 1974, Dragulescu 1995, Dragulescu and Macalik 1997, Hagyó 2003, Čarni et al. 2004, Dimopoulos et al. 2005). For Eastern Europe, information is available for the Desna floodplain (Ukraine, Shelyag-Sosonko et al. 1987) where *E. palustris* is confined to the *Phalaridetum arundinaceae* that covers the periodically flooded narrow hollows. In the Lower Volga valley (Golub and Mirkin 1986, Golub and Saveljeva 1991, Golub and Kuzmina 1997) the species occurs in *Phragmitetea* communities (reed and sedge associations: *Phragmitetum australis*, *Sagittario-Sparganietum*, *Calystegio-Phragmitetum*, *Beckmannio-Rorippetum austriacae*, *Cirsio incani-Caricetum distichae*), in *Molinio-Arrhenatheretea* communities (wet meadows: *Rumici-Eleocharitetum palustris*, *Rumici-Tragopogonetum orientale*, *Stachyo-Achilletum septentrionalis*), in *Glycyrrhizetea glabrae* communities (steep meadow slopes: *Cichorio-Lactucetum serriolae*, *Lepidio-Cynodontetum*), in halophytic *Bolboschoenetea* communities (*Bolboschoeno-Inuletum britannicae*, *Bolboschoeno-Glycyrrhizetum echinatae*), and also in floodplain oak-elm forests (*Poo angustifoliae-Quercetum roburi*).

Distribution range

Within its distribution range, *Euphorbia palustris* occurs in regions varying strongly in continentality (Fig. 3), showing a kind of azonale pattern in this respect. Table 3 lists statistics for selected climatic variables that seem important for the limitation by abiotic factors at the distribution range scale.

Table 3 - Climate statistics for selected variables throughout the distribution range of *Euphorbia palustris*. Climate data are extracted from WORLDCLIM (Hijmans et al. 2005). *AMT* = annual mean temperature, *TMIN* = minimum temperature of coldest month, *MT_WQ* = mean temperature of warmest quarter, *AP* = annual precipitation, *MP_CQ* = mean precipitation of coldest quarter. Variable minimum, 5th percentile, 95th percentile, maximum, mean, range, standard deviation, and coefficient of variation are given.

Climate variable	min	P 5th	P 95th	max	range	mean	sd	cv
<i>AMT</i> [°C]	2.14	4.10	11.24	18.67	16.53	7.83	2.22	0.28
<i>TMIN</i> [°C]	-20.80	-16.10	-1.20	6.80	27.60	-8.67	4.59	-0.53
<i>MT_WQ</i> [°C]	12.40	16.47	22.56	27.32	14.92	19.41	1.82	0.09
<i>MAP</i> [mm]	160	391	829	1982	1822	577.68	144.86	0.25
<i>MP_CQ</i> [mm]	34	86	190	583	549	123.04	37.84	0.31

The lowest mean annual temperatures occur at the easternmost range limit in the southern Ural mountain region (Bashkortostan). They are the consequence of the long and cold winters with mean minimum temperatures down to -20 °C. Highest mean annual temperatures (14-18°C) are measured in S European lowlands below 45° northern latitude. Here, *E. palustris* is restricted to isolated coastal wetland habitats. Along with the wide continentality amplitude, the species occurs under much varying precipitation regimes. The lowest values (160-340 mm/a) are measured at the lower Volga and Ural valleys in the steppe zone of the south-eastern range sector, where the species is independent of regional precipitation due to its restriction to areas inundated by spring floods fed from snowmelt in northern regions. Because of this spatial difference between the often mountainous catchment areas and the lowland river habitats, the within-range winter precipitation values (*MP_CQ*), ranging between 34 and 583 mm, are highly variable and seem to be of low importance. Maximum precipitation (1000-2000 mm/a) is present only at higher elevations (perhaps partly inexact geo-referenced) exposed to moist western air masses (northern Spain, Jura Mountains, northern Italy, western Balkan Peninsula, and the Colchic region). While the species appears to be rather independent of precipitation (*cv* = 0.25), it shows relatively high summer warmth requirements (*cv* = 0.09). Minimum values of below 15 °C are confined to isolated occurrences at higher elevations (but see above) and the coastal populations in Norway. However, 90% of the geographical distribution range is situated at locations with mean summer temperatures between 16.5 and 22.5 °C (*MT_WQ*, Table 3).

Response to abiotic factors

In Central Europe, *Euphorbia palustris* is frequently recorded from surrogate habitats in which abiotic conditions are less favourable than those in its natural habitats. The species is, due to its longevity, able to exist under these deteriorated environmental conditions for decades, although recruitment of the populations is impossible in most cases.

In a study of twelve populations of *E. palustris* in North-western Germany over three years, the differences in seed production across sites between years were strongly affected by soil quality via weather conditions (Wärner et al. submitted; Table 1), particularly in terms of excessive or relatively low precipitation and its influence on soil moisture. Seed production was highest (on average 812 seeds per plant) when weather conditions conformed to the long-term mean. As the species prefers relatively dry conditions in summer in contrast to a preference for floodings in winter (Ellenberg et al. 1991), constantly high soil moisture over spring and summer reduces growth and seed production. The negative relationship between the latter and nitrogen content is possibly caused by the low activity of soil organisms under wet conditions making the nutrients unavailable to the plants. The number of shoots per plant increased with decreasing C/N ratio. The recruitment in the populations (proportion of seedlings), however, declined with decreasing C/N ratio and content of organic matter (carbon content). Furthermore, the number of seedlings was positively affected by winter floodings, providing free space for seed germination and seedling establishment.

While soil pH and phosphate content had no effects on plant performance (Wärner et al. submitted), both parameters had a significant impact on the growth and survival of individuals in a re-introduction experiment. Under extreme shade in reed populations, seed production is reduced and plants grow to above-average height to reach to the light. Recruitment was basically not observed under these conditions.

Life cycle and biology

Life cycle

Euphorbia palustris is a long-lived hemicryptophyte, only occasionally it can behave as a geophyte (Krumbiegel 2002), as the horizontal stem axes separated from the rootstock have the ability to overwinter in the soil and to resprout in the following growing sea-

son. The rootstock of a plant that had been dug out and divided into several pieces continued to grow after re-planting. The species' life span is not well known; however, observations within the plant inventory programme of Lower Saxony in Germany indicate that it may live for several decades. A life span of 5 to 50 years is given by Kleyer et al. (2008). A thorough age determination through the analysis of annual rings of the root is impossible since the species does not form a persistent root (see Morphology).

In addition to sexual reproduction via seeds, *Euphorbia* may reproduce vegetatively by forming short horizontal stem axes that emerge from the soil (C. W., personal observations; von Kirchner et al. 1908). However, in 12 natural populations that were observed over a period of three years, this way of clonal growth was observed only in 1% of all surveyed individuals. This finding is corroborated by microsatellite genotyping of all individuals in another population in which we found only two neighbouring individuals out of 100 with the identical genotype, indicating a low fraction of clonal growth within sites. Thus, successful reproduction is most likely dependent on seeds. During its generative life cycle stage the species normally flowers and forms seeds each year. Abiotic factors like unfavourable weather conditions, however, may inhibit flowering and seed set (Wärner et al. submitted).

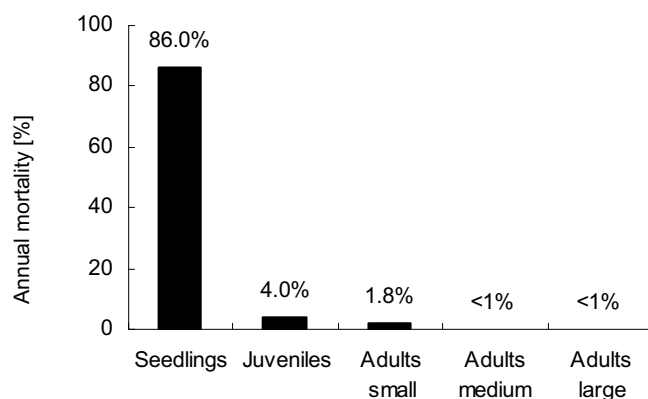


Fig. 5 - Annual mortality of seedlings, juveniles and adult (small, medium, large) plants of *Euphorbia palustris*. Demographic data were gathered between 2005 and 2007 in one dynamic and two static natural populations (with $n > 100$ plants) in North-western Germany.

Detailed investigations of the demography of *E. palustris* were conducted in relatively large populations at three sites in North-western Germany. Two of the populations can be considered as static because of a lack of recruitment, whereas one population with seedling establishment was classified as dynamic. Four different life cycle stages are distinguished: seed, seedling, juvenile, and adult (small, medium, large). At the juvenile stage, we also found dormant individuals (2.5%) whose above-ground organs were not

visible for a whole growing season. While annual seedling mortality is high (86%), the mortality of juveniles and adults falls below 5% (Fig. 5). Individuals grow in height until they have reached the adult stage and a medium size, then only the number of flowering shoots increases (Fig. 6). Senescent plants decrease in height, the number of shoots, and flowering shoots. Also in younger established plants the number of shoots may decrease in unfavourable years, even though plant size generally increases up to a certain age (Table 4).

