ENVIRONMENTAL AND HUMAN INFLUENCES ON TROPICAL TREELINE FORMATION: INSIGHTS FROM THE REGENERATION ECOLOGY OF *POLYLEPIS* SPP. IN THE PÁRAMO DE PAPALLACTA, ECUADOR

Dissertation (kumulativ)

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

vorgelegt der
Naturwissenschaftlichen Fakultät I – Biowissenschaften
der Martin-Luther-Universität Halle-Wittenberg

von
Diplombiologe Arne Cierjacks
geboren am 04.04.1972 in Karlsruhe

Gutachterinnen und Gutachter
1. Prof. Dr. rer. nat. habil. Isabell Hensen
2. Prof. Dr. rer. nat. habil. Helge Bruelheide
3. PD Dr. rer. nat. Michael Kessler

Halle (Saale), Dezember 2006
Verteidigt am 20.03.2007

urn:nbn:de:gbv:3-000011760
[http://nbn-resolving.de/urn/resolver.pl?urn=nbn%3Ade%3Agbv%3A3-000011760]

CONTENT

SUMMARY

Tropical-alpine treelines are characterized by discontinuous forest patches forming abrupt boundaries with the adjacent grassland vegetation. This also holds true for the tropical-Andean forests formed by *Polylepis* spp. *Polylepis* forests have been listed as one of the most endangered forest ecosystems of the world for which efficient conservation strategies are urgently needed. Although the peculiar vegetation pattern has frequently been attributed to anthropogenic disturbances, quantitative or experimental studies on the consequences of land use and environment for the current treeline position are limited. Knowledge on regeneration processes is crucial to the understanding of treeline formation and future stand development, however, recruitment patterns with associated environmental and human factors at *Polylepis* treelines still remain poorly understood because most previous studies derive from temperate, as opposed to tropical, ecosystems.

The studies which comprise this thesis deal with the impact of altitude, canopy cover, litter depth, grazing and burning on the reproduction of two *Polylepis* species in the Páramo de Papallacta, Ecuador. In particular, I analysed flowering, fruit set, seed viability, seedling emergence and survival as well as stand structure of *Polylepis incana* and *P. pauta*. The data on natural regeneration *in situ* were supplemented by sowing experiments at the upper treeline and after burning in order to discriminate effects of microsite conditions from those of seed availability. Due to the abundance of *Gynoxis acostae* in central Ecuadorian *Polylepis* forests, this species was additionally included into the assessment of post-fire regeneration. As well as contributing to the general theoretical framework on treeline ecology, this study aims at providing recommendations for the practical application of the scientific results. Based on the presented data, potential reforestation and conservation activities are described in the synthesis section at the end of this work.

In *P. incana*, the numbers of inflorescences, seedlings and saplings per m² decreased significantly with increasing altitude. The upslope decrease of tree height indicates growth limitations of the adult trees, which also affect the development of flowers and fruits. Sowing experiments at the upper distribution limit revealed a very low seedling emergence and survival, in comparison with results obtained in greenhouse and field experiments at lower altitudes. Sowing did not lead to higher seedling numbers than in the control plots. I conclude that low seedling numbers at high altitudes are the consequence of hampered germination due to harsh climatic conditions. In addition, lower inflorescence numbers indicate a reduced seed production, which might lead to lower seedling numbers. The number of asexual ramets, however, showed no altitudinal trends, which implies a higher importance of vegetative reproduction at the upper treeline.

The number of *P. pauta* inflorescences also decreased significantly upslope, but I found no evidence that seedlings, saplings or stand structure were influenced by altitude – presumably due to the low altitudinal range of this species, which covers only some 400 vertical metres. However, seedling emergence following sowing experiments at the upper treeline was clearly lower than at lower altitudes, and sowing increased seedling number exclusively in the sheltered conditions prevailing in existing forest stands. Following a linear regression, in both forest types the position of the current upper treeline in Ecuador coincides with a decline in inflorescence numbers to zero at about 4100 m asl for *P. incana*, and at about 4200 m asl for *P. pauta*. Nevertheless, I found no evidence of a change in seed viability with altitude.

Canopy cover affected seedling, sapling and ramet numbers significantly in both *Polylepis* species. While seedlings prevailed in the forest interior, sapling and ramet numbers were highest at the forest edge. Thus, the observed life stages show pronounced responses to edge effects. Climatic measurements indicated colder, but less extreme conditions below the canopy in forests compared to on the open paramo. I suggest that these microclimatic differences affect seedling emergence, and particularly so in the highest forest stands. As artificial sowing at these altitudes hardly increased seedling emergence within the forests, if at all, the differences in seedling numbers along the edge cannot be attributed to differences in seed rain. However, seed rain might be an important factor for the regeneration of both *Polylepis* species at lower altitudes. Sapling and ramet numbers, in contrast, responded rather to light conditions than to thermal effects. Hence, the species might be considered as being light demanding, which is supported by the low percentage of stems in narrow diameter classes in the forest interior. Consequently, the *Polylepis* forests of the Páramo de Papallacta mainly rejuvenate at the forest boundaries or in gaps. The overall ramet number was clearly higher in *P. incana* than in *P. pauta*, which emphasizes the relevance of asexual reproduction in this species.

Study sites are grazed but only to a limited extent. Ungulate trampling had a positive impact on the seedling abundance of both *Polylepis* species, presumably due to the removal of the litter layer. This corresponds to a significantly higher seedling emergence after litter removal in the sowing experiments. However, artificial litter addition did not lead to declining

seedling numbers, which might be ascribed to experimental difficulties in establishing a deep and dense litter layer. Herbivore browsing was scarce in the study area and there was no evidence for a negative impact on tree recruitment or stand structure. Hence, grazing at low to moderate intensities proved to be a sustainable land use practice in these forest communities.

In contrast, seedling emergence after burning was clearly reduced. Sowing increased seedling numbers of *P. incana* both in the burned and the unburned plots, which were exclusively located in the lower distribution range of the species. Reduced seedling numbers thus have to be attributed to the decrease in seed rain after canopy burning and to the destruction of the seed bank by fire rather than to climatic constraints. Nevertheless, the extreme climatic conditions at higher altitudes might further aggravate the negative consequences of burning. In contrast, sapling numbers clearly increased after burning, again due to the improvement of light conditions. In terms of its behaviour after burning, *P. incana* might be characterized as an obligate seeder with high tree mortality and low ramet numbers in the burned treatments compared to *Gynoxis acostae* with its vigorous resprouting capacity, which might explain the high percentage of the latter species in the study area. *Polylepis pauta* also showed lower seedling emergence after burning, although this result was not significant. There was no impact of sowing, which might be ascribed to the fact that burned areas and unburned plots were located at the upper distribution limit of the species, where germination is strongly hampered by climatic constraints.

In summary, my results on tree regeneration clearly indicate different regeneration patterns at the upper treeline in comparison to forest boundaries at lower altitudes. The low recruitment at the highest distribution limit characterizes this treeline as being natural due to the harsh climatic conditions. A further upslope migration by means of sexual regeneration seems unlikely, unless climatic conditions change. Consequently, the climatic growth limitations at the upper forest border of *P. incana* and *P. pauta*, which affect growth of adult trees, saplings and ramet populations, equally hampers the production of flowers and seeds as well as seedling recruitment. In contrast, forest boundaries below this altitude did not show any limitations in generative or vegetative reproduction, and the forest edge actually proved to be a zone of high natural recruitment. I conclude that these forest borders have to be attributed to human influences. As there were no negative effects of cattle grazing or woodcutting in the study area, I suggest that fire is the main factor driving boundary formation at lower altitudes. This is particularly probable as fire most commonly affects the otherwise reproductively dynamic edge zones, thus leading to a delay of tree recruitment. According to these findings,

the patchy discontinuous vegetation pattern found at tropical-alpine treelines in Ecuador is a consequence of the burning regime.

The study provides recommendations for forest conservation and restoration. Compulsory fire prevention will be the most important measure in order to maintain and to increase the forest cover by natural regeneration. Moreover, the establishment of firebreaks through the mowing of tussock vegetation around the existing remnants might be helpful in order to prevent grass paramo fires from spreading to forest fragments. In contrast, changes in the grazing regime will not be necessary. The positive consequences derived from changing light conditions and litter removal provide relevant knowledge for sapling production in nurseries and for plantation. Reforestation activities should consider the importance of the shelter from extreme climatic conditions provided by the remaining forest stands, which is particularly important at higher altitudes. Above 3900 m asl, any restoration effort will be difficult and time-consuming. Hence, conservation of the remaining stands should be of a higher priority.

