Effects of fragmentation on pollination and regeneration of South American *Polylepis australis* woodlands

Dissertation (kumulativ)

Zur Erlangung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.)

vorgelegt der

Mathematisch-Naturwissenschaftlich-Technischen Fakultät (mathematisch-naturwissenschaftlicher Bereich) der Martin-Luther-Universität Halle-Wittenberg

von

Diplom-Biologin Peggy Seltmann
geboren am 25.02.1976 in Erlabrunn

Gutachterin bzw. Gutachter:
1. Prof. Dr. rer. nat. habil. Isabell Hensen
2. Prof. Dr. rer. nat. habil. H. Bruelheide
3. Prof. Dr. rer. nat. habil. Markus Fischer

Halle (Saale), 2006

[urn:nbn:de:gbv:3-000010852](http://nbn-resolving.de/urn/resolver.pl?urn=nbn%3Ad%3Agbv%3A3-000010852)
TABLE OF CONTENTS

CHAPTER I: EFFECTS OF FRAGMENTATION ON POLLINATION AND REGENERATION OF SOUTH AMERICAN POLYLEPIS AUSTRALIS WOODLANDS – INTRODUCTION AND OVERVIEW
  Forest fragmentation and consequences ........................................... 3
  Polylepis forests ................................................................................ 5
  Study species and area ........................................................................ 7
  Aims and questions ............................................................................ 10
  Survey of methods and results, and first conclusions ......................... 11
  References ......................................................................................... 13

CHAPTER II: MATING SYSTEM, OUTCROSSING DISTANCE EFFECTS AND POLLEN AVAILABILITY IN THE WIND-POLLINATED TREELINE SPECIES POLYLEPIS AUSTRALIS
  Abstract ....................................................................................... 17

CHAPTER III: BIPARENTAL INBREEDING DEPRESSION, GENETIC RELATEDNESS AND PROGENY VIGOUR IN A WIND-POLLINATED TREELINE SPECIES IN ARGENTINA
  Abstract ....................................................................................... 18

CHAPTER IV: WOODLAND FRAGMENT SIZE, POLLINATION EFFICIENCY AND REPRODUCTIVE SUCCESS IN NATURAL POPULATIONS OF WIND-POLLINATED POLYLEPIS AUSTRALIS (ROSACEAE) TREES
  Abstract ....................................................................................... 19

CHAPTER V: VARIATION IN SEED MASS AND ITS EFFECTS ON GERMINATION IN POLYLEPIS AUSTRALIS: IMPLICATIONS FOR SEED COLLECTION
Abstract ............................................................................................................ 20

CHAPTER VI:   COMPREHENSIVE CONCLUSIONS ..................... 21

CHAPTER VII:  ANHANG
  Erklärung über den persönlichen Anteil an den Publikationen .......... 24
  Curriculum vitae ......................................................................................... 27
  Publikationsliste ....................................................................................... 29
  Eigenständigkeitserklärung ..................................................................... 30
CHAPTER I

EFFECTS OF FRAGMENTATION ON POLLINATION AND REGENERATION OF SOUTH AMERICAN POLYLEPIS AUSTRALIS WOODLANDS – GENERAL INTRODUCTION AND OVERVIEW

Forest fragmentation and consequences

Worldwide, large areas of continuous forests are rapidly becoming fragmented as a result of human activities. Across the globe, forests have been cut for reasons of wood production, burnt or clear-cut to produce grasslands for livestock, agricultural lands or urban areas, changing in this way the face of many forest landscapes (Ellenberg, 1979; Spies, 1998). Remaining forests are often highly fragmented and their defining characteristics modified. These transformations are connected with a loss of ecosystem functions formerly provided by the original closed forests. Forests are important, for example, for controlling soil erosion, increasing water catchment capacity of the area and providing habitat for wildlife (Hunter, 1990; Fjeldså & Kessler, 1996; Spies, 1998).