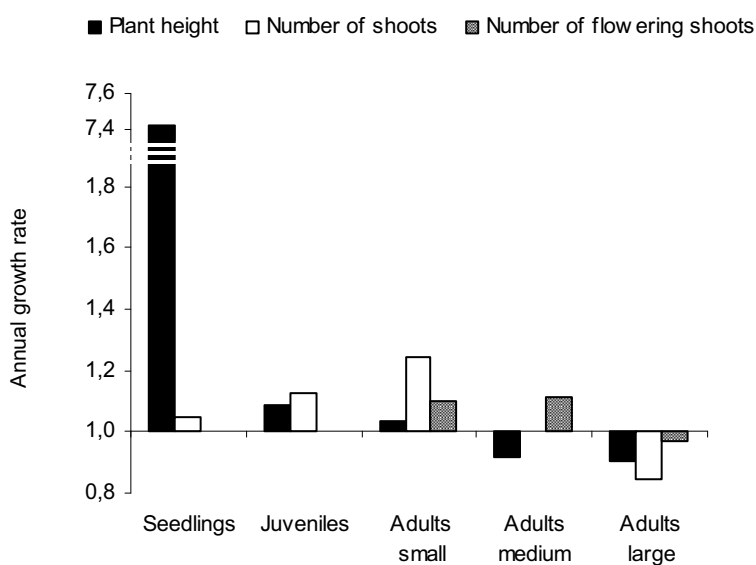


Fig. 6 - Annual growth rates ($\lambda = A(t)/(A(t_0)^{1/N})$) of plant height, the number of shoots and the number of flowering shoots of seedlings, juveniles and adult (small, medium, large) plants of *Euphorbia palustris*. Demographic data were gathered between 2005 and 2007 in three natural populations in North-western Germany ($n > 100$ plants).

Table 4 - Mean changes in total plant height, the number of shoots and the number of flowering shoots (only adult plants) of one dynamic (with recruitment) and two static (without recruitment) populations of *Euphorbia palustris* in North-western Germany. Demographic data were gathered in 2005, 2006 and 2007 ($n > 100$ in each population).

Plant traits		Dynamic population	Static population I	Static population II
Mean % change in total height	2005-06	47.4	-7.4	-19.6
	2006-07	36.6	10.9	10.9
Mean change in no. of shoots	2005-06	1.73	1.69	-7.58
	2006-07	0.40	-2.32	1.66
Mean change in no. of flowering shoots	2005-06	-0.71	2.45	5.91
	2006-07	-0.47	-2.20	-7.18

Spatial distribution of plants within populations

Although vegetative reproduction via horizontal stem axes is possible, lateral growth is limited and individuals are therefore usually easily recognisable. Owing to its shrub-like habit, one adult individual may occupy an area of up to 2 m². This large plant size causes the low average population density of 0.46 individuals / m². Static and aged populations (see Life cycle) are even less dense with only 0.17 individuals / m², whereas dynamic populations may reach an average density of 1.31 individuals / m².

Phenology

In North-western Germany, shoot elongation of the deciduous *Euphorbia palustris* starts in March, and in early April the first leaves are unfolded. Shoots grow from above-ground buds that have been initiated in the previous year. The main period of vegetative growth lasts from mid-April to mid-June. Inflorescences appear in late April, reach peak flowering in mid-May and finish flowering in mid-June. At the time of fruit ripening (from the end of May till the end of July), sterile branches already overtop the inflorescences because shoot elongation ends only after seed maturity has started during the first half of July. All bracts turn green with seed maturity. When all seeds are shed at the beginning of August the above-ground parts start to degenerate. In autumn, the leaves sag from the crimson-coloured shoots which determine the colour of the whole population. The shoots completely die off during winter but remain on the plant as grey stems and wither for the most part over the course of the following growing season.

Reproduction

In general, *Euphorbia palustris* reaches sexual maturity at the beginning of the third or fourth growing season. Occasionally, flowering occurs already in one year-old individuals. The species is monoecious, the reduced female and male flowers form a pseudoflower (cyathium) and show pronounced protogyny at the level of the cyathium.

However, within one inflorescence, male and female flowers are present at the same time potentially allowing for geitonogamy, but pollination experiments demonstrated that caged and manually self-pollinated flowers do not generate any seeds ($n = 8$ and $n = 9$ inflorescences) indicating pronounced self-incompatibility. The species, thus, has an obligate outcrossing breeding system. *E. palustris* is exclusively pollinated by insects, mostly by flies (Muscidae, Conopidae; Knuth, 1898). Typical pollinators also include

Table 5 - Number, weight and size of seeds. Wärner et al. 2009: The number and weight of seeds was measured in populations of the Weser and Elbe systems in North-western Germany in 2005, 2006 and (2007) (number $n \geq 180$ plants; weight $n \geq 2000$ seeds). Klotz et al. 2002: Data on seed size was obtained from the database BiolFlor. Hölzel and Otte 2004a: Seed weight was calculated for populations of the northern Upper Rhine River ($n \geq 1000$). Bojňanský and Fargašová 2007: Data on seed size were collected in the Carpathian Mountains. —: no data available.

Seed trait	Number			Weight [mg]			Size (length x width x thickness) [mm]			
	Year	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean	Minimum	Maximum
<i>Wärner et al. 2009</i>	2005	812 ± 840	159	325	9.7 ± 2.2	5.6	13.4	—	—	—
	2006	302 ± 217	49	753	9.4 ± 1.2	7.6	11.4	—	—	—
	2007	198 ± 223	0	714	—	—	—	—	—	—
<i>Klotz et al. 2002</i>	—	—	—	—	8.2	—	—	3.3 x 2.7 x 2.6	2.8 x 2.4 x 2.2	3.7 x 3.2 x 3.2
<i>Hölzel and Otte 2004a</i>	—	—	—	—	10.5	—	—	—	—	—
<i>Bojňanský and Fargašová 2007</i>	—	—	—	—	—	—	—	—	3.2 x 2.6	3.7 x 3.0

syrrhids, as well as beetles (Scarabidae, Dermastidae, Chrysomelida, Cerambicidae, Curculionidae, Elateridae), wasps (Braconidae, Tenthredinidae, Chrysidae), ants (Formicidae) and medium-tongued bees (Apidae). Vroege et al. (1987) report a possible case of arachnophily (spider pollination). Insects are attracted by the ostentatious yellow nectar-glands and bracts forming a showy inflorescence. The nectar contains fructose, glucose and sucrose (Papp 2004a). A characteristic weak musty odour may preferentially attract flies. The species' self-incompatibility system and its dependence on insect pollination were identified as the most important reasons for the reduced reproductive success of small populations in North-western Germany (Wärner et al. submitted).

A female flower has three ovules, each fruit thus usually contains three seeds. More rarely, two or four seeds are formed in a flower. Plants analyzed in 7 populations near Halle (Saale) had on average 14.5 flowering shoots (SD $\pm$ 12.3, $n = 47$), each bearing 146 cyathia ($\pm$ 68) and producing 109 seeds ($\pm$ 95). Only 38 ($\pm$ 51) seeds per inflorescence (i.e., 28.5%) were blackish and proved to be viable, while 72.5% were pale brown or brown and non-viable due to herbivory or an aborted embryo. The seed : ovule ratio

was 0.244.

The number of fruits (159 ± 388 , $n = 591$) and seeds (477 ± 1.165 , $n = 591$; Table 5) per plant varied significantly between three years in populations of North-western Germany, whereas the weight of well-developed viable seeds ($9.50 \text{ mg} \pm 2.19$, $n = 4.480$) calculated from data from two growing seasons changed only marginally. Mean seed mass values given in other studies, however, differed considerably from our own data. On average, seeds are 3.3 mm long, 2.7 mm wide and 2.6 mm high (Table 5).

The primary dispersal of seeds is autochorous and achieved by the bursting of the desiccated capsules and subsequent centrifuging. Seeds can be transported up to a few metres by this mechanism. As seeds fall relatively fast to the ground at a terminal velocity of 4.08 m / s ($\text{SD} \pm 0.04$, $n = 50$), wind dispersal is unlikely (Poschlod et al. 2003). Owing to their oleiferous elaiosom (caruncula), seeds may also be dispersed by foraging ants. Even though floodplains are not considered as typical habitats for these animals, the summer drought may enable the ants to colonize the sites during seed maturity. As *E. palustris* often occurs along rivers, long-distance dispersal by water is possible. Seeds contain aerenchyma and float on water. Buoyancy experiments showed that 50% of the germinable seeds still floated after 7 days and 30% longer than 50 days. Moreover, zoochorous dispersal of seeds attached to the plumage of birds was speculated about as another potential agent for long-distance dispersal (Hegi 1975, von Kirchner et al. 1908), but this seems unlikely due to the high weight and large size of the seeds. Up to now, detailed studies of the dispersal mechanisms and distances are lacking.