ZUSAMMENFASSUNG

Tropisch-alpine Waldgrenzen sind meist durch einen abrupten Wechsel zur umliegenden Grasvegetation charakterisiert, und die betreffenden Waldbestände bestehen aus kleinflächigen unzusammenhängenden Populationen. Dem gleichen Muster folgen auch die tropisch-andinen *Polylepis*-Wälder Südamerikas. *Polylepis*-Wälder gehören zu den bedrohtesten Waldökosystemen der Erde – daher werden wirkungsvolle Naturschutzstrategien dringend benötigt. Obwohl die besonderen Vegetationsmuster häufig menschlichen Störungen zugeschrieben wurden, ist die Wirkung von Landnutzung und Standortfaktoren auf die aktuelle Physiognomie der Waldgrenze bisher kaum untersucht worden. Insbesondere quantitative Erhebungen und experimentelle Arbeiten fehlen fast vollständig. Die Kenntnis der Regenerationsprozesse könnte nützliche Hinweise über Waldgrenzenbildung und die zukünftige Bestandsentwicklung liefern; allerdings sind die Verjüngungsmechanismen an der Waldgrenze und die zugrundeliegenden abiotischen, biotischen und anthropogenen Einflüsse nach wie vor kaum verstanden, da die Mehrzahl der verfügbaren Daten aus temperaten und nicht tropischen Breiten stammt.

Die vorliegende Arbeit untersuchte den Einfluss von Höhe üNN, Kronendeckung, Streutiefe, Beweidung und Feuer auf die Reproduktion zweier *Polylepis*-Arten im Páramo de Papallacta, Ecuador. Hierfür wurden Blüten- und Fruchtbildung, Keimfähigkeit, Keimung und Keimlingsüberleben sowie die Bestandsstruktur von *Polylepis incana* and *P. pauta* analysiert. Daten zur natürlichen Regeneration am Standort wurden durch Aussaatexperimente an der oberen Waldgrenze bzw. nach Bränden überprüft, um zwischen Habitatunterschieden und Diasporenverfügbarkeit unterscheiden zu können. Da *Gynoxis acostae* in *Polylepis*-Wäldern Zentralecuadors sehr häufig ist, wurde diese Art in die Betrachtung der Regeneration nach Bränden einbezogen. Neben einem Beitrag zur allgemeinen Theorie der Waldgrenzenökologie hat diese Arbeit zum Ziel, Empfehlungen für die praktische Anwendung der wissenschaftlichen Ergebnisse zu liefern. Dementsprechend wurden Aufforstungs- und Naturschutzaktivitäten formuliert, die in der Synthese am Schluss dieser Arbeit beschrieben sind.

Bei *P. incana* nahm die Anzahl der Blütenstände, Keimlinge und Jungpflanzen mit zunehmender Höhe ab. Die Abnahme der Baumhöhe mit der Höhenlage zeigt Wachstumsbegrenzungen an, welche offensichtlich auch die Blüten- und Fruchtentwicklung beeinflussen. Aussaatversuche an der oberen Verbreitungsgrenze erbrachten sehr geringe

Keimungs- und Überlebensraten im Vergleich zu Ergebnissen aus Gewächshaus- und Feldversuchen in tieferen Lagen. Künstliche Aussaat an der Waldgrenze führte nicht zu höheren Keimlingszahlen als in den Kontrollflächen. Man kann daraus schließen, dass die geringen Keimlingszahlen in großer Höhe zum einen die Folge von extremen klimatischen Bedingungen in den oberen Waldbeständen sind. Zum anderen weisen die geringeren Blütenstandszahlen in den oberen Beständen darauf hin, dass auch verringerte Diasporenproduktion eine Rolle spielen kann. Die Zahl asexuell gebildeter Ramets zeigte dagegen keine Abhängigkeit von der Höhenlage, was insgesamt zu einer erhöhten Bedeutung von vegetativer Reproduktion an der oberen Waldgrenze führt.

Die Zahl der *P. pauta*-Blütenstände nahm ebenfalls mit der Höhenlage ab, während ein Einfluss der Höhe auf Keimlinge, Jungpflanzen oder Bestandsstruktur nicht nachgewiesen werden konnte. Das ist wahrscheinlich auf die schmalere Höhenamplitude zurückzuführen, denn die Art besetzt nur 400 Höhenmeter. Trotzdem waren die Keimlingszahlen nach Aussaatversuchen an der oberen Waldgrenze deutlich niedriger als in tieferen Lagen und Aussaat führte ausschließlich in den geschützten Bedingungen innerhalb der vorhandenen Bestände zu höheren Keimlingszahlen.

In beiden Waldgesellschaften fällt die Lage der oberen Waldgrenze mit der Höhe zusammen, an der die Blütenstandszahl gemäß linearer Regression null ergeben würde, nämlich bei 4100 m üNN für *P. incana* und 4200 m üNN für *P. pauta*. Eine Änderung der Diasporenqualität mit der Höhe konnte hingegen nicht nachgewiesen werden.

Die Kronendeckung hatte signifikanten Einfluss auf die Keimlings-, Jungpflanzen- und Rametzahlen beider Arten. Während Keimlinge hauptsächlich im Waldesinneren aufkamen, waren Jungpflanzen- und Rametzahlen am Waldrand am höchsten. Waldrandeffekte wirkten sich also deutlich unterschiedlich auf die beobachteten Lebensstadien aus. Klimamessungen belegten kühlere, aber ausgeglichenere Bedingungen unter der Kronenschicht verglichen mit der umgebenden Grasparamo-Vegetation. Daher lässt sich schlussfolgern, dass mikroklimatische Unterschiede die Keimung beeinflussen, insbesondere in den höher gelegenen Waldbeständen. Da Aussaat in diesen Höhen, wenn überhaupt, nur innerhalb der Wälder zu einer höheren Keimungsrate führte, lassen sich die unterschiedlichen Keimlingszahlen in den Waldrandtransekten nicht ausschließlich auf evtl. kleinräumige Unterschiede im Diasporenregen zurückführen. Trotzdem kann der Diasporenregen ein wichtiger Faktor in tieferen Lagen sein. Im Gegensatz dazu waren Jungpflanzen- und Rametzahlen eher von den Einstrahlungsbedingungen als vom thermischen Mikroklima abhängig. Beide Arten sind also Lichtarten, was auch durch den geringen Anteil von Stämmen in den unteren Durchmesserklassen im Waldinneren unterstützt wird. Folglich verjüngen sich die *Polylepis*-Wälder des Páramo de Papallacta überwiegend am Waldrand oder in Bestandslücken. Die Gesamtzahl der *P. incana*-Ramets war deutlich höher als bei *P. pauta*, was die Bedeutung vegetativer Regeneration in dieser Art hervorhebt.

Viehtritt hatte eine positive Wirkung auf die Keimlingszahl. Dies ist wahrscheinlich auf die Verringerung der Streuschicht zurückzuführen, was auch durch die signifikant höhere Keimungsrate nach experimenteller Streuentfernung in den Aussaatversuchen bestätigt wird. Trotzdem führte künstliche Streuzugabe nicht zu einer Verringerung der Keimlingszahl, was durch unzureichende Streutiefe und -dichte in den Experimenten begründet sein könnte. Die Nutztiere fraßen im Untersuchungsgebiet nur selten an Zweigen oder Blättern, und es gab keine Hinweise auf negative Auswirkungen auf Verjüngung oder Bestandstruktur. Die vorherrschende Beweidung bei niedriger bis mittlerer Intensität stellte sich also als nachhaltige Landnutzung dieser Waldgesellschaften heraus.

Im Gegensatz dazu war die Keimung nach Bränden deutlich reduziert. Experimentelle Aussaat erhöhte die Keimlingszahlen von *P. incana* sowohl in den gebrannten als auch in den ungestörten Flächen, wobei dieses Experiment im unteren Verbreitungsbereich der Art durchgeführt wurde. Die nach Brand verringerten Keimlingszahlen müssen daher der Verringerung des Diasporenregens nach Kronenbrand und der durch Feuer zerstörten Diasporenbank zugeschrieben werden und nicht mikroklimatischen Einflüssen. Trotzdem ist es möglich, dass die extremen klimatischen Bedingungen in größerer Höhe die negativen Konsequenzen von Bränden noch verstärken. Dagegen war die Anzahl der etablierten Jungpflanzen in den gebrannten Flächen deutlich höher, was wiederum auf die besseren Einstrahlungsbedingungen zurückzuführen ist. Bezüglich des Verhaltens nach Bränden lässt sich *P. incana* als “obligate seeder” mit hohen Mortalitätsraten und geringen Rametzahlen in den gebrannten Flächen charakterisieren. Im Gegensatz dazu verfügt *Gynoxis acostae* über eine ausgeprägte Fähigkeit zur Stockausschlagsbildung, was ihren hohen Anteil im Untersuchungsgebiet erklären könnte. Auch *P. pauta* wies geringe Keimlingszahlen nach Bränden auf, was jedoch nicht statistisch abgesichert werden konnte. Bei dieser Art hatte Aussaat keinen Einfluss auf die Keimlingszahlen, da sich die gebrannten und nicht gebrannten Flächen an der oberen Verbreitungsgrenze der Art befanden.

