Universität für Bodenkultur Wien

Präsentation
von geförderten Projekten der Stiftung ´120 Jahre Universität für Bodenkultur´

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IMPRESSUM

Präsentation
von geförderten Projekten
der Stiftung ´120 Jahre Universität
für Bodenkultur´

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REDAKTION UND LAYOUT

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Geleitwort

Die Universität für Bodenkultur steht für Nachhaltigkeit, ein Konzept, das aus der Forstwirtschaft heraus entwickelt wurde. Gerade heute, in Zeiten globaler wirtschaftlicher Veränderungen und des Klimawandels sind praxisgerechte aber wissenschaftsbasierte Innovationen und Managementkonzepte in der Forstwirtschaft notwendig. Gerade die Naturräume sind unterschiedlichsten Nutzungsansprüchen aus der Gesellschaft ausgesetzt. Tourismus, Naturschutz, Jagd und etwa Schutz vor Naturgefahren sind mit den Erfordernissen einer nachhaltigen Forstwirtschaft in Einklang zu bringen. Forstwissenschaftliche Forschung ist daher gerade heute auf hohem Niveau gefragt und höchst notwendig. Die Universität für Bodenkultur hat in ihren einschlägigen Departments und Instituten eine international sehr angesehene und auch nachgefragte Expertise in den Forstwissenschaften anzubieten. Dabei ist es gleichermaßen wichtig, den Forschungs- und Innovationsprozess engagiert weiterzutreiben und insbesondere in den wissenschaftlichen Nachwuchs zu investieren.

Die Universität für Bodenkultur ist in diesem Zusammenhang unserem Absolventen und Ehrensenator Dipl.-Ing. Rupert Hatschek überaus dankbar. Er hat bereits 1992 eine Stiftung an der BOKU (120 Jahre Universität für Bodenkultur) zur Unterstützung der forstwissenschaftlichen Forschung begründet, mit viel persönlichem Einsatz vorangetrieben und mit seinem Fachwissen bereichert. Zahlreiche NachwuchswissenschafterInnen kamen in der Zwischenzeit in den Genuss von Förderungen der von ihnen vorgeschlagenen Projekte und konnten damit das forstwissenschaftliche Fachwissen bereichern und die eigene wissenschaftliche Karriere weitertreiben. Die vorliegende Publikation fasst die Ergebnisse einiger der in den letzten Jahren durchgeführten und in der Vortragsveranstaltung am 25. Oktober 2011 an der BOKU präsentierten Projekte zusammen. Diese Veranstaltung ist das zweite Symposium, das zum Ziel hat, die Ergebnisse der aus der Stiftung geförderten Projekte an die Öffentlichkeit zu bringen.

Ich danke den AutorInnen für die Mitwirkung und wünsche Ihnen eine interessante Lektüre.

Martin H. Gerzabek

Rektor

Ehrensenator DI Rupert Hatschek
Stifter

Vorwort

Die nachhaltigen Veränderungen der wirtschaftlichen Randbedingungen sollen uns in Erinnerung bringen, dass jedes Land sich darauf besinnen muss, seine Stärken weiter auszubauen. Die Universität für Bodenkultur und die österreichische Forstwirtschaft sind ohne Zweifel eine dieser Stärken des Landes, auf die wir stolz sein können, unsere Leistungen lassen sich sehen. Wir müssen aber stets daran arbeiten, nicht stehen zu bleiben.

Es war mir eine Freude im Jahr 1992 die Stiftung ´120 Jahre Universität für Bodenkultur´ gründen zu können. In harmonischer Zusammenarbeit mit den Herren in der Jury konnten wir 44 Preisträger auswählen, die Förderungssumme beträgt bisher größenordnungsmäßig EUR 175.000,-.

Um die Forscherinnen und Forscher mit ihren Arbeiten einem breiteren Kreis bekanntzumachen, ist der Gedanke entstanden, den PreisträgerInnen Gelegenheit zu geben, sich und ihre Arbeit vorzustellen. Ich hoffe, diese Vorstellungen, die wir auch in Zukunft machen wollen, helfen nicht nur den jungen WissenschafterInnen in ihrer Laufbahn, sie mögen auch die forstliche Forschung, die lebenswichtig ist, anregen und die Verbindung zwischen Bodenkultur und Praxis vertiefen.

Ich wünsche Ihnen viel Freude bei der Lektüre der Beiträge!

Rupert Hatschek

Stiftung ´120 Jahre Universität für Bodenkultur´

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PROJEKTE

Die PreisträgerInnen

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Zum Einfluss der Photoperiode und der Nahrungsqualität auf den Schlupf- und Brutbeginn des Buchdruckers (*Ips typographus*)

Studies on the influence of photoperiod and the quality of the breeding material on the emergence of the bark beetle Ips typographus

Photoperiode und Entwicklung von *Ips typographus*

Dipl.-Ing. Nina Dobart

Zusammenfassung

In dem Projekt wurde der Einfluss der Photoperiode auf die Entwicklung des Borkenkäfers, *Ips typographus,* von zwei verschiedenen Herkünften untersucht. Für die Analyse des Einflusses der Nahrungsqualität wurden Käfer auf Stämme angesetzt, die im Frühling und im Herbst geerntet worden waren. Die Analyse der geschlüpften Jungkäfer zeigte, dass eine kurze Tageslänge sowohl eine hemmende Wirkung auf den Schlupf der Jungkäfer als auch auf ihre Brutbereitschaft hat. Die Konservierung der Stämme, die einer Lagerung im Winter entspricht, und die daraus resultierende Abnahme der Bastqualität, hatten ebenfalls einen negativen Einfluss auf die Entwicklung der Käfer. Die daraus gewonnenen Ergebnisse können zur genaueren Abschätzung der Entwicklung der Käfer im Jahresverlauf herangezogen werden.

Abstract

In this project, the influence of the photoperiod and the quality of the breeding material on the development and the breeding success of the bark beetle, *Ips typographus,* from two different populations, were analysed. To test the influence of the breeding material, beetles were put on logs which were harvested in spring and autumn. It was shown, that a short photoperiod delays the emergence itself, and decreases the breeding success of the emerged filial beetles. The conservation of the logs, which simulates the overwintering of the logs, results in a decrease of the breeding material, which hinders the development of the filial beetles. These results could be used to precise prediction models of the beetle´s development within a season.

1. Einleitung

Für die Stabilität der nord- und mitteleuropäischen Fichtenwälder stellen Massenvermehrungen des Borkenkäfers *Ips typographus* (Buchdrucker) derzeit wohl das bedeutendste Problem dar. Im Zusammenhang mit einer Klimaerwärmung und häufigerem Eintreten von extremen Witterungsereignissen ist prinzipiell damit zu rechnen, dass das Risiko von Borkenkäfer-Gradationen in Zukunft noch deutlich zunehmen wird (SCHOPF 1997). Dies betrifft vor allem die montanen und subalpinen Fichtenwaldregionen, in denen durch die Erwärmung die Entwicklung des Borkenkäfers beschleunigt und somit auch dort zum Teil zwei Generationen pro Saison etabliert werden können.

Die Entwicklung des Buchdruckers in Mitteleuropa kann bei geeigneten Temperaturbedingungen meist über zwei Generationen pro Jahr (= multivoltin) erfolgen, es ist allerdings auch bekannt, dass ein Teil der Population auch unter entwicklungsgünstigen Bedingungen meist nur eine Generation/Jahr anlegt (univoltine Populationen) (NETHERER et al. 2001). Inwieweit neben der Photoperiode auch die Bastqualität für den Schlupf und die Brutbereitschaft der Käfer eine Rolle spielt, wurde in dieser Arbeit untersucht.

2. Projektziele und Fragestellung

In dem vorliegenden Projekt sollte der Einfluss der Photoperiode und der Qualität des Brutmaterials auf die Schlüpf- und Brutbereitschaft der Käfer untersucht werden. Zusätzlich wurde eine univoltine und eine multivoltine Population für die Versuche verwendet.

Folgende Hypothesen sollten anhand der geplanten Untersuchungen überprüft werden:

- Die Brutqualtiät frischer Stämme ist im Frühjahr besser als im Herbst; Käfer, die auf diesen Stämmen gezüchtet werden, weisen eine höhere Schlüpfrate und Brutbereitschaft auf als solche, die sich im Herbst entwickeln.
- Bei Käfern der univoltinen Population ist der Schlupf und die Brutbereitschaft trotz Langtag-Bedingungen gehemmt.
- Bei Käfern der multivoltinen Population sind die Schlüpfrate und die Brutbereitschaft nur unter Kurztag-Bedingungen gehemmt.

3. Methode

3.1 Brutexperimente

Für die Versuche wurden zwei unterschiedliche Photoperioden verwendet: Langtag (LT: 16h Licht: 8h Dunkelheit) und Kurztag (KT: 8h Licht: 16h Dunkelheit).

Die Käfer der getesteten Hochlagen-Population (HL) stammten aus dem Nationalpark Gesäuse (1500 m); die Population aus der Tieflage (TL) aus Prinzersdorf, NÖ (450 m). Für die Versuche wurden Käfer aus dem Freiland ans Institut gebracht und hier Dauerzuchten etabliert.

Um den Einfluss von Frühling- und Herbstholz untersuchen zu können, wurde schon vor Beginn der Versuche im Frühjahr 2007 ein Baum gefällt und Stammstücke davon zur Konservierung tiefgefroren (-20°C). Die Brutqualität der Rinde sollte so bis zur Durchführung der Versuche erhalten bleiben, damit Käfer der gleichen Generation zugleich an Stammstücken von Frühling und Herbst getestet werden konnten.

Je hundert Käfer einer Herkunft wurden auf die frischen und konservierten Stämme angesetzt, und die besiedelten Stämme auf die zwei Photoperioden aufgeteilt.
Die aus den Stämmen schlüpfenden Jungkäfer wurden täglich abgesammelt und nach Ausfärbungsgrad und Geschlecht sortiert. Die Weibchen wurden anschließend hinsichtlich des Entwicklungszustandes der Gonaden und ihrer tatsächlichen Brutbereitschaft untersucht. Nach dem Versuchsende - elf Wochen nach Ansatz der Parentalkäfer - wurden die Stämme entrindet und die Anzahl der nicht geschlüpften, arretierten Käfer bestimmt. Diese wurden analog zu den geschlüpften Käfern untersucht und aus dem Verhältnis der geschlüpften und arretierten Käfer wurden die Schlüpfraten ermittelt.

3.2 Bestimmung des Entwicklungszustandes der Ovarien

Geschlüpfte und nicht geschlüpfte Weibchen wurden in Ringerlösung seziert und die präparierten Gonaden fotografiert. Die Fläche der Gonaden wurde mit dem Bildbearbeitungsprogramm „Adobe Photo Shop“ nachgezeichnet und anschließend die Flächengröße mit dem Computerprogramm „LUCIA“ ermittelt (Abbildung 1).

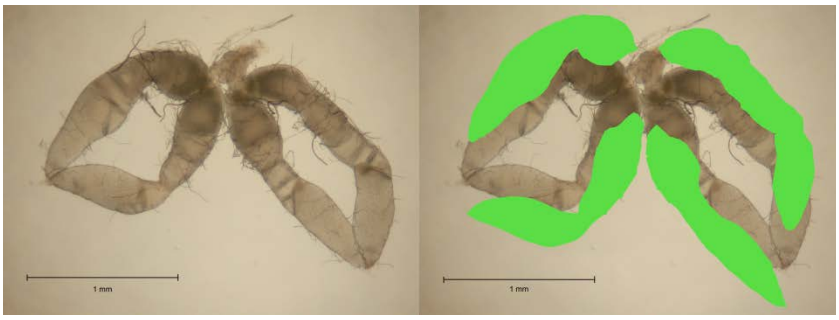

Abbildung 1: Foto einer Gonade eines Borkenkäfer Weibchens, deren Flächen nachgezeichnet wurden, um so deren Größe genau ermitteln zu können.

3.3 Bestimmung der Brutbereitschaft der geschlüpften Jungkäfer

Um die tatsächliche Brutbereitschaft der geschlüpften Jungkäfer zu testen, wurden diese wiederum an frische Stämme bei LT und 20 °C mittels Kapselzwinger angesetzt. Männchen, die sich nicht innerhalb von zwei Tagen in die Rinde eingebohrt hatten, wurden durch neue Käfer ersetzt („getauscht“). Ebenso wurden Weibchen, die nicht innerhalb von 24h in die Rammelkammer eingedrungen waren, durch neue ersetzt („getauscht“). Die Stämme wurden vierzehn Tage nach dem letzten, erfolgreich eingebohrten Weibchen entrindet und die Anzahl der angelegten Bruten („erfolgreiche RK, erfolgreiche Brutanlagen“) ermittelt. Die Brutanlagen selbst wurden hinsichtlich der Länge der Muttergänge, der Anzahl der Einischen sowie der entwickelten Larven ausgewertet.

4. Ergebnisse und Diskussion

Wie sich während der Versuche herausstellte, hatte die Konservierung der Stämme einen deutlichen negativen Einfluss auf die Qualität des Brutmaterials für die Käfer. Schon wenige Tage nach dem Auftauen der Stämme und Ansetzen der Käfer trat auf den Stirnflächen, und in späterer Folge auch auf der Rinde, ein starker Befall durch saprophytische Pilze auf, wodurch die Denaturierung des Bastes beschleunigt und einen stark hemmenden Effekt auf die Entwicklung der Käfer ausgeübt wurde. Dadurch konnte der Unterschied der Bastqualität zwischen Frühling- und Herbstholz nicht mit der gleichen Käfergeneration untersucht werden. Allerdings hatte die Konservierung der Stämme den gleichen Effekt wie man sich bei der Überwinterung von Stammstücken im Freiland bei tiefen Temperaturen erwarten kann. Dadurch konnte anhand der konservierten Stämme simuliert werden, wie sich die Abnahme der Bastqualität im Winter auf die Entwicklung der Käfer auswirkt.

4.1 Schlüpfergebnisse

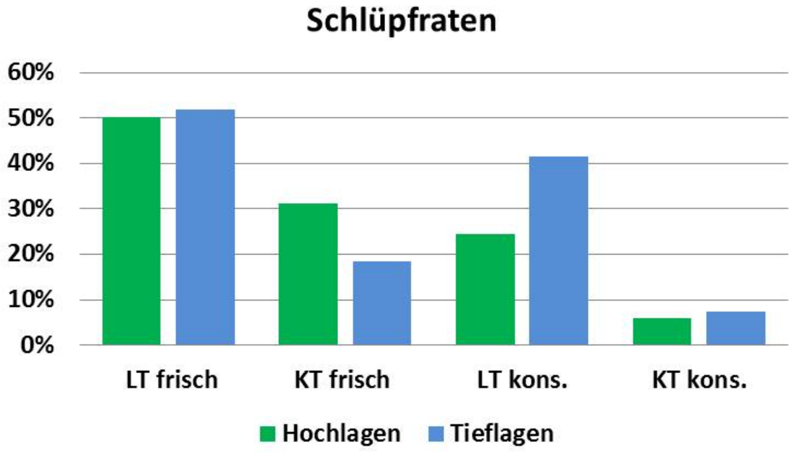

Abbildung 2: Schlüpfraten, in Prozent der Gesamtanzahl an entwickelten Käfern der beiden Herkünfte, die sich in den frischen und in den konservierten Stämmen, sowie unter Langtag (LT) und Kurztag (KT) Bedingungen, entwickelt hatten.

Käfer der TL- und der HL-Population, die sich unter LT-Bedingungen in frischen Stämmen entwickelt hatten, unterschieden sich nicht bezüglich ihrer Schlüpfraten (50%). Unter KT- Bedingungen hingegen verblieben signifikant mehr Käfer in den Stämmen als unter LT- Bedingungen. Die Schlüpfrate war unter KT-Bedingungen bei Käfern der HL-Population mit 30% signifikant höher als die der TL-Population mit weniger als 20% (Abb.2).

Der Schlupf setzte bei Käfern, die sich unter LT-Photoperiode auf frischen Stämmen entwickelten, früher ein und war früher abgeschlossen. Unter KT-Bedingungen hingegen war der Schlupf der Käfer verzögert, es bohrten sich weniger Käfer pro Tag aus den Stämmen aus.

Die Konservierung der Stämme hatte einen starken negativen Effekt auf die Reproduktion der Käfer: es entwickelten sich bei vergleichbaren Versuchsgruppen 3-5 mal weniger Käfer in den konservierten Stämmen als in den frischen. Auch verblieben bei beiden Herkünften unter LT- als auch unter KT-Bedingungen signifikant mehr Käfer in den konservierten Stämmen. Die Schlüpfraten der Käfer betrugen meist nur ca. 50 % von denen aus frischen Stämmen (Abb.2).

4.2 Gonadale Entwicklung

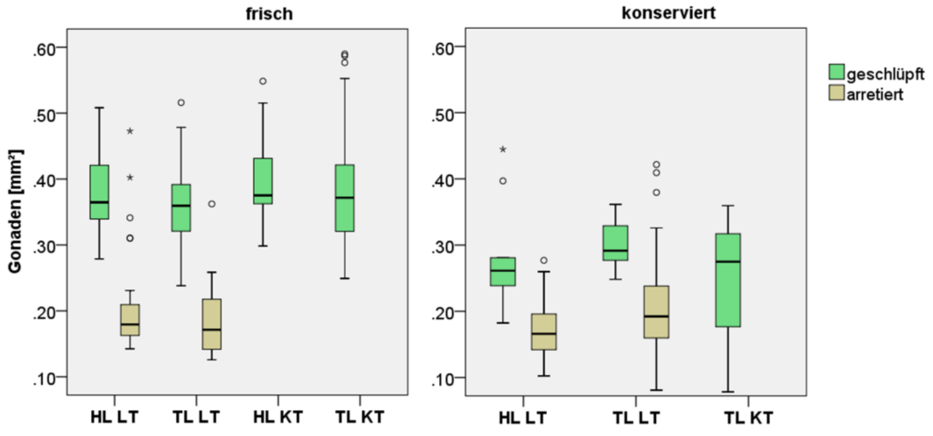

Abbildung 3: Gonaden der untersuchten Jungkäfer der Hochlagen (HL) und der Tieflagen (TL) Population, die sich unter Langtag (LT) und Kurztag (KT) Bedingungen entwickelt hatten und während der Versuche aus den Stämmen ausbohrten (während) und nach Versuchende noch arretiert waren (nach), getrennt nach frischen und konservierten Brutstämmen.