Germination

Under experimental field conditions (Hölzel and Otte 2004a) and in the laboratory, the seeds of *Euphorbia palustris* showed the ability to germinate directly after shedding: Seeds sown in an experiment germinated to more than 80% in July and August of the same growing season, while only a small proportion germinated in the springs of the following two growing seasons. In contrast, in natural populations in North-western Germany, germination was observed only in spring.

When seeds are dry-stored at room temperature for several weeks, most of them fall in a secondary induced physical dormancy (Hölzel and Otte 2004a). Experiments in a growth chamber showed that only 18% of the seeds germinated after storage and most seeds were dormant (Fig. 7), but stratification increased the germination percentage

considerably. Nearly all seeds (95%) germinated if they were treated with a high concentration (2 mg / ml) of Gibberelline acid (GA). Wet stratification at 4 °C for six or 12 weeks resulted in a germination percentage of 74%. The start and velocity of germination, however, were enhanced under cold-wet stratification (4 °C), as most seeds already germinated on the second day of the experiment (Fig. 7). After a treatment with 2 mg/ml GA, a similar germination percentage was not reached before day ten. Highest germination rates were achieved under moist conditions at a light and temperature regime of 14 h / day at 20-25 °C and 10 h / night at 15-20 °C.

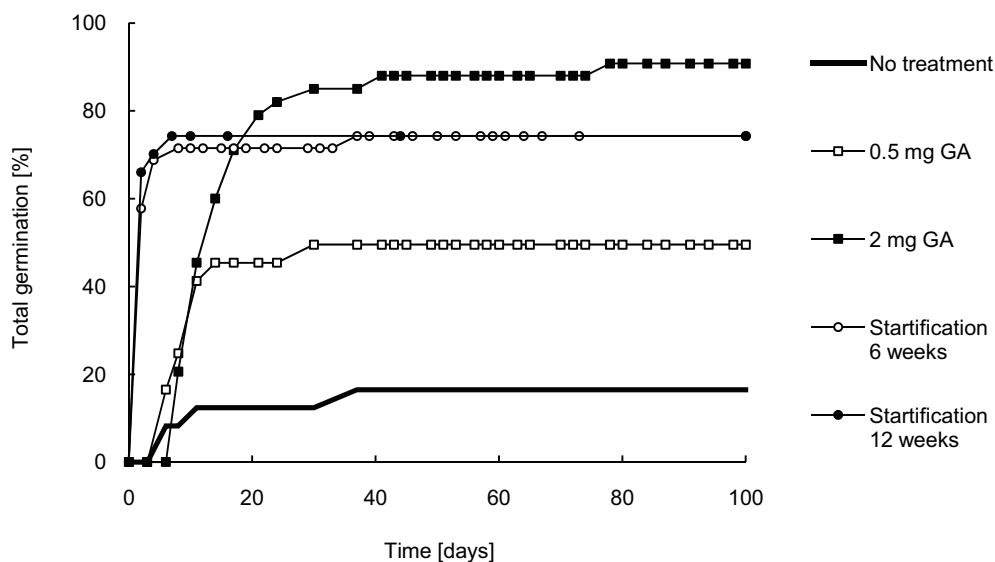


Fig. 7 - Total germination of a mixture of 100 seeds collected in 8 *Euphorbia palustris* populations in North-western Germany. The germination curves show the chronological sequence over 100 days for different pre-treatment of the seeds: no treatment, treatment with 2 mg/ml Gibberellin acid, treatment with 0.5 mg/ml Gibberellin acid, cold-wet stratification for 6 weeks and cold-wet stratification for 12 weeks. Seeds were placed on a double layer of wet filter paper in Petri dishes and kept in a growth chamber at a temperature and light regime of 14 h/day at 25 °C and 10 h / night at 20°C.

The radicle emerged, at the earliest, two days after the start of the germination experiment. During the following seven days, the radicle kept on elongating until the two cotyledons were unfolded. The species forms a long epicotyl and a thick hypocotyl (Fig. 2) and belongs to the epigeal germination type (Rauh 1937). In a common garden experiment it was shown that seedlings in their first year can form up to 14 leaves and reach a height of up to 10 cm.

In the field, seeds of *E. palustris* are only present in the upper layer (0-5 cm) of the soil with a maximum of 70 seeds / m² (Hölzel and Otte 2004b). The authors calculated a seed accumulation index, which expresses the tendency of a species to accumulate seeds in the soil on a scale from 0 (transient) to 100 (persistent). According to this index, the seed bank of *E. palustris* with a value of 16 was classified as more or less transient.

In natural populations, germination is dependent on open sites originating from winterly inundations. In North-western Germany, most populations of *E. palustris* are cut off from flooding events and seedling establishment is thereby hampered, causing the populations to be over-aged and static.

Response to competition and management

According to the model of primary ecological strategies after Grime (1988), *E. palustris* is classified as intermediate between a competitor and a stress-tolerator (Frank and Klotz 1990, Klotz et al. 2002). This strategy is characteristic for perennial competitive plants in extreme habitats, for example swamps. *Euphorbia* is suppressed by highly dominant, tall-growing species like reeds and willows. Annual autumnal mowing of reed resulted in an increase in seed production from 159 seeds per plant to 280 in the following growing season and to 380 two seasons later, even though, in other, untreated populations of the region, seed production decreased during this time due to unfavourable weather conditions. If the species has accomplished reproduction, mowing is not deleterious for its viability in spite of its general sensitivity to mowing. Furthermore, the species is sensitive to trampling but very tolerant of grazing (Klotz et al. 2002). Muller (2002) suggested, in order to preserve the species, to abandon land use, to cut only the colonizing shrubs from time to time, or to conduct only a low-intensity agricultural management in its habitat. The crucial factors for the permanent survival of a population are, however, winterly inundation in combination with summer drought, i.e., conditions typical for the natural sites of the species. Only these conditions enable seedling establishment and avoid competitive replacement by other species. As most populations at present suffer from the lack of winter flooding, habitats should be re-attached to the natural river dynamics.

Small population size has strong negative effects on the reproductive success of *E. palustris*, possibly due to reduced pollinator services in small populations (Winter et al. 2008, Wärner et al. submitted). Thus, a further important management measure for in-

creasing population growth would be the enlargement of suitable habitats, possibly supported by augmentation of additional plant material. Another possible, but labour-intensive measure to preserve *E. palustris* would be the reintroduction of the species to restored sites where the species has gone extinct. A reintroduction experiment showed that the plants used in such conservation measures should be at least one year old to enhance survival and long-term establishment.

Herbivores and pathogens

In North-western Germany, damage by browsing deer was observed from June onwards. Leaves and infructescences were browsed while the stems were spared. Between 20 and 71% of the plants in the affected populations were damaged, but this appeared to have no effect on the fitness and viability of individuals in the following growing season. As most populations were static, it was not possible to detect a negative impact on the recruitment of populations through the reduction of seeds.

It appears that *E. palustris* is only weakly affected by phytophagous insects, most likely due to the deterrent effect of latex production. In our field studies in Germany insect feeding on the leaves was not observed. Together with the habitually similar species *E. virgata* and *E. lucida*, *E. palustris* is the sole food plant for *Chamaesphecia palustris* and *C. hungarica* (Lepidoptera, Sesioidea) which feed on roots and stems (FUNET 2009). *Aphthona violacea* (Coleoptera, Chrysomelidae) has been reported to be oligophagous on *E. palustris* and *E. lucida* (cited in Nowierski et al. 2002), and *Oberea euphorbiae* (Coleoptera, Cerambycidae) to be monophagous on *E. palustris*. Remaudiere and Leclant (2000) report on an aphid species *Acyrtosiphon (Aphis) euphorbiae* to feed on *E. palustris* in Turkey. Bud galls on the species are formed by *Drasineura schulzei* (Diptera, Cecidomyiidae) (Gagne 1990). Larvae of an unknown insect feeding on the embryo within the seeds were found in 29% of all seeds in populations near Halle, Germany.

Phytopathogenic fungi known to attack *E. palustris* include the powdery mildew *Podosphaera (Sphaerotheca) euphorbiae* (Erysiphales) (Nagy and Kiss 2006). Another species-specific fungus is *Plagiostoma euphorbiae* (Diaporthales) (Sogonov et al. 2008). In one of three growing seasons, an orange-coloured, not yet identified fungus was found in several populations in North-western Germany. It caused the withering of the infructescences and inhibited the maturation of the seeds of many plants.

Papp (2004b) found an antimicrobial effect of plant extracts from *E. palustris* against the bacteria *Bacillus subtilis*, *Staphylococcus aureus*, *Escherichia coli* and *Candida albicans*.

Mycorrhiza

No information available.

Physiological data

No information available.