As documented by several studies, the restriction of formerly common tree species to small and isolated fragments may subsequently lead to increased inbreeding depression because of cumulative effects of genetic drift (e.g. Fischer & Matthies, 1997; Gigord et al., 1998; Hedrick & Kalinowski, 2000; Glémin et al., 2001). While inbreeding usually refers to the mating of closely related individuals, inbreeding depression is defined as reduced fitness of the offspring of related mates compared to the offspring of randomly mated individuals (Hedrick & Kalinowski, 2000). Genetic drift in small populations can lead to decreased fitness in all, or nearly all, of their
individuals compared to larger populations (Hedrick & Kalinowski, 2000). In accordance, the potential for inbreeding depression has been demonstrated in various animal-pollinated species (e.g. Aizen & Feinsinger, 1994; Moran-Palma & Snow, 1997; Fischer & Matthies, 1997; Larson & Barrett, 2000; Garcia Collevatti et al., 2001; Stacy, 2001), and for a number of conifers (e.g. Krakowski et al., 2003; Wang et al., 2004). However, very little is known about biparental inbreeding depression in wind-pollinated woody angiosperms.

Furthermore, both fragmentation of woodlands and small fragment size may reduce pollen availability and thus, limit reproduction. While preliminary experimental evidence suggests that reproduction in populations of wind-pollinated trees is pollen-limited under certain conditions (e.g. Perry & Knowles, 1990; Allison, 1990; Holm, 1994; Knapp et al., 2001), a consensus on this issue has yet to be achieved (studies in contrast: e.g. Dow & Ashley, 1998; Streiff et al., 1999).

In addition, abundant theory postulates a reduction in gene flow among fragmented populations of many species, including numerous maladaptive consequences which can follow from genetic isolation (Ellstrand & Elam, 1993; Smouse & Sork, 2004). In contrast to the general assumption of extensive pollen flow in wind-pollinated trees (e.g. Adams & Burczyk, 2000; Hamrick & Nason, 2000), recent studies by Knapp et al. (2001), Sork et al. (2002) and Satake & Iwasa (2002) have lead to the conclusion that short-distance dispersal of pollen tends to be common, and that increased fragmentation could ultimately result in reproductive failure in wind-pollinated tree species (Koenig & Ashley, 2003).

Thus, for successful conservation efforts of remaining fragments it is crucial to gather knowledge both on reproductive processes and on gene transfer of the involved tree species. This applies particularly to highly fragmented ecosystems where it is indispensable to assess whether progressive habitat degradation, size reduction and increasing isolation actually accelerate further declines in populations. A substantiated knowledge on gene transfer is especially important because gene flow is one of the key factors determining species responses to fragmentation (Burczyk et al., 2004).

The next chapters focus on the genus *Polylepis* with the intention of highlighting its mating system, possible scenarios of gene transfer and reproductive responses to forest fragmentation.
**Polylepis forests**

The genus *Polylepis* R. & P. (Rosaceae, Sanguisorbeae) includes about 28 wind-pollinated species of short to tall trees and shrubs of usually gnarled shape. The bark of *Polylepis* consists of numerous layers of thin, dark red exfoliating sheets as a protection against low temperatures (Simpson, 1979; Fjeldså & Kessler, 1996). While all species of *Polylepis* have compound imparipinnate leaves, the number of pairs of leaflets varies within and among species. The genus is distributed along the South American Andes (Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile and North-Argentina) and in the Córdoba mountains, Argentina (Simpson, 1979; Simpson, 1986; Kessler, 1995a; Kessler, 1995b; Schmidt-Lebuhn et al., submitted; Fig.1). Some of the species grow in the area of the tropical upper mountain forest, the others in isolated stands far above a closed treeline up to an altitude of 5.200m a.s.l. where they form the world’s highest woodlands (Troll, 1959).

Figure 1. Approximate distribution of *Polylepis* (from: Schmidt-Lebuhn, 2005)

Once assumed to be patchy by nature, *Polylepis* forests are now recognized to be highly endangered due to human impact (Fjeldså, 2002; Kessler, 2002; Purcell et al., 2004; Renison et al., 2006). Exploitation of South American high mountains since Incan times has greatly reduced forest areas. Recent forests occupy only about one percent of their original area in the eastern Bolivian Andes and about three percent in Peru (Fjeldså & Kessler, 1996; Purcell et al., 2004). In other countries, the extent of *Polylepis* forest loss is not quantified but likely to be equally high (Renison et al., 2006).
In consequence, several recent studies have investigated the effects of anthropogenic activities on *Polylepis* forests (e.g. Acosta, 1986; Hensen, 2002; Renison et al., 2002; Teich et al., 2005; Renison et al., 2006). Much effort has been done to achieve a substantiated knowledge on successful reforestation of the endangered habitats (Kopta, 1985; Brandbyge & Holm-Nielsen, 1987; Renison & Cingolani, 1998; Ibisch, 2002; Renison & Cingolani, 2002; Renison et al., 2002; Renison et al., 2005). However, reforestation may be hampered due to the low seed viability or/and low germination rates reported for several *Polylepis* species (Pretell Chiclote et al., 1985; Brandbyge & Holm-Nielsen, 1987; Reynel & Leon, 1990; Hensen, 1994; Renison et al., 2004). In this context, Renison et al. (2004) investigated the effects of habitat degradation on *P. australis* and detected both a positive relationship between seed viability and soil conditions, and a negative correlation with soil erosion. In addition, reforestation success may be negatively affected by the vigour of the seedlings. Indeed, Renison et al. (2005) found that seedling growth during their first five years was faster when seedlings derived from seeds collected in a large, well-preserved forest than from seeds collected in smaller forest fragments.