Es gab keine Unterschiede bezüglich der Gonadengröße zwischen HL- und TL-Käfern von frischen Stämmen, die sich während dem Versuch ausbohrten. Auch zwischen Käfern, die sich unter LT- und KT-Bedingungen entwickelt hatten, gab es keine Unterschiede (Abb. 3). Allerdings hatten Weibchen, die nach Versuchende noch im Stamm verblieben waren, weniger weit entwickelte Gonaden: sie waren deutlich kleiner und es waren keine reifen Eier in den Eischläuchen der weiblichen Fortpflanzungsorgane feststellbar.

Käfer, die sich in konservierten Stämmen entwickelt hatten und schlüpften, hatten signifikant kleinere Gonaden als die Weibchen, die aus frischen Stämmen geschlüpft waren. Wie schon bei den Versuchen mit frischen Stämmen, waren in den konservierten Brutstämmen die Gonaden der geschlüpften Weibchen weiter entwickelt als die der arretierten (Abb. 3).

Bei den arretierten Käfern gab es keine Unterschiede zwischen denen, die sich in frischen Stämmen entwickelt hatten, zu jenen aus konservierten Stämmen. Arretierte Käfer, die sich unter KT-Bedingungen entwickelt hatten, konnten nicht untersucht werden, da sich bei diesen Gruppen zu wenige Käfer entwickelt hatten, um alle Untersuchungen durchführen zu können.

4.3 Brutbereitschaft- Kapselansätze

Die Brutversuche konnten nur mit Käfern aus frischen Stämmen durchgeführt werden, da sich aus den konservierten Stämmen zu wenige Käfer während der Versuche ausbohrten. Zum Test der Brutbereitschaft der Jungkäfer wurden diese, nachdem sie sich aus den Versuchsstämmen ausgebohrt hatten, wiederum an frische Stammstücke angesetzt und bei 20°C und LT-Bedingungen gehalten.

Männchen der HL-Population, die sich unter LT-Bedingungen entwickelt hatten, mussten häufiger getauscht werden als jene der TL-Population. Allerdings unterschieden sich die beiden Gruppen nicht signifikant voneinander. Bei der TL-Population aus LT-Bedingungen legten 15% der eingebohrten Käfer keine Rammelkammer an („eingebohrt“); es wurde nur ein zusätzlicher Ernährungsfraß unter der Rinde durchgeführt. Käfer, die sich unter LT-Bedingungen entwickelt hatten, waren erfolgreicher im Einbohren in die Rinde als Käfer von KT-Bedingungen.
Keines der angesetzten Weibchen musste gewechselt werden, allerdings führten bei der TL- LT- und bei beiden KT-Varianten ca. 10% nur einen weiteren Ernährungsfraß durch, und legten keine Eier ab.

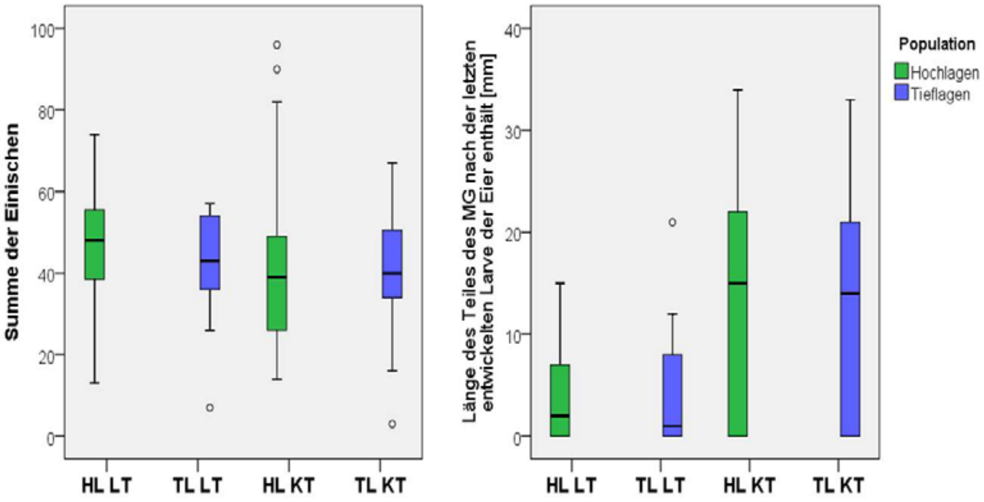

Abbildung 4: Die Summe der Einischen sowie die Länge des Anteils am Muttergang der nach der letzten geschlüpften Larve noch Eier enthält, untersucht an den Hochlagen und den Tieflagen Populationen die sich zuvor bei Langtag (LT) und Kurztag (KT) Bedingungen entwickelt hatten.

Die Herkunft der Käfer und die Photoperiode hatten keinen Einfluss auf die Länge der Muttergänge und die Anzahl der darin abgelegten Eier (Abb. 4). Die Anzahl der entwickelten Larven hingegen, die sich in Bruten der Käfer aus LT-Bedingungen entwickelten hatten, war signifikant höher als bei Bruten der Käfer aus KT-Bedingungen. Im Gegensatz dazu war der Anteil an Eiern nach der letzten geschlüpften Larve signifikant höher in Bruten von Käfern aus KT-Bedingungen (Abb.4).
Dies zeigt, dass Mutterkäfer, die sich unter KT-Bedingungen entwickelt hatten und dann auf LT-Bedingungen transferiert wurden, eine längere Zeit für die Eiablage benötigten; offensichtlich waren diese Käfer direkt nach dem Schlupf noch nicht eiablagebereit.

5. Schlussfolgerungen und Ausblick

Die Photoperiode hatte keinen Einfluss auf die Entwicklung der Bruten, da sich unter Kurztag- und Langtag Bedingungen gleich viele Käfer entwickelten, wohl aber auf das Schlüpfverhalten der Jungkäfer. Der Schlupf der unter KT-Bedingungen entwickelten Käfer war deutlich verzögert und ein Großteil der Käfer verblieb nach der Entwicklung weiter im Brutstamm (70-80%).

Die Photoperiode hatte keinen Einfluss auf die Größe der Gonaden der Käfer. Einzig die Gonaden der im Stamm arretierten Käfer waren, sowohl bei den LT- als auch der KT-Weibchen, deutlich kleiner.

Die Gonaden der geschlüpften Käfer waren unter KT- und LT-Bedingungen gleich groß. Allerdings zeigten Brutversuche mit geschlüpften Jungkäfern ein differenzierteres Bild: Käfer, die sich unter LT-Bedingungen entwickelt hatten, zeigten eine höhere Brutbereitschaft, und ihre Brutanlagen waren zum Vergleichszeitpunkt weiter entwickelt als bei Käfern die sich unter KT-Bedingungen entwickelt hatten. In den Anlagen der KT-Käfer waren noch mehr Eier zu finden, da diese später abgelegt worden waren und daraus noch keine Larven geschlüpften waren.

Die Effekte der Konservierung entsprechen aber den Bedingungen der Überwinterung von Stämmen bei Temperaturen unter -15°C. Daher kann dieser Versuch durchaus als Indiz für die Abnahme der Bastqualität während des Winters, im Vergleich zu frischen Stämmen aus dem Herbst, herangezogen werden.

Die erwarteten Unterschiede im Schlupf und Brutverhalten zwischen den beiden Voltinismustypen konnten nicht gefunden werden, da auch die Hochlagen-Population vorwiegend aus multivoltinen Individuen bestand.

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Project report for the award “120 Jahre Universität für Bodenkultur“

SUSTAINABLE FOREST MANAGEMENT IN THE WALNUT FRUIT FORESTS IN KYRGYZSTAN

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Abstract

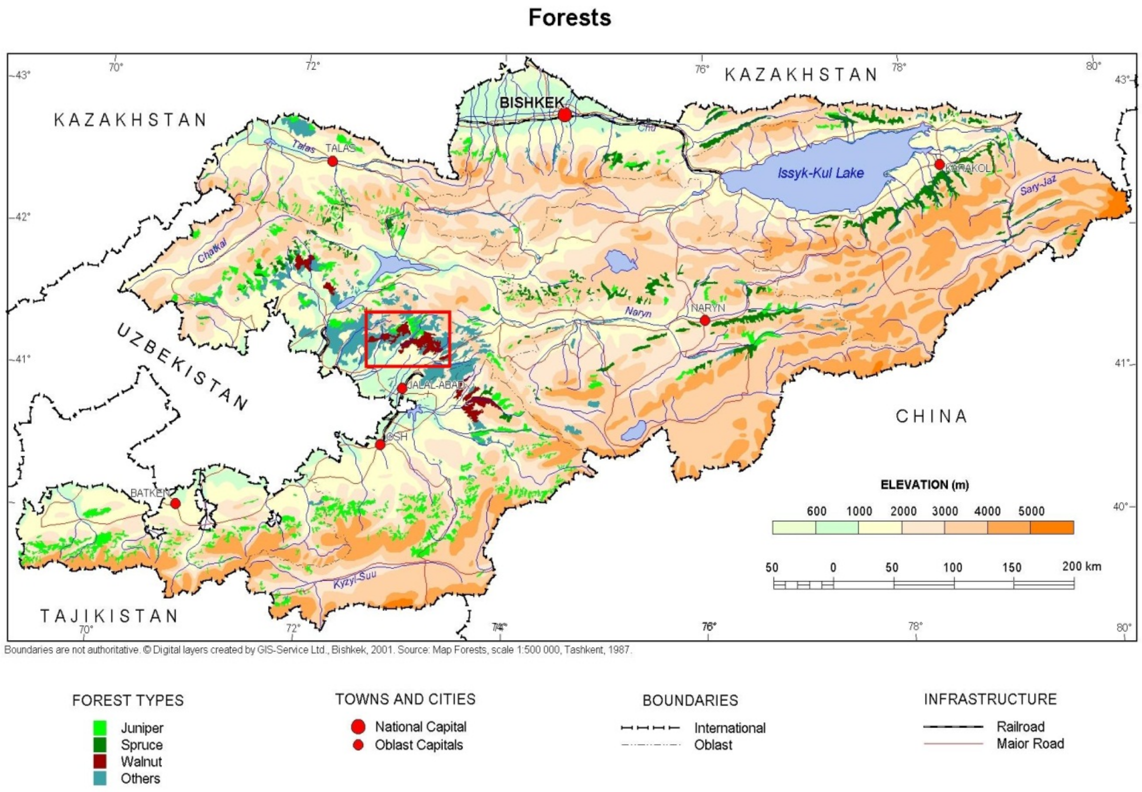
The management of the walnut fruit forests is one of the key issues of the forest sector in Kyrgyzstan to address the challenges in conserving forest resources, assure socio-economic efficiency and the livelihood of people. However, there is an urgent demand to assess sustainable forest management (SFM), which generally involves the use of Criteria and Indicators (C&I). In our case study Multi-Criteria Analysis (MCA) techniques have been applied following five steps: environmental setting, development of C&I, analysis of preferences, development of management strategies and selecting the best alternative. The approach was applied at the forestry management unit. In general, 7 criteria and 45 indicators have been identified using rating, ranking and pairwise comparison techniques within the Analytical Hierarchy Process (AHP). Futhermore, four different management strategies have been developed and the performances of the strategies were assessed within a AHP model. Accordingly, forest health, forest productivity and socio-economic functions of forests are found as the most important aspects in a SFM of the walnut forests. Our findings highlight the importance of C&I and its future application for policy implications. Moreover, the increased involvement of local stakeholders in the decision making process and their genuine participation in forest management was seen as a major benefit of such processes. Additionally, the dissemination of the basic issues of SFM and the capacity building will be stimulated by the C&I process in the walnut forests of Kyrgyzstan.

1. Introduction

Sustainable forest management (SFM) has recently become the primary goal of forestry institutions worldwide (Mendoza and Prabhu, 2000b). After the United Nations Conference on Environment and Development (UNCED) held in Rio in 1992, international efforts towards implementing sustainable forestry at different levels have shown significant progress, including the ecological, economic and social aspects (Brang et al., 2002; Wolfslehner et al., 2005).C&I for SFM are tools which can be used to collect and organize information in a manner that it is useful in conceptualizing, evaluating, communicating and implementing SFM (Prabhu et al., 1998). In this context, Multi-Criteria Decision Making Methods (MCDM) are an appropriate and useful approach for supporting the process of generating criteria and indicators (C&I) for monitoring, evaluation and assessment (Mendoza and Prabhu, 2003). MCDM techniques are capable of accommodating diverse views, objectives and perspectives of stakeholders and enable collaboration in planning and decision making (Mendoza and Prabhu, 2000b; 2003). More recently, the Analytical Hierarchy Process (AHP) has been applied in multi-objective forest management and land use planning due to its simplicity, flexibility and high effectiveness in analyzing complex decision making (Mendoza et al., 1999; Vacik and Lexer, 2001). Thus, there is a need to examine the applicability of C&I for evaluating SFM at the national as well as field levels by the use of MCDM. The aim of this contribution is to demonstrate the use of C&I to identify the best management option for a sustainable forest management of the walnut fruit forests in Kyrgyzstan by using the AHP.

2. The walnut fruit forests

The walnut fruit forests are located in the south of Kyrgyzstan. These forests are regarded as the main source for the livelihoods of the local people. However, due to a socio-economic recession following independence, there have been increased pressures on forest resources due to uncontrolled grazing, firewood collection and the consumption of non-timber forest products. In 1998, the Collaborative Forest Management (CFM) Programme was introduced. The basic concept of CFM is that a working partnership between the key stakeholders in particular the local users and the relevant forest authorities is established (Carter et al., 2003). This partnership could be strongly enhanced by the use of C&I for SFM in evaluating current management activities and formulating sustainability measures. Therefore a case study was conducted including Arstanbap, Kara-Alma, Kaba and Ortok enterprises (Fig.1), which covers about 72,760 ha of forest area, with 36,304 ha covered with walnut tree stands (*Juglans regia*) and other fruit trees species and about 23,810 inhabitants (Abdymomunov, 2003; Forest Inventory, 2003).



Boundaries are not authoritative. © Digital layers created by GIS-Service Ltd., Bishkek, 2001. Source: Map Forests, scale 1:500 000, Tashkent, 1987.

Figure 1: Map of Kyrgyzstan. The study is marked with a rectangle (Source: GIS Servise, Ldt. Bishkek)

3. Methodological approach

The methodological approach taken in this study can be classified into five steps (Fig. 2). In the first stage, the environmental setting was defined by collecting background information for context studies (i.e. socio-economic, institutional and bio-physical assessments) and establishing contacts with different stakeholders. In the bottom-up C&I development process, a SWOT analysis and resource assessment were employed, which firstly involved the identification of problems and the development of a vision statement, set of objectives and criteria through 6 different workshops at local as well as regional levels with 112 stakeholders and experts. In the third stage, rating and pairwise comparison methods of multi-criteria analysis (MCA) were used in order to filter and compare the C&I from different stakeholder groups and to judge their practicability, relevance and general acceptance. In the fourth stage, different management strategies were developed by experts and discussions about the performance of the strategies with regard to the criteria were held. In the last stage, developed strategies were evaluated and judged according to the selected C&I with the help of multi-criteria decision making techniques and their applicability discussed.

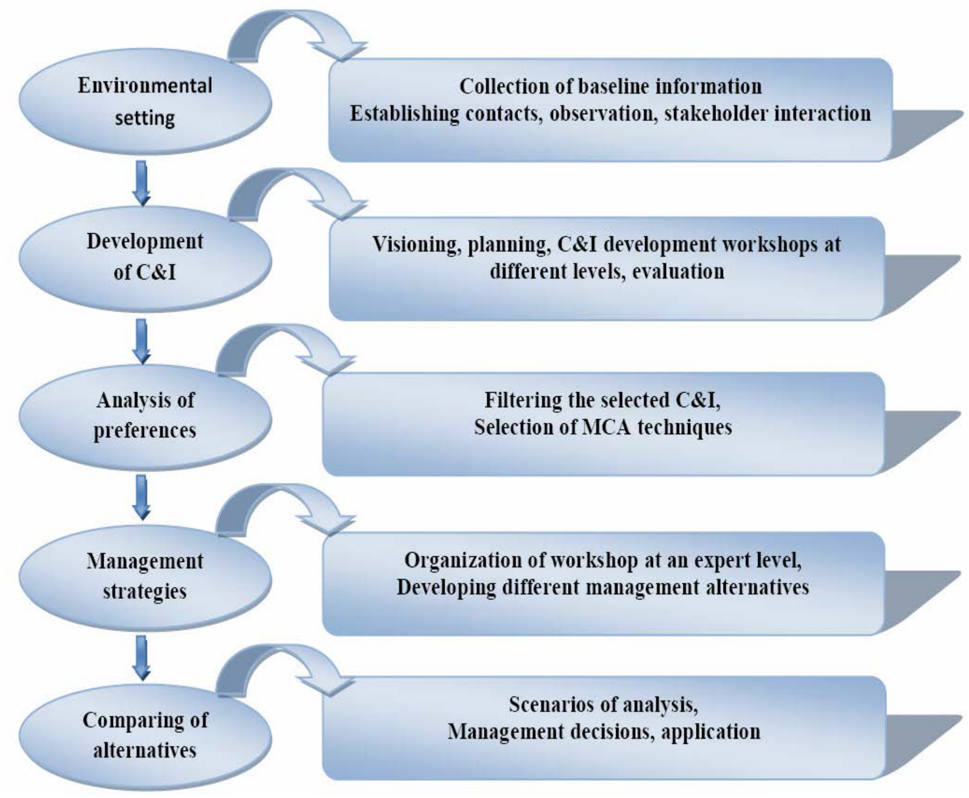


Figure 2: Methodological approach for developing C&I for evaluating sustainable forest management strategies

4. Application

In total, 7 criteria and 45 indicators were identified by the help of 48 stakeholders comprising foresters, social workers, farmers and employers for evaluating SFM (Fig.3). Rating, ranking and pairwise comparison techniques were used to derive the preferences on the C&I set by the stakeholders. In this study, for the rating a score between 1-100 was assigned and the ranks were assigned following a nine-point scale (depending on the number of indicators related to each criterion). Pairwise comparisons were done on the base of rating and ranking inputs provided by stakeholders and the priorities were calculated with the eigenvalue method by the use of the Expert Choice Software.

Figure 3: Photos from the various workshops

The results obtained from rating and ranking (arithmetic mean) and pairwise comparison (geometric mean) derived from the 48 stakeholders for the criteria level is shown in Tab (1). The enhancement of forest health and vitality (C3) and the production functions of forests (C4) were found to be the highly-preferred criteria. The socio-economic function of the forests (C6) has been preferred as the second most important criteria among all.