Biochemical data

All parts of *E. palustris* contain latex, a characteristic of the genus *Euphorbia*. It partly consists of different terpene esters (e.g., 20-desoxyingenol) that are, depending on the species, slightly or highly caustic and skin-irritant, and have tumor-enhancing qualities. Data on the effects of the latex of *E. palustris* is scarce, but it seems that the above-mentioned properties are only weakly pronounced in this species. Most likely, the latex protects the plants against phytophagous insects and snails. Although the species is described as poisonous to grazing animals (List and Hörhammer 1973), intensive herbivory by deer and the absence of cutaneous reactions indicate that the latex of this species has only weak effects on mammals and humans. When sap gets into the eye, however, burning or stinging pain with blurred vision has been reported (Eke et al. 2000) and wearing eye protection is recommended when working with *Euphorbia* species.

Bondarenko et al. (1969) found different phenol compounds in the latex of the above-ground parts of *E. palustris* and identified them as quercetin, kaempferol, myricetin, steppogenin, (+)-robidanol, (+)-robidanol gallate, gallic acid, hyperoside, isomericitrin, stepposide, 3-rhamnoglycosides of quercetin and 3-rhamnoglycoside of kaempferol. In addition, the tanning agent catechine and phorbine were extracted from the plant (Nordal and Ogner 1964). The root stocks contained 21-23% tanning agents (cited in Hegenauer 1966). The combination of flavonol glycosides, stepposide and robidanol gallate is known to release muscle cramps, to enhance the excretion and the function of the choler and to increase capillary strength. In general, flavonoids, for example as quercetin, kaempferol and myricetin, feature antioxidant activities and function as a protection from herbivores, bacteria, fungi and viruses.

Genetic data

E. palustris is diploid ($2n = 2x = 20$). Genetic variability was analysed at 7 microsatellite loci (Durka in press) in 23 local populations in two German regions (Wärner et al. submitted, Durka unpubl. results). Measures of genetic diversity (mean values for number of alleles $A = 5.2$, expected heterozygosity $H_e = 0.67$, inbreeding coefficient $F_{is} = -0.03$) showed high levels of within-population diversity and values typical for outcrossing species. While allelic diversity (A) was positively correlated with population size, indicating genetic drift, expected heterozygosity (H_e) was not. Local populations were strongly differentiated genetically in the two German regions studied with $F_{ST} = 0.228$ and 0.139 and standardised $F_{ST}' = 0.667$ and 0.506 , respectively. Genetic distance among populations was only weakly correlated to geographic distance in one region. Overall, these analyses show that genetic drift is strong, leading to a loss of diversity within small populations, and that current amounts of gene flow among sites cannot counteract genetic drift. Consequently, gene exchange by pollen or seed should be facilitated by site management enabling functional connections by flooding.

Hybrids

Hybrids of *E. palustris* have not been reported so far.

Status of the species

Although *E. palustris* is a relatively rare species throughout its entire distribution area and occupies sites that are heavily affected, at least in densely populated Central Europe, by human influence, it is neither included in the IUCN red list of threatened species (IUCN 2009) nor in the compilation of Central European plants requiring special attention from nature conservation authorities (Schnittler and Günther 1999). However, the species is mentioned in four national Red lists: According to IUCN-criteria, it is categorized as vulnerable in Germany (Ludwig and Schnittler 1996; for its decline see Fig. 4), the Netherlands (Weeda 1990), Switzerland (Moser et al. 2002) and Austria (Niklfeld, 1999), not only due to its rarity, but also to the ongoing loss and deterioration of its habitats along the flood plains. The species is characterized as generally rare and significantly declining in France (Lombard and Arnal 2001), where it is protected by law in several provinces. Furthermore, *E. palustris* is protected at the national level in Germany (Bundesamt für Naturschutz 2005). Here, the following processes are recog-

nized as being responsible for its decline: (i) cultivation, (ii) peat and soil mining, (iii) destruction of particular small-scale habitats (e.g., fringes, ditches, hedgerows), (iv) melioration, drainage and afforestation of wet meadows, and (v) grassland transformation into crop fields (Korneck et al. 1998). In North-western Germany where the species is critically endangered, the most important reasons for its decline are, apart from habitat fragmentation, the regulation of watercourses and lowering of the ground water table. In addition, winterly inundation is essential for the recruitment of the populations. As a consequence of the cut-off from flooding dynamics, most populations in this region are over-aged and static and occur in surrogate habitats as ditch banks, field edges and abandoned grasslands. The consequence is that the species will, in spite of its longevity, continue to decline steadily. Only selective management measures might stop or reverse this development.

Loss of populations is reported also from southern range parts. A decline appears to take place in Catalonia due to habitat alteration and destruction (Sáez and Soriano, 2000). All occurrences in Southern Italy refer to historical findings that could not be confirmed in recent times (Marchioli et al. 2000). The localities Zambana and Rovereto in Northern Italy (Trentino) are reported by Prosser and Sarzo (2002) to have gone extinct. Several of the populations shown for Friuli Venezia Giulia (Poldini 2002) and for Venetia-Oriental (Zanetti 1997) are also indicated as having disappeared. Most of the isolated lake-wetland occurrences in Turkey are highly endangered by human impact, and several of the lakes dried out. One of the isolated outposts in the extreme southeast was destroyed by the construction of an airport.

Owing to its large colourful inflorescence and high stature, *E. palustris* is also used as an ornamental plant (Bosi et al. 2009). It has proved to be particularly successful when planted into native grasslands to enhance visual appeal of urban parks (Hitchmough 2009). Today the species is commercially traded worldwide for gardening of terrestrial sites, ponds and wetlands. Furthermore, *E. palustris* is also used as medicinal plant. The root is applied against fever and the latex against warts (List and Hörhammer 1973). Whether and how these human activities have affected or will influence populations in natural habitats or enable invasive spread outside its natural range is unknown.

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Zusammenfassende Diskussion und Empfehlungen für den Naturschutz



Oben links: Auspflanzen einer einjährigen nachgezogenen Euphorbia palustris zur Wiedereinbürgerung (Foto: Cord Wärner).

Oben rechts: Aussaatfläche für Samen von Euphorbia palustris. Die Ursprüngliche Vegetation wurde entfernt (Foto: Christina Wärner).

Unten links: Standort zur Wiedereinbürgerung von Euphorbia palustris im renaturierten Quellbereich des Holßeler Bachs im Einzugsgebiet der Weser (Foto: Christina Wärner).

Unten rechts: Nachzucht von Euphorbia palustris-Setzlingen im Frühbeet (Foto: Christina Wärner).

Zusammenfassende Diskussion

Welche Auswirkungen hat Habitatfragmentierung auf ausdauernde Stromtalpflanzen?

Das Hauptziel der vorliegenden Arbeit war es, ein allgemeines Muster für die Reaktion von ausdauernden Stromtalpflanzen auf Habitatfragmentierung zu finden. Dazu wurden vier bzw. fünf gefährdete Stromtalarten hinsichtlich ihres langfristigen Überlebens (*E. palustris*, *P. longifolium*, *S. officinalis*, *S. paludosus*) und ihrer Reproduktion (*E. palustris*, *L. palustris*, *P. longifolium*, *S. officinalis*, *S. paludosus*) in den Flusssystemen der Weser und Elbe untersucht. Eine geringe Populationsgröße und in geringem Maße auch die Isolation der Populationen - beides unmittelbare Folgen der Fragmentierung von Standorten - konnten dabei generell als Ursachen für die Einschränkungen in der Vitalität der Pflanzen identifiziert werden.

Die Ergebnisse zeigen deutlich, dass der starke Rückgang der Untersuchungsarten hauptsächlich auf hohe Aussterberaten kleiner Populationen (≤ 25 Individuen) zurückzuführen ist, während die räumliche Isolation der Populationen keine Relevanz hat (s. Kap. 3.1). Auffällig ist jedoch, dass innerhalb eines Zeitraumes von durchschnittlich etwa 15 Jahren nur wenige der kleinen Populationen in ihrer Größe abgenommen haben und der Faktor Zeit keine Auswirkungen auf den Aussterbeprozess bzw. die Veränderung der Populationsgröße hat. Beides gibt Anlass zu der Vermutung, dass die Populationen aufgrund kurzfristig wirkender Ereignisse unmittelbar ausgestorben sind. Die meisten der möglichen Ursachen für die höhere Aussterbewahrscheinlichkeit kleiner Populationen wie demographische Schwankungen, genetische Drift oder Störung biotischer Interaktionen führen allerdings bei ausdauernden Arten, wenn überhaupt, eher langfristig zum Aussterben und sind deshalb abhängig von der Zeit (vgl. Eriksson und Ehrlén 2001). Lediglich plötzlich auftretende Veränderungen der Umweltbedingungen können diese Populationen direkt auslöschen. Da Umweltkatastrophen für das Untersuchungsgebiet im Untersuchungszeitraum auszuschließen sind, kommen nur menschlich bedingte plötzliche Ereignisse wie Kultivierung, Landnutzungsänderungen oder der Einsatz von Pestiziden für die hohen Aussterberaten in Betracht.