However, despite substantial evidence of the negative impact of fragmentation and habitat degradation on *Polylepis* reproduction, no specific studies exist which have investigated the mating system and pollination biology of *Polylepis* species, and, based on that, pollination-based responses to fragmentation.

Well-founded knowledge of the mating system of a species is an essential prerequisite for evaluating the dependence of seed production and progeny attributes on pollination rate and type, and may subsequently lead to a greater understanding of the mechanisms of gene flow within and between populations (Barrett & Eckert, 1990).

In the following, defining characteristics of *Polylepis australis* as representative for the genus are discussed in detail.
Study species and area

*Figure 2.* Collection localities of *Polylepis australis* Bitter (from: Simpson, 1997)

*Figure 3.* *Polylepis australis* Bitter. (A) branch (B) flower. (C) fruit (from: Simpson, 1979).

*Polylepis australis* Bitter is the southernmost *Polylepis* species, endemic to Argentina where it occurs in the mountains of the provinces of Jujuy, Salta, Catamarca, Tucumán, Córdoba and San Luis (Simpson, 1979; Fig. 2). It is the only native species that forms forests in the higher mountains of Central Argentina (Renison et al., 2004).

The species comprises shrubs and trees that are 1.5 to 14m in height (Simpson, 1986). Its racemiform pendulous inflorescences are 1.8 to 7.3cm long catkins that are produced annually. They may carry up to twelve perfect wind-pollinated flowers with typical anemophilous features such as reduced inconspicuous corollas, protogyny and a large stigmatic surface area (Fig. 3, 4). Each flower is 0.7-1.0cm in diameter with three or four green sepals and 8–16 stamens (Simpson, 1979; Fig. 3, 4). Anthers are red, conspicuous and open by longitudinal slits (Fig. 4). The stigma is uniformly expanded and fimbrillate (Simpson, 1986; Fig. 3, 4). Self-pollination is precluded by protogyny, i.e. temporal staggering of sexual maturity within the flower with stigmas being receptive only before the anthers open. *Polylepis australis* pollen is arranged in monads, more or less spheroidal in shape, 58–76µm wide and 3-colporate (Simpson, 1986; Fig. 5). Flowers generally develop one ovule (with only few exceptions where
Effects of fragmentation on pollination and regeneration of *Polylepis australis*

two are formed, personal observation), and fruits are mostly single seeded nutlets that are enclosed in a turbinate and winged receptaculum (Fig. 3).

![Figure 5. *Polylepis australis* pollen grains (20x), Photo: Andrea Cocucci.](image)

Investigations were carried out in the Córdoba mountains, Central Argentina (31º 34’ S, 64º 50’ W). The mean annual temperature is 8°C, and there is no frost-free period. Mean annual precipitation is 840mm with most rainfall concentrated in the warmer months between October and April (Cabido et al., 1987). Woodlands are dominated almost exclusively by *P. australis* trees (Cingolani et al., 2004) whose stands can be found between 900 and 2,884m a.s.l.

Human intervention and forest fragmentation probably started 8000 years ago when the first Amerindians settled in the area and started using burning techniques for hunting (Berberían, 1999; Pastor, 2000). After European settlement, forests further declined and degradation proceeded due to fire, introduction of cattle grazing and utilization of timber and firewood (Cabido & Acosta, 1985; Kopta, 1999; Cingolani et al., 2004; Renison et al., 2004).
Effects of fragmentation on pollination and regeneration of *Polylepis australis*

**Figure 4.** *Polylepis australis* Bitter. (A) Inflorescence with flowers in the male phase (anthers opened); (B) Longitudinal section of a flower in the male phase; (C) Branch with inflorescence and young infructescences. Photos: A. Cocucci.
Aims and questions