Table 1: Preferences of criteria based on rating, ranking and pairwise comparisons (PWC) methods (n=48)

Criteria	Arith. mean rating	sdv. of rating	Arith. mean ranking	sdv. of ranking	Gmean of priorities (PWC)
C1. Maintenance of forest ecosystems	11.9	1.12	3.90	1.76	0.095
C2. Maintenance of forest biodiversity	12.6	4.40	3.58	1.76	0.110
C3. Enhancement of forest health and vitality	15.8	6.28	2.75	0.89	0.149
C4. Productive functions of forests	17.0	8.50	2.65	1.72	0.143
C5. Protective functions of forests	15.5	8.40	3.10	1.48	0.132
C6. Socio-economic functions and conditions	15.1	6.70	3.15	1.17	0.132
C7.The legal and institutional frameworks	12.1	5.60	3.79	1.03	0.010

5. Development and evaluation of management strategies

An expert workshop was organized in order to define the forest management strategies. The experts developed four strategies: the first strategy (MS I) was developed by the foresters' group on the basis of the current management plan. It represents technical issues, as it is more oriented towards forest production, protection and the policy of forest management. The second strategy (MS II), which was generated by the researchers' group, concentrates more on socio-economic and ecological measures. MS (III) is a conservation strategy developed by the ecologists, which focuses mainly on biodiversity conservation, forest health and the maintenance of forest ecosystems. Finally, MS IV strategy concentrates on socio-economic and policy issues, and was developed by administrative workers from the forested areas. All management strategies were designed in terms of their practical applicability, incorporating several concepts of SFM and opportunities for forest development. Moreover, an assessment of the four management strategies has been done according to the content analysis of the existing action plans and the collection of base line information.

Furthermore, the AHP technique has been employed to select the best strategy for SFM by comparing the performance of all 45 indicators. The overall performance of a management strategy was determined by utilizing the geometric mean of the preferences expressed by the different stakeholder groups. According to the overall results, strategy MS II was found to be the best management strategy, MS I as the second best alternative, and MS IV had the lowest priority in general (Fig.4).

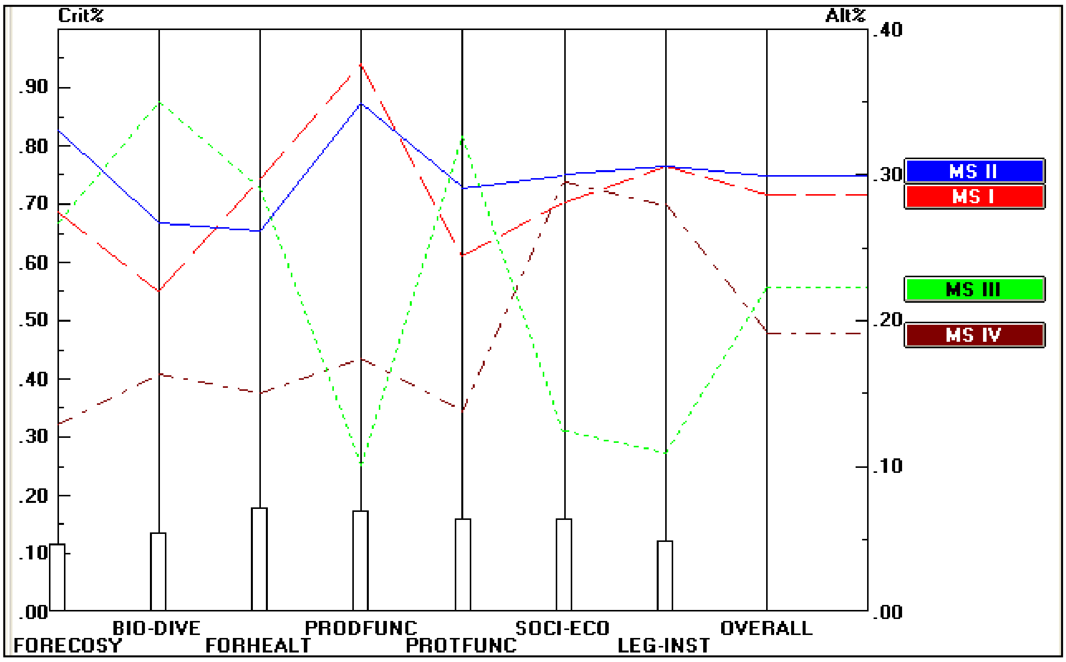


Figure 4: Sensitivity analysis of the general priorities of management strategies based on geometric mean of the synthesed judgment to the all stakeholders (n=48)

Moreover, the results based on the preferences of the individual stakeholder groups' were more or less similar to the overall preferences using the geometric mean, except for the foresters group, whose first priority was to select MS I (Tab.2).

Table 2: General priorities of management strategies based on geometric mean of the synthesized judgment with respect to the different stakeholder groups

Management strategies	Foresters		Social workers		Employers		Farmers		All stakeholders	
	Rank	Priority	Rank	Priority	Rank	Priority	Rank	Priority	Rank	Priority
MSI	1	0.298	2	0.289	2	0.301	2	0.279	2	0.281
MSII	2	0.296	1	0.301	1	0.307	1	0.299	1	0.299
MSIII	3	0.219	3	0.226	3	0.223	3	0.232	3	0.223
MSIV	4	0.187	4	0.183	4	0.169	4	0.191	4	0.191

6. Conclusion

In total, 7 criteria and 45 indicators were identified and four different management strategies have been derived from the identified needs and expectations by various experts and stakeholders. This approach utilized multi-criteria decision making techniques and several participatory methods to identify their multi-dimensional characteristics of the current management system. The results of our study supported the practical use of the MCA approach taken, as the interests and preferences were systematically analysed and the expectations of different stakeholders were identified. Moreover, the findings of this research highlight the importance of C&I and its future application for policy implications. Forest health, productivity and socio-economic functions of forests are found as the most important aspects in a SFM of the walnut forests. All stakeholders recognized the elements of non timber forest products development and access to the market as important to improve the livelihood of the people. The study helped to seek the options for income generation activities and to increase the productivity of resources. Moreover, the increased involvement of local stakeholders in the decision making process and their genuine participation in forest management was seen as a major benefit of such processes. Additionally, the dissemination of the basic issues of SFM and the capacity building will be stimulated by the C&I process in the walnut forests of Kyrgyzstan.

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Nährstoffbilanzmodelle und forstliche Standortskarten als Basis für eine nachhaltige Biomasseproduktion

Combining nutrient balance models and site maps as a basis for sustainable forest biomass production

Nährstoffbilanzmodelle

Ao.Univ.Prof. Dipl.-Ing. Dr. Klaus Katzensteiner

Projektteam
Die Arbeiten wurden teilweise im Rahmen der Lehrveranstaltung, LFÜ Standorts-lehre/Ertragslehre & Bakkalaureatsarbeit' durch die Studierenden Michael Kollnig, Harald Oblasser, Christian Norz und Jörg Oberhollenzer, betreut von Klaus Katzensteiner und Otto Eckmüllner durchgeführt.

Zusammenfassung

Der Bedarf an forstlicher Biomasse als Energieträger wird zunehmend über die Nutzung von Schlagabraum gedeckt. Die Entnahme von Ästen, Reisig und Nadeln in Durchforstung und Endnutzung führt zu unverhältnismäßig hohen Nährstoffverlusten am Standort. Die Produktivität und damit die Menge entzogener Nährstoffe sind von Baumart und Standort abhängig. Die Resilienz des Standorts ist unter anderem eine Funktion der Nährstoffbilanz. Nährstoffbilanzmodelle sind ein Weg um die Nachhaltigkeit der forstlichen Produktion zu überprüfen. In der Arbeit wurde dieser Ansatz für eine Standortseinheit im BOKU-Lehrforst Rosalia getestet. Existierende Inventur- und Standortsinformationen wurden über Bestimmungen der Nährstoffvorräte entlang einer Wuchsreihe ergänzt. Unterschiedliche Nutzungsszenarien zeigen Möglichkeiten und Grenzen nachhaltigen Nährstoffmanagements auf.

Abstract

The demand for forest biomass as an energy source is increasingly met by the utilization of harvesting residues. The extraction of marginal biomass dimensions: branches, twigs and leaves, both in thinning and final harvest, leads to an excessive loss of nutrients from the site. The productivity and thus the amount of nutrient removal with biomass are site and species dependent. The resilience of the site is a function of the nutrient balance. Nutrient balance models are a way to assess the sustainability of forest production. Within the project, a nutrient balance approach has been tested for a selected site unit of the BOKU-school forest at Rosalia. Existing forest inventory data and soil analytical data have been combined with the determination of nutrient stocks along a chronosequence. Different utilization *scenarios highlight possibilities and limits of sustainable forest nutrition management.*

1. Einleitung

Aufgrund ambitionierter nationaler und internationaler Vorgaben für die Nutzung erneuerbarer Energieträger z.B. dem EU-Biomasse-Aktionsplan (CEC, 2005) und den EU 20-20-20 Zielen (CEC, 2008) steigt auch der Druck zur Nutzung von Biomasse aus dem Wald für die energetische Verwertung. Die österreichischen Ziele für 2020 betragen 34 % erneuerbare Energieträger – ein Teil davon soll über Waldbiomasse gedeckt werden. Durch die Installation von Biomasse-KWK-Anlagen ist bereits derzeit regional eine hohe Nachfrage nach Biomasse aus dem Wald zu verzeichnen (Katzensteiner und Nemestothy, 2007). Der Bedarf an forstlicher Biomasse für die energetische Nutzung wird daher zunehmend auch über Sortimente welche ehemals am Schlag verblieben (Schlagabraum) gedeckt. Schon früh wurde vor möglichen negativen Auswirkungen der Nährstoffentzüge durch Nutzung ‚marginaler' Sortimente wie Feinreisig und Nadeln gewarnt und diese mit den Auswirkungen von Streunutzung und Schneitelung in der Vergangenheit verglichen (Krapfenbauer, 1983; Kreutzer, 1979). Nachhaltige forstliche Produktion ohne Einsatz von Bodenhilfsstoffen und Düngern ist ja nur möglich, weil bei Ernte von Holz in relativ langen Umtriebszeiten nur geringe Nährstoffmengen entzogen werden. Nährstoffverluste bei der konventionellen Nutzung von Derbholz i.R. werden in der Regel über Einträge aus der Atmosphäre und über Mineralverwitterung ausgeglichen. Die Entnahme von Ästen, Zweigen und Nadeln bzw. Blättern bei Durchforstung und Endnutzung führt zu weitaus höheren Nährstoffverlusten vom Standort. Werden solche erhöhte Nährstoffentzüge nicht über Düngungsmaßnahmen kompensiert, ist die Nachhaltigkeit der forstlichen Produktion nicht mehr gewährleistet. Feldversuche zeigen Zuwachseinbussen von bis zu 20 Prozent in den ersten Jahrzehnten nach Vollbaumnutzung im Vergleich zur Entnahme von Stammholz in Rinde (Nord-Larsen, 2002, Egnell und Valinger 2003, Sterba et al. 2003). Helmisaari et al. (2011) zeigten eine negative Korrelation zwischen Zuwachs und entzogener Nährstoffmenge bei Vollbaumnutzung. Die Zuwachsverluste durch Vollbaumnutzung lassen sich in Helmisaaris Arbeit durch Düngung kompensieren. Da aber für die Herstellung von Düngemitteln erhebliche Mengen fossiler Energieträger nötig sind, wird der positive Effekt der energetischen Verwertung der Restbiomasse – Einsparung fossiler Energieträger - deutlich reduziert.

Meiwes et al. (2008) weisen darauf hin, dass Biomasseentzüge aus dem Wald differenziert betrachtet werden müssen. Dabei sind einerseits die einzelnen (Nähr-)Stoffe getrennt zu betrachten, andererseits ist die Nährstoffausstattung des Standorts zu beachten. Die Produktivität und damit auch die Nährstoffentzüge sind standortsabhängig. Die Resilienz eines Standorts hängt wiederum von der Nährstoffbilanz ab. Bilanzmodelle sind eine Möglichkeit die Nachhaltigkeit der forstlichen Produktion abzuschätzen. Allerdings benötigen diese Modelle zahlreiche Eingangsparameter für die Kalibrierung weshalb ihre Anwendung bisher vorwiegend auf Langzeitversuchsflächen mit entsprechend guter Datenlage beschränkt blieb. Akselsson et al. (2007 a, b) verwendeten Nährstoffbilanzmodelle zur Abschätzung der Nachhaltigkeit der forstlichen Produktion im Hinblick auf die Versorgung mit basischen Kationen für Schweden. Die Modellrechnungen zeigen für weite Bereiche Schwedens negative Bilanzen bei Vollbaumnutzung. Ein ähnlicher Ansatz wurde von Sverdrup et al. (2006) für verschiedene Baumarten für einen Standort in Südschweden gewählt. Diese Studie verweist allerdings auf große Unsicherheiten bei der Abschätzung der Nährstoffauswaschung in den Bilanzmodellen. In Österreich wandten Englisch und Reiter (2009) Nährstoffbilanzmodelle im Rahmen der Studie, Holz- und Biomasseaufkommen für Österreich' mit Datensätzen der Österreichischen Waldinventur an. Meiwes et al. (2008) schlagen eine einfache Klassifikation von Standorten anhand des Anteils der in der Biomasse gebundenen Nährstoffe am pflanzenverfügbaren Vorrat (Pflanze+Boden) vor. Je nach Klasse ist eine größere oder geringere Bandbreite für die Nutzungsintensität zulässig. Nach Englisch und Reiter (2009) ist den vorher vorgestellten Ansätzen Vollbaumnutzung auf etwa der Hälfte der Probeflächen der Österreichischen Waldinventur nachhaltig möglich und sollte auf etwa einem Viertel der Flächen gänzlich unterbleiben.

2. Projektziel und Fragestellung

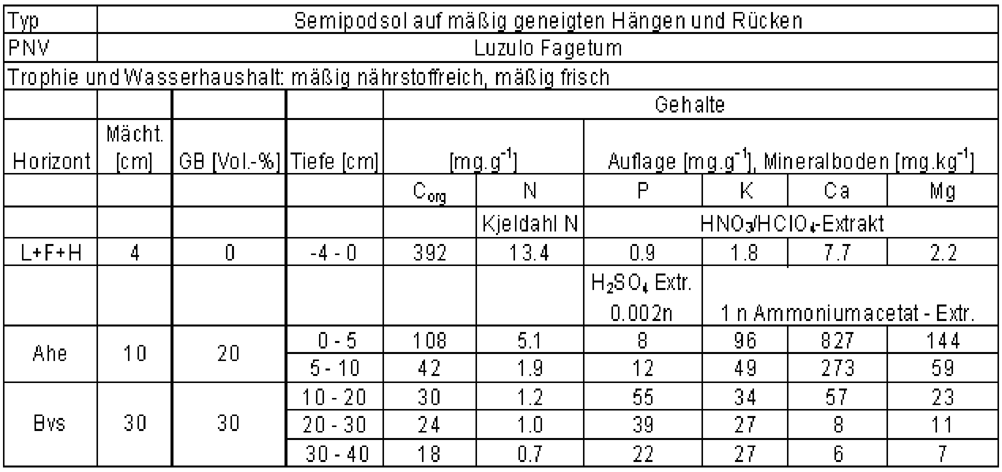
In dem Projekt wird die Anwendbarkeit von Nährstoffbilanzmodellen beispielhaft auf Ebene eines Forstreviers getestet. In weiterer Folge sollen derartige Modellansätze im Rahmen klassischer Standortskartierungsverfahren eingesetzt werden und damit die Nutzbarkeit von Standortskarten für betriebliche Entscheidungsprozesse deutlich verbessern. Für eine ausgewählte Standortseinheit im Lehrforst Ofenbach-Rosalia der BOKU werden Nährstoffvorräte sowie Nährstoffbilanzen für unterschiedliche Managementszenarien gerechnet. Das Projekt fördert die Anwendungsmöglichkeit dieser Konzepte für betriebliche Überlegungen. Die Methoden sollen in weiterer Folge in der Lehrveranstaltung ‚Lehrforstübungen Standortslehre/Ertragslehre (912.110)' eingesetzt und für unterschiedliche Standortsbedingungen und Nutzungsszenarien angewandt und weiterentwickelt werden.

3. Material und Methoden

3.1 Standort und Boden

Für den Lehrforst Ofenbach-Rosalia liegt eine forstliche Standortstypenkarte mit Bodenbeschreibungen und chemischen Analysedaten vor (Gasch 1985, Weidinger 1988). Auf Basis dieser Arbeiten wurden in der Abteilung 20 Bestände auf einem dominierenden Standortstyp mit durchschnittlicher Nährstoffausstattung ausgewählt (Tabelle1). Die Bestände liegen auf ca. 600 m Seehöhe auf einem mäßig geneigten Nordwesthang. Die Fichte wurzelt flach, der Hauptwurzelraum reicht bis in ca. 40 cm Mineralboden.

Tabelle 1: Charakteristika des Standortstyp 3 der Standortskarte Lehrforst, Revier Pernitz Teil Ofenbach 1:10.000, Stand 1985 (Gasch 1985, Weidinger, 1988).



Typ	Semipodsol auf mäßig geneigten Hängen und Rücken								
PNV	Luzulo Fagetum								
Trophie und Wasserhaushalt: mäßig nährstoffreich, mäßig frisch									
				Gehalte					
Horizont	Mächt. [cm]	GB [Vol.-%]	Tiefe [cm]	$[mg.g^{-1}]$		Auflage $[mg.g^{-1}]$, Mineralboden $[mg.kg^{-1}]$			
				C_{org}	N	P	K	Ca	Mg
					Kjeldahl N	$HNO_3/HClO_4$-Extrakt			
L+F+H	4	0	-4 - 0	392	13.4	0.9	1.8	7.7	2.2
						H_2SO_4 Extr. 0.002n	1 n Ammoniumacetat - Extr.		
Ahe	10	20	0 - 5	108	5.1	8	96	827	144
			5 - 10	42	1.9	12	49	273	59
Bvs	30	30	10 - 20	30	1.2	55	34	57	23
			20 - 30	24	1.0	39	27	8	11
			30 - 40	18	0.7	22	27	6	7

Die Lagerungsdichte für die Mineralbodenhorizonte wurde nach Callesen et al. (2003) über die Kohlenstoffgehalte nach Formel 1 abgeschätzt. Für Auflagehumus wurde eine Lagerungsdichte von 0.12 $g.cm^{-3}$ angenommen. Die Stoffvorräte über die Durchwurzelungstiefe wurden nach Formel 2 berechnet.