Nichtsdestotrotz gibt die Untersuchung ebenfalls Hinweise darauf, dass die Folgen von Habitatfragmentierung bei ausdauernden Stromtalpflanzen auch zu einem langfristig ablaufenden Aussterbeprozess führen können. Es konnte nämlich gezeigt werden, dass der reproduktive Erfolg aller Untersuchungsarten in kleinen und teils auch isolierten Populationen eingeschränkt ist, möglicherweise aufgrund reduzierter Bestäubung

oder des Verlustes genetischer Diversität (Kap. 3.2). Dieser Umstand führt vermutlich langfristig zum Aussterben der Populationen, da nach Giplin und Soulé (1986) Populationen, die eine bestimmte Größe unterschritten haben, aufgrund abnehmender Pflanzenfitness stetig weiter an Größe verlieren.

Anhand der Art *E. palustris* wurde weiterhin untersucht, inwieweit der Verlust genetischer Diversität verantwortlich für die reduzierte Fitness in kleinen Populationen ist. Dabei hat sich gezeigt, dass kleine Populationen zwar insgesamt eine geringere Anzahl von Allelen aufweisen als große Populationen, aber auf Individuenebene die Allelfrequenz und die erwartete Heterozygotität ähnlich hoch sind (Kap. 3.3). Dies mag darauf zurückzuführen sein, dass selbstinkompatible, langlebige Arten wie *E. palustris* eine geringe Anfälligkeit gegenüber den negativen Effekten kleiner Populationsgröße auf die genetische Konstitution aufweisen. Der Verlust genetischer Diversität aufgrund genetischer Drift wird einerseits durch die Selbstinkompatibilität, die nahe Inzucht ausschließt, minimiert und andererseits durch die Langlebigkeit verlangsamt, da das Ausmaß genetischer Drift von der Anzahl der durchlaufenen Generationszyklen abhängt (Hartl und Clark 1989). Letztere ist bezogen auf die 200-jährige Fragmentierungsgeschichte des Untersuchungsgebietes (s. Kap. 2) bei dieser langlebigen Art immer noch gering. Trotz des kaum sichtbaren Zusammenhangs zwischen genetischer Diversität und Populationsgröße konnte jedoch die Abhängigkeit der Pflanzenfitness von der genetischen Diversität bei *E. palustris* nachgewiesen werden: Die Samenproduktion einer Population sinkt mit abnehmender Anzahl der Allele ihrer Individuen. Damit ist nicht ausgeschlossen, dass im Laufe einiger Generationszyklen, in denen der Verlust genetischer Diversität durch Drift in kleinen Populationen voranschreiten würde, eine schlechte genetische Konstitution u.a. Ursache für eine geringe Fitness der Pflanzen dieser Populationen sein könnte. Für die derzeitige Einschränkung im Samenansatz kleiner Populationen ist jedoch vermutlich eine zu geringe Bestäubung verantwortlich. *E. palustris* ist ausschließlich auf die Bestäubung durch Insekten angewiesen, die kleine Populationen häufig verschmähen, da sie diese als unattraktiv empfinden oder sie erst gar nicht lokalisieren (Sih und Baltus 1987, Jennersten 1988). Dieses Ergebnis lässt sich jedoch nicht uneingeschränkt auf andere Stromtalarten übertragen. Die übrigen vier untersuchten Arten beispielsweise sind zwar auch mehr oder weniger langlebig und ebenfalls insektenbestäubt, lassen jedoch auch Selbstbestäubung zu, so dass ein Verlust genetischer Diversität kleiner Populationen durch Inzucht innerhalb eines Individuums eher möglich wäre als bei *E. palustris*.

Neben den Auswirkungen von Populationsgröße und Isolation wurde ebenfalls der Einfluss der Habitatqualität (u.a. Lichtverfügbarkeit und Bodenparameter) auf das Überleben und die Reproduktion der vier bzw. fünf Arten untersucht. Die Degradierung von Standorten kann eine Folge sowohl der Habitatfragmentierung an sich als auch allgemeiner Umweltveränderungen wie z.B. von Luftverschmutzung oder einer Absenkung der Grundwasserspiegel sein. Da die Habitatqualität eben auch von solchen Faktoren bestimmt wird, die unabhängig von der Fragmentierung der Standorte sind, wird sie in der vorliegenden Arbeit als eigenständige Einflussgröße neben der Fragmentierung betrachtet. Die Untersuchung hat gezeigt, dass die Habitatqualität wie auch die Isolation der Populationen wesentlich geringere Auswirkungen auf das Überleben (Kap. 3.1) und die Reproduktion (Kap. 3.2) der untersuchten Arten hat als die Populationsgröße. Da bei keiner der Arten ein Zusammenhang zwischen Populationsgröße und Habitatqualität vorhanden ist (Kap. 3.2), besteht vermutlich auch keine indirekte Wirkung der Habitatqualität über die Populationsgröße auf das Überleben und die Reproduktion. Diese Ergebnisse müssen jedoch unter dem Gesichtspunkt betrachtet werden, dass eventuell entscheidende Parameter der Habitatqualität nicht gemessen wurden. Weiterhin wurden innerhalb der Analyse zu den Auswirkungen von Habitatfragmentierung und Habitatqualität auf das Überleben alle vier untersuchten Arten aufgrund statistischer Erfordernisse in einen gemeinsamen Datensatz eingeschlossen. Möglicherweise sind so spezifische Reaktionen der Arten auf einzelne Parameter der Habitatqualität nicht sichtbar geworden. Diese Vermutung wird dadurch bekräftigt, dass die Arten zumindest in ihrem reproduktiven Verhalten - wenn auch schwach - unterschiedlich auf einzelne Faktoren der Habitatqualität reagieren (Kap. 3.2).

Die Situation der gefährdeten Untersuchungsarten wird sich auch künftig verschlechtern. Eine Projektionsmatrix prognostiziert, dass binnen 117 Jahren nahezu alle der untersuchten Populationen ausgestorben sein werden, auch die großen (Kap. 3.1). Letztere bleiben jedoch am längsten bestehen. Zudem ist ebenfalls davon auszugehen, dass im Untersuchungsgebiet kaum neue Populationen entstehen werden, da es an potentiellen Standorten mangelt und die Degradierung und Veränderung der Landschaft durch den Menschen weiterhin voranschreitet. Für den rasanten Aussterbeprozess scheint es noch nicht einmal langfristig wirkender Ursachen wie z.B. dem Verlust genetischer Diversität kleiner Populationen oder der Verschlechterung der Habitatqualität zu bedürfen. Allein kurzfristige menschliche Aktionen, die insbesondere die kleinen Popu-

lationen unmittelbar vernichten, sind so massiv, dass sie den anderen Mechanismen zuvorkommen (s.u.).

Die Übertragbarkeit der oben erläuterten Ergebnisse auf andere ausdauernde Stromtalpflanzen bestätigt sich insbesondere dadurch, dass die Untersuchungsarten trotz der Unterschiede in gewissen Standortansprüchen und Reproduktionssystemen (s. Kap. 2) ein weitestgehend einheitliches Muster in ihrer Reaktion auf Habitatfragmentierung zeigen: Überleben und Reproduktion sind in kleinen Populationen eingeschränkt. Seit längerer Zeit fordert die Wissenschaft die Forschung nach solchen allgemeinen Mustern hinsichtlich der Auswirkungen von Habitatfragmentierung auf Pflanzengruppen mit bestimmten Merkmalen, in bestimmten Lebensräumen oder Regionen, um konkrete Anweisungen für das Management von fragmentierten Ökosystemen geben zu können (z.B. Hobbs und Yates 2003). Das hier erzielte Ergebnis liefert einen konkreten Beitrag zu dieser Problematik. Da die Suche nach derlei allgemeinen Mustern relativ aufwendig ist, gibt es bisher nur wenige weitere Studien auf diesem Gebiet (z.B. Jacquemyn 2004, Kolb 2005, Aguilar 2006, Honnay und Jacquemyn 2007), so dass auch künftig ein erhöhter Forschungsbedarf besteht.

Welche allgemeingültigen Aussagen lassen sich für Pflanzenarten fragmentierter Standorte ableiten?