The central aim of the current investigation is not only to improve the knowledge on the pollination biology and the mating system of *Polylepis* but also, moreover, to assess pollination-based responses of *Polylepis* to fragmentation. An additional goal was to contribute to the knowledge on possibilities for successful reforestation. Thus, *Polylepis australis* was used to answer the following main questions:

- Is self-pollination possible? Are there differences in the reproductive output of self- and cross-pollinated flowers? Does the distance between mates affect seed mass and germination? Are there any indications for pollen limitation and for pollen longevity being a limiting factor in the pollination process? (*CHAPTER II*)

- Is there a relationship between genetic similarity and geographic distance in *P. australis* woodland fragments? Do outcrossing distances influence genetic variability and vigour of the progeny? What scenarios of gene transfer are most likely to be occurring in *P. australis* woodland fragments at the current fragmentation level? (*CHAPTER III*)

- How are the relationships between woodland fragment size, natural pollination and reproductive success in *P. australis* woodland fragments? (*CHAPTER IV*)

- To what extent does the seed mass affect *P. australis* seed germination? Does the knowledge on this relationship contribute to successful reforestation? (*CHAPTER V*)
Survey of methods and results, and first conclusions

**CHAPTER II**...deals with effects of hand-selfing, varying outcrossing distances of up to 30km and pollen addition on seed mass and seed germination of *Polylepis australis*. In addition, pollen germination on the stigma and pollen tube growth were investigated to determine compatibility resulting from selfing and outcrossing, as well as pollen longevity.

To test for self-fertilization and the effect of outcrossing distances, flowers of *P. australis* individuals equally distributed between two woodland fragments were hand-pollinated with self-pollen and with cross-pollen belonging to different distance-classes. Pollen addition experiments were performed in four woodland fragments differing in size.

The results suggest a potential for inbreeding depression through selfing and crosses within woodland fragments. However, the results also indicate that pollen flow between *P. australis* woodland fragments is still effective at the current fragmentation level. In coincidence, results suggest that *P. australis* pollen grains remain viable long enough to complete the pollination process even over longer distances. Furthermore, even in case of relatively small woodland fragments, pollen availability does not seem to limit reproductive success.

**CHAPTER III**...focuses on the relationships between parental genetic similarity, outcrossing distances and progeny vigour as measured by N metabolism capacity of the seedlings. Genetic variability and vigour of the resulting progeny were contrasted with progeny from open pollinated flowers.

Seedlings resulting from seeds that had been obtained by crosses with pollen belonging to different distance-classes (chapter II) were used for the evaluation of the N metabolism capacity. All remaining seedlings served as plant material for genetic analysis (RAPD-PCR). Leaf tissue from focal females and from pollen donors from each of the respective distance classes was used to assess parental genetic similarity.

The study revealed a continuous decrease of parental genetic similarity with spatial distance among mates and an increase of N metabolism capacity with increasing distances of pollen provenance. It can be concluded that genetic similarity between focal females and pollen donors can be seen as an underlying factor for biparental inbreeding depression in the study species. Consequently, this is the first
study providing evidence of biparental inbreeding in a wind-pollinated angiosperm tree.

However, the results confirm and underline the assumption of fragment connectivity at the current fragmentation level as derived from chapter II. Effective long distance pollen-mediated gene flow can be assumed, counteracting problems of inbreeding depression observed under present day conditions. Thus, the mentioned results contribute to the general assumption of extensive pollen flow in wind-pollinated trees.

CHAPTER IV...To test for the hypothesis of effective fragment connectivity as concluded in chapter II and III, this chapter deals with the relationships between woodland fragment size, natural pollination and reproductive success of *P. australis*, comparing natural pollination and reproduction between four different woodland fragment sizes (three woodland fragments each, totalling twelve woodland fragments).

The results demonstrated that while flowers collected from trees of different fragment sizes received similar pollen loads on their stigmas, they also displayed a tendency of having an increased percentage of pollen tubes at the top of the styles with increasing fragment size. This finding gives reason to assume an increased natural pollination in larger woodland fragments and can likely be explained by the breeding system and the identity of pollen grains contained in the naturally deposited pollen loads. However, this would be in contrast to the results of the previous chapters indicating effective reproductive and genetic connectivity of woodland fragments through effective pollen-mediated gene flow. Furthermore, the study also revealed increasing progeny leaf area and biomass with increasing fragment size. Based on these findings, it was concluded that impaired vigour of *P. australis* progeny resulting from woodland fragmentation is due to inbreeding problems that are specific to this species and/or due to decreased habitat quality in small fragments.