Formel 1: $BD = 1.685 - 0.1045\sqrt{C}$

BD…Lagerungsdichte $[g.cm^{-3}]$, C…organischer Kohlenstoff $[mg.g^{-1}]$

Formel 2:

$$Stoffvorrat = \sum_{Bodenhorizonte} 10 * Stoffgehalt * BD * Horizontmächtigkeit * (1 - Skelettgehalt / 100)$$

Stoffvorrat $[g.m^{-2}]$, Stoffgehalt $[mg.g^{-1}]$, BD $[g.cm^{-3}]$, Horizontmächtigkeit [cm], Skelettgehalt [Vol.-%]

3.2 Oberirdische Biomasse entlang einer Wuchsreihe

Drei möglichst reine Fichtenbestände unterschiedlicher Altersklassen (III, IV und V) wurden im Sinn einer Wuchsreihe ausgesucht. In jedem Bestand wurden fünf Winkelzählproben gemessen. Im weiteren wurden in jeder Altersklasse je eine Fichte**,** die in etwa dem 17er, 50er und 83er Quantil der Grundflächenverteilung (aller Bäume inklusive anderer Baumarten) entsprach, ausgewählt. Eine Einschränkung war, dass die Bäume keine biotischen oder abiotischen Schäden aufweisen sollten. Nach Fällung wurden Stockhöhe, Länge des gefällten Stammes und Kronenlänge und das Baumalter über Zählung der Jahrringe bestimmt. Die Krone wurde in Sechstel unterteilt und in jedem Sechstel alle Astbasisdurchmesser gemessen. Für Äste mit einem Durchmesser < 10 mm wurde nur die Anzahl bestimmt. Für die weiteren Untersuchungen wurden je Kronensechstel zwei repräsentative, unbeschädigte Äste ausgewählt, geerntet, in unbenadelte und benadelte Teile getrennt und deren Teilfrischmassen bestimmt. Von den in 10 cm Stücke zerkleinerten benadelten Fraktionen wurden nach sorgfältiger Durchmischung jeweils ca. 300 g Teilprobe herausgewogen.

Ebenso wurden von den unbenadelten Astteilen zwei repräsentative Teilstücke entnommen. Unterhalb des Kronenansatzes wurde der Basisdurchmesser aller Totäste gemessen, ein repräsentativer Ast geworben, gewogen und eine Teilprobe entnommen. Weiters wurde von jedem Baum in Brusthöhe und am Kronenansatz eine Baumscheibe entnommen. Die Teilproben wurden gekühlt ins Labor transportiert. Von den Stammscheiben wurden nach Bestimmung der Durchmesser und Rindenstärke Keile entnommen und in Holz und Rindenanteile getrennt. Die benadelten Astanteile wurden nach Vortrocknung bei 40°C in Reisig und Nadeln zerteilt. Anschließend wurden alle Proben bei 105° C bis zur Gewichtskonstanz getrocknet und ihre Massen bestimmt. Die Stammvolumina in Rinde wurden über BHD und Höhe mit Hilfe der Formzahlfunktionen nach Pollanschütz (1974) errechnet. Die Rindenanteile wurden über ihre Kreisflächenanteile an den Stammscheiben errechnet. Die Dichte von Holz und Rinde wurde von versiegelten Teilproben pyknometrisch bestimmt und damit die jeweiligen Massen an Stammholz und Rinde hochgerechnet.

Die Trockenmassen je Ast nach unbenadelten Astteilen, Reisig und Nadeln wurden durch Multiplikation der jeweiligen Gesamtfrischmassen mit den Faktoren Trockenmasse zu Frischmasse der Teilproben hochgerechnet und auf die jeweilige Astbasisfläche bezogen. Über Multiplikation der aus zwei Probeästen gemittelten Trockenmassen je cm² Astbasisfläche mit der Summe aller Astbasisflächen im jeweiligen Kronensechstel (Ästen < 10 mm, die nur gezählt worden waren, wurde ein Durchmesser von 7,8 mm unterstellt), wurden Nadel-, Reisig- und Asttrockenmasse je Kronensechstel für die Einzelbäume errechnet. Die Teiltrockenmassen (Holz, Rinde, Äste, Reisig, Nadeln) wurden für jeden Einzelbaum getrennt aufsummiert und auf Masse je m² Kreisfläche in Brusthöhe hochgerechnet. Multipliziert mit jeweils einem Drittel der Grundfläche ergibt dies den Anteil der Biomasse von Holz, Rinde, Nadel und Ast im Teilkollektiv. Die Summe Biomassen der Teilkollektive ergibt die Gesamtbiomasse des jeweiligen Bestandes.

3.3 Nährstoffvorräte entlang einer Wuchsreihe

Von den Nadel-, Reisig- und Astproben wurden baumweise über die Biomassenanteile je Kronensechstel gewichtete Mischproben hergestellt und vermahlen. Ebenso wurden baumweise Proben von Holz- und Rinde aus Brusthöhe und Kronenansatz entsprechend ihren Biomasseanteilen vermahlen. Kohlenstoff und Stickstoff wurden mit einem Leco TruSpec CN Elementaranalysator bestimmt. Die Bestimmung der Elemente P, S, K, Ca und Mg erfolgte im $HNO_3/HClO_4$-Aufschluß mittels ICP-OES (Perkin Elmer Optima 3000 XL). Über die Biomassenfraktionen wurden die Kohlenstoff- und Nährstoffvorräte einzelbaumweise hochgerechnet und anschließend wie bei den Biomassen beschrieben die Bestandesvorräte ermittelt.

3.4 Nährstoffentzüge

Für die Nährstoffentzüge wurden zwei Szenarien über die Umtriebszeit in Anlehnung an Eckmüllner (2006b) gerechnet. Nach den Stammzahlleitlinien von Pollanschütz soll die Stammzahl einen Wert von 20000/Oberhöhe [m] nicht überschreiten. Je nach Ausgangsstammzahl und Bonität wachsen Bestände unterschiedlich rasch in einen für Schneebruch kritischen Bereich. Durch den Pflanzverband, Zeitpunkt und Intensität von Stammzahlreduktion bzw. Durchforstung kann das Verhältnis Höhe zu Durchmesser der Zukunftsstämme (H/D-Wert) unterhalb eines kritischen Bereichs gehalten werden. Szenario 1 unterstellt eine hohe Stammzahlhaltung unter in Kaufnahme eines hohen Risikos, Szenario 2 unterstellt starke frühzeitige Eingriffe. Die dabei anfallenden Biomassenkompartimente wurden über den Grundflächenmittelstamm mit allometrischen Funktionen nach Eckmüllner (2006a) errechnet. Über die aus den Untersuchungen aus der Wuchsreihe gewonnenen mittleren Nährstoffgehalte von Stammholz in Rinde, Ästen, Reisig und Nadeln wurden potentielle Nährstoffentzüge hochgerechnet. Bei der auf der untersuchten Standortseinheit herrschenden Bonität fallen diese dargestellten Entzüge über einen Zeitraum von 100 Jahren an.

3.5 Nährstoffbilanzen

Für eine Umtriebszeit für unterschiedliche Nutzungsszenarien werden Nährstoffbilanzen (Delta Nährstoffkapital = Eintrag aus der Atmosphäre + Freisetzung aus der Mineralverwitterung + Düngung - Austrag mit dem Sickerwasser - Austrag durch Ernte) errechnet. Für den jährlichen Austrag über Ernte werden die nach 3.4 berechneten potentiellen Nährstoffentzüge über Ernte und einer unterstellten Ausbeute bei Nutzung (Stammholz i.R. 80 %, bei Vollbaumnutzung 90 % Stammholz i.R. plus 70 % Äste, Reisig und Nadeln) durch die Umtriebszeit von 100 Jahren dividiert. Als Eintrag aus der Atmosphäre wird für N, S, K, Ca und Mg der Durchschnitt der österreichischen ICP Forest-Level II Flächen herangezogen (Smidt, 2008). Für P Deposition und Leaching werden Daten von Ilg et al. 2009 übernommen (Median für ICP Forest Level II Fichtenbestände in Deutschland). Da die Datenbasis für die Modellierung der Raten der Mineralverwitterung mit PROFILE (Warfvinge and Sverdrup 1992, Sverdrup and Warfvinge 1995) nicht ausreicht, werden diese vorläufig für ähnliche Böden von Sverdrup et al. (2006) übernommen. Ebenso wurden die Raten der Nährstoffauswaschung an der Untergrenze des Wurzelraumes geschätzt. Die aus der Literatur übernommenen bzw. geschätzten Daten dienen nur zur Veranschaulichung des Gesamtmodells.

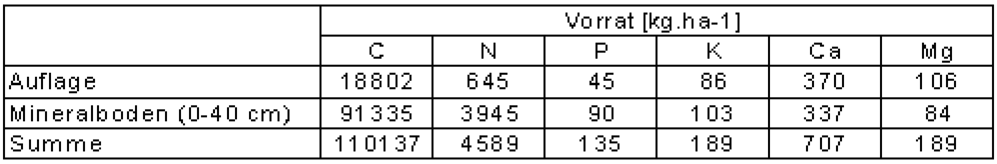
Die Modellergebnisse werden für eine Klassifikation des Standortes nach seiner Vulnerabilität herangezogen und die Einschätzung mit einfacheren, auf wenigen Standortsparametern basierenden Klassifikationsansätzen verglichen.

4. Ergebnisse und Diskussion

4.1 Biomassen und Stoffvorräte im Boden und in der oberirdischen Biomasse

Tabelle 2 zeigt die in der Auflage und im Oberboden als pflanzenverfügbar erachteten Elementgehalte. Es zeigt sich, dass besonders von den basischen Kationen ein wesentlicher Anteil der Auflage gebunden ist. Die Kaliumausstattung des Systems ist gering, ebenso die extrahierbaren Phosphorgehalte.

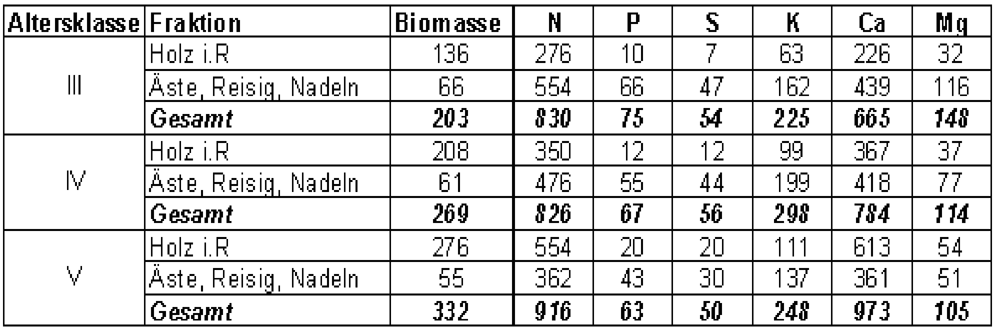
Tabelle 2: Nährstoffvorrat in der Auflage (Gesamtgehalte) und im Mineralboden (C, N gesamt, P im H2SO4-Extrakt, K, Ca, Mg extrahierbar im Ammonacetatextrakt)



	Vorrat [kg.ha-1]					
	C	N	P	K	Ca	Mg
Auflage	18802	645	45	86	370	106
Mineralboden (0-40 cm)	91335	3945	90	103	337	84
Summe	110137	4589	135	189	707	189

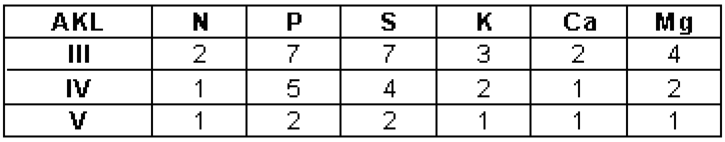
Tabelle 3 zeigt, dass die Vorräte an Ästen, Reisig und Nadeln, ebenso wie die darin gebundenen Nährstoffvorräte von der III bis zur V Altersklasse leicht abnehmen. Das Verhältnis Nährstoffe in Ästen + Reisig + Nadeln zu Nährstoffe in Stammholz i.R. ist in der jüngsten Altersklasse besonders weit, vor allem für Phosphor.

Tabelle 3: Biomasse [Mg.ha^{-1}] und Elementvorräte [kg.ha^{-1}] entlang der Wuchsreihe



Altersklasse	**Fraktion**	**Biomasse**	**N**	**P**	**S**	**K**	**Ca**	**Mg**
III	Holz i.R	136	276	10	7	63	226	32
	Äste, Reisig, Nadeln	66	554	66	47	162	439	116
	Gesamt	***203***	***830***	***75***	***54***	***225***	***665***	***148***
IV	Holz i.R	208	350	12	12	99	367	37
	Äste, Reisig, Nadeln	61	476	55	44	199	418	77
	Gesamt	***269***	***826***	***67***	***56***	***298***	***784***	***114***
V	Holz i.R	276	554	20	20	111	613	54
	Äste, Reisig, Nadeln	55	362	43	30	137	361	51
	Gesamt	***332***	***916***	***63***	***50***	***248***	***973***	***105***

Tabelle 4: Verhältnis von Biomasse und Nährstoffvorräten in Ästen + Reisig + Nadeln zu Nährstoffvorräten von Stammholz i. R für unterschiedliche Altersklassen



AKL	**N**	**P**	**S**	**K**	**Ca**	**Mg**
III	2	7	7	3	2	4
IV	1	5	4	2	1	2
V	1	2	2	1	1	1

Meiwes et al. (2008) schlagen Schwellwerte für Nutzungsrestriktionen auf Basis der Anteile ‘Oberirdische Nährstoffvorräte in der Biomasse eines Altbestandes’ am Gesamtvorrat (austauschbarer Vorrat basischer Kationen, Gesamtvorrat in der Auflage und im Bestand, Gesamtvorräte für N und P). In Abhängigkeit von diesen Schwellwerten werden Nutzungseinschränkungen vorgegeben (Tabelle 5). Nach dieser Einschätzung sind vor allem im Hinblick auf die Phosphorausstattung aber auch auf die Phosphorvorräte für den Standortstyp 3 im Lehrforst erhebliche Nutzungseinschränkungen vorhanden. Die Nutzung des Schlagabraumes sollte jedenfalls unterlassen werden da durch frühere intensive Streunutzung das Nährstoffkapital des Standorts bereits erschöpft ist. Hohe Immissionsraten haben vermutlich in den vergangenen 50 Jahren zusätzlich zu Auswaschungsverlusten basischer Kationen geführt.

Tabelle 5: Vorgeschlagene Schwellwerte für den prozentuellen Anteil der in der oberirdischen Biomasse gespeicherten Nährstoffe am verfügbaren Gesamtvorrat in Biomasse & Boden für unterschiedliche Nutzungen (verändert nach Meiwes et al. 2008) und Vergleichswert für einen Bestand der V. Altersklasse auf Standortstyp 3.

N	P	K +Ca + Mg			Nutzungsvorschlag
60 - 80	25 - 40	50 - 90			Ernte v. (stärkerem) Stammholz i.R.
30 - 60	10 - 25	25 - 50			Belassen von Blättern/Nadeln & Feinreisig
1 - 30	1 - 10	1 - 10			Vollbaumnutzung möglich
Untersuchungsbestand					
N	P	K	Ca	Mg	
17	32	57	58	36	Ernte v. (stärkerem) Stammholz i.R.

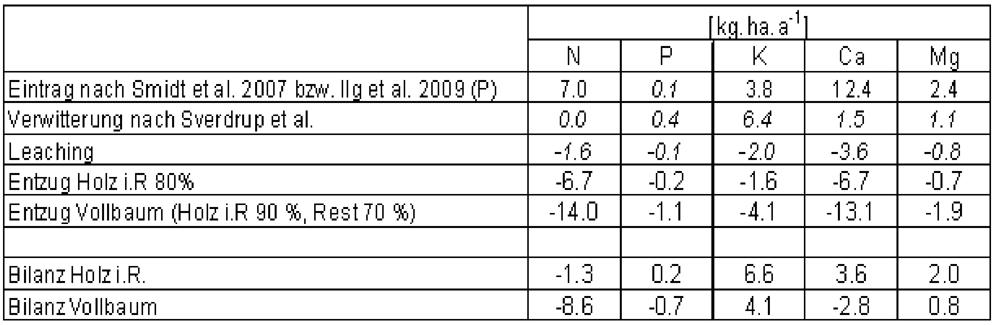
4.2. Szenariobasierte Modellierung

Tabelle 6 veranschaulicht die potenziellen Mehrerträge an Biomasse für verschiedene Durchforstungsszenarien und die damit verbundenen Nährstoffentzüge über die Umtriebszeit. Mehrerträgen an Biomasse von 23 bzw. 27 % stehen exorbitant höhere Nährstoffverluste, vor allem bei Phosphor gegenüber. Diese potenziellen Entzüge liegen im oberen Bereich der von Helmisaari et al. (2011) et al. in Skandinavien gemessenen Werte, für Magnesium sogar deutlich darüber. Unterstellt man realistische Nutzungsszenarien ergeben sich über eine Umtriebszeit von 100 Jahren gerechnet die in Tabelle 7 dargestellten jährlichen Entzüge.

Tabelle 6: Potenzielle Biomasse- und Nährstoffentzüge über die Umtriebszeit (Szenario 1: frühzeitige, intensive Eingriffe, Szenario 2: konservative späte Nutzung mit hohem Schneebruchrisiko)

		Biomasse [Mg.ha^{-1}]		N [kg.ha^{-1}]		P [kg.ha^{-1}]		K [kg.ha^{-1}]		Ca [kg.ha^{-1}]		Mg [kg.ha^{-1}]	
		Holz i.R.	A+F+N	Holz i.R.	A+F+N	Holz i.R.	A+F+N	Holz i.R.	A+F+N	Holz i.R.	A+F+N	Holz i.R.	A+F+N
Szenario 1	1.DF	38	18	72	138	3	17	17	49	72	118	8	23
	2.DF	63	20	120	153	4	19	28	55	119	131	13	26
	Vorlichtung	138	31	262	237	9	29	61	85	261	203	29	40
	Räumung	205	35	390	267	14	33	91	96	387	230	43	45
	Summe	444	104	844	795	30	97	196	286	839	683	93	133
Szenario 2	1.DF	23	18	44	138	2	17	10	49	43	118	5	23
	2.DF	51	20	97	153	3	19	23	55	96	131	11	26
	Vorlichtung	148	36	281	275	10	34	65	99	280	236	31	46
	Räumung	219	47	416	359	15	44	97	129	414	308	46	60
	Summe	441	121	838	925	30	113	195	333	833	794	92	155
		Potenzieller Mehrentzug durch Nutzung der 'Restbiomasse' über die Umtriebszeit im Verhältnis zu Holz i. R. [%]											
Szenario 1			23		94		326		146		81		143
Szenario 2			27		110		381		171		95		168

Tabelle 7: Hypothetische jährliche Nährstoffbilanzen für einen Fichtenbestand in der Abteilung 20 auf Standortstyp 3 im Lehrforst



	[kg.ha.a^{-1}]				
	N	P	K	Ca	Mg
Eintrag nach Smidt et al. 2007 bzw. Ilg et al. 2009 (P)	7.0	*0.1*	3.8	12.4	2.4
Verwitterung nach Sverdrup et al.	*0.0*	*0.4*	*6.4*	*1.5*	*1.1*
Leaching	*-1.6*	*-0.1*	*-2.0*	*-3.6*	*-0.8*
Entzug Holz i.R 80%	-6.7	-0.2	-1.6	-6.7	-0.7
Entzug Vollbaum (Holz i.R 90 %, Rest 70 %)	-14.0	-1.1	-4.1	-13.1	-1.9
Bilanz Holz i.R.	-1.3	0.2	6.6	3.6	2.0
Bilanz Vollbaum	-8.6	-0.7	4.1	-2.8	0.8

Trotz aller Unsicherheiten bei der Schätzung von Verwitterung und Nährstoffauswaschung zeigt sich, dass konventionelle Nutzung von Stammholz in Rinde das Nährstoffkapital am Standort nicht beeinträchtigt. Die leicht negative Stickstoffbilanz ist vermutlich auf Unterschätzung der tatsächlichen Einträge in diesem emittentennahen Gebiet zurückzuführen. Die Vollbaumnutzung führt in jedem Fall zu negativen Bilanzen bei mehreren Nährstoffen und damit zu einer langfristigen Reduktion des Standort-kapitals.