Seit den 80er Jahren haben sich viele Untersuchungen mit den unterschiedlichsten Auswirkungen von Habitatfragmentierung auf Pflanzenpopulationen befasst. Für einige in diesem Zusammenhang aufgestellte Hypothesen konnten zahlreiche Beweise erbracht werden, während andere sich nur schwer belegen lassen. Häufig wurde gezeigt, dass kleine und teilweise auch isolierte Populationen eine geringere genetische Diversität aufweisen als große nicht isolierte, und dass dies eine reduzierte Pflanzenfitness zur Folge hat (Leimu et al. 2006). Außerdem konnte gezeigt werden, dass fragmentierte Populationen seltener von Bestäubern besucht werden als nicht fragmentierte, was einen geringeren Samenansatz bedingt (Jennersten 1988, Kwak et al. 1998). Ob die reduzierte Fitness in kleinen und isolierten Populationen letztendlich zum Aussterben führt, wurde bisher lediglich durch Modelle nahegelegt (Erikson und Ehrlén 2001). Generell gibt es nur wenige Beweise dafür, dass fragmentierte Populationen überhaupt ein höheres Aussterberisiko aufweisen als nicht fragmentierte Populationen (aber s. Fischer und Stöcklin 1997, Matthies et al. 2004). Dies wurde jedoch in der vorliegenden Arbeit bestätigt,

da das Überleben der untersuchten Populationen fast ausschließlich von der Populationsgröße bestimmt wurde (Kap. 3.1). In den meisten Studien konnten erhöhte Aussterberaten kleiner Populationen für langlebige Arten bisher nicht nachgewiesen werden, was in der Regel durch die langen Generationszyklen der Arten erklärt wird (z. B. Schleuning und Matthies 2009). Anhand von Modellen beispielsweise wurde für einen Zeitraum von 50 Jahren nur ein äußerst geringes Aussterberisiko fragmentierter Populationen ausdauernder Arten prognostiziert (Eriksson und Ehrlén 2001). In der vorliegenden Untersuchung wurde allerdings für einen verhältnismäßig kurzen Zeitraum von knapp 15 Jahren das Gegenteil bewiesen. Da die Landschaft im Untersuchungsgebiet stark vom Menschen dominiert ist, werden vermutlich die meisten Populationen durch plötzliche Handlungen kurzfristig ausgelöscht, so dass ein vielleicht langfristig ablaufender Aussterbeprozess aufgrund reduzierter Pflanzenfitness in kleinen Populationen schon im Vorfeld unterbrochen wird. Deshalb und vermutlich auch aufgrund des relativ kurzen Zeitraumes von nur knapp 15 Jahren konnte auch in dieser Arbeit kein Beweis erbracht werden, dass die hier gefundene reduzierte Pflanzenfitness in fragmentierten Populationen zum Aussterben führt. Um diese Annahme eventuell verifizieren zu können, sollten künftig verstärkt mögliche Auswirkungen reduzierter Pflanzenfitness auf die Demographie von Populationen in den Mittelpunkt von Untersuchungen gerückt werden.

In drei aufeinanderfolgenden Untersuchungsjahren konnte für *E. palustris* gezeigt werden, dass die aufgedeckten Zusammenhänge zwischen Reproduktion, Populationsgröße, genetischer Diversität und Habitatqualität in Abhängigkeit von den Witterungsbedingungen der jeweiligen Vegetationsperiode variieren. Entsprechend der Witterung in etwa dem langjährigen Mittel, war die Populationsgröße der entscheidende Einflussfaktor für die Samenproduktion. Wichen die Witterung deutlich vom langjährigen Mittel ab, insbesondere im Hinblick auf die Niederschlagsmengen, wurde die Samenproduktion teilweise von der genetischen Diversität, aber hauptsächlich von der Habitatqualität, die wiederum stark vom Niederschlag beeinflusst wird, bestimmt. Möglicherweise verbirgt sich hinter diesem Mechanismus auch ein Grund für die häufig widersprüchlichen Untersuchungsergebnisse hinsichtlich der Auswirkungen von Habitatfragmentierung auf die Fitness von Pflanzenpopulationen. Dieses Ergebnis bestärkt Empfehlungen, dass die Datenaufnahme für solcherlei Untersuchungen in mehreren aufeinanderfolgenden Jahren erfolgen sollte, um aussagekräftige Resultate zu erzielen (Hobbs and Yates 2003, Rabasa et al. 2009).

Empfehlungen für den Naturschutz

Die Grundintention jeglicher ökologischer Forschungsarbeit muss das Erlangen eines besseren Verständnisses von Ökosystemen einschließlich der darin ablaufenden Prozesse und der beteiligten Organismen sein, um den Schutz und die Entwicklung dieser zu forcieren. Das in der vorliegenden Untersuchung aufgedeckte Reaktionsmuster von ausdauernden Stromtalpflanzen in einer fragmentierten Landschaft schafft eine wissenschaftliche Grundlage für die Empfehlung notwendiger Maßnahmen zum Erhalt und zur Entwicklung dieser gefährdeten Artengruppe. Die Ergebnisse zeigen, dass akuter Handlungsbedarf besteht, da ein nahezu völliges Erlöschen der untersuchten Populationen binnen weniger als 120 Jahren prognostiziert werden konnte (Kap. 3.1). Die Situation wird weiterhin dadurch verschärft, dass die Möglichkeiten der Etablierung neuer Populationen im Untersuchungsgebiet aufgrund des Mangels an potentiell Lebensraum und des häufigen Verlust der Arten vom lokalen Artenpool eingeschränkt sind.

Die folgenden Empfehlungen gelten sowohl für Populationen in Nordwestdeutschland als auch für solche ähnlich fragmentierter Landschaften und sollen eine erste, allgemeine Anleitung sein.

(1) Erhalt bestehender Populationen

Primäres Ziel muss sein, noch bestehende Populationen zu erhalten, um zunächst den allgemeinen regionalen Rückgang der Artenzahl ausdauernder Stromtalpflanzen zu stoppen. Dabei sollte auch in den Schutz kleiner Populationen investiert werden, da sie im Hinblick auf die Erhaltung genetischer Diversität eine wichtige Rolle spielen (Lesica und Allendorf 1992, Fischer und Matthies 1998, Greimler und Dobeš 2000, Oostermeijer 2000). Die meisten Populationen liegen jedoch außerhalb von Schutzgebieten in der konventionell genutzten Agrarlandschaft, so dass die Überwachung dieser eine besonders schwierige Aufgabe darstellt. Die Erfahrung hat gezeigt, dass viele Landbesitzer und -bewirtschafter in der Regel nicht von dem Vorkommen gefährdeter oder sogar auf Bundesebene besonders geschützter Arten auf oder in der Nähe ihrer Flächen wissen. Selbst die Kommunen, die für die Unterhaltung von Straßenrändern und Gräben, den häufigen Ersatzlebensräumen für Stromtalpflanzen, sorgen, sind zumeist nicht unterrichtet. Da das erhöhte Aussterben von Populationen ausdauernder Stromtalpflanzen verstärkt auf plötzliche Handlungen des Menschen wie z.B. Kultivierung, Landnutzungsänderung oder dem Einsatz von Pestiziden zurückzuführen ist (Kap. 3.1), sollten

Naturschutzbehörden diese Personen und Stellen besser informieren und aufklären, um damit die Aussterbeereignisse zu minimieren (vgl. Andres und Westhus 2000).

(2) Vergrößerung bestehender Standorte und ihrer Populationen

In einem nächsten Schritt sollte sich der Entwicklung bestehender Populationen gewidmet werden. Da in der vorliegenden Untersuchung gezeigt werden konnte, dass eine geringe Populationsgröße das Überleben und die Reproduktion stark einschränkt, müssen Voraussetzungen für natürliches Populationswachstum oder Populationsvergrößerung durch Einbringung von Pflanzenmaterial geschaffen werden (vgl. Primack und Drayton 1997). Dort, wo es die landschaftlichen Strukturen zulassen, sollte die Fläche eines Standortes gemäß den Ansprüchen der Art (s.u.) so vergrößert werden, dass sich die Population entweder selbständig ausbreiten oder durch Einbringung von Pflanzenmaterial (s.u.) erweitert werden kann. Weiterhin hat die Untersuchung ergeben, dass Populationen ab einer Größe von 100 Individuen geringere Aussterberaten aufweisen, eher groß bleiben, und höhere Chancen haben, eine Populationsgröße von über 1000 Individuen zu erreichen, im Vergleich zu Populationen von 25 Individuen und weniger (Kap. 3.1). Demgemäß sollte bei der Durchführung von entsprechenden Managementmaßnahmen auf eine Populationsmindestgröße von 100 Individuen geachtet werden.