Zusammenfassend zeigen die Ergebnisse zur Regeneration deutliche Unterschiede zwischen der oberen Waldgrenze und Waldrändern in tieferen Lagen auf. Die geringe

Verjüngung an der oberen Verbreitungsgrenze charakterisiert diese Waldgrenze als natürlich. Eine weitere Aufwärtsausbreitung über sexuelle Regeneration ist unwahrscheinlich, solange sich das Klima nicht ändert. Die klimatischen Wachstumsbeschränkungen, welche sich auf Altbäume, Jungpflanzen und Ramets auswirken, betreffen im Falle von *P. incana* und *P. pauta* offensichtlich auch die Blüten- und Diasporenbildung sowie die Keimlingsdynamik. Waldränder unterhalb dieser oberen Waldgrenze wiesen dagegen keinerlei Beschränkungen in der generativen oder vegetativen Reproduktion auf. Im Gegenteil: die Waldränder waren sogar Zonen außerordentlich hoher natürlicher Verjüngung. Folglich sind diese Vegetationsgrenzen menschlichen Einflussfaktoren zuzuschreiben. Da es keine negativen Auswirkungen der Beweidung mit Kühen im Untersuchungsgebiet gab, ist Feuer als Hauptfaktor für die Randbildung in tieferen Lagen anzusehen. Dies ist vor allem deshalb wahrscheinlich, da Feuer meist die reproduktive Randzone schädigt und so zu einer verzögerten Verjüngung führt. Aufgrund dieser Ergebnisse ist die mosaikartige unzusammenhängende Vegetationsstruktur tropisch-alpiner Waldgrenzen in Ecuador mit hoher Wahrscheinlichkeit eine Folge des Feuerregimes.

Die vorliegende Arbeit hat naturschutzrelevante Bedeutung. Verbindliche Feuerregelungen stellen die vordringlichste Maßnahme zur Erhaltung bzw. Ausdehnung der Waldfläche durch natürliche Regeneration dar. Außerdem kann die Einrichtung von Feuerschutzstreifen durch das Abmähen der Grasvegetation rund um die Waldfragmente hilfreich sein, um ein Übergreifen von Grasparamobränden auf die Wälder zu verhindern. Demgegenüber wird eine Veränderung des Beweidungsregimes nicht als notwendig erachtet. Der Einfluss der Einstrahlungsbedingungen und der Streuverringerung ist bei der Jungpflanzenproduktion in Baumschulen und bei Aufforstungen zu beachten. Außerdem sollte bei Aufforstungsaktivitäten die ausgleichende Wirkung der verbleibenden Waldbestände auf das Mikroklima bedacht werden, was besonders in höheren Lagen bedeutend ist. Über 3900 üNN werden jegliche Wiederaufforstungsbemühungen schwierig und zeitaufwändig sein. Daher sollte in den höher gelegenen Beständen strenger Schutz der verbleibenden Waldfragmente allerhöchste Priorität haben.

RESUMEN

La línea de bosque tropical se caracteriza por tener parches de bosques discontinuos, los cuales forman bordes abruptos que limitan con el pajonal. Esta característica está presente en los bosques tropicales-andinos de *Polylepis* spp. Los bosques de *Polylepis* son uno de los ecosistemas forestales más amenazados del mundo y es urgente buscar estrategias eficientes para su conservación. Aunque el patrón peculiar de la vegetación se ha atribuido frecuentemente a la intervención humana, se han efectuado hasta el momento solamente pocos estudios cuantitativos o experimentales que se dedican a las consecuencias del uso de tierra y del medio ambiente sobre la posición actual de la línea de bosque. El conocimiento de los procesos de regeneración es indispensable para entender la formación de la línea de bosque y el desarrollo de los bosques en el futuro. Se cuenta con pocos estudios sobre la regeneración en la línea de bosque y los factores involucrados, como aquellos realizados en ecosistemas temperados y no tropicales.

El objetivo del presente estudio fue el investigar el impacto de la altitud, el dosel, la profundidad de hojarasca, el pastoreo y la quema sobre la regeneración de dos especies de *Polylepis* en el Páramo de Papallacta, Ecuador. En particular, se analizaron la floración, producción de semillas, viabilidad de semillas, germinación y supervivencia de las plántulas tal como la estructura poblacional de *Polylepis incana* y *P. pauta*. Además de la regeneración natural *in situ*, se realizaron experimentos de siembra en el límite superior de la distribución de las especies y después de las quemas para distinguir los efectos del hábitat y de la lluvia de semillas. Debido a la abundancia de *Gynoxys acostae* dentro de los bosques de *Polylepis* en el centro del Ecuador, se incluyó a esta especie para la investigación de la regeneración después de la quema. Con el fin de contribuir a la teoría general de la ecología de la línea de bosque, se intentó dar recomendaciones para la aplicación práctica de los resultados científicos. En base de los datos presentados, se proponen actividades de reforestación y de conservación en la síntesis proporcionada al final de este estudio.

En *P. incana*, el número de inflorescencias, plántulas y plantas jóvenes por metro cuadrado se redujeron significativamente con la altitud. La disminución de la altura de los árboles con la altitud indica limitaciones del crecimiento de las plantas adultas, la misma que influye en el desarrollo de flores y semillas. Después de la siembra experimental realizada en el límite superior de las especies, la emergencia y la supervivencia de las plántulas fueron menores que en otros experimentos efectuados en el campo y en viveros a menores altitudes.

La siembra no incrementó el número de plántulas en comparación de los cuadrados de control. En conclusión, a mayor altitud hay menor cantidad de plántulas por la limitada germinación a causa de las extremas condiciones climáticas. Además, el menor número de inflorescencias indica una reducida producción de semillas que también podría provocar una menor cantidad de plántulas. Sin embargo, el número de rebrotes generados asexualmente no mostró una tendencia altitudinal indicando que la reproducción vegetativa sea más relevante en la línea de bosque que la regeneración generativa.

El número de inflorescencias de *P. pauta* también disminuyó con la altitud, pero no se encontró influencia altitudinal sobre las plántulas, las plantas jóvenes o la estructura poblacional del bosque. Esto podría ser debido a la distribución menos amplia de la especie, cubriendo solamente alrededor de 400 metros de altitud. No obstante, la germinación después de la siembra experimental fue claramente menor que en altitudes menores y la siembra aumentó el número de plántulas exclusivamente en condiciones de mayor temperatura dentro de los bosques. Según una regresión linear, la posición actual de la línea de bosque coincide en las dos especies con la reducción del número de inflorescencias a cero que se estimó para *P. incana* a 4100 msnm y para *P. pauta* a 4200 msnm. No se detectó ningún cambio en la viabilidad de las semillas con la altitud.

El dosel tuvo un impacto significativo sobre el número de plántulas, plantas jóvenes y rebrotes en ambas especies. Se encontró mayor número de plántulas en el interior de los bosques mientras que en el borde predominaron las plantas jóvenes y los ramets. Las etapas de vida observadas mostraron un comportamiento diferente en relación con los efectos de borde. Las mediciones climáticas indicaron condiciones más frías pero menos extremas bajo el dosel en comparación con el páramo abierto. Estas diferencias climáticas podrían tener efectos negativos sobre la germinación y es más probable en mayores altitudes. La diferencia en el número de plántulas a lo largo del límite de bosque no se pueden atribuir a la lluvia de semillas, ya que haya aumentado exclusivamente dentro de los mismos con la siembra experimental.

No obstante, la lluvia de semillas podría ser relevante para la regeneración de ambas especies en altitudes más bajas. Por otro lado, las plantas jóvenes y los ramets son influenciados por las condiciones de luz que por efectos térmicos. De esta manera, las especies se consideran de alta demanda de luz, fomentando el hecho de que se encuentra un porcentaje bajo de troncos delgados dentro del bosque. En consecuencia, los bosques de *Polylepis* del Páramo de Papallacta generalmente se regeneran en los bordes o en claros de

bosque. El número total de ramets de *P. incana* fue superior que el de *P. pauta*, demostrando la importancia de la reproducción vegetativa en la primera especie.

En los sitios de estudio existe pastoreo de ganado vacuno con intensidades bajas y medias. El pisoteo de ungulados tenía un impacto positivo sobre la abundancia de plántulas en ambas especies de *Polylepis*, que supuestamente es a causa de la eliminación de la capa de hojarasca. Esto coincide con un número significativamente más alto de plántulas en los tratamientos sin hojarasca de los experimentos con siembra. No obstante, la adición artificial de hojarasca no disminuyó el número de plántulas, que podría ser por dificultades experimentales estableciendo una densa y profunda capa de hojarasca.

El ramoneo de herbívoros se observó escasamente en el área de estudio y no se probó un efecto negativo alguno sobre la regeneración o la estructura poblacional de los bosques. El pastoreo de intensidades bajas a medias se puede considerar como sustentable en estos ecosistemas.