5. Schlussfolgerungen und Ausblick

Die Untersuchung zeigt die Anwendbarkeit von Nährstoffbilanzmodellen zur Entscheidungsunterstützung für Nutzungsplanung für konkrete Standorts- und Bestandessituationen. Einmal mehr ist auch die fehlende experimentelle Datenbasis für die Modellierung von Verwitterung und Nährstoffausträgen auf dieser Untersuchungs-ebene erkennbar. Hier sollten für die dominierenden Standortstypen im BOKU Lehrforst langfristige Monitoringkonzepte entwickelt und umgesetzt werden. Im Rahmen von Übungen, Bakkalaureats- und Diplomarbeiten sollen Nährstoffvorräte und Bilanzen für weitere Standortstypen und Baumarten erarbeitet werden.

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Wolbachia in the spruce bark beetle *Pityogenes chalcographus* (Coleoptera, Scolytinae) and consequences for bark beetle control

Wolbachia im Kupferstecher, *Pityogenes chalcographus* (Coleoptera, Scolytinae)

Wolbachia im Kupferstecher

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Zusammenfassung

Der Kupferstecher *Pityogenes chalcographus* gehört zu den wichtigsten Schädlingen in eurasischen Fichtenstandorten. Kreuzungsversuche in den 70er Jahren zeigten Inkompatibilität von Käfern verschiedener Herkunft. Diese Befunde wurden als Hinweis auf eine Rassendifferenzierung infolge eiszeitlicher Trennungsereignisse interpretiert. Eine Analyse der mtDNA von *P. chalcographus* zeigte, dass die Populationen des Kupferstechers in zwei geographisch getrennte Gruppen in Nordost- und Mitteleuropa gegliedert sind. Zusätzlich wurden noch zwei weitere Gruppen gefunden, die in Italien und am Balkan vorkommen. *Wolbachia* sind Endosymbionten und sind in vielen Insektenarten nachgewiesen worden. Diese α-Proteobakterien sind maternal vererbt und können das Reproduktionsverhalten des Wirts drastisch verändern so können sie z.B. cytoplasmatische Inkompatibilität induzieren, d.h. *Wolbachia* infizierte Männchen erzeugen mit nicht infizierten Weibchen keine Nachkommen. *Wolbachia* ist daher ein potentieller Kandidat für den Einsatz im biologischen Pflanzenschutz. Dieser Endosymbiont kann durch CI Populationen minimieren bzw. Genotypen mit bestimmten Eigenschaften in eine Population bringen. Nachdem das mitochondriale Genom wie *Wolbachia* maternal vererbt ist, könnte *Wolbachia* für die Inkompatibilität und somit auch für die mitochondriale Verteilung von *P. chalcographus* in Europa verantwortlich sein. In diesem Projekt wurden zwei unterschiedliche *Wolbachia* Linien (*w*Cha1 and *w*Cha2) in sehr geringer Konzentration gefunden. Es wurde kein Infektionsunterschied zwischen den europäischen Populationen gefunden.

Abstract

Wolbachia are obligatory endosymbiotic α-proteobacteria found in many insect species. They are maternally transmitted and often exhibit reproductive phenotypes like cytoplasmic incompatibility. *Pityogenes chalcographus* is a bark beetle causing severe damage in spruce stands. Its European populations are divided into several mitochondrial clades separated by partial crossing barriers. In this study we tested a large sample set covering the natural range of the beetle in Europe for the presence of *Wolbachia* and associations between infection pattern and mitotypes using a highly sensitive nested PCR technique. 35.5% of the individuals were infected with the endosymbiont and two distinct strains were identified. Both strains occur in low titre not accessible by conventional detection methods. The infections are present all over Europe, unlikely to cause the partial crossing barriers in this host and uncoupled from mitochondrial clades. This pattern is indicative for populations evolving towards endosymbiont loss and for repeated intraspecific horizontal transfer of Wolbachia. Alternatively, the low titre infections found in *P. chalcographus* are yet another example for *Wolbachia* that can persist in host species at low densities and frequencies.

1. Introduction

Wolbachia are obligatory endosymbiotic α-proteobacteria found in numerous arthropod and filarial nematode species (Werren et al, 2008). The genus *Wolbachia* contains more than six taxonomic supergroups including supergroup A and B that are found in insects. Estimations on the rate of infected insect species vary from approximately 20% (Werren and Windsor, 2000) to up to 76% (Jeyaprakash and Hoy, 2000) based on conventional PCR and more sensitive long PCR approaches. Taking low frequency infections into account, a recent meta-analysis by Hilgenböcker et al. (2008) estimates more than 65% of insect species to harbour *Wolbachia*. *Wolbachia* are usually maternally inherited and have developed sophisticated methods to alternate the host's reproductive system in order to increase the ratio of infected female offspring. Cytoplasmic incompatibility (CI) is the most common phenotype in insects and has been observed in many arthropod species (Hoffmann and Turelli, 1997). It leads to embryonic death of fertilized eggs when infected males mate with uninfected females, while matings with infected females are compatible. This leads to a reproductive advantage of infected over uninfected females and infection frequencies will rise over generations. The maternal inheritance of *Wolbachia* creates a strong association with the maternally inherited mitochondrial DNA (mtDNA). In newly infected populations, mtDNA of the initially infected individuals often hitchhikes through the population with the expanding *Wolbachia* and replaces original haplotypes (Hurst and Jiggins, 2005).

Worldwide more than 6000 species of bark and ambrosia beetles are described, forming the Scolytinae (Wood, 1982). They mostly live in living or dead woody substrates, communicate by pheromones (Byers, 2004), are commonly associated with blue stain or ambrosia fungi (Kirisits, 2004) and have hence the potential to cause substantial economic damage. An initial small scale survey of *Pityogenes chalcographus*, a bark beetle species that commonly infests spruce stands, did not detect *Wolbachia* infections in

Austrian populations (Riegler 1999). While the latter survey was performed using conventional PCR techniques, a long PCR approach following the protocol of Jeyaprakash and Hoy (2000) yielded 14.3% positive reactions in 189 European individuals (Avtzis, 2006).

During the 1970s, Führer (1976, 1977) performed crossing experiments with *P. chalcographus* and observed a significant decline in offspring numbers when female beetles from Central Europe mated with male beetles from Northern Europe, while the effect was not detected in reciprocal crosses. Mitochondrial Cytochrome Oxidase I (COI) gene sequences of European *P. chalcographus* populations revealed 58 haplotypes (Avtzis et al., 2008). Phylogenetic analysis yielded three major clades with a maximum sequence divergence of 2.33%. These were numbered from I to III, with clade III being further divided into four subclades, a, b, c and d. Almost 80% of all individuals showed haplotypes that grouped either in clade I or in clade IIIa. Although broadly sympatric, clade I haplotypes were most frequently detected in the northern regions of Europe while clade IIIa haplotypes were dominant in Central Europe. Avtzis et al. (2008) demonstrated the reproductive barriers between the Northern and the Central European populations and assigned incompatible individuals to the major mitochondrial clades I and IIIa, respectively.

2. Aims

For this study a highly sensitive nested PCR approach was used to survey the *wsp* gene of over 300 *P. chalcographus* individuals with characterized mtDNA. PCR products were cloned and sequenced in order to analyse the *Wolbachia* diversity in *P. chalcographus*. PCR-RFLP was then applied for strain discrimination and infection patterns were compared with mtDNA haplotype distribution and geographic origin of the beetles. Two new strains were determined, characterized as *w*ChaA and B using the multilocus sequence typing system (Baldo et al., 2006) and their density estimated by using a semiquantitative approach.

3. Materials and Methods

Sample collection and DNA extraction

For a phylogenetic study, *P. chalcographus* adults were collected in 39 different European locations between 2003 and 2005 (Avtzis et al., 2008). To avoid biased haplotype diversity of the maternal inherited endosymbiont and mitochondria, only one individual per mother gallery was used. Specimens were stored in 96% ethanol at -20°C. DNA of whole individual beetles was extracted using the GenElute Mammalian DNA extraction Kit (Sigma) following the protocol of the manufacturer. DNA was eluted in 50 µl and stored at -20°C. Single *Drosophila simulans* flies infected with *w*Ri and *D. melanogaster* flies infected with *w*Mel were extracted and stored in the same way. 344 beetles from 31 locations with known mtDNA haplotype were selected for *Wolbachia* detection.

Wolbachia detection

All procedures for *Wolbachia* detection were performed in a separated lab not used for DNA extraction, microbiological or post-amplification procedures. Fresh aliquots of chemistry were used at least every two days. Only pipettes equipped with filter tips were used and bench surfaces were repeatedly cleaned with 70% ethanol. As standard PCR repeatedly failed to consistently detect *Wolbachia* in extracts, we applied an extensively optimized nested PCR technique amplifying the endosymbionts *wsp* gene on a 96 well thermocycler in a total volume of 10 µl containing: 1x Mg-free buffer, 1.5 mM $MgCl_2$, 100 µM dNTPs, 0.2 µM of each primer and 0.25 u Taq polymerase. For 1st PCR, primers 81F and 691R (Braig et al. 1998) and 0.8 µl template DNA were used and reactions were overlaid with 15 µl mineral oil (Sigma) to avoid formation of aerosols. PCR conditions were 95°C for 2 min followed by 15 cycles at 94°C for 30 sec, 55°C for 45 sec, 72°C for 1 min. 2nd PCR was performed using newly designed internal primers wspif (5'-gtggtggtgcatttggttataaaatgg-3'; position 146 on the 81F/691R PCR product) and wspir (5'-cataagaaccgaaataacgagctccag-3'; position 508 on the 81F/691R PCR product) and 0.5 µl of the 1st PCR product as template. PCR conditions were 95°C for 2 min followed by 30 cycles at 94°C for 30 sec, 60°C for 45 sec, 72°C for 1 min. 8 µl of the 2nd PCR product were loaded to 2% agarose gels and DNA was stained with ethidium bromide and visualized by UV transillumination. 10^{-3}, 10^{-4} and 10^{-5} ng of a control plasmid created by ligating a full length *w*Cha-A *wsp* insert into the pTZ57R plasmid vector (Fermentas) were included in each 96 well detection batch. Furthermore, four wells containing sterile water were distributed over the plate to serve as negative control. Batches showing weak or no signal at 10^{-4} ng or signals in the negative controls were excluded from the analysis and repeated using fresh aliquots of PCR chemistry.

Estimation of Wolbachia density

The detection limit of the nested PCR approach was evaluated using 10^{2} to 10^{-7} ng/µl dilution series of the control plasmid. Sensitivity was compared to conventional *wsp* PCR as described by Braig et al. (1998). DNA content from three individual insect extracts of *P. chalcographus* samples, infected with *w*Cha-A, *w*Cha-B and not infected, respectively, from *D. melanogaster* infected with *w*Mel and from *D. simulans* infected with *w*Ri was determined photometrically. Dilution series covering the 1:5 to 1:100 range were produced from these extracts and amplified for *wsp* using the conventional protocol (Braig et al., 1998) and the nested protocol described above. A similar sized amplicon from EF1α was amplified using the primers EF-2255 and EF-3015 (Cognato and Vogler, 2001) (760 bp, T_a=58°C) for *P. chalcographus*. For *Drosophila*, the new primers Dmel-EF-F (5'-accggccacttgatctacaa-3') and Dmel-EF-R (5'-gatcaagcacttgccctctg-3') (618 bp, T_a=55°C) were used. Cycling conditions were 95°C for 2 min followed by 32 cycles at 94°C for 30 sec, T_a for 45 sec, 72°C for 1 min and a final elongation at 68°C for 15 min. Products were visualized as described above.

Cloning and Sequencing

A 0.8 µl aliquot of the PCR products from six *Wolbachia* positive beetles originating from Norway, Sweden, Finland, Poland, Germany and Greece was ligated into the pTZ57R vector of the InstaClone PCR cloning kit (Fermentas) according to the instructions of the manufacturer. The ligated plasmids were used for transformation of competent JM109 *E. coli* cells and four white colonies from each reaction were picked and transferred to liquid medium. After overnight growth, plasmid DNA was extracted by alkaline lysis (Sambrook et al., 1989). Sanger sequencing was performed by a commercial provider. Retrieved sequences were edited manually, aligned using ClustalX (Thompson et al., 1997) and compared with *Wolbachia* sequences from GenBank by BLAST analysis.

PCR-RFLP

Based on the retrieved *wsp* sequences, polymorphic restriction sites were identified using the NEBcutter software (Vincze et al., 2003). The *w*Cha-A fragment contains one XapI restriction site resulting in bands at 97 and 265 bp, respectively. *w*Het contains two restriction sites resulting in bands at 94, 97 and 171 bp. *w*Cha-B is not cut by XapI giving one 362 bp band (Fig. 2). 58 positive individuals were selected for PCR-RFLP characterization. A mix containing 1x Tango Buffer (Fermentas), 10 µl PCR product and 5 u XapI (Fermentas) was incubated at 37°C for 2 hours. After enzyme inactivation at 70°C for 5 min electrophoresis was performed on a 3% agarose gel and DNA was visualized as described above.

mtDNA analysis

To assess potential contamination of bark beetle samples from the Jarvenpää (Finland) population with parasitoid DNA, the mitochondrial COI gene of two beetles from this location, one showing the PCR-RFLP pattern of *w*Cha-B and one the aberrant pattern, was amplified using the universal primers PAT (5'- TCC ATT GCA CTA ATC TGC CAT ATT A-3') and DICK (5'- CCA ACA GGA ATT AAA TTT TAG AGA TTA GC-3'; Simon et al., 1994). Identical PCR chemistry as for *Wolbachia* detection was used and cycling conditions were 95°C for 2 min followed by 35 cycles at 94°C for 30 sec, 55°C for 45 sec, 72°C for 1 min. PCR products were cloned as described above. Six colonies of each sample were picked and resulting sequences were analyzed by BLAST search.

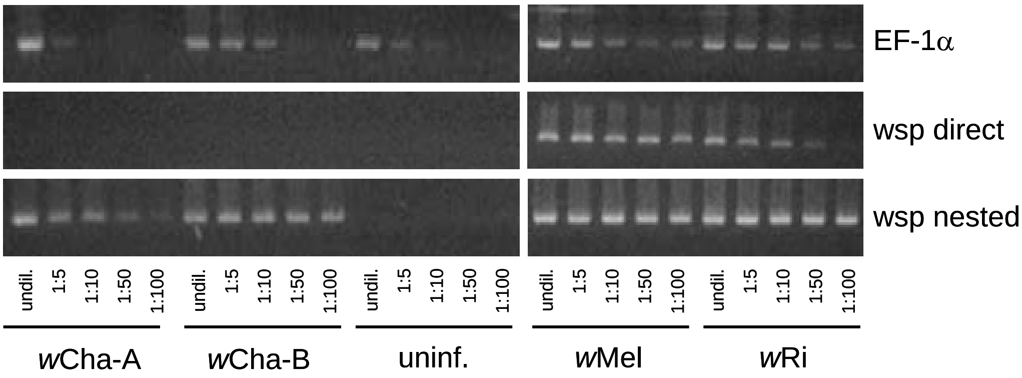

Figure 1: Semiquantitative estimation of *Wolbachia* density - Dilution series of single individual DNA extracts from *P. chalcographus* single infected with *w*Cha-A and *w*Cha-B, uninfected beetles and *D. melanogaster* infected with *w*Mel and *D. simulans* infected with *w*Ri were amplified with primers targeting the nuclear single copy gene EF-1α and the *Wolbachia* surface protein gene *wsp*, either by conventional direct or by nested PCR. Signal intensity suggests that the relative concentration of *Wolbachia* in the bark beetle is at least a factor of ten lower than in the fruit fly.

MLST characterization

For each *w*Cha strain, two single infected beetle samples giving strong bands in nested *wsp* PCR were selected for MLST characterization. As amplification using universal and supergroup specific primers following the protocol of Baldo et al. (2006) gave no visible bands, 0.5 µl of these PCR reactions were used as template in a second round of amplification under the same conditions as in the first round. Products with visible bands were cloned as described above and four to eight white colonies per product were picked for sequencing.

Statistical analysis

A regional grouping was performed for statistical analysis. 'Northern Europe' contains all populations north of 55° latitude. 'Apennine' and 'Balkans' are the populations associated with the two peninsulas. 'Eastern Europe' contains all populations south of 55° latitude and east of 20° longitude that do not belong to the Balkans. All other populations were subsummized as 'Central Europe'. Clade specific grouping depends on the individual mtDNA sequence of each sample. For analysis of regional or clade specific significance of *Wolbachia* distribution, uni- and multivariate ANOVA as implemented in SPSS 15 was used. Duncan's multiple comparison procedure based on the Studentized range test with an $\alpha=0.05$ was applied to test for homogenous groups.

4. Results

Wolbachia density and prevalence

The sensitivity of the *Wolbachia* survey was calibrated by including a standardised plasmid control. Conventional PCR with 81F and 691R primers of the single copy *wsp* gene had a detection limit of 10^{-2} ng plasmid DNA in 10 µl total reaction volume. The nested PCR technique allowed reliable detection of 10^{-4} ng, with faint bands still visible at 10^{-5} ng (Fig. 1). Thus, nested PCR enhances the *wsp* detection limit by an order of two to three magnitudes.