(3) Verringerung der Distanzen zwischen Populationen

Die räumliche Isolation von Populationen wurde ebenfalls als einschränkender Faktor für ausdauernde Stromtalpflanzen identifiziert, wenn auch in geringerem Maße als die Populationsgröße und ausschließlich für die Reproduktion mancher der untersuchten Arten (Kap. 3.2). Der reduzierten reproduktiven Fitness dieser Populationen können zwei Hauptursachen zugrunde liegen: (1) Mangelnder Genaustausch mit anderen Populationen kann in der Folge von genetischer Drift einen Verlust genetischer Diversität und damit eine geringere Pflanzenfitness bewirkt haben (Young et al. 1996) und (2) verminderte Bestäubung kann, weil die isolierten Populationen von Bestäubern nicht gefunden wurden, zu einem geringeren Samenansatz geführt haben (Jennersten 1988, Kwak et al. 1998, Steffan-Dewenter und Tschardt 1999). Die Situation von isolierten Populationen zu verbessern, stellt den Naturschutz jedoch vor eine schwierige Aufgabe. Auf Dauer können mangelnder Genfluss und mangelnde Bestäubung nur durch Anbindung der Populationen an ein Metapopulationssystem behoben werden. Dazu müssten neue Populationen als „Trittsteine“ geschaffen werden, um die Distanzen zwischen den Populationen zu verringern und Barrieren für den notwendigen Genfluss wie Siedlung-

gen oder große Agrarflächen zu umgehen. Eine Empfehlung für die maximale Entfernung zwischen Populationen lässt sich allerdings kaum geben, da diese stark von der Pflanzenart, ihren Pollenvektoren und ihren Mechanismen zur Samenausbreitung abhängt (Kwak et al. 1998). Die meisten Bestäuber sind jedoch in der Lage, Distanzen von mindestens 100 m zurückzulegen (ebd.). Die Ansiedlung neuer Populationen lässt sich allerdings in der heutigen, stark vom Menschen genutzten Landschaft kaum realisieren. Die Maßnahme eignet sich eher innerhalb von Schutzgebieten und großangelegten Kompensationsflächen, wo die Landschaft zu Schutzzwecken frei verfügbar ist und das spätere Management der Standorte kontrolliert wird. Populationen, die völlig isoliert in einem stark genutzten Gebiet liegen - wie viele - und damit kaum Überlebenschancen haben, könnten in letzter Konsequenz in ein Schutzgebiet überführt werden. Diese Methode ist jedoch äußerst riskant und bedarf eines genauen Wissens über die Eigenschaften und Ansprüche der betreffenden Art, um erfolgreich zu sein (Gordon 1994).

Die Einbringung genetischen Materials in Form von Samen oder Pflanzen anderer Populationen zur genetischen Aufwertung isolierter Populationen stellt ebenfalls eine mögliche Hilfsmaßnahme dar. Bei der Wahl einer Spenderpopulation muss darauf geachtet werden, dass diese möglichst in der Nähe der Empfängerfläche oder -population liegen, um einerseits autochthone Ökotypen zu erhalten und andererseits die genetische Veränderung der lokalen Flora gering zu halten (Wright 1943, van Groenendael et al. 1998). Das Pflanzenmaterial sollte möglichst aus verschiedenen Populationen stammen, um die Chance der Populationsetablierung durch den Einsatz einer großen Bandbreite an Ökotypen zu erhöhen (Wright 1943, Luijten et al. 2002). Diese Art der Hilfsmaßnahme, die auch zur Verbesserung der genetischen Konstitution kleiner Populationen angewendet werden könnte, steht jedoch in der Diskussion, da das Risiko der Fremdzuchtdepression bei den Nachkommen besteht (z.B. Fischer und Matthies 1997).

(4) Verbesserung der Standortbedingungen

Die Habitatqualität im Hinblick auf Lichtverfügbarkeit, Bodenparameter und Parameter der umgebenden Vegetation hatte zwar in der vorliegenden Untersuchung im Vergleich zur Populationsgröße einen wesentlich geringeren Einfluss auf Überleben und Reproduktion von ausdauernden Stromtalpflanzen, konnte aber als bestimmende Größe für das Auftreten von Keimlingen in Populationen von *E. palustris* identifiziert werden (Kap. 3.4). Da sich die Art kaum vegetativ vermehrt, ist die Fähigkeit zur generativen

Verjüngung essentiell für das Überleben ihrer Populationen, auch wenn diese aufgrund ihrer Langlebigkeit Jahrzehnte ohne die Etablierung von Nachkommen an einem Standort bestehen können. Das Vorkommen von Keimlingen ist abhängig von einer eher geringen Deckung der Vegetation (maximal 85%) und einem relativ hohem Gehalt an organischer Substanz im Boden (mindestens 6% Kohlenstoff). Beide Faktoren deuten darauf hin, dass solche Standorte zeitweise überschwemmt sind. *E. palustris* bevorzugt wie viele andere Stromtalpflanzen winterliche Überschwemmung und relative sommerliche Trockenheit (Hejný 1960, Burkart 2001). Überflutungen, die weit bis ins Frühjahr hinein bestehen, beschränken die Zeit für die Aktivität von Bodenorganismen, wodurch der Gehalt an organischer Substanz im Boden relativ hoch ist. Weiterhin kann das Wachstum vieler Pflanzenarten erst entsprechend später einsetzen, so dass Lücken in der Vegetation verbleiben, die potentielle Standorte für Keimlinge bieten (Bornette und Amoros 1996). In 75% der untersuchten Populationen kamen innerhalb von 3 Jahren keine Keimlinge auf, was u.a. auf eine nicht ausreichende winterliche Überflutung hindeutet. Lediglich ein Wiederanschluss der Standorte an die natürliche Flusssynamik mit ihren spezifischen hydrologischen Verhältnissen könnten das Überleben dieser meist überalterten Populationen sichern. Wiedervernässungsmaßnahmen lassen sich in der Regel jedoch nur in Schutzgebieten oder auf großangelegten Kompensationsflächen realisieren. Für Populationen außerhalb dieser bieten sich kaum solche Hilfsmaßnahmen an, was angesichts ihres hohen Anteils am Gesamtbestand alarmierend ist. Da *E. palustris* als äußerst typische Stromtalpflanze (Korsch 1999) stellvertretend für viele andere Stromtalarten steht, ist das Problem mangelnder Verjüngung verbunden mit einer Überalterung der Populationen vermutlich eine starke Bedrohung nicht nur für diese Art allein.

(5) Renaturierung alter bzw. Nutzung neuer Lebensräume

Stromtalpflanzen leiden stark unter dem Verlust und der Degradierung ihrer Lebensräume, was der hohe Anteil an gefährdeten Arten widerspiegelt (s. Kap. 1). Die Wiederherstellung alter Lebensräume und die Schaffung neuer im Rahmen von Renaturierungsmaßnahmen oder der Anlage von Retentionsraum bietet eine wichtige Chance für die Entwicklung vieler Arten. Häufig sind diese jedoch aus dem lokalen oder sogar regionalen Artenpool verschwunden, und eine Regeneration aus der Samenbank ist eher unwahrscheinlich (Hölzel et al. 2006), ebenso wie der Sameneintrag im Zuge von regelmäßigen Überschwemmungen (Donath et al. 2003). Demzufolge kann eine Wieder-

besiedlung oder eine Neubesiedlung nicht ohne Hilfsmaßnahmen erfolgen. Die Wiedereinbürgerung oder die Neuansiedlung von Arten ist jedoch mit einem immens hohen Arbeits- und Kostenaufwand, großem Know-How und gleichzeitig einer sehr geringen Erfolgsquote verbunden (Falk und Olwell 1992, Primack und Drayton 1997, Drayton und Primack 2000). Primack und Drayton (1997) leiten aus eigenen Experimenten ab, dass maximal 30% der ausgepflanzten Individuen überleben. Das erfordert bei einer Populationsmindestgröße von 100 Individuen (s.o.) das Auspflanzen von mindestens 333 Exemplaren. Weiterhin geben die Autoren für ausdauernde Arten an, dass sich lediglich eine von hundert Populationen auf Dauer etabliert. Dies bedeutet, dass man 33 300 Individuen nachziehen und 100 potentielle Standorte finden müsste, um eine einzige Population dauerhaft anzusiedeln. Mit voranschreitender Forschung zu Ansiedlungsmaßnahmen mag die Erfolgsquote jedoch deutlich ansteigen. Solche Maßnahmen sind dennoch notwendig, damit die hier untersuchten Arten langfristig in einer ausreichenden Anzahl an Populationen im Gebiet weiterexistieren. Ein in kleinem Rahmen angelegtes Wiedereinbürgerungsexperiment mit *E. palustris* hat gezeigt, dass sich die Art problemlos aus Samen nachziehen und später auspflanzen lässt, und dass 70% der Populationen die ersten zwei Jahre überlebt haben. Weiterhin hat der Versuch ergeben, dass sich mindestens einjährige Pflanzen besser etablieren als Keimlinge und Setzlinge, was den Ergebnissen vieler anderer Untersuchungen entspricht (z.B. Drayton und Primack 2000, Luijten et al. 2002). Ob das Experiment langfristig erfolgreich ist, misst sich am Reproduktionserfolg und letztendlich am Populationswachstum.

Insgesamt gesehen bedarf der langfristige Schutz und die Entwicklung von Stromtalpflanzen in der Kulturlandschaft relativ kosten- und arbeitsaufwendiger Managementmaßnahmen. Gemeinsame Projekte von Forschungseinrichtungen und Naturschutzbehörden könnten eine Finanzierung vereinfachen. Zudem könnte die Wissenschaft von den regionalen Kenntnissen und Befugnissen der Behörden profitieren und im Gegenzug ihr Fachwissen z.B. über die Eigenschaften und Ansprüche gefährdeter Arten einbringen. Zunächst müssen jedoch beide Parteien den Schutz von Stromtalpflanzen stärker in ihren Fokus rücken.