CHAPTER V...This chapter analyses the influence of seed mass and seed provenance on the germination probability of *P. australis* seeds. In order to conduct the analyses, seeds from five woodland fragments distributed in two regions of the
Córdoba mountains were collected, weighed and tested for germination and viability. Woodland fragments differed in size, topographical position and altitude.

Results indicated a high positive correlation between germination probability and seed mass. Thus, selecting seeds on the basis of mass is an appropriate way to enhance germination prospects for reforestation projects. However, highest germination probabilities were given at varying seed mass values depending on geographical region, woodland fragment or tree identity. Therefore, it is suggested to collect the relatively heaviest available seeds for breeding, although the absolute seed mass of a given region, fragment or tree may be low over-all.

References


CHAPTER II

MATING SYSTEM, OUTCROSSING DISTANCE EFFECTS AND POLLEN AVAILABILITY IN THE WIND-POLLINATED TREELINE SPECIES POLYLEPIS AUSTRALIS

Together with A. Cocucci, D. Renison, A. Cierjacks & I. Hensen
- Basic and Applied Ecology -

Abstract

Isolation and small population size resulting from habitat destruction and fragmentation may negatively affect plant fitness via increased levels of inbreeding and pollen limitation. However, effects of fragmentation may vary with regard to life form and breeding system and have not been very well studied in wind-pollinated trees. Here, we studied the effects of hand-selfing, varying outcrossing distances of up to 30km and pollen addition on seed mass and seed germination of Polylepis australis (Rosaceae), an anthropogenically fragmented wind-pollinated treeline species endemic to Argentina. Furthermore, we investigated pollen germination on the stigma and pollen tube growth to determine compatibility resulting from selfing and outcrossing, as well as pollen longevity. All hand pollinations resulted in variable seed masses and variable seed germination across maternal trees, but selfing reduced seed germination with significant differences between results for open pollination and outcrosses at 30km. In addition, we found a tendency for pollen germination and pollen tube growth to decrease following selfing. Between-fragment crosses resulted in a trend of higher reproductive output than within-fragment crosses, whereas values were similar between open pollination and between-fragment crosses. Our observations documented that P. australis is characterized by an exceptionally long period of pollen viability and that, even in small fragments, pollen addition did not increase reproductive success. Our results suggest a potential for inbreeding depression through selfing and within-fragment crosses. However, the results also indicate that pollen flow between P. australis woodland fragments is still effective at the current fragmentation level, counteracting negative effects resulting from reproductive isolation.
BIPARENTAL INBREEDING DEPRESSION, GENETIC RELATEDNESS AND PROGENY VIGOUR IN A WIND-POLLINATED TREELINE SPECIES IN ARGENTINA

Together with I. Hensen, D. Renison, K. Wesche, S. Ploch, J. Rondan Dueñas, A. Cocucci & K. Jung
- Plant Biology (submitted) -

Abstract

Background and Aims Limited gene flow and resulting spatial genetic structure are generally considered as being the primary controlling factors in the dynamics of biparental inbreeding depression in a wide range of plant species. However, wind-pollinated angiosperm trees have not been adequately studied in this respect. The present study analyses the relationships between parental genetic similarity, outcrossing distances and progeny vigour in Polylepis australis (Rosaceae), a wind-pollinated treeline species endemic to Argentina.

Methods We investigated whether spatial genetic structuring occurs in anthropogenically fragmented P. australis woodlands of the Córdoba Mountains. We also performed a controlled crossing experiment using pollen collected from distances of 20m, 1km and 30km. Genetic variability (using RAPD-PCR) and vigour (N metabolism capacity) of the resulting progeny were contrasted with progeny from unmanipulated flowers.

Key Results We found a continuous decrease in parental genetic similarity with spatial distance among mates and an increase both in genetic variability and N metabolism capacity in the progeny produced from pollen at increasing distances.