Wolbachia density in *P. chalcographus* was compared to the density in high titre infected standard *Drosophila* lab strains using dilution series and the single copy elongation factor 1α (EF1α) gene as reference (Fig. 2). The DNA concentration of all *Pityogenes* and *Drosophila* extracts was in the range 49 to 65 ng/µl. Successful amplification of EF1α was possible for all dilutions down to 1:100 in *Drosophila* and down to the 1:10 dilution in *P. chalcographus.* Direct *wsp* amplification yielded bands for all dilutions in *w*Mel and down to 1:50 in *w*Ri, but no amplicons in *P. chalcographus.* Using nested *wsp* PCR, all dilutions of infected beetles and flies gave clear bands.

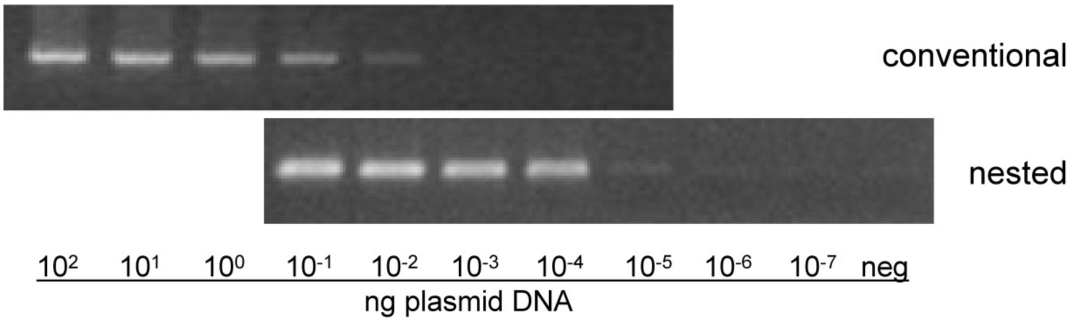

Figure 2: Detection limit of conventional and nested PCR - Dilution series of a plasmid containing a full length *wsp* insert were amplified by conventional (primers 81F and 691R, 35 cycles) and nested PCR. The nested approach enhances the detection limit from 10^{-2} to 10^{-5} ng DNA.

The sensitive nested PCR technique yielded positive signals in 122 out of 344 individuals (35.5%). The highest *Wolbachia* infection rate with 100% positive samples was observed in the populations Harz (Germany) and Hajnowka (Poland) while the samples from Raon sur Plaine and Massif Central II (France), Asiago (Italy) and Chojnice (Poland) contained no infected beetles. Grouping by geography revealed a significantly lower *Wolbachia* prevalence in the Apennine (Italy) and Northern and Central Europe than in Eastern Europe while the Balkans form an intermediate group (Table 1).

Genotyping and distribution of Wolbachia strains
Sequencing of 22 plasmids carrying the *wsp* PCR product revealed three distinct *Wolbachia* sequence variants, of which two belong to the A and one to the B supergroup: *w*Cha-A (GenBank EU878035) shows 99% homology to a *Wolbachia* isolated from the bark beetle *Xylosandrus germanus* (AB359040). *w*Cha-B is identical to previously detected *Wolbachia* in *P. chalcographus* (DQ993183) and shows high homology to *w*Ain from *Tipula aino* (AF481165). One *wsp* sequence variant (EU878036) was only observed once in an individual from the population Jarvenpää (Finland) and was 99% similar to *w*Het from the hymenopteran parasitoid *Leptopilina heterotoma* (AJ634746). Sequencing of six plasmids containing the mitochondrial COI amplicon of the Finnish *w*Cha-B infected beetle gave the expected *P. chalcographus* mtDNA allele. In the individual showing the *w*Het PCR-RFLP pattern, five plasmids contained *P. chalcographus* mtDNA, and one plasmid gave a divergent sequence (EU878037) with over 80% homology to mtDNA of the braconid wasp genera *Peristenus* and *Cotesia*.

From 58 positive individuals characterized by PCR-RFLP, 53 were infected with *w*Cha-A and seven with *w*Cha-B (Table 2, 3). 55 beetles were single-infected and in three beetles originating from Drama (Greece) and Zwardon (Slovakia) both strains were observed.

After two rounds of MLST amplification, *w*Cha-A gave strong bands for *ftsZ* and multiple, weak bands for *gatB* when supergroup A specific primers were used. Standard primers for these two genes and all primers for the other MLST loci gave no visible product. After cloning and sequencing, a consensus *ftsZ* sequence of *w*Cha-A was retrieved (GenBank FJ444853). No *gatB* sequences were found in the cloned plasmids. *w*Cha-B showed clear bands for all MLST loci after re-PCR with standard and supergroup B specific primers and consensus sequences are available under GenBank FJ444854 – FJ444858. All sequences were furthermore submitted to http://pubmlst.org/*wolbachia*/. *ftsZ* of *w*Cha-A is identical with allele 32. The allelic profile of *w*Cha-B is *gatB* = 39, *coxA* = 73, *hcpA* = 104 (new allele), *ftsZ* = 7 and *fbpA* = 161 (new allele).

Table 1*: Wolbachia* prevalence was surveyed by nested PCR. Groups with the same letters are not significantly different (Duncan's multiple comparison procedure based on the Studentized range test, α=0.05).

Region	**n tested**	**n positive**	**% positive**
Northern Europe	87	28 ^{a}	32.2
Central Europe	138	44 ^{a}	31.9
Apennine	51	13 ^{a}	25.5
Balkans	21	9 $^{a\,b}$	42.9
Eastern Europe	47	28 ^{b}	59.6
Total	**344**	**122**	**35.5**

Table 2: Strain discrimination was achieved by RFLP of nested PCR products. For each strain, groups with the same letters are not significantly different (Duncan's multiple comparison procedure based on the Studentized range test, α=0.05). Clades II and IIIc were excluded from the statistics due to low sample size. Note that the sum of *w*Cha-A and *w*Cha-B positive samples might be higher than *n* due to double infected individuals.

Clade	**n tested**	***w*Cha-A**	**% *w*Cha-A**	***w*Cha-B**	**% *w*Cha-B**
I	21	16 ^{a}	76.2	4 ^{a}	19.0
II	1	1	100	0	0
IIIa	29	29 ^{b}	100	3 ^{b}	10.3
IIIc	1	1	100	0	0
IIId	6	6 ^{b}	100	0 ^{b}	0
Total	**58**	**53**	**91.4**	**7**	**12.1**

BLAST analysis of the supergroup specific *ftsZ* gene showed highest homology of *w*Cha-A to a *Wolbachia* of the muscoid fly *Calyptratae sp.* (GenBank EU126372). *w*Cha-B is homologous to *Wolbachia* isolate 34 from *Nasonia vitripennis* (GenBank DQ842333).

Wolbachia distribution and mtDNA clade affiliation

For both *w*Cha-A and *w*Cha-B significant difference between clade I and the subgroups of clade III was shown. While all *Wolbachia* infected members of clade III harboured *w*Cha-A, this strain contributed 76,2% of the infections in clade I. *w*Cha-B caused 19,0% of the infections in clade I, compared to 10.3% in clade IIIa and 0% in clade IIId (Table 2).

Geographically, wCha-A was observed in 100% of the beetles from Central Europe, Apennine and the Balkans. In Northern Europe, this strain contributed to 75% of the total infections. *w*Cha-B was found as a single infection in 18.8% of the *Wolbachia* harbouring beetles in Northern Europe and as *w*Cha-A+*w*Cha-B double infection in 33.3% on the Balkans. The other regions showed lower rates of *w*Cha-B infections. Strain specific regional differences were not significant with α=0.05 (Table 3).

Table 3: No significant differences between regions are supported when Duncan's multiple comparison procedure based on the Studentized range test with α=0.05 was applied on the original data.

Region	**n tested**	***w*Cha-A**	**% *w*Cha-A**	***w*Cha-B**	**% *w*Cha-B**
Northern Europe	16	12	75	3	18.8
Eastern Europe	10	9	90	1	10
Central Europe	22	22	100	1	4.5
Apennine	4	4	100	0	0
Balkans	6	6	100	2	33.3
Total	**58**	**53**	**91.4**	**7**	**12.1**

5. Discussion

Within the last two decades, several large *Wolbachia* surveys of insect populations have been published. Most surveys assumed that infections are approaching fixation, have high maternal transmission rates, assessed few samples per species and applied conventional PCR (Werren and Windsor, 2000). These surveys suggested a global equilibrium of about 20% of infected species. More recent results show an increasing proportion of infected species when larger sample numbers are analyzed, as the rate of infected individuals within a species may differ significantly from 100% and be as low as 3.1% (Sun et al. 2007). Thus it can be assumed that the results of screening strategies that are based on few samples per species are biased towards an underestimate of infected species (Hilgenboecker et al., 2008). Furthermore, 28S rDNA was often used as reference gene to evaluate DNA quality of *Wolbachia* negative samples (Werren and Windsor, 2000). In insects 40 to 1023 copies of rDNA are present per cell (Prokopowich et al., 2003), much more than the expected copy number of highly replicating *Wolbachia* strains (McGraw et al., 2003). It is questionable if multicopy genes are reliable reference amplicons for the verification of negative *Wolbachia* diagnosis, especially when the existence of low titre infections not traceable by conventional PCR techniques is considered (Jeyaprakash and Hoy, 2000).

Here we present the first Europe-wide survey of *Wolbachia* in the economically important forest pest species *P. chalcographus* using a large sample set of 344 individuals and a nested PCR approach that proved to be two to three orders of magnitude more sensitive than conventional PCR. An overall infection rate of 35.5% was detected. The infections were detected all over Europe with a slight increase in infection frequencies in eastern and south-eastern regions. Cloning, sequencing and PCR-RFLP revealed the existence of at least two *Wolbachia* strains in *P. chalcographus*. *w*Cha-A was the major strain contributing to 100% of the infections in Southern and Central Europe but decreasing to a fraction of 75% in Northern Europe. *w*Cha-B was in average responsible for 12.1% of all infections, never exceeding a 33.3% proportion in local populations.

Wolbachia density is usually measured by quantitative PCR of *wsp* amplicons and a similar sized product of a host's single copy nuclear gene (McGraw et al., 2002; Berticat et al., 2002; Mouton et al., 2003; Maroja et al., 2008). In case of *P. chalcographus* this method could not be utilized as conventional *wsp* amplification did not yield enough product for SyBr green detection in qPCR (data not shown). Therefore, a semiquantitative approach using dilution series of beetle DNA and two high titre infected lab strains of *Drosophila* which serve as standard positive controls in *Wolbachia* surveys (e.g. Zhou et al. 1998) was chosen. Amplification of the nuclear reference gene EF1-α in *P. chalcographus* was lower by a factor of 10 when compared with the fly extracts, suggesting a lower amount of amplifiable template in almost identical total DNA concentrations from beetles and flies. Assuming the same template bias for *wsp*, comparison of conventional PCR suggests that the *Wolbachia* density in *P. chalcographus* is at least 10 times lower than in *w*Ri and more than 10 times lower than in *w*Mel. The estimated density of *Wolbachia* in *Drosophila* is 5 copies per cell for *w*Ri in head, thorax and abdomen extracts (McGraw et al. 2002) and 10 copies per cell for *w*Mel in head extracts. Thus we infer that the *Wolbachia* density in *P. chalcographus* is lower than one copy per cell in whole specimen extracts, and lower than the estimated densities of other *Wolbachia* infections. Nested PCR is approaching its detection limit in the 1:100 dilution of *w*Cha-A, but still performing well at this dilution for *w*Cha-B. As both strains do not yield a direct PCR product in the first PCR run, the gain in sensitivity testing genomic DNA is definitely higher than 100-fold, supporting the observations from plasmid standards. Effects due to potential loss of DNA during storage can be excluded in our analysis as mitochondrial and nuclear targets of numerous samples amplified without difficulty over the entire period from extraction to submission of this paper.

Difficulties in *Wolbachia* detection originating from low bacterial densities were previously described in lice (Floate et al., 2006). In this group of insects spanning eight taxonomic families all species seem to be infected with *Wolbachia*, but infections sometimes remain in low density or affect only a part of the individuals of a population. Miller and Riegler (2006) observed highly localised *Wolbachia* infections in neotropical *Drosophila* species.

While the use of *wsp* is established for the diagnosis of A and B group *Wolbachia* (Kikuchi and Fukatsu, 2003), its potential for strain characterization is limited due to frequent recombination (Baldo et al., 2005; Werren and Bartos, 2001). Recently, a MLST system based on five housekeeping genes was introduced in order to overcome this issue (Baldo et al., 2006). Our attempts to characterize the *w*Cha strains were constrained by amplification problems due to low bacterial densities, and standard protocols to apply MLST in low titre infections are yet to be developed. Using re-PCR we were able to retrieve the *ftsZ* gene sequence for *w*Cha-A and a complete characterization of *w*Cha-B. The association of the strains to supergroup A and B is supported by both *wsp* and *ftsZ* sequences.

When parasitized insects are sampled, universal primers may amplify trace amounts of parasitoid DNA and cause erroneous results (Greenstone, 2006). Technical procedures to circumvent parasitoid contamination like removal of the abdomen prior to DNA extraction are not always reliable. Careful sequence analysis will give hints on possible artefacts. In this study, one *Wolbachia* strain only found in a population from Finland showed sequence homology to hymenopteran *Wolbachia*. Mitotyping of the affected insect by direct sequencing of PCR products resulted in clear chromatograms with no ambiguous peaks (Avtzis et al., 2008) but cloning and re-sequencing of the COI gene revealed a contamination with DNA of braconid wasps that was not visible on the direct sequence reads. Due to this finding we assume that this strain is most likely the infection of a co-extracted parasitoid and not associated with the bark beetle.

The dynamics of a *Wolbachia* infection are shaped by host fitness effects and vertical transmission rate. Given that infected females either suffer a fitness cost or that transmission rate is lower than 100%, excess of a threshold frequency is required before infection rates can increase towards fixation. Frequencies below this threshold will lead to a decrease of infection frequency and loss of *Wolbachia* (Werren, 1997; Hoffmann and Turelli, 1997). Established *Wolbachia* associations allow several possible long term trajectories: co-evolution of host and endosymbiont may lead to increased transmission and decreased fitness costs (Turelli, 1994), cycles of invasion may be followed by eventual endosymbiont loss (Hurst and McVean, 1996) or parasitic endosymbionts may develop towards mutualism (Fenn and Blaxter, 2006; Brownlie and O’Neill, 2005). The infection frequency of 35.5% observed in *P. chalcographus* is far from fixation and bacterial density is low. A similar situation is described for the *w*Mel strain of *Drosophila melanogaster,* a *Wolbachia* strain that exhibits variable infection frequencies and a weak CI phenotype in field populations (Merçot and Charlat, 2004; Hoffmann et al., 1998). It is likely that a beneficial fitness effect of *w*Mel maintains this infection at the observed level (Hoffmann et al., 1998; (Teixeira et al., 2008; Hedges et al., 2008).

According to conventional understanding of *Wolbachia* dynamics, *w*Cha-A and *w*Cha-B have entered a phase of decay and *P. chalcographus* populations currently evolve towards the loss of *Wolbachia* (Hurst and McVean, 1996). However, it is also possible that a yet unidentified beneficial fitness effect conserves the infection frequency of the endosymbiont in certain environmental conditions.

Comparison of infection patterns and mtDNA showed that *w*Cha-A and *w*Cha-B are present in both major mitochondrial clades and it is unlikely that they are responsible for the observed crossing barriers in this species. While the reproductive phenotype of these strains remains unknown, species invaded by CI inducing *Wolbachia* will undergo indicative changes in their mtDNA distribution, i.e. the mitochondrial haplotype of the first infected females will hitchhike through the population replacing any prior variation

(Werren, 1997), or, in case of multiple CI agent infections, deep mtDNA structure in linkage disequilibrium with the endosymbiont may be maintained despite of migration, resembling the patterns expected for large, old populations (Hurst and Jiggins, 2005). In opposite, uncoupling of *Wolbachia* and mtDNA is indicative rather for repeated horizontal transfer events within the genus than for a single infection event before the separation of the host's major clades (Baldo et al., 2008) or for rare paternal transmission (Hoffmann et al., 1990). Sporadic loss of the endosymbiont in some lineages may have further shaped its current distribution. Bark beetles are often associated with wood colonizing fungi (Kirisits, 2004) of which several are known to produce antibacterial substances (Robbins et al., 1945; Zrimec et al., 2004). This association may account for environmental curing of the infection (Hoffmann et al., 1990, Wade and Stevens, 1994), while hymenopteran parasitoids would act as source for horizontal transfer and re-infection (Vavre et al., 1999; Baldo et al., 2008).

6. Conclusion

What does the analysis of *P. chalcographus* contribute to our understanding of *Wolbachia* infections? (i) For a comprehensive understanding of a species infection status it is necessary to examine more than a few individuals, ideally from different geographic localities, as an unknown amount of species can be infected at very low frequencies. (ii) Individuals showing negative results in conventional PCR can not be readily interpreted as uninfected. Low titre strains only become traceable by high sensitive approaches like the nested PCR used in this study. Such approaches are prone to environmental contamination and extensive precautions against false positive results must be taken, including clean-room working conditions, separation of lab space for sample preparation, amplification and post-amplification handling, introduction of numerous negative controls in each sample batch and sequence analysis of retrieved amplicons. (iii) Singly copy nuclear genes should be used for quality control of DNA extracts as multicopy nuclear 28rDNA or mtDNA overestimate the amplification efficiency of low titre and localised *Wolbachia* infections. (iv) In species that are afflicted by parasitoids special care has to be taken in order not to misinterpret endosymbionts of the parasitoid as those of the originally targeted host. (v) *P. chalcographus* is a potential new model system to study the fate of low frequency and low titre infections. In case of a recent threshold transgression, no matter in which direction, substantial fluctuations in infection frequencies should become observable within few generations. On the other hand, equilibrium at the current infection level would suggest actions of elusive beneficial *Wolbachia* traits. (vi) Finally, deep genetic structure, formation of non-*Wolbachia* mediated crossing barriers and the uncoupling of mtDNA and *Wolbachia* makes *P. chalcographus* an excellent species of interest for the study of horizontal and paternal endosymbiont transmission.