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Zusammenfassung

Innerhalb Mitteleuropas zählen über 100 Gefäßpflanzenarten zu den sogenannten Stromtalpflanzen, die durch die Verbreitung entlang von Flusstälern charakterisiert sind. Der Verlust und die Degradierung ihres Lebensraumes aufgrund von Flussregulierung, Deichbau, Kultivierung der Auen und Intensivierung der Landwirtschaft haben zu ihrer überdurchschnittlich hohen Gefährdung beigetragen. Viele Populationen sind heutzutage durch die Fragmentierung ihrer Standorte in der Größe reduziert und räumlich voneinander isoliert, was eine Reihe von negativen Auswirkungen auf ihre Überlebensfähigkeit haben kann. Abhängig von ihren Eigenschaften, wie dem Verbreitungsmuster oder der Lebensform, gibt es Unterschiede zwischen Arten bzw. Artengruppen, in welchem Maße und in welcher Weise sie beeinflusst werden. Deshalb war es Hauptziel der vorliegenden Arbeit, ein allgemeines Muster für die Reaktion von ausdauernden Stromtalpflanzen auf Habitatfragmentierung zu finden, um wiederum Empfehlungen für den Schutz dieser gefährdeten Artengruppe geben zu können. Dazu wurden Untersuchungen auf Populationsebene in den stark fragmentierten Flusstälern des Weser- und Elbesystems im nordwestdeutschen Raum durchgeführt.

Zunächst wurden die Auswirkungen von Habitatfragmentierung auf die Populationssterberaten und Veränderungen der Populationsgröße, und damit auf das regionale Überleben von ausdauernden Stromtalpflanzen, anhand vier gefährdeter Arten untersucht: *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus*. Der starke Rückgang der Untersuchungsarten ist hauptsächlich auf hohe Aussterberaten kleiner Populationen (≤ 25 Individuen) zurückzuführen, während die räumliche Isolation keine Relevanz hat. Mit hoher Wahrscheinlichkeit haben anthropogenbedingte, plötzliche Ereignisse wie Kultivierung, Landnutzungsänderungen oder der Einsatz von Pestiziden die Populationen kurzfristig vernichtet. Bei unveränderten Verhältnissen werden binnen weniger als 120 Jahren nahezu alle der untersuchten Populationen ausgestorben sein. Dies betrifft auch die großen (> 100 Individuen) ungeachtet ihres Vorteils, ihre Größe eher halten zu können und der vergleichsweise höheren Chance, eine Populationsgröße von über 1000 Individuen zu erreichen.

In einem nächsten Schritt wurde analysiert, ob die negativen Auswirkungen von Habitatfragmentierung die Reproduktion in Populationen von *Euphorbia palustris*, *Lathyrus palustis*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio*

paludosus einschränken und damit auch langfristig zum Aussterben führen könnten. Der reproduktive Erfolg aller untersuchten Arten war in kleinen und teils auch isolierten Populationen reduziert, möglicherweise aufgrund von mangelnder Bestäubung und / oder dem Verlust genetischer Diversität. In einer weiterführenden Untersuchung an *E. palustris* konnte der Verlust genetischer Diversität in kleinen Populationen jedoch nicht eindeutig belegt werden, was vermutlich in direktem Zusammenhang mit der Langlebigkeit der Art steht.

In allen Teiluntersuchungen hatte die Habitatqualität, gemessen an Lichtverfügbarkeit, Bodenparametern und Parametern der umgebenden Vegetation, zwar einen wesentlich geringeren Einfluss als die Populationsgröße auf Überleben und Reproduktion der Untersuchungsarten konnte aber als bestimmende Größe für die Verjüngung in Populationen von *E. palustris* identifiziert werden. Vegetationslücken und ein hoher Anteil organischer Substanz im Boden - vermutlich hervorgerufen durch langandauernde winterliche Überflutungen - ermöglichen die Etablierung von Keimlingen. Die Abtrennung von der natürlichen Flusssdynamik z.B. durch Deichbau hat letztendlich zu einer Überalterung vieler Populationen geführt.

Weitere Beobachtungen an Populationen von *E. palustris* in drei aufeinanderfolgenden Untersuchungsjahren haben gezeigt, dass Zusammenhänge zwischen Reproduktion, Populationsgröße, genetischer Diversität und Habitatqualität in Abhängigkeit von den Witterungsbedingungen der jeweiligen Vegetationsperiode variieren. Um aussagekräftige Resultate hinsichtlich der Effekte von Habitatfragmentierung auf die Pflanzenfitness zu erhalten, sollten deshalb Datenaufnahmen grundsätzlich in mehreren aufeinanderfolgenden Jahren stattfinden.

Angesichts der negativen Auswirkungen von Habitatfragmentierung auf die Vitalität ausdauernder Stromtalpflanzen und der damit verbundenen alarmierenden Prognosen müssen Maßnahmen zum Erhalt und zur Entwicklung dieser gefährdeten Artengruppe ergriffen werden. Aus der vorliegenden Arbeit lassen sich folgende Empfehlungen ableiten: Vergrößerung von Standorten und Populationen, Verringerung der Distanzen zwischen Populationen, Wiederanschluss von Standorten an die natürliche Flusssdynamik, Nutzung renaturierten und neugeschaffenen potentiellen Lebensraumes zur Wiedereinbürgerung bzw. Neuansiedlung von Populationen.

Summary

In Central Europe, more than 100 vascular plant species are exclusively or predominantly confined to the basins of large rivers: the so-called river corridor plants. As the natural habitats along the rivers have been destroyed and degraded by the regulation of watercourses, the building of dikes, land reclamation and agricultural intensification, they may account for an above-average proportion of endangered species. Due to the fragmentation of their habitats, many populations are small and highly isolated and this may threaten the viability of populations. The degree and the way in which species are impacted can vary between species or groups of species, respectively, depending on their traits, such as their distribution pattern or their life-form. The aim of this study was therefore to find a general pattern reflecting the fragmentation effects on perennial river corridor plants and to advise conservation measurements for these species. The study was carried out in the highly fragmented floodplains of the Weser and Elbe systems in North-western Germany.

The first objective of the study was to assess the effects of habitat fragmentation on the extinction of populations and the changes in population sizes of four endangered perennial river corridor plants: *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus*. High extinction rates of small populations (≤ 25 individuals) could be identified as the most probable cause for the decline of the species studied while the isolation of populations had no effect. Sudden environmental stochasticity induced by human activity, such as land reclamation, changes in land use, or utilization of pesticides, may have led to extinction in the short-term. If conditions stay unchanged, nearly all of the surveyed populations will have become in less than 120 years. This also includes the large populations (> 100 individuals) even though they have a much higher chance of survival or even growth to a size of 1000 individuals and more.

In a next step, we analyzed whether the negative effects of habitat fragmentation would reduce reproduction in fragmented populations of *Euphorbia palustris*, *Lathyrus palustis*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Senecio paludosus* and would thus lead to extinction of populations in the long-term, too. Reproductive success of all species studied was reduced in small but not always in isolated populations. This is possibly due to limited pollination and/or the loss of genetic variation. In a

following investigation on *E. palustris*, the loss of genetic variation in small populations was, however, not clearly confirmed and this was probably caused by the longevity of the species.

Overall, the effects of habitat quality, such as light availability, soil parameters and parameters of the surrounding vegetation, on the survival and the reproduction of the species studied were considerably less pronounced compared to the effects of population size. However, the recruitment of populations of *E. palustris* was determined by gaps in the vegetation and a relatively high content of organic matter in the soil, both indicating abundant winterly floodings. Consequently, most populations are static and aged since they are completely cut off from the dynamics of the river due to the construction of dikes.

Further investigations on *E. palustris* over three years showed, that the relationships between reproductive success, population size, genetic variation, and habitat quality varied depending on the weather conditions of each growing season. Thus, studies concerning the impact of habitat fragmentation on the fitness of plant populations should preferably be based on surveys conducted over several consecutive years.

In conclusion, river corridor plants are highly threatened by habitat fragmentation and will be further on the decline throughout the study area. The following management measures based on the findings of this study should be included in a conservation plan of this species group to stop or reverse this development: increase of population area and sizes, improvement of the connectivity between populations, re-attachment of habitats to natural river dynamics, utilisation of restored flood plains for reintroduction or introduction of species.

Anhang (Appendix, Kap. 3.4)

List of references including phytosociological relevés with E. palustris from Central and northern Europe

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We also used relevés from the Dutch database provided by Stephan M. Hennekens, from the Czech database provided by Lubomir Tichy and from the Austrian database provided by Wolfgang Willner.