En cambio, el aparecimiento de plántulas después de la quema fue claramente reducida. La siembra aumentó el número de plántulas de *P. incana* tanto en los cuadrantes quemados como en los no quemados ubicados en bajas altitudes. Esto implica que el bajo número de plántulas son consecuencia de la lluvia de semillas menos fuerte después de la quema del dosel y también de la destrucción del banco de semillas por el fuego, mientras que efectos climáticos no tuvieron un impacto en este caso. Sin embargo, los impactos climáticos podrían desempeñar un papel en bosques quemados situados en altitudes mayores. Al contrario, plantas jóvenes se observaron claramente de forma más frecuente después de las quemas que es por causa del aumento de la radiación solar antes mencionada.

La regeneración de *P. incana* después de la quema depende casi enteramente de semillas, mientras que se observó un porcentaje alto de mortalidad en los adultos y bajo en rebrotes. *Gynoxys acostae* tiene alta capacidad de rebrotar después del fuego, que posiblemente causa la abundancia de esta especie en el área de estudio.

En los bosques de *P. pauta* se encontró también un número reducido de plántulas después de la quema, aunque este resultado no se comprobó estadísticamente. En la siembra no se observó un efecto alguno por el hecho de que los cuadrantes quemados y no quemados se ubicaron en el límite superior de esta especie, en donde la germinación es limitada por los efectos climáticos.

En resumen, los resultados presentados indican claramente patrones diferentes de regeneración en la línea superior de bosque en comparación con los bordes de bosques en

altitudes más bajas. La regeneración en el límite de distribución más alto, demuestra que esta línea de bosque es natural por las condiciones climáticas. No es probable que por regeneración generativa se de el crecimiento de las especies cada vez a mayor altitud, suponiendo que el clima principalmente no cambie.

En consecuencia, las limitaciones climáticas en el crecimiento al límite superior de *P. incana* y *P. pauta* que afectan el crecimiento de las plantas adultas y jóvenes (rebrotes) también disminuyen la producción de flores y semillas, inhibiendo los procesos de germinación. En cuanto a los bordes del bosque ubicados en altitudes más bajas, no presentaron ninguna limitación la reproducción generativa o vegetativa. Además, se probó que estas zonas son de alta regeneración natural. Como conclusión los bordes son producidos por la intervención humana.

No se observaron efectos negativos del pastoreo o de la tala de madera en el área del estudio. El fuego es el mayor factor para la formación de bordes de bosque en altitudes menores porque la frecuencia de las quemas afecta directamente el límite del bosque. Esto causa un retraso grave de reproducción por ser la zona más productiva en cuanto a la regeneración. En base a estos resultados, la distribución discontinua de los bosques tropicales alto-montanos podría ser el producto del régimen de fuego en estos bosques.

Además, el estudio tiene relevancia para la conservación y reforestación de los bosques de *Polylepis*. La prevención de fuegos forestales parece la actividad más importante para conservar el área forestal y al mismo tiempo incentivar para permitir la regeneración natural. El establecimiento de corredores rompe-fuegos, cortando el pajonal junto a los remanentes de bosque, evitaría que los fuegos de pajonal se extiendan hacia los bosques. Por otro lado, el cambio del sistema de pastoreo no parece necesario. El impacto positivo de la luz y la eliminación de hojarasca son conocimientos relevantes para la producción de plantines en vivero y para la reforestación.

Es importante que en actividades de reforestación se considere el abrigo que brindan los remanentes de bosque en particular en las zonas altas. La conservación de los remanentes debe ser prioritario porque a altitudes mayores de 3900 msnm todos los esfuerzos en reforestación serán difíciles y tomarán mucho tiempo.

ACKNOWLEDGEMENTS

This study was part of the project “regeneration ecology of tropical timberlines” kindly funded by the Deutsche Forschungsgemeinschaft (DFG). First of all, I want to thank my wife Silja and my daughters Karla and Mareike for their company in Ecuador, which enabled and strengthened my commitment to this study. I thank Prof. Dr. Isabell Hensen and Dr. Karsten Wesche for their continuous scientific and emotional support during all phases of this project. Nadine Rühr, Silvia Salgado, Juan Enrique Iglesias are thanked for their great contributions to this work and for their warm company during field work. In addition, I thank Sebastian Ploch for assistance in the field. I gratefully acknowledge the fruitful collaboration with Dr. Hugo Navarrete, Susana León-Yánez and Dr. Katya Romoleroux from the Herbario QCA of the Pontificia Universidad Católica del Ecuador. Special thanks go to Dr. Alfonso Gortaire, Alicia and Esteban Gortaire (Quito), Pablo Ochoa (Quito) as well as to Dr. Francisco Gangotena (Pifo) and his family for their support during all stages of the work in Ecuador and for their friendship. This work would not have been possible without the people from the farmer associations in Itulcachi and Inga Alto as well as Camilo Ponze, who helped during fencing. Prof. Dr. Helge Bruelheide and Dr. Ilona Leyer, University of Marburg, provided useful comments on the statistical analysis. I am grateful to Birgit Müller and Christine Voigt for the germination experiments and the genetic analysis, which will be crucial for the continuation of this work. Prof. Dr. Antoine Cleef from the Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, and Dr. Robert Hofstede, IUCN South America, are thanked for interesting discussions. Dr. Daniel Renison revised the project planning at the beginning of the study and gave me the opportunity to participate in the conference “Ecología y conservación de bosques montanos” in Argentina. Martin Stanley encouraged me to write a proposal for a reforestation project in the Páramo de Papallacta. I thank Gustavo Mosquera, Mateo Espinosa and Galo Pillajo from Fundación Antisana for their interest in this work and their collaboration. Danny McCluskey repeatedly checked my English. Finally, I give thanks to all the colleagues at the Institute of Biology/Geobotany and Botanical Garden in Halle, Germany, in particular to Dr. Peggy Seltmann, Beatrix Vonlanthen, Katrin Ronnenberg and Matthias Pietsch for their great company.

1 INTRODUCTION

REGENERATION AT TROPICAL-ALPINE TREELINES

Treelines are among the most conspicuous vegetation patterns in plant ecology, but despite numerous research efforts the underlying mechanisms of treeline formation are still controversially discussed (*e.g.* Tranquillini 1979, Stevens and Fox 1991, Sveinbjörnsson 2000, Körner 2003a). Climatic measurements at a wide range of treelines have revealed a close correlation between thermal thresholds and treeline position (5-7°C mean growing season temperature; Körner 1998, Körner and Paulsen 2004), implying the presence of a common climatic driver, which operates both at the regional and global scale (Jobbágy and Jackson 2000). However, any treeline position is often locally modified by anthropogenic disturbance (Miehe and Miehe 1994) or biotic interactions such as herbivory (Cairns and Moen 2004). In addition, substantial influence is exerted by the tree species themselves (Körner and Paulsen 2004).

Concerning possible mechanisms of treeline formation, Körner (2003a) distinguishes five principle hypothesises. The *stress hypothesis* refers to growth limitations due to repeated damage by frosts; whereas the *disturbance hypothesis* attributes reduced tree growth to mechanical damage by wind, snow break, herbivory or pathogens. The *carbon balance hypothesis* relates insufficient tree growth at treelines to a lack of photosynthetic CO_2 fixation ("carbon source-related", *e.g.* Carbera *et al.* 1998), while the sink-related *growth limitation hypothesis* attributes this to limited synthesis of complex organic compounds for plant tissues and structures. Recent studies provide evidence for a sink-related limitation in biomass production as carbon supply at the majority of treelines does not seem to be a constraint (Hoch and Körner 2003, 2005; Körner 2003b). And finally, the *regeneration hypothesis* ascribes treeline formation to regeneration failure.

An investigation into the dynamic processes behind natural regeneration at treelines may therefore provide useful hints for the understanding of treeline formation. Differences in species' dispersal and recruitment behaviour can, among other factors, explain historic treeline shifts (Dullinger *et al.* 2004). In particular, seedling emergence and survival may be critical for tree recruitment at higher altitudes (Wardle 1985, Cuevas 2000, Germino *et al.*

2002, Holtmeier 2003, Smith *et al.* 2003). The focus on regeneration has two major advantages in comparison to mere consideration of growth patterns of adult trees. Firstly, it broadens the view from the ecophysiology of adult plant individuals to a perspective of population dynamics and thus allows for the projection of future stand development. Secondly, the various life stages a plant passes through during generative reproduction show a very high plasticity to environmental factors (Fenner 2000, Körner 2003a). Hence, the dynamic processes are visible within much less time in comparison to the observation of adult populations that are characterized by very low growth rates (Colmenares 2002, Körner 2003a). However, one has to bear in mind that regeneration is not compulsory for the existence of forest stands at high altitudes as forests may persist without natural recruitment for centuries after they have established under, presumably, more favourable conditions in the past (Körner 2003a). Hence, the absence of regeneration at present does not necessarily explain the formation of treelines, and should rather be considered as an indicator for future stand development.