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Bodenbildung entlang von Klima- und Substrataltersgradienten: Veränderungen von mineralogischen, physikalischen, chemischen und biologischen Bodeneigenschaften und daraus resultierende Effekte auf ökologische Bodenfunktionen

Soil formation along gradients of climate and substrate age: Variations in mineralogical, physical, chemical and biological soil properties and resulting effects on ecological soil functions

Bodenbildung entlang von Klima- und Substrataltersgradienten

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Zusammenfassung

Die Habilitationsschrift fasst meineForschungsarbeiten über Bodenbildung und -entwicklung entlang von Umweltgradientenzusammen. Ich untersuchte Böden entlang von Klimagradienten (Climosequenzen)und entlang von unterschiedlich altem Ausgangsmaterial (Chronosequenzen). Dabeizeigten sich deutliche Trends in mineralogischen, physikalischen, chemischen undbiologischen Bodenparametern, die sich ihrerseits auf ökologische Bodenfunktionensowie Bodengefährdungen auswirken. Ähnliche Forschungsansätze werden auch inZukunft eine wichtige Rolle in der bodenkundlichen Forschung spielen, umeinerseits die Langzeitauswirkungen des Klimawandels besser einzuschätzen(Climosequenzen) und andererseits genauere Aufschlüsse über Kohlenstoffanreicherungund Bodenneubildungsraten zu erhalten (Chronosequenzen).

Abstract

The habilitation dossier summarizes my research work on soil formation and development along environmental gradients. I studied soil formation along gradients of climate (climosequences) and substrate age (chronosequences), and found clear trends in mineralogical, physical, chemical and biological soil properties, which affected ecological soil functions as well as soil threats. Similar approaches will play an important role in the future of *soil research, for example to evaluate long-term impacts of climate change on soil ecosystems (climosequences) and to quantify rates of carbon accumulation and soil neo-formation (chronosequences).*

1. Introduction - Soil forming factors

Soils form a thin, living skin on the earth's land surface. They are dynamic systems influenced by a number of soil forming factors and processes (Jenny, 1941; Simonson, 1959).

The Russian geographer Vasily Vasili'evich Dokuchaev (1846 - 1903) introduced the concept that geographical variations in soil type could be explained in relation not only to the underlying geology, but also to climate, plants and organisms, relief, and the time available for soil development (Dokuchaev, 1883). This concept was later formalized by Hans Jenny (1899 - 1992) with a mathematical equation that relates the properties of a soil to independent factors that determine the processes of soil formation (Jenny, 1941):

$$s = f(cl, o, r, p, t, ...)$$

where any soil property (s) is a function of climate (cl), organisms including soil biota, vegetation and humans (o), relief / topography (r), parent material / lithology (p), and time / soil age (t). Jenny saw these factors not as formers or forces, but as state factors that define the state of the soil system. He left the ellipsis open (*…*) to indicate that there might be additional factors in the function.

In theory, Jenny's equation could be solved mathematically if the effects and interactions of all state factors are known. In practice, the complex nature of soil ecosystems precludes this option in most cases. Soil scientists have therefore approached the state factor equation empirically by experimentation or field observation. A commonly employed method has been the variation of a single factor while keeping the other factors constant (as much as possible). Soil changes have been studied along sequences of varying climate (climosequences), vegetation (biosequences), relief (toposequences), parent material (lithosequences) and time (chronosequenes). This has led to the development of empirical models that describe the effect of a given soil forming factor on pedogenesis using climofunctions, biofunctions, topofunctions, lithofunctions and chronofunctions, respectively.

In this context, it is important to point out that the development of soils may not only proceed along one predestined pathway leading to a single steady state. The complex and dynamic nature of soils rather suggests multidirectional changes along several possible evolutionary pathways (Huggett, 1998).

2. Soil formation along climatic gradients (climosequences)

Over the past decade, global climate change and its impacts on natural and managed ecosystems have attracted considerable attention in the scientific community (e.g. IPCC 2007a, 2007b). The *Fourth Assessment Report of the Intergovernmental Panel on Climate Change* predicts a global average surface warming in the range of 1.1 to 6.4°C until the end of the 21st century and considerable alterations in the amount, timing and intensity of regional and global precipitation patterns (IPCC, 2007a).

Climate change may affect a variety of soil properties and processes, such as the soil water balance, carbon (C) and nitrogen (N) cycling, structural stability and erosion, as well as mineral transformations and surface reactions (Rounsevell et al., 1999). Soil organic matter (SOM) has received special attention in this context, because of its key role in many important soil processes, its rapid response to environmental changes and its feedback to the atmospheric climate system. Accordingly, C sequestration and temperature sensitivity of soil C dynamics have become hot research topics in recent years (s. reviews by Schimel et al., 2001; Hungate et al., 2003; Freibauer et al., 2004; Lal, 2004; Smith, 2005; Davidson and Janssens, 2006; Kirschbaum 2006). Manipulation experiments such as artificial soil warming (e.g. Melillo et al., 2002; Gu et al., 2004) have provided useful information on short-term soil responses to changed climatic conditions; however, such experiments offer little insight into responses that occur over longer periods involving weathering and mineral transformations. Indeed, it is these often irreversible processes that provide the framework within which short-term dynamics operate. Climate gradient studies help fill this gap by exploiting “space-for-time” substitution (Rustad, 2008).

Observations along natural climatic gradients (altitudinal or latitudinal) have increased our understanding of longer-term ecosystem responses to climate change. Soil climosequences are, by definition, sequences of soils whose variations are caused by differences in climatic conditions. In nature, vegetation almost always co-varies along climatic gradients. Therefore, most soil climosequences are implicitly also biosequences, investigating the combined effects of climatic differences and associated differences in vegetation composition.

2.1 Changes in weathering and mineralogy along climatic gradients

Relatively few climosequence studies have investigated long-term pedogenic processes, such as chemical weathering and clay mineral transformations. Along an altitudinal climosequence in the Italian Alps, Egli et al. (2003) found elemental losses and smectite contents to be greatest in high-elevation (subalpine) forests near the timberline, while the contents of hydroxy-interlayered clay minerals showed an inverse trend, which was likely a result of greater leaching (higher precipitation, lower evapotranspiration) with increasing elevation and pronounced podzolization near the timberline. In the same climosequence, Mirabella and Egli (2003) showed that in soils with a higher degree of weathering, an evolution of trioctahedral to dioctahedral mineral structures was evident and lower layer charges were observed in smectites. Along a volcanic arid-to-humid climosequence in Hawaii, Chadwick et al. (2003) reported increasing elemental leaching losses and decreasing pH, base saturation and effective cation exchange capacity with increasing humidity.

Soils derived from volcanic deposits (Andisols) often exhibit unique physical and chemical properties, such as low bulk density, high water retention, variable charge characteristics and strong phosphate retention, which have been largely ascribed to the presence of active amorphous weathering products, such as allophane, imogolite, ferrihydrite and Al/Fe-humus complexes (e.g. Kimble et al., 2000; Dahlgren et al., 2004). Climatic conditions and their effects on the degree of leaching and soil solution chemistry play an important role in volcanic weathering pathways and secondary mineral neogenesis (Rasmussen et al., 2007). Temperature also plays a decisive role in the formation of active amorphous materials or crystalline minerals, with crystallization promoted as climate becomes warmer and drier (Schwertmann, 1985).

Allophane and halloysite are the dominant components in the clay fraction of many volcanic soils around the world. Parfitt et al. (1983) proposed a weathering scheme for rhyolitic ash, in which halloysite is the dominant clay mineral where the mean annual precipitation is less than approximately 1500 mm, and allophane predominates above 1500 mm. Along these lines, many subsequent studies on volcanic soils in different parts of the world have confirmed the importance of rainfall and leaching in mineral formation (e.g., Parfitt et al., 1984; Stevens and Vucetich, 1985; Takahashi et al., 1993; Nieuwenhuyse et al., 2000).

Soil climosequence studies along the slopes of volcanoes have further assessed the effect of climate on weathering and mineral formation (Chartres and Pain, 1984; Nizeyimana et al., 1997). On an extinct volcano in Rwanda, Nizeyimana et al. (1997) found decreasing allophane contents and increasing halloysite contents with decreasing elevation, which they attributed to a concomitant decrease in rainfall. Chartres and Pain (1984) found a similar weathering pattern with elevation in highland Papua New Guinea, although there precipitation increased with decreasing elevation. They suggested that lower rates of evapotranspiration with increasing altitude caused greater leaching, thus favoring the formation of allophane. Egli et al. (2007), who investigated a soil sequence along an elevation gradient from subtropical to subalpine climate zones in the Etna region (Sicily), found that weathering as related to the proportion of crystalline Fe-oxyhydroxides or the kaolinite concentration in the clay fraction was greater at the lower-elevation sites.

In our studies on ~3000-yr-old volcanic deposits in the temperate Ecuadorian Andes (Zehetner et al., 2003, **H1**), we found an expressed altitudinal soil zonation, which we attributed to climatic differences resulting in different leaching regimes and differences in SOM decomposition. At high elevations, we observed accumulation of organic matter (OM) and formation of allophane and Al-humus complexes, whereas at low elevations, topsoils contained less than 1% organic carbon (OC) and halloysite dominated clay mineralogy. On >400,000-yr-old volcanic deposits in subtropical Taiwan, we also found strong influence of climate on the pedogenesis of volcanic soils (Tsai et al., 2010, **H2**). Like in the Andes, the high-elevation soils contained high amounts of OM and active amorphous materials (e.g. allophane, ferrihydrite), whereas the low-elevation soils contained thermodynamically more stable minerals (e.g. kaolinite, hematite). On both volcanic climosequences, andic soil properties[1] increased with elevation, resulting in taxonomic sequences from low-elevation Inceptisols (Cambisols) to high-elevation Andisols (Andosols).

In the course of pedogenesis on volcanic deposits, soil properties undergo dramatic changes, thus changing the soils' resistance to water erosion. While fresh volcanic deposits with low cohesiveness may be particularly prone to erosion (Nammah et al., 1986), progressive development of volcanic soils leads to increased structural stability and decreased soil erodibility. Mature Andisols generally show strong resistance to water erosion,

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[1] Andic soil properties result mainly from the presence of allophane, imogolite, ferrihydrite and Al/Fe-humus complexes, which are typical weathering products in volcanic deposits (Dahlgren et al., 2004).

which has been ascribed to the presence of highly stable soil aggregates resulting in high permeability and rapid rainfall infiltration (Warkentin and Maeda, 1980; Dahlgren et al., 2004). However, erosion of Andisols has been reported to involve fragmentation of larger aggregates by raindrop impact and subsequent transport of smaller, stable aggregates of low bulk density by surface runoff (Rodríguez Rodríguez et al., 2002).

The impacts of the above-mentioned climate-dependent soil formation in volcanic landscapes on variations in the soils' infiltration capacity and resistance to erosion had not been analyzed previously. In Zehetner and Miller (2006, **H3**), we showed that the runoff - erosion behavior of volcanic soils is strongly affected by their pedogenic development. The accumulation of OM and the formation of active amorphous materials at high elevations have led to the formation of very stable aggregate structure. These soils remained wetable when air-dried, showed very high infiltration capacity and low potential for runoff generation and soil erosion. On the other hand, low OM contents and absence of active amorphous materials at low elevations have led to the formation of weakly aggregated soils, which were susceptible to surface crusting, runoff and soil erosion.

Soils formed on volcanic deposits have the reputation of being fertile and highly productive; however, as discussed above, the properties of these soils strongly depend on their pedogenic pathways, which are considerably affected by climate. Resulting mineralogical differences may have important bearings on the biogeochemical cycling in agro-ecosystems of volcanic landscapes. Active amorphous materials, for example, are known for their strong retention of phosphate (e.g., Wada, 1989; Parfitt, 1989; Dahlgren et al., 2004) and for their stabilizing effects on SOM (e.g., Parfitt et al., 1997; Gijsman and Sanz, 1998; Parfitt et al., 2001). In Zehetner and Miller (2006, **H4**), we showed that the climate-dependent differential pedogenesis of soils along volcanic slopes significantly affected the altitudinal distribution of many fertility-relevant soil properties, such as OM content, pH, cation exchange capacity, phosphate retention and phosphorus (P) availability.

2.2 Changes in soil organic matter and microbiology along climatic gradients

As we observed along volcanic slopes in the Andes and Taiwan, many climosequence studies report soil organic carbon (SOC) and N concentrations / stocks to increase with decreasing temperature (e.g. Hart and Perry, 1999; Ganuza and Almendros, 2003; Garten, 2004; Kane et al., 2005; Kueppers and Harte, 2005; Dai and Huang, 2006); however, the findings in the literature are not unequivocal. For example, Leifeld et al. (2005) showed that while SOC *concentrations* under permanent grassland increased linearly with altitude in the Swiss Alps, no relationship was found between altitude and SOC *stocks*, which was a result of shallow soils and high rock contents at high elevations. Garcia-Pausas et al. (2007) even reported decreasing SOC stocks with increasing elevation in grasslands of the Pyrenees, which they attributed to temperature limitation of net primary production. In our studies in the Austrian Limestone Alps, we found increasing SOC stocks from 900 to 1500 m above sea level (asl), which decreased again from 1500 to 1900 m asl (Djukic et al., 2010, **H5**). We attributed this decrease mainly to harsh climate and short growing seasons at high elevations, which limits net primary production and C inputs to the soil.

Several climosequence studies have provided insight into the temperature-dependence of OM turnover dynamics under natural steady-state conditions. For example, Simmons et al. (1996) reported slower forest floor OM decomposition under cooler conditions along a climatic gradient. Hitz et al. (2001) found that in alpine grasslands, above-ground phytomass, production rate and turnover time decreased while the importance of below-ground phytomass and its production rate increase with altitude. Kane et al. (2003) reported decreasing soil respiration with decreasing temperature and shorter growing season along an elevation gradient. Likewise, Garten (2004) reported *in-situ* loss rate of ^{13}C from labelled forest soils to be inversely related to elevation and directly related to mean annual temperature. On the other hand, Kueppers and Harte (2005) found no significant climate trends of total annual soil CO_2 flux along a climatic gradient in the Rocky Mountains.

Recent studies on litter decomposition along climatic gradients have confirmed the influence of temperature and moisture on decomposition processes, but also emphasized the importance of litter composition / quality in this context (Sjögersten and Wookey, 2004; Cornelissen et al., 2007; Parton et al., 2007). Cornelissen et al. (2007) concluded that the warming-induced expansion of shrubs with recalcitrant leaf litter across cold biomes could actually result in a negative feedback to global warming.

Other climosequence studies have revealed climate-induced differences in SOM characteristics and soil microbial community composition. Amelung et al. (1997) reported that polysaccharides persisted less and alkyl structures were enriched in warmer areas of the Great Plains prairie. Amelung et al. (1999a) found that increasing precipitation and temperature led to decreasing proportions of bacterial-derived amino sugars and increasing proportions of glucosamine (produced by fungi) in native grassland soils. In the finer particle size fractions of the same soils, the degree of lignin decomposition decreased with increasing temperature, possibly because there was a lack of additional C sources needed for the cometabolic decay of lignin (Amelung et al., 1999b). Martin-Neto et al. (1998) showed that OM humification increased with increasing rainfall in an arid-to-humid climosequence of the Argentine Pampa grassland. Faz Cano et al. (2002) reported that soils of the mesomediterranean zone had a higher content of O-alkyl C and a lower content of aromatic C than soils of the warmer thermomediterranean zone of southern Spain. Kane et al. (2005) showed that the proportion of (relatively labile) light-fraction SOM decreased with increasing heat sum in interior Alaska. Similarly, Dalmolin et al. (2006) found increasing proportions of O-alkyl C with increasing elevation (cooler and moister climate) in southern Brazil, which indicates accumulation of OM with larger carbohydrate contents and is a sign of a lower degree of OM decomposition. In our studies in the Austrian Limestone Alps, we found the aliphatic Fourier-transform infrared (FTIR) band (2920 cm^{-1}) to be lower in low-elevation forest sites compared to high-elevation shrubland and grassland sites; however, most other FTIR bands did not change with altitude but were related to specific site conditions, such as vegetation composition and associated differences in soil pH (Djukic et al., 2010, **H5**).

A few studies have pointed out shifts in microbial community composition along altitudinal / climatic gradients. For example, in the Austrian Central Alps, the fungal population and relative amount of Gram-negative bacteria increased with increasing elevation (Margesin et al., 2009), while decreasing diversity of soil fungi with increasing elevation had been reported earlier (Schinner and Gstraunthaler, 1981). Furthermore, Ma et al. (2004) reported for China and Giri et al. (2007) for India that bacterial population was negatively correlated with elevation. In contrast, Männistö et al. (2007) found that microbial community composition in tundra soils was relatively similar at different elevations as long as the soil pH was similar. Also, changes in microbial activity have been reported along altitudinal / climatic gradients. Soil microbial activity measured by dehydrogenase activity (Margesin et al., 2009), other enzyme activities and CO_2-evolution (Schinner, 1982) decreased with increasing elevation (and decreasing temperature). However, in the former study (Margesin et al., 2009), relative microbial activities (relative to the activity at optimum temperature) were significantly higher in alpine than in subalpine soils, which shows that soil microorganisms may be well adapted to the prevailing climatic conditions.

Climate warming is expected to cause an upward migration of vegetation zones (e.g. Dullinger et al., 2003), which will entail changes in microbial community composition and function in a given elevation zone. In our studies in the Austrian Limestone Alps, we found the fungal biomarkers ergosterol and phospholipid fatty acid (PLFA) 18:2w6,9 to be significantly higher in low-elevation forest sites compared to high-elevation shrubland and grassland sites; however, again soil pH was an important determinant of other microbial parameters, such as bacterial PLFAs and microbial activity (Djukic et al., 2010, **H6**).

3. Soil formation along substrate age gradients (chronosequences)

As climate and other soil forming factors continue to act upon soils, these progressively develop over time. For example, the above-mentioned Andisols form rapidly in humid climates and develop into other soil types as soil age and degree of weathering increase (Ugolini and Dahlgren, 2002), e.g. very old and highly weathered volcanic soils may no longer be Andisols, but may have developed into Oxisols. We know from a well-established 4 million-yr-old chronosequence in Hawaii that under tropical weathering conditions, Andisols develop into Oxisols between 150,000 and 1.4 million years (Crews et al., 1995). Similarly, Nieuwenhuyse et al. (2000) found Andisols in <18,000-yr-old volcanic deposits and Oxisols in 450,000-yr-old deposits in humid tropical Costa Rica. In our studies in the temperate Ecuadorian Andes, we found andic properties in both ~3000-yr-old recent soils and >40,000-yr-old buried paleosols (Zehetner et al., 2003, **H1**), and in subtropical Taiwan, we still found Andisols in >400,000-yr-old volcanic deposits (Tsai et al., 2010, **H2**).