Conclusions Genetic similarity between focal females and pollen donors can be seen as an underlying factor for biparental inbreeding depression in P. australis. However, there was no difference between N metabolism capacity resulting from open pollination and that from crosses between distant fragments. Furthermore, the progeny resulting from long-distance crosses was closely related to that of open pollinated progeny. On the whole, our results suggest fragment connectivity in P. australis through effective long distance pollen-mediated gene flow with no effective inbreeding depression problems observed under present day conditions.
CHAPTER IV

WOODLAND FRAGMENT SIZE, POLLINATION EFFICIENCY AND REPRODUCTIVE SUCCESS IN NATURAL POPULATIONS OF WIND-POLLINATED POLYLEPIS AUSTRALIS (ROSACEAE) TREES

Together with D. Renison, A. Cocucci, I. Hensen & K. Jung

Abstract

It is well known that fragmentation is likely to negatively affect the reproductive success of a species. Despite of this fact, studies on the effects of fragmentation on reproductive success in combination with effects on natural pollination of wind-pollinated tree species are very rare. In this study, we analyzed the relationships between woodland fragment size, natural pollination, reproductive success and progeny vigour of the highly fragmented wind-pollinated treeline species Polylepis australis (Rosaceae) in Argentina. We conducted our study in the high mountains of Córdoba, comparing natural pollination and reproduction between four woodland fragment sizes. Flowers collected from trees of the different fragment sizes received similar pollen loads on their stigmas. Results showed a non-significant trend of increased percentages of germinated pollen grains on the stigma and of percentages of pollen tubes reaching the styles in trees derived from larger woodland fragments. Furthermore, our study revealed a parallel linear increase in leaf area and biomass of 40 days old seedlings with increasing fragment size. The findings confirm that woodland fragmentation negatively affects the vigour of P. australis progeny. Future research will need to clarify whether impaired P. australis progeny vigour resulting from woodland fragmentation is due to inbreeding problems specific to this species or to decreased habitat quality in small fragments.
CHAPTER V

VARIATION IN SEED MASS AND ITS EFFECTS ON GERMINATION IN POLYLEPIS AUSTRALIS: IMPLICATIONS FOR SEED COLLECTION

Together with I. Leyer, D. Renison & I. Hensen

- New Forests -

Abstract

South American Polylepis mountain forests are recognised as being one of the most endangered forest ecosystems in the world. Reforestation measures have been strongly recommended but may be hampered due to the very low seed germination reported for several Polylepis species. In order to facilitate reforestation we analysed the influence of seed mass on germination probability for Polylepis australis seeds in the Córdoba mountains (central Argentina). We collected seeds from 43 trees distributed throughout 5 woodland fragments located within two regions differing in size, topographical position, and altitude (1900 and 2200m a.s.l.). Seeds of Polylepis australis exhibited a great variation in terms of mass and percent seed germination among individual trees and among geographical regions. The results of logistic regression showed that germination probability was highly correlated with seed mass. However, the explained deviance significantly increased by including the region, the woodland fragment and especially the individual tree in addition to seed mass in the regression models. We conclude that selecting seeds on the basis of mass is an appropriate way to enhance germination prospects for reforestation projects. However, no absolute mass values are applicable in this context as the highest germination probabilities were reached at varying seed mass values depending on geographical region, woodland fragment or individual tree. We suggest collecting the relatively heaviest available seeds, even though the absolute seed mass may be low.
CHAPTER VI

COMPREHENSIVE CONCLUSIONS

The data presented herein provide evidence for long distance pollen-mediated gene flow rendering the wind-pollinated *Polylepis australis* fairly resistant to reproductive isolation via forest fragmentation. As population connectivity and gene flow into patches may serve to mitigate the effects of inbreeding depression (Richards, 2000), this fact should contribute to the persistence of fragmented *P. australis* woodlands.

The assumption of effective pollen flow and of genetic connectivity is underlined by the results of low genetic differentiation of *P. australis* in the Córdoba mountains and by studies on other species of this genus (Schmidt-Lebuhn et al., in press.). In consequence, the present results should be transferable to other *Polylepis* species and contribute to the general assumption of extensive pollen and gene flow in wind-pollinated trees. Thus, previous assumptions of very limited pollen dispersal in *Polylepis*, such as suggested by Graf (1986) and Fjeldså & Kessler (1996) can not be confirmed.

However, it was also found that effective pollen movement over substantial distances is *essential* for maintaining seedling fitness and, in consequence, for natural regeneration of *P. australis* woodlands. To specify a precise critical minimum distance of effective pollen flow, further investigations are necessary. Nevertheless, a complete isolation of natural stands interrupting pollen exchange due to ongoing
land-use practices would involve a high potential for loss of the natural reproduction capacity of remaining fragments.

Despite of the fact that the mating system of *P. australis* is extraordinarily efficient at producing highly out-bred individuals and ensuring long distance pollen-mediated gene flow, the tendency of regressing natural pollination in trees derived from small woodland fragments compared to larger ones indeed indicates the beginning of a decline in the naturally deposited outcrossed pollen load in small *P. australis* woodland fragments. However, the amount of compatible pollen may be still adequate to arrive at comparable reproductive success.

In addition, the reported increase in progeny biomass and leaf area with increasing fragment size leads to the conclusion that there are inbreeding-related problems (e.g. Heschel & Paige, 1995; Cascante et al., 2002) but would be in contrast to the results mentioned above indicating effective reproductive and genetic connectivity of woodland fragments. However, a possible complementary explanation for this finding is related to habitat quality. There are several studies suggesting that fragmentation is more a matter of habitat degradation within small fragments (Harrison & Bruna, 1999). Furthermore, the growing conditions of a parent plant may influence both the number and the quality of its progeny (e.g. Weiner et al., 1997; Gianoli & González-Teuber, 2005). In coincidence, small fragments of *P. australis* can be found mostly in steep rocky areas protected from fires and livestock but providing unfavourable growing conditions (Teich et al., 2005; Renison et al., 2006).

Considering the results presented in chapters II to IV, it becomes apparent that even if there is genetic connectivity between isolated fragments, this connectivity cannot compensate for the loss of quantity and quality of the progeny of isolated origin and its negative effects on the regeneration of *P. australis* woodlands. Although not tested directly, considering the fact that most *Polylepis* woodland stands throughout South America are also highly fragmented and degraded (Fjeldså & Kessler, 1996), the potential of regeneration problems following fragmentation, isolation and degradation may also be of importance for other species of the genus.

Therefore, in order to maintain progeny vigour, a clear conservation strategy is needed to avoid further fragmentation and isolation accompanied by ongoing degradation of *Polylepis* habitat throughout its entire range of distribution.

References


Anhang

CHAPTER VII

ANHANG

Erklärung über den persönlichen Anteil an den Publikationen

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

Chapter II

Datenerhebung:
- Bestäubungsversuche, Sammeln der Blüten und Früchte: 100%
- Auswiegen der Samen: 60%
- Durchführung der Keimversuche: 100%
- Ermittlung der Pollenlebensfähigkeit: 100% (nach Hinweisen von A. Cocucci)

Datenanalyse: 100% (nach Hinweisen von K. Wesche)

Schriftliche Umsetzung: 90% (Korrektur durch D. Renison, A. Cocucci und I. Hensen)

Chapter III

Datenerhebung:
- Bestäubungsversuche, Sammeln der Blüten und Früchte: 100%
- Anzucht und Kultivierung der Keimlinge: 100%
• Isotopenanalyse (Probenaufarbeitung, Bestimmung des N-Gehaltes nach Kjeldahl, 
\(^{15}\)N-Isotopenanalytik): 90% (Einarbeitung und Unterstützung durch K. Jung und 
Technische Angestellte des UFZ Leipzig)
• Sammeln des Blattmaterials für genetische Analysen: 100%
• molekularbiologische Laborarbeiten durch Sebastian Ploch

_Datenanalyse:_
• Genetische Analysen: genetische Ähnlichkeit: 100%; genetische Diversität und 
genetische Distanzen: 60% (Unterstützung durch Juán Rondán Dueñas)
• Analysen zur \(^{15}\)N-Isotopenanalytik: 100% (nach Hinweisen von K. Wesche)

_Schriftliche Umsetzung:_ 95% (Korrekturen durch D. Renison, I. Hensen und K. Jung)

**Chapter IV**
fragment size, pollination efficiency and reproductive success in natural populations 
of wind-pollinated _Polylepis australis_ (Rosaceae) trees. _Forest Ecology and 
Management_.

_Datenerhebung:_
• Sammeln von Blüten und Früchten: 100%
• Pollenzählung, Ermittlung Pollenkeimung und Anteil an Pollenschläuchen mittels 
Epifluoreszenzmikroskopie: 100% (nach Hinweisen von A. Cocucci)
• Anzucht und Kultivierung der Keimlinge: 100%
• Ermittlung der Fitnessparameter der Keimlinge (ausgenommen Isotopenanalyse): 
100%
• Isotopenanalyse: Probenaufarbeitung: 100%; \(^{15}\)N-Isotopenanalytik durch I. Flügel 
vom UFZ Leipzig

_Datenanalyse:_ 100%

_Schriftliche Umsetzung:_ 97% (Korrekturen durch D. Renison, I. Hensen und K. Jung)

**Chapter V**
and its effects on germination in _Polylepis australis_: Implications for seed collection. 
_New Forests_.

_Datenerhebung:_
• Sammeln der Samen: 100%
• Auswiegen der Samen: 60%
• Durchführung der Keimversuche: 100%
• Durchführung der TTC-Tests: 50%

_Datenanalyse:_ 50% (Logistische Regressionen durch I. Leyer)

_Schriftliche Umsetzung:_ 90% (Unterstützung durch I. Leyer; Korrekturen durch D. Renison 
und I. Hensen)
Co-Autoren in alphabetischer Reihenfolge und deren Status:
Cocucci, A.A., Dr.
Dueñas, R.J., Dr.
Hensen, I., Prof. Dr.
Jung, K., Prof. Dr.
Ploch, S., Student
Renison, D., Prof. Dr.
Wesche, K., Dr.

Bestätigung des betreuenden Hochschullehrers

Prof. Dr. Isabell Hensen
Curriculum vitae

Name: Peggy Seltmann
Geburtsdatum: 25.02.1976
Geburtsort: Erlabrunn

Ausbildung
1990 – 1994 Gymnasium Schwarzenberg
Abitur
1994 – 2000 Universität Leipzig, Fakultät für Biowissenschaften/Pharmazie und Psychologie
Studium Biologie (Diplom)
• Schwerpunktfächer: Spezielle Botanik, Ökologie, Spezielle Zoologie, Geologie
• Thema der Diplomarbeit: Untersuchungen zur Ökologie der Loranthaceae und Viscaceae am Oberen Orinoco (Venezuela)
• Abschluss Diplom, Prädikat: sehr gut

Praktika & Kurse
Botanisch-ökologisches Feldpraktikum innerhalb des Projektes „Untersuchungen zur Phänologie, Blüten- und Fruchtökologie der Bäume eines amazonischen Tieflandregenwaldes"

Vegetationsökologisches Praktikum innerhalb der Projekte „Vorrangflächen für Naturschutz in der Bergbaufolgelandschaft Westsachsens und Nordthüringens“ und „Übertragung und Weiterentwicklung eines robusten Indikationssystems für ökologische Veränderungen in Auen"

09/2000 Namibia & Südafrika
Vegetationsökologisches Feldpraktikum innerhalb des Projektes „Evolution und Ökologie der Vegetation der afrikanischen Trockengebiete, insbesondere Analyse der Auswirkungen verschiedener Landnutzungsformen und Umweltveränderungen auf die Vegetation und den zu beobachtenden Wandel der Biodiversität“ (BIOTA – Biodiversity Monitoring Transect Analysis)
Anillaco/La Rioja (Argentinien)

**Workshop on Pollination Ecology**
Leitung: Prof. Dr. Amots Dafni (University of Haifa, Israel)

---

**Berufserfahrung**

**07/1997 – 10/1998**  
*Floristische Kartierung* im Rahmen der Erstellung des Verbreitungsatlasses der Gefäß- und Farnpflanzen Sachsens


*Universität Leipzig, Institut für Spezielle Botanik*  
*Wissenschaftliche Hilfskraft*

**08/2001 – 10/2002**  
*Landschaftsplanungsbüro Adrian, Leipzig*  
*Freie Mitarbeiterin*

**04/2002 – 03/2006**  
*MLU Halle-Wittenberg, Institut für Geobotanik und Botanischer Garten*  
**Wissenschaftliche Mitarbeiterin und Promotionskandidatin**

- Dozententätigkeit
- Titel der Dissertation: „Effects of fragmentation on pollination and regeneration of South American *Polylepis australis* woodlands“ (Kooperationsprojekt MLU Halle-Wittenberg – Nationaluniversität Córdoba, Argentinien)

**02/2005**  
*Dozent im Rahmen des internationalen Kurses: „Ökologie und Schutz von Bergwäldern“ („Ecología y Conservación de Bosques Montanos“) in Córdoba, Argentinien*

seit **04/2006**  
*MLU Halle-Wittenberg, Institut für Geobotanik und Botanischer Garten*  
*Dozententätigkeit (Lehrauftrag)*
Publikationsliste

Publikationen in Fachzeitschriften und Büchern


Tagungsbeiträge


Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit bisher weder der Mathematisch-Naturwissenschaftlich-Technischen Fakultät der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle/Saale, den

Peggy Seltmann