Unfortunately, most of the data on recruitment at treelines derive from temperate latitudes (Tranquillini 1979, Hättenschwiler and Smith 1999), whereas very little information is available for tropical treelines (Rundel *et al.* 2003, Byers 2000, Hoch and Körner 2005). At temperate latitudes, treelines are characterized by a rather continuous transition of growth forms towards the upslope plant communities. In contrast, tropical treelines are usually abrupt and formed by scattered forest patches (Miehe and Miehe 1994, Körner 2003a). The reasons for this discontinuous distribution pattern in the tropics have been subject to a long-standing debate (Ellenberg 1958, 1979, 1996; Walter und Medina 1969, Miehe and Miehe 1994), which has focussed particularly on the high-Andean genus *Polylepis* (Rosaceae, tribe: Sanguisorbeae). This genus comprises 28 species distributed throughout the Andean cordillera from northern Argentina to Venezuela (Schmidt-Lebuhn *et al.* 2006). *Polylepis* spp. occur in woodlands up to 5200 m asl and thus rank together with the conifers of the Himalayan Mountains as the highest natural occurring trees. Due to their restricted distribution in small fragmented remnants subjected to human disturbances such as grazing, fire and woodcutting, *Polylepis* forests have been listed as one of the most endangered woodland ecosystems in the world (UNEP-WCMC 2004). The conservation and restoration of *Polylepis* forests is currently given high priority (*e.g.* Kessler 1995, Fjeldså and Kessler 1996, Sarmiento 2000a, 2000b; Purcell and Brelsford 2004, Aucca and Ramsay 2005).

Earlier publications attributed the existence of scattered *Polylepis* woodlands far above the closed forest line to special edaphic and microclimatic conditions at the forested sites, and denied the possibility of a higher forest extension in the past (Troll 1959, Walter und Medina 1969, Simpson 1979). More recent studies emphasized the impact of human disturbances as a principal cause of the discontinuous distribution (Cabido and Acosta 1985, Lægaard 1992, Lauer *et al.* 2001, Sarmiento and Frohlich 2002), which was already proposed by Ellenberg as early as 1958. However, there is, at present, very little quantitative evidence for anthropogenic influence on *Polylepis*' distribution. The implications from palynological data for the Andes remains contradictory mostly due to the fact that *Polylepis* pollen is easily confused with that of *Acaena* – a closely related genus of the same tribe, which is herbaceous and not restricted to woodlands (Kessler 1995, Chepstow-Lusty *et al.* 2005). A recent study from Bolivia considered *Polylepis* forests as an important component of the Altiplano vegetation of the last glacial maximum (Chepstow-Lusty *et al.* 2005), but pollen diagrams from central Ecuador did not provide conclusive evidence of higher forest coverage in historic times (Wille *et al.* 2002). Teich *et al.* (2005) describe that animal browsing might retard woodland recovery of *Polylepis* woodlands in Argentina. Kessler (1995), who studied the diameter distributions of stands submitted to grazing and burning in comparison to stands under more or less undisturbed conditions, describe, at most, weak influences of grazing by ungulates such as sheep, goats, cattle and camelids. In contrast, he showed the detrimental effect of burning on tree recruitment. A combination of both disturbance regimes proved to cause the most severe degradation. Hensen (2002) also attributes the current *Polylepis* distribution in the Eastern cordillera of Bolivia to human disturbance, as do Renison *et al.* (2006), who revealed that the low cover of *P. australis* in Argentina is at least in part caused by anthropogenic factors. These assessments, however, rely on rather local and non-formal observations of recruitment patterns, whereas a systematic quantitative approach is as yet largely absent.

In Bolivia and Peru, recent assessments of seedling and sapling numbers revealed no relations between generative regeneration and altitude or the position of the upper treeline (Byers 2000, Hoch and Körner 2005), although no quantitative results are reported. In contrast, a variety of studies – both from temperate and tropical forests – show the relevance of edge effects to regeneration (Chen *et al.* 1992, Benítez-Malvido 1998, Laurance *et al.* 1998, Abe *et al.* 2002, Burton 2002, Sanford *et al.* 2003, Hewitt and Kellman 2004), which may also influence the life stages of single plant species differently (Harper *et al.* 2005) and depend on the particular disturbance regime (Weyenberg *et al.* 2004). Similar patterns might also be expected at treelines, but I know of no published studies on edge effects at tropical treelines.

The availability of safe sites, where conditions are suitable for germination and seedling establishment, determines the success of sexual recruitment and varies considerably among different tree species (*e.g.* Crow 1992, Bonfil and Soberón 1999, Narukawa and Yamamoto 2002, Mori *et al.* 2004). The presence of safe sites depends on specific environmental and human influences and can therefore provide useful information on dynamic processes in seedling populations. In *Polylepis*, litter, shelter by rocks and competition with herbaceous vegetation have been expected to influence seedling number and establishment: Smith (1977) suggested a positive effect of sheltered microsites and a negative effect of interspecific competition on seedling survival. Renison and Cingolani (1998) analysed the impact of substrate (sand, litter and soil) on seedling emergence of *P. australis*, but they did not find significant differences between the substrates, although germination was highest on bare soil. Seedling survival was not influenced by microsite conditions, but growth was limited at so-called “degraded microsites” (Renison *et al.* 2005). In addition, sapling growth was highest under sheltered conditions (Renison *et al.* 2002a). However, the safe sites of *Polylepis* remain poorly understood and further research is needed.

In summary, available knowledge on the regeneration ecology of *Polylepis* is still not sufficient to understand the observed distribution pattern of the remaining stands and to assess the potential of future forest development. Therefore, a focus on regeneration is given in the present study in order to complement the knowledge of the dynamic processes in *Polylepis* forests and the human and environmental factors involved.

OBJECTIVES AND OUTLINE OF THE STUDY

The overall objective of this study was to determine the main environmental and human influences on the regeneration of *Polylepis incana* Kunth and *P. pauta* Hieron. in the Páramo de Papallacta, Ecuador. I studied the regeneration traits of these species and possible impacts of altitude, canopy cover, litter depth, vegetation cover, grazing and burning in order to assess the importance of these factors on future stand development and to provide an explanation for the present distribution patterns. In particular, flowering, fruit set, seed viability, seedling emergence and survival as well as stand structure of the species were analysed.

This study comprises five chapters. The first one includes an overview of the area, species and forest stands. In the following chapters, findings on the environmental and human influences on treeline regeneration are presented. Chapter 2 assesses regeneration in the interior forest at different levels of altitude and grazing. It presents figures for inflorescences, seedlings, saplings and ramets as well as seed quality and stand structure of 15 forest stands in the study area. The chapter elaborates on the following questions: (1) How does altitude affect flowering, fruit set, seed quality and seedling establishment of both *Polylepis* species? (2) How is stand structure influenced by altitude? (3) What is the impact of trampling on these parameters?

The third chapter deals with seedling, sapling and ramet numbers along 36 transects running perpendicular to forest edges in order to assess the impact of canopy cover on recruitment patterns. For *P. incana*, which covers a wide range of altitudes and grazing levels, the impact of these factors was analysed in order to test the findings of the second chapter. In particular, I assessed the following questions: (1) How do seedling, sapling and ramet numbers differ among edge, open and interior habitats? (2) Is there any impact of altitude or grazing by domestic and wild ungulates on recruitment?

The fourth chapter derives from an experimental study carried out on 18 permanent plots located at the interior, the boundary and outside the forest at the upper distribution limit of the species. I analysed the impact of canopy cover, experimental sowing and litter depth on seedling emergence and survival of *P. incana* and *P. pauta* focusing on the following questions: (1) Is seedling emergence of two *Polylepis* species at the tropical treeline influenced by experimental sowing, canopy cover and litter depth? (2) Is there any impact of canopy cover or litter layer on seedling survival?

Chapter 5 compares seedling emergence and survival in 6 burned and 6 undisturbed permanent plots after experimental sowing. Due to the importance of *Gynoxis acostae* Cuatrec. in the study area, the regeneration patterns of this species were compared with those of *Polylepis incana*. The fifth chapter analyses the impact of burning, sowing and litter depth in order to give answers to the following study questions: (1) What is the impact of burning on seedling emergence, and is there any influence of experimental sowing, litter removal or study species? (2) Is there an interaction of seedling survival with burning or litter depth in any of the two species? Only the data of *P. incana* are presented, because here burned sites with comparable conditions concerning altitude, position within the forest (all plots were located in forest gaps) and absence of woodcutting were available. A similar experiment was performed for *P. pauta*, but due to ecological differences between the plots the data were difficult to interpret. However, a short overview of the *P. pauta* results is given in the synthesis and the respective statistical analysis is shown in the appendix.

The sixth chapter provides a synthesis of the results presented. It summarizes environmental and human influences of the regeneration of *P. incana* and *P. pauta* and provides comprehensive conclusions. In addition, it contains recommendations for possible conservation and reforestation activities in the study area.

STUDY SITE

Geology and land use

The Páramo de Papallacta comprises an area of about 580 km² located in the eastern cordillera of the Ecuadorian Andes between the Cayambe and Antisana volcanoes at altitudes between c. 3500 and more than 5700 m asl (Figure 1). The geology of the area is characterized by plio-pleistocene vulcanites covered by pyroclastic and aeolian sediments ("cangahua"; Lauer *et al.* 2001). Soils have been classified as Andosols, with a slightly acidic pH and a high content of allophanes (Lauer *et al.* 2001). Properties of the top soil along the altitudinal gradient are given in chapter 2. The reported soil-chemical data are within the range reported from other *Polylepis* forests in Ecuador (Fehse 1999). The high content of volcanic ashes in the soil causes a high aggregate stability, which prevents soil degradation following agricultural activity (Podwojewski and Germain 2005).

Following the nomenclature of Lauer *et al.* (2001), the study area covers the geoecological subunits of the Páramo de Papallacta itself (Páramo de Papallacta *sensu stricto*) and the El Tablon-Páramo de Guamaní. The Páramo de Papallacta is a plateau-like landscape characterized by young glacial lakes, bogs and moraines formed by an icecap during the Younger Dryas (Clapperton *et al.* 1997). This subunit is largely covered by the Antisana and Cayambe-Coca reserves and is of major importance to the water supply of Quito (Pugh and Sarmiento 2004). However, conflicts between land users and conservation agencies concerning burning and hunting activities are still common (Mena Vásconez 1995). The Páramo de Guamaní is situated on the western slopes of the eastern cordillera and consists mainly of U-shaped valleys that deepened in the course of erosion processes of huge cangahua layers. The proximity to the Antisana, the Cayambe-Coca as well as to the Cotopaxi reserves gives this subunit pivotal importance as an ecological corridor between the reserves and as a buffer zone between the Antisana reserve and the capital Quito. However, there are no protected areas in the Páramo de Guamaní as most of the area is privately owned.

The destruction of *Polylepis* forests presumably began more than 10 000 years ago with the use of fire by early hunters (Kessler 1995). In central Ecuador, village-based agro-pastoral economies have existed since 3000-4000 years B.P. (Brush 1982). *Polylepis* forests are thought to have played an important role in prehispanic Andean cultures (Capriles and Flores Bedregal 2002). The high population density in the period of Andean high cultures gave rise to an already reduced forest cover before the arrival of the Spaniards, at least in Bolivia and Peru (Kessler 1995, Hensen 2002).

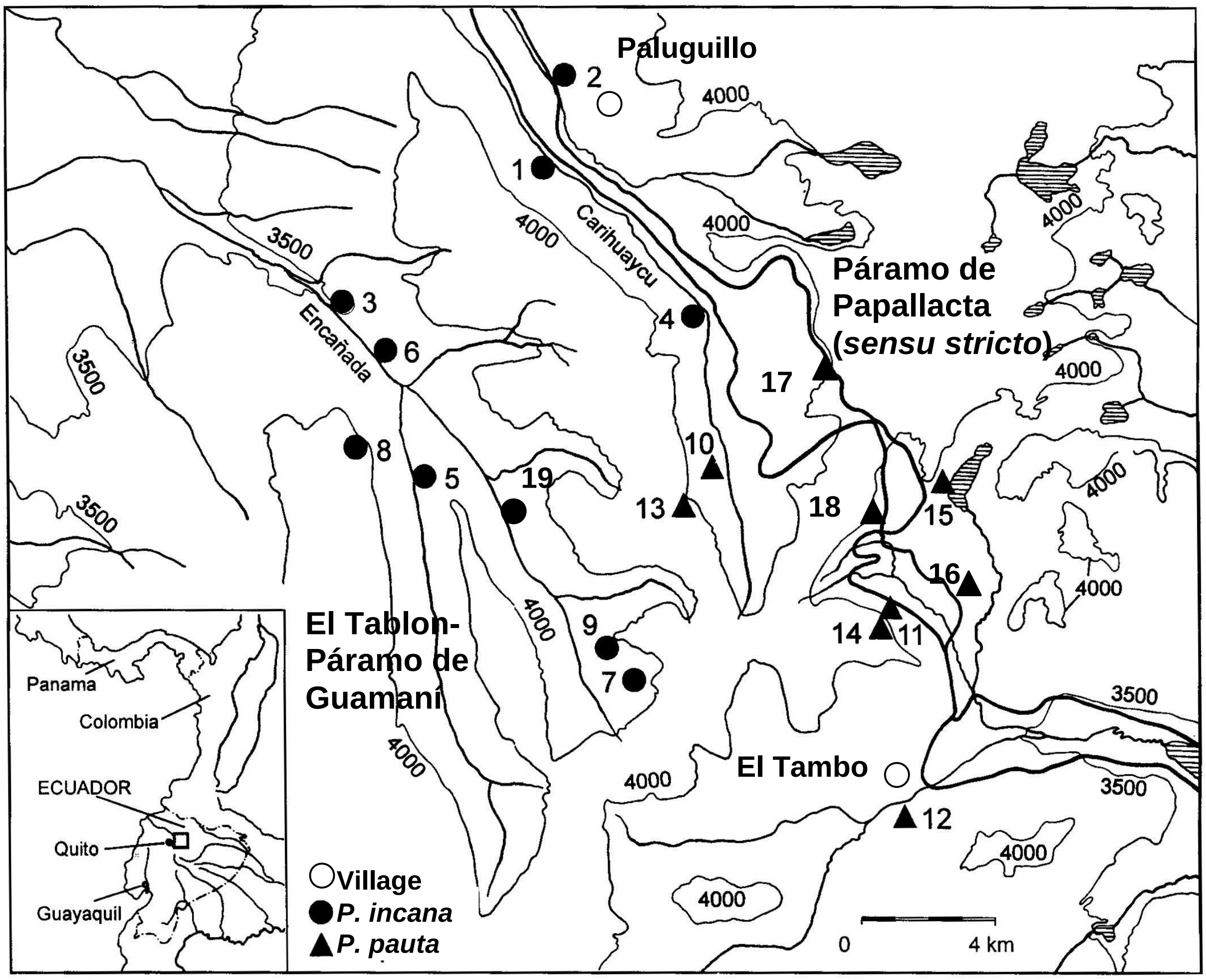

Figure 1. Study area and position of the investigated forest stands. 1-15 Forest numbers according to chapter 2. Transects (Chapter 3): 1: Transects 3, 4; 2: Transect 5; 4: Transects 7, 8; 5: Transect 9; 6: Transects 1, 2, 6; 7: Transect 18; 8: Transects 13-16; 9: Transect 17; 10: Transects 19-21; 12: Transect 27; 13: Transects 28-30; 14: Transects 25, 26, 31; 15: Transect 35; 16: Transects 22-24; 17: Transects 32-34; 18: Transect 36; 19: Transects 10, 11, 12. Permanent plots (Chapter 4): 8: *P. incana*; 13: *P. pauta*. Permanent plots (Chapter 5): 6.

After the Spanish conquest, the land use history of the study area is characterized by the former hacienda system, which was already established in the study area in the 16th century, and was abandoned following land reform in the 1960s (Alarcón and Segovia 2001). The introduction of European land-use practices has heavily accelerated forest destruction (Ulloa and Jørgensen 1993, Hensen 2002). Before the 1960s, the study area was used for sheep grazing, which caused severe degradation of the paramo vegetation (Grubb 1970). Over the last 40 years, cattle farming has been the most common land use practice, and according to interviews with land owners, farmers and park rangers the management system has persisted at comparable intensities during this period.

Figure 2. (a) Silvipastural use in stand 1, *P. incana*, and fence posts from *Polylepis* wood. (b) Woodcutting and charcoal production in stand 6, *P. incana*. (c) Wildfire in stand 6. (d) Charcoal production in stand 6. Stand numbers refer to Figure 1.

In the Páramo de Papallacta *sensu stricto*, there are only a small number of human settlements with El Tambo (about 20 households) and Paluguillo (about 15 households) being the most relevant of those situated in the distribution range of the *Polylepis* forests. However, the establishment of an oil pipeline, hydroelectric plants as well as a new road to Papallacta have all led to significant human disturbances in the area, and despite patrolling of park rangers wildfires are frequent. Grazing in these villages is restricted to fenced areas around the settlements, and livestock is only in a few cases allowed to penetrate deeply into forested areas. A couple of meadows are maintained applying a silvipastural system, in which large overstorey trees of the former forest are left standing, whereas the herbaceous layer is sown with pasture species such as *Festuca* spp., *Lolium perenne* or *Dactylis glomerata*. Cattle form the main livestock, but more recently farmers have also attempted to introduce camelids and goats. Grazing intensity is low (0.13-0.15 animal per ha) with the exception of the silvipastural fields where animal load is at 1.25 animals per ha.

The upper parts of the Páramo de Guamaní are divided between the Itulcachi, Inga Bajo and Inga Alto estates (Alarcón and Segovia 2001). The former represents one of the oldest haciendas in Ecuador, which was founded in the 16th century. The Inga property derives from a former hacienda established in 1830. All properties were handed over to the village people during the land reform of the 1960s giving the local population a leaseholder status whilst people from Inga Alto obtained land titles in 1977 (Alarcón and Segovia 2001). There are only a few houses in the area which provide shelter from rain to the farmers. The whole area is used for cattle grazing (Alarcón and Segovia 2001, Crissman 2003). Overall grazing intensity ranges between 0.15 and 0.44, but due to the lack of fences along the property boundaries, cattle roam freely in the whole area including the forests depending on fodder availability. In addition, about 60 horses are kept in the paramo belt and also small numbers of wild ungulates such as white-tailed deer (*Odocoileus virginianus*) or mountain tapir (*Tapirus pinchaque*) may be found in the area. The grazing is accompanied by burning of the grass paramo in order to promote resprouting of younger more palatable leaves. There is no obvious systematic approach concerning the fire regime, but fire frequency at any given plot may be estimated at one fire event every five to ten years (pers. obs.). These fires only scarcely affect entire forests patches in the area, but many forest edges show clear signs of burning (Figure 2c). Following the recent construction of a new access road in 2001 (Segovia 2002), charcoal production followed by the establishment of meadow and farm land has taken place in the Páramo de Guamaní. Such practices have led to a notable decrease in forest cover (Segovia 2002; Figures 2b, d).

Climate

Due to the equatorial position of the Páramo de Papallacta, the climate shows little annual variation which is exclusively dictated by the rainfall seasons. However, there are pronounced local differences affected by altitude, slope and circulation patterns (Lauer *et al.* 2001). Temperature measurements carried out in the course of this study revealed an altitudinal lapse rate in mean soil temperature of 0.73 K/100 m on the western slope, and 0.78 K/100 m in the eastern part (Figure 3; chapter 2). On the western slope, the highest rainfall is received between March and May, and September and November, whilst on the eastern slope the rainfall season is between June and August (Lauer *et al.* 2001).

The nearest climate station (Papallacta, 3160 m asl) reports a mean annual temperature of 8.3°C and a mean precipitation of 1433 mm (Bendix and Rafiqpoor 2001). Along the upper treeline at 4017 m asl, mean soil temperature at a depth of 10 cm was 5.9°C, compared to the ground level temperature of 5.4°C (minimum -2.3°C, maximum 32.3 °C: according to own measurements within a *P. pauta* forest stand performed between March 2005 and February 2006). This exceeds the values reported by Bendix and Rafiqpoor (2001) by more than 1 K. Within the sampling period, 19 days with night frosts were recorded.

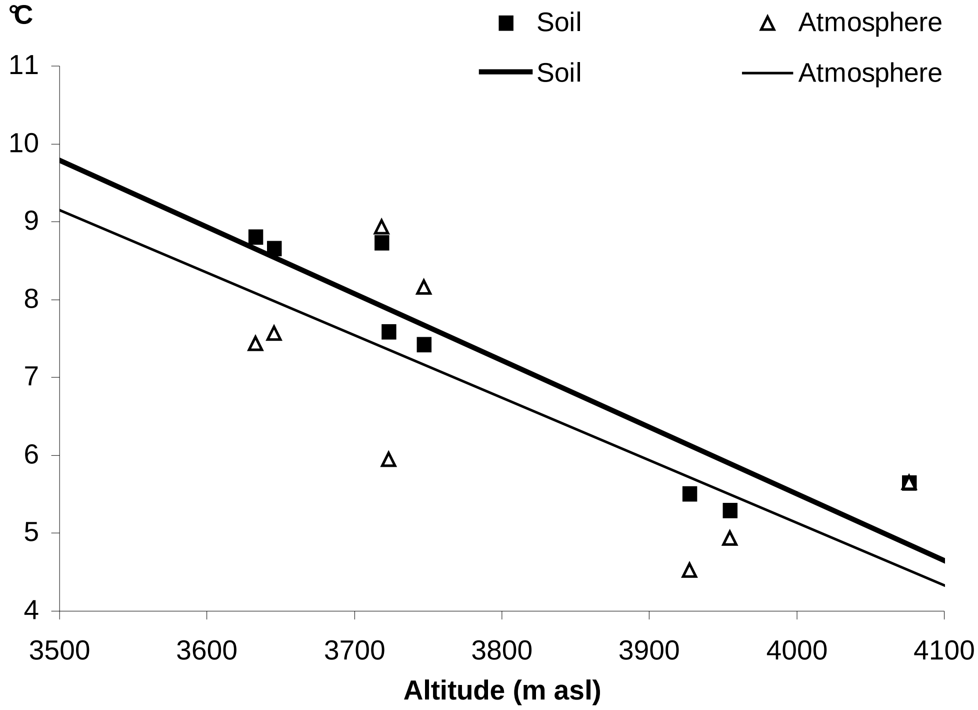

Figure 3. Soil and atmospheric temperature within *P. incana* stands on the western slope at different altitudes in the study area measured simultaneously between the 10th and 13th of July, 2004.

The microclimatic conditions provided by the forests themselves are expected to play a crucial role during recruitment at treeline, as there are pronounced microclimatic gradients along forest edges (Chen *et al.* 1995, Kremsater and Bunell 1999, Gehlhausen *et al.* 2000). Therefore, temperature profiles inside and outside the forest stands were compared (Figure 4; chapter 3). The variation of daily temperatures is much lower in the forest interior, but mean temperatures are about 2 K lower than outside, which corresponds to the data of Bendix and Rafiqpoor (2001). Night frosts were measured exclusively in the exterior of the forest. Unfortunately, our climatic data are widely incomplete due to the fact that the majority of data loggers failed to measure. Many long-term measurements were absent particularly due to the high humidity at the study sites, which affected data loggers' functioning. Future studies on the issue should take this climatic constraint into account and use more robust data loggers.

The ongoing changes of temperature in the Andes in the course of global warming, which are estimated to be 0.1 to 0.3°C/decade between 1939 and 1998 (Vuille and Bradley 2000; Republic of Ecuador 2000), may have significant influence on the findings of this study. In particular, high rates of recruitment at the upper limit of tree occurrence might lead to erroneous conclusions about the anthropogenic influence on current forest distribution, as possible increases in forest cover may be related to warmer climates (Camarero and Guitierrez 2004) rather than to decreasing land use. Therefore, I investigated the forest distribution history by interviews conducted with the land owners and with older farmers. These revealed that neither the position of the upper treeline nor the management system have markedly changed in the past 40 years. However, historical documents on stand dynamics were not available for the study area.

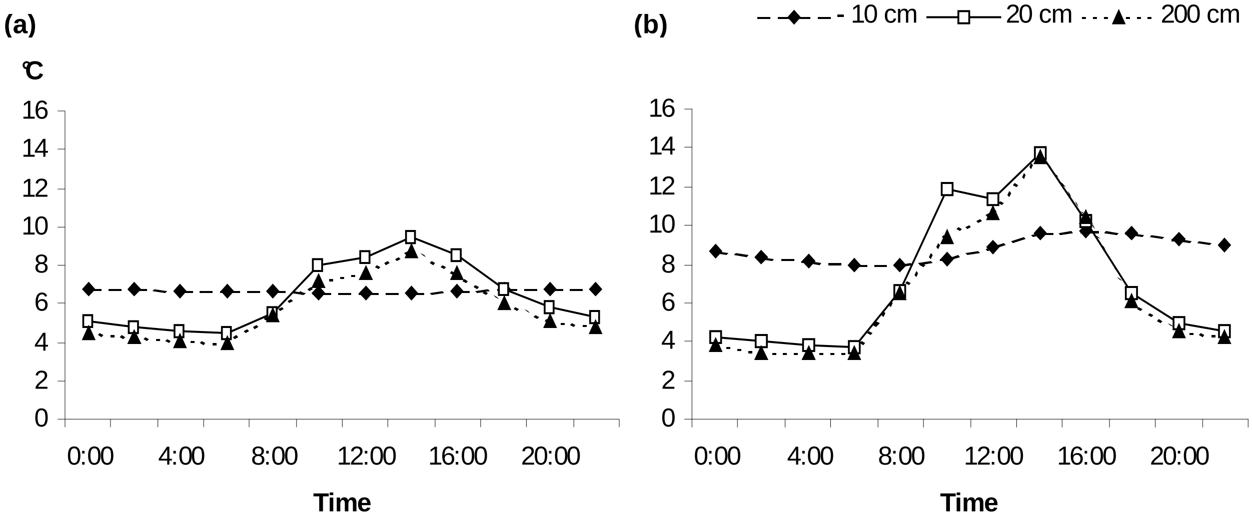

Figure 4. Soil temperature (at a depth of 10 cm) and atmospheric temperatures at 20 cm and 200 cm above ground. (a) Within a *P. pauta* stand at 4017 m asl, (b) in the exterior of this stand (means of data measured simultaneously at both locations between 23rd of February and 10th of March 2005).

STUDY SPECIES AND VEGETATION

The genus *Polylepis* belongs to the wind-pollinated tribe Sanguisorbeae within the rose family (Rosaceae). The genus comprises 28 species (Schmidt-Lebuhn *et al.* 2006), which are endemic to the Andean mountain range from Argentina and Chile to Venezuela. Systematically, *Polylepis* is closely related to the shrubby genus *Acaena*, which is distributed with c. 100 species circumpolarily on the southern hemisphere. *Polylepis* presumably evolved from the *Acaena* section *Elongatae* during the middle Miocene (c. 15 million years), when the Andes reached elevations of around 1500 m for the first time (Kessler 1995).

All species are arborescent with heights between 1 and 27 m (Simpson 1979) and are characterised by an exfoliating bark that consists of numerous thin papery layers. The leaves are compound and imparipinnate. The stipules are fused around the branch forming a sheath (Simpson 1979). The flowers are apetalous and clearly proterogynous. The fruits are one-seeded nutlets (hereafter referred to as seeds, Simpson 1979). In addition, vegetative reproduction via ramets derived from rooting horizontal branches is frequent (Kessler 1995). *Polylepis* is associated with arbuscular mycorrhiza (Menoyo 2004), which might explain the high rates of biomass accumulation even under harsh climatic conditions (Velez *et al.* 1998, Fehse *et al.* 2002).

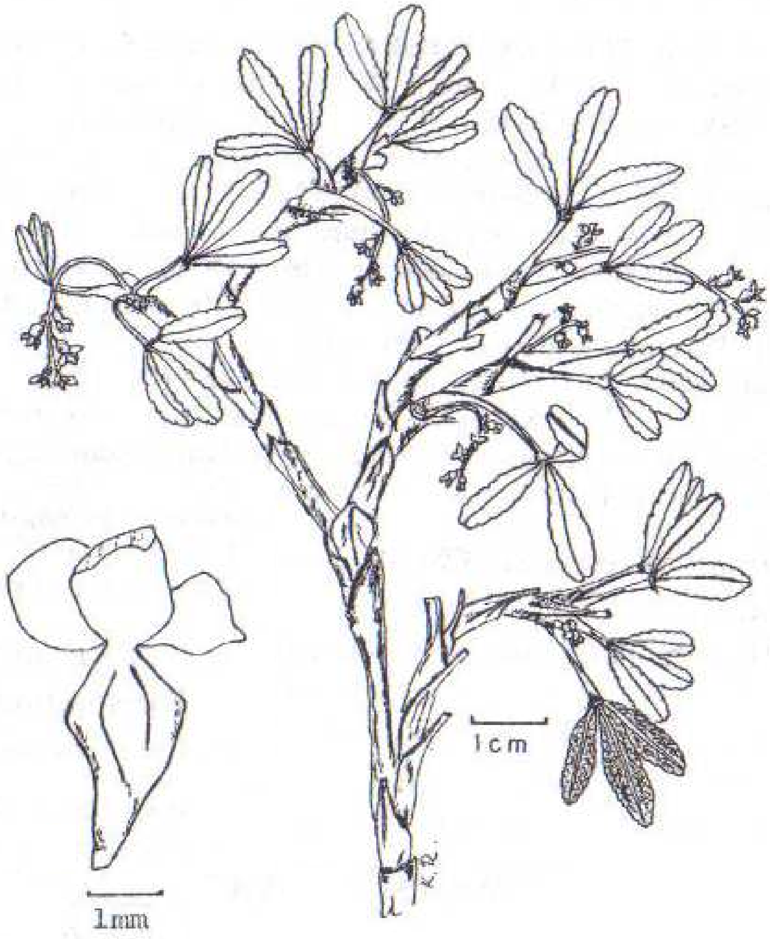

Figure 5. Flowering branch and seed of *Polylepis incana* Kunth (from Romoleroux 1996).

Polylepis has a well-adapted carbon assimilation system with a low compensation point allowing photosynthesis even at low temperatures (Rada *et al.* 1996). In addition, *Polylepis* *sericea* is known to adjust its leaf osmotic potential according to diurnal temperature changes, which reduces the risk of frost damage (Smith and Young 1987). Specific triterpenes and flavonoids have been isolated in *P. incana* (Catalano *et al.* 1995), *P. racemosa* (Neto *et al.* 2000) and *P. quadrijuga* (Velez *et al.* 1998), which are in part cytotoxic and decrease the palatability to herbivores (Neto *et al.* 2000). These compounds characterize the chemotaxonomy of *Polylepis* at subfamily, tribe and genus level. However, the taxonomy on species and subspecies level is still discussed due to the frequent occurrence of hybrids (Romoleroux 1996, Schmidt-Lebuhn *et al.* 2006). Recent genetic analyses indicate a complex phylogeny arising from hybridisation of two *Acaena* species and subsequent chloroplast introgression (Kerr 2003).

Figure 6. (a) Inflorescence of *Polylepis pauta.* (b) Ramet population at the forest edge of stand 8 (*P. incana*). (c) Excavated ramets of *P. pauta* with rootlets.

This study focussed on *Polylepis incana* and *P. pauta* – the most abundant species in the Páramo de Papallacta. Both species have been classified as vulnerable according to the IUCN Red List (IUCN 2006). *Polylepis incana* is characterized by having three leaflets per leaf and short inflorescences with 3-10 flowers (Figure 5; Romoleroux 1996). The lower surfaces of the leaflets show a typical pubescence with very short yellow hairs and a resinous exudate.

The species is distributed from central Ecuador to southern Peru in rather arid situations (Simpson 1979). In contrast, *Polylepis pauta* bears long, rarely ramified inflorescences with 10 to 40 flowers (Figure 6a), and leaves composed of 8-10 leaflets (Figure 7; Romoleroux 1996). Its distribution ranges from northern Ecuador to southern Peru along the humid eastern slopes of the Andean cordillera (Simpson 1979). Both *Polylepis* species reach a maximum height of 12 m (Romoleroux 1996). Flowers and seeds are produced continuously without a pronounced seasonality. *Polylepis pauta* produces seeds with spiny protuberances on the surface, which indicate a limited epizoochorous dispersal capacity (Simpson 1986). This is unlikely for the winged seeds of *Polylepis incana*, which are rather ballochorous. In addition, both species have the capacity to produce asexual ramets (Figures 6b, c).

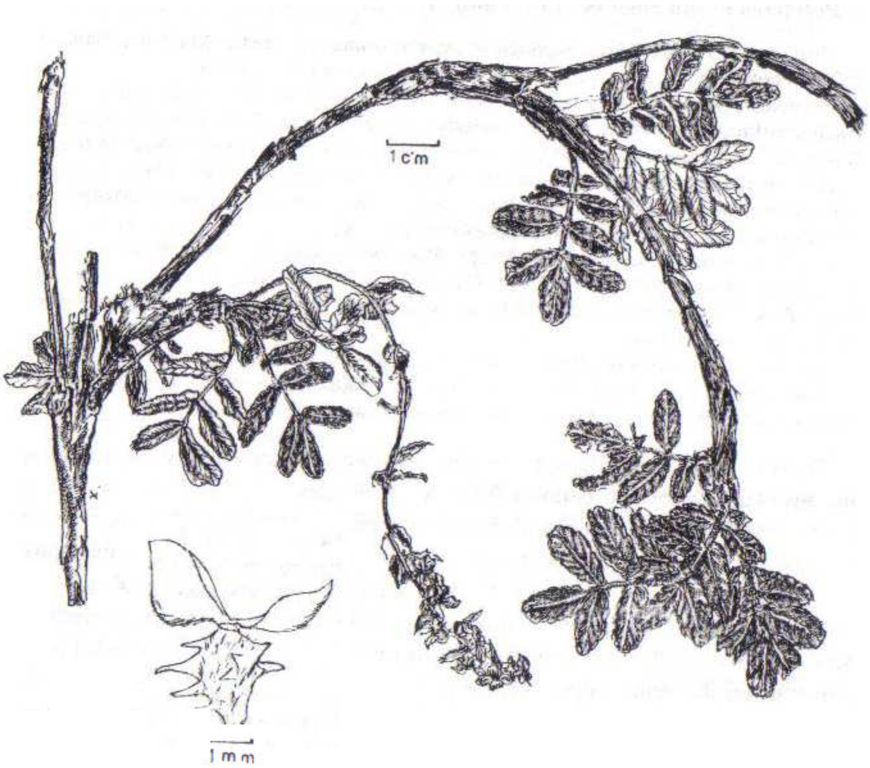

Figure 7. Branch and seed of *Polylepis pauta* Hieron. (from Romoleroux 1996).

Polylepis incana prevails in the western part of the study area and grows at altitudes between 3500 and 4100 m asl, whereas *P. pauta* is predominant in the eastern part with an altitudinal range of between 3700 and 4100 m asl. However, the distribution limits of the species are far less clear than stated by Lauer *et al.* (2001). Many forests mapped as *P. incana* stands on the western slope of the cordillera were actually stands dominated by *P. pauta* (Figure 1). In the contact zone of both distribution areas, the species coexisted and frequently formed hybrids. The situation was further complicated by the occurrence of a third species, *P. sericea*, which is closely related to *P. pauta* and morphologically and – at least in Ecuador –

genetically very similar (Simpson 1979, Segovia-Salcedo