Soil chronosequence studies have enhanced our understanding of directions and rates of pedogenic processes. As with climosequences, a difficulty of chronosequences is holding all soil forming factors constant except time. Notably, climate has been changing in earth’s history, even within relatively short periods (e.g. Jouzel et al., 2007; Frank et al., 2010), and vegetation and topography are unlikely to have remained unchanged for millennia or more. Nevertheless, well-dated soil chronosequences are the only way of studying how pedogenesis operates over centuries and longer periods. Soil chronosequences have been established in different environmental settings (s. review by Huggett, 1998). These include glacial moraines, sand dunes, landslide scars, abandoned pastures, burnt patches, old mining areas, lava flows, fluvial landforms and marine terraces. In a very comprehensive chronosequence study, Wardle et al. (2004) combined various chronosequence types in tropical, temperate and boreal zones (i.e. sand dunes, fire sequences, glacier forelands, volcanic lava flows and marine terraces) to find that in the long-term absence of catastrophic events, ecosystem development enters a decline phase, in which the substrate N:P ratio increases, indicating increasing P limitation over time. This was associated with reductions in litter decomposition rates, P release from litter and microbial biomass and activity (Wardle et al., 2004).

3.1 Fluvial soil chronosequences

3.1.1 Changes in iron oxide crystallinity during floodplain soil development

In fluvial environments, most chronosequence studies have covered thousands to millions of years and so provided information on long-term pedogenic trends. These include mineralogical changes (Dorronsoro and Alonso, 1994) combined with specific surface area increase (White et al., 1996) as well as pH decrease (Vidic and Lobnic, 1997). Under moist conditions, increasing clay accumulation, clay translocation and rubification have been observed (Dorronsoro and Alonso, 1994; Engel et al., 1996; Leigh, 1996; Vidic and Lobnic, 1997), while under drier conditions, accumulation of pedogenic carbonate (Eash and Sandor, 1995; Nordt et al., 1998) and silicon (Kendrick and Graham, 2004) has been reported. Commonly observed long-term trends in floodplain soils include increasing iron (Fe) oxide contents (Dorronsoro and Alonso, 1994; Engel et al., 1996; Leigh, 1996) and crystallinity (Shaw et al., 2003; Kendrick and Graham, 2004) with soil age.

During weathering, Fe is released from Fe-bearing minerals, and depending on the predominant environmental conditions (temperature, redox conditions, soil solution chemistry, presence of clay and organic ligands), various pedogenic Fe oxides can precipitate (Cornell and Schwertmann, 1996). In the dynamic soil system, Fe oxides transform continuously into one another. Under oxic soil conditions, the highly crystalline goethite and hematite are thermodynamically the most stable pedogenic Fe compounds. They accumulate in older soils due to the reduction and leaching of poorly crystalline Fe oxides and their conversion into more crystalline forms by multiple redox oscillations (Cornell and Schwertmann, 1996; Miller et al., 2001; Thompson et al., 2006). In soils, the ratio of oxalate-extractable Fe (from amorphous or poorly crystalline hydrous oxides and OM; Fe_o) to dithionite-extractable Fe (from crystalline and non-crystalline hydrous oxides; Fe_d) decreases with duration of pedogenesis and indicates increasing Fe oxide crystallinity. In our studies in the Danube floodplain, we showed a remarkable increase in Fe oxide crystallinity within a few centuries of floodplain soil formation (Lair et al., 2009, **H7**). In a chronofunction model, we linked Fe oxide crystallinity (Fe_o/Fe_d) to soil age measured with ^{137}Cs and optically stimulated luminescence (OSL) dating (Lair et al., 2009, **H7**).

3.1.2 Soil organic matter accumulation during floodplain soil development

Several studies on primary riparian succession have shed light on processes dominating earlier stages of ecosystem evolution. For example, Luken and Fonda (1983) as well as Walker (1989) found that N-fixing alder trees (*Alnus* spp.) significantly raised soil N pools during the initial decades of primary succession. Similar soil N accumulation was reported by Adair et al. (2004) for ecosystems that lack N-fixing vegetation and was attributed to N inputs with freshly deposited sediments. In an extensive study on the Tanana River floodplain in interior Alaska, van Cleve et al. (1993) found steep increases of SOM and cation exchange capacity within the first 50 years of primary succession, which leveled off between 100 and 200 years of succession. For the same sites, Kaye et al. (2003) determined accumulation rates of stabile and labile SOC and N, which decreased exponentially with terrace age (1 to 270 yr). Also on the Tanana River, Kielland et al. (2006) found decreasing net N mineralization per mass SOM across a primary successional sequence, suggesting that SOM quality decreased in the course of floodplain ecosystem evolution. Kaye et al. (2003) estimated OC accumulation at ~45 g m^{-2} yr^{-1} over ~25 years and at ~23 g m^{-2} yr^{-1} over ~100 years. Similar rates have also been shown for OC accretion during soil formation on other landforms, such as glacial moraines (~30 g m^{-2} yr^{-1} over ~70 years; Burt and Alexander, 1996) and volcanic mudflows (~14 g m^{-2} yr^{-1} over 80 to 600 years; Lilienfein et al., 2003). Compared to the above studies, OC accumulation proceeded much faster in the Danube floodplain soils of our studies. Calculated mean C sequestration rates (in the top 20 cm) were up to 180 g m^{-2} yr^{-1} over the last ~25 years and around 100 g m^{-2} yr^{-1} over the last ~100 years (Zehetner et al., 2009, **H8**). However, intensive cultivation severely compromised the high C sequestration potential of these soils. Our studies also showed that SOM pools reached a steady state within a few decades of floodplain evolution (Zehetner et al., 2009, **H8**). This compares well with primary succession across alpine glacier forelands, where the fraction of microbial biomass C was more or less constant from the first years of soil development on (Conen et al., 2007), and functional microbial diversity and enzyme activities were at steady state after 50 years (Tscherko et al., 2003).

3.1.3 Phosphorus transformations during floodplain soil development

Walker and Syers (1976) devised a conceptual model describing P transformations as a function of soil development. According to this model, primary mineral P dominates in the early stages of pedogenesis and slowly dissolves with time. The released P is partly taken up by organisms, thus entering the organic pool, and partly sorbed onto surfaces of secondary minerals. With progressing soil development, the latter fraction gets incorporated into the structures of pedogenic oxides. The model further shows an asymptotic decline of total P toward a terminal steady state, at which time occluded and organic P prevail and losses from the system approximately equal gains (Walker and Syers, 1976).

The Walker and Syers model was later supported by an extensive review of P fractionation studies that covered a wide range of soil types representing different development stages (Cross and Schlesinger, 1995). Likewise, Crews et al. (1995) found that soil P pools along the above-mentioned 4-million-yr chronosequence in Hawaii followed the model of Walker and Syers (1976). Primary mineral P comprised about 80% of total P contents at a 300-yr-old site, about 60% at a 2100-yr-old site, and decreased to 1% after 20,000 years of pedogenesis. Organic P contents increased from the youngest site to a maximum after 150,000 years of soil development and then declined again. Occluded P contents increased steadily with soil age (Crews et al., 1995). Unfortunately, the initial several hundred years of weathering and soil formation were not well resolved in this study.

Other studies in humid and tropical environments found notable shifts in biogeochemical P fractions within a few hundreds of years. For example, Singleton and Lavkulich (1987) reported a decline of primary mineral P in the upper 10 cm of a sandy soil chronosequence on Vancouver Island from about 190 mg kg^{-1} at a 127-yr-old site to about 10 mg kg^{-1} at a 550-yr-old site. Schlesinger et al. (1998) studied the distribution of biogeochemical P fractions in soils developing on the pyroclastic material of the 1883 Krakatau eruption. After 110 years of soil development, they found most soil P still in the primary mineral form; however, losses of primary mineral P from surface horizons were accompanied by marked accumulations of organic P.

Under the dry and temperate climate of Central Europe, for which slower changes in P biogeochemistry might be expected compared to humid and tropical conditions, we found significant transformations from primary mineral P to organic P within less than 250 years of soil development (Zehetner et al., 2008, **H9**). The mean dissolution rates of primary mineral P decreased exponentially with increasing soil age from ~1.6 g m^{-2} yr^{-1} over ~15 years to ~0.04 g m^{-2} yr^{-1} over ~550 years, and were almost an order of magnitude higher than rates reported for tropical environments (Zehetner et al., 2009, **H10**).

3.1.4 Impacts of floodplain soil development on contaminant retention

As evident from the above discussion, soil properties undergo significant changes with progressing pedogenesis, which are caused by a variety of processes that operate at different time scales, such as accumulation and transformation of OM, formation of secondary clay minerals and oxides as well as acidification (Buol et al., 2003). Depending on the specific dominant processes of soil formation, the soils' retention capacity for contaminants can be increased or decreased during soil development. Floodplain soils are in their early stages of development, with the deposited river sediments only slightly altered by the processes of soil formation. Little is known how these initial soil changes affect the retention behavior of contaminants in floodplains.

A soil's retention capacity for contaminants is affected by a number of properties, such as grain-size distribution, pH, OM content and composition, clay mineralogy, pedogenic oxides and redox state. Generally, increasing contaminant retention was observed with increasing contents of clay and pedogenic oxides (e.g. Alloway, 1999; Delle Site, 2001). 2:1-type clay minerals (e.g. smectite) and amorphous oxides increase the retention of ionic contaminants compared to 1:1-type clay minerals (e.g. kaolinite) and crystalline oxides, respectively (Hubbard, 2002). In the soil environment, cation retention increases while anion retention decreases with increasing soil pH. This is due to an increasing portion of negatively charged surfaces, especially on SOM and hydrous oxide minerals (e.g. Delle Site, 2001; Bradl, 2004). Retention of non-polar compounds increases linearly with content and hydrophobicity of SOM (e.g. Grathwohl, 1990).

In our studies on the Danube floodplain, we demonstrated that progressing pedogenesis resulted in increasing retention capacity for Cu and Cd (Graf et al., 2007, **H11**; Lair et al., 2008, **H12**). Sequential fractionation of Cu freshly added to the soil showed a significant decrease of “weakly bound” Cu coupled with an increase of “strongly bound” Cu with increasing soil age (Lair et al., 2009, **H13**). Compared to Cu, Cd generally shows a more mobile behavior in the environment (e.g. Alloway, 1999). We found a slight but significant increase of Cd retention and decreasing amounts of “easily desorbable” Cd with increasing soil age (Lair et al., 2009, **H13**). For the retention of phosphate, however, no age trend was found within 500 years of pedogenesis. Here, the grain-size distribution and oxide content inherited from the parent sediments still override pedogenic changes (Lair et al., 2009, **H14**). Generally, the neo-formation of pedogenic oxides results in increasing P retention capacity over time (e.g. Carreira and Lajtha, 1997), except for volcanic soils, in which strongly P-sorbing amorphous constituents weather into oxides (e.g. Olander and Vitousek, 2005). In our study area, 500 years of pedogenesis have not resulted in sizeable neo-formation of pedogenic oxides that would have led to a clearer trend in P retention with soil age. Other studies have shown that pedogenic Fe oxides (Fe_d) accumulate over longer time periods. For example, in a study at Lake Michigan, no significant Fe_d increase was found within 5200 years (Barrett, 2001), while under more intense weathering conditions in northern Georgia, USA, Fe_d increased from approximately 12 to 22 g kg^{-1} within 14,000 years (Leigh, 1996). Under the climatic conditions of our study area, neo-formation of pedogenic oxides is not expected to significantly affect P retention until after several thousand years of soil development.

In the Danube floodplain soils of our studies, the retention of naphthalene strongly correlated with SOM contents and increased from the island sites (low in OM) to sites on the floodplain that had rapidly accumulated OM (cf. Zehetner et al., 2009, **H8**). Grassland exhibited the highest retention capacity for naphthalene followed by forest and extensively cultivated cropland. Naphthalene retention in intensively cultivated soils was clearly below the trends of the other ecosystems (Lair et al., 2009, **H13**). These results demonstrate that intensive agricultural practices, which deplete SOM contents, considerably decrease the soils' retention capacity for non-polar compounds.

3.2 Soil organic matter accumulation in volcanic chronosequences

Besides for contaminant retention, SOM is important for a variety of soil functions, e.g. it provides plant nutrients that become available as it decomposes, it improves a soil's water-holding capacity and stabilizes soil structure. In light of climate change, soils have come into increased scrutiny because of their relatively large OC pool (soil+litter: ~1500 Pg C, compared to ~550 Pg C in vegetation and ~780 Pg C in the atmosphere; Houghton, 2007). It has been shown that volcanic soils (Andisols) contain the highest amounts of OC among all mineral soil types (Eswaran et al., 1993). The large humus accumulation frequently observed in volcanic soils has been ascribed to high plant productivity and large OM inputs (Dahlgren et al., 2004) as well as to stabilization of SOM by active amorphous materials (Torn et al., 1997). Another important factor in the preservation of SOM in volcanic soils is burial by repeated additions of volcanic deposits (Dahlgren et al., 2004). This rejuvenates volcanic landscapes and creates newly aggrading ecosystems that may sequester OC rapidly. Volcanic soils may so act as important sinks in the global terrestrial C cycle. In a recent review (Zehetner, 2010; **H15**), I combined data from available studies conducted on Holocene volcanic deposits in different parts of the world to assess SOC accumulation. I found exponentially decreasing accumulation rates with increasing soil age, dropping below 10 g C m^{-2} yr^{-1} after ~1000 years of soil development. The obtained trends were similar for soils of contrasting climate zones. I estimated an upper limit of global OC sequestration in volcanic soils of 20 Tg yr^{-1}, which is at most 25% of the C degassing from terrestrial volcanoes (Mörner and Etiope, 2002) and less than 1% of the "residual land sink" of C (Denman et al., 2007). I concluded that contemporary OC sequestration in volcanic soils is less important than CO_2 consumption by chemical weathering of volcanic deposits (Dessert et al., 2003) and plays a negligible role in the global terrestrial C cycle.

4. Conclusions and outlook

Soil gradient studies have - despite inherent methodological limitations - provided valuable insights into the effects of soil forming factors on soil properties and processes. Along climatic gradients (climosequences) and substrate age gradients (chronosequenes), trends in mineralogical, physical, chemical and biological soil properties have been detected. The observed trends further affected ecological soil functions, such as the production function and the buffer-filter-transformer function, as well as soil threats, such as runoff and erosion.

In future research, soil climosequence studies will continue to play an important role in the study of climate change impacts on soil ecosystems. In this context, climosequence studies, investigating longer-term impacts, shall be combined with soil monitoring and experimental manipulations (e.g. artificial soil warming), which study medium-term and short-term impacts, respectively. Soil chronosequence studies will continue to provide insights into directions and rates of pedogenesis under different environmental conditions. In light of global change, the temporal dynamics of SOC shall deserve special attention in this context. Soil chronosequence studies will further be essential for determining the rates of weathering and soil neo-formation as a basis for the establishment of maximum tolerable soil erosion rates.

Soil gradient studies will undoubtedly continue to be vital methodological tools in soil science with expected major contributions to basic and applied science and with outcomes relevant for policy makers and the general public.

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Publications of the presented habilitation dossier

Publications on soil formation along climatic gradients (climosequences)

H1 ZEHETNER, F., W.P. MILLER, and L.T. WEST (2003). Pedogenesis of volcanic ash soils in Andean Ecuador. **Soil Science Society of America Journal** 67, 1797-1809. (*first author, estimated contribution: 80%*)

H2 TSAI, C.C., Z.S. CHEN, C.I. KAO, F. OTTNER, S.J. KAO, and F. ZEHETNER (2010). Pedogenic development of volcanic ash soils along a climosequence in Northern Taiwan. **Geoderma** 156, 48-59. (*senior and corresponding author, estimated contribution: 50%*)

H3 ZEHETNER, F., and W.P. MILLER (2006). Erodibility and runoff – infiltration characteristics of volcanic ash soils along an altitudinal climosequence in the Ecuadorian Andes. **Catena** 65, 201-213. (*first and corresponding author, estimated contribution: 90%*)

H4 ZEHETNER, F., and W.P. MILLER (2006). Soil variations along a climatic gradient in an Andean agro-ecosystem. **Geoderma** 137, 126-134. (*first and corresponding author, estimated contribution: 90%*)

H5 DJUKIC, I., F. ZEHETNER, M. TATZBER, and M.H. GERZABEK (2010). Soil organic-matter stocks and characteristics along an Alpine elevation gradient. **Journal of Plant Nutrition and Soil Science** 173, 30-38. (*corresponding author, estimated contribution: 40%*)

H6 DJUKIC, I., F. ZEHETNER, A. MENTLER, and M.H. GERZABEK (2010). Microbial community composition and activity in different Alpine vegetation zones. **Soil Biology and Biochemistry** 42, 155-161. (*corresponding author, estimated contribution: 40%*)

Publications on soil formation along substrate age gradients (chronosequences)

H7 LAIR, G.J., F. ZEHETNER, M. HRACHOWITZ, N. FRANZ, F.-J. MARINGER, and M.H. GERZABEK (2009). Dating of soil layers in a young floodplain using iron oxide crystallinity. **Quaternary Geochronology** 4, 260-266. (*corresponding author, estimated contribution: 40%*)

H8 ZEHETNER, F., G.J. LAIR, and M.H. GERZABEK (2009). Rapid carbon accretion and organic matter pool stabilization in riverine floodplain soils. **Global Biogeochemical Cycles** 23, GB4004, doi:10.1029/2009GB003481. [featured as *research highlight* in **Nature Reports Climate Change**, vol. 3, July 2009, www.nature.com/reports/climatechange] (*first author, estimated contribution: 50%*)

H9 ZEHETNER, F., G.J. LAIR, F.-J. MARINGER, M.H. GERZABEK, and T. HEIN (2008). From sediment to soil: floodplain phosphorus transformations at the Danube River. **Biogeochemistry** 88, 117-126. (*first author, estimated contribution: 50%*)

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H11 GRAF, M., G.J. LAIR, F. ZEHETNER, and M.H. GERZABEK (2007). Geochemical fractions of copper in soil chronosequences of selected European floodplains. **Environmental Pollution** 148, 788-796. (*estimated contribution: 20%*)

H12 LAIR, G.J., M. GRAF, F. ZEHETNER, and M.H. GERZABEK (2008). Distribution of cadmium among geochemical fractions in floodplain soils of progressing development. **Environmental Pollution** 156, 207-214. (*corresponding author, estimated contribution: 30%*)

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H15 ZEHETNER, F. (2010). Does organic carbon sequestration in volcanic soils offset volcanic CO_2 emissions? **Quaternary Science Reviews**, doi:10.1016/j.quascirev.2010.03.003. (*single author, contribution: 100%*)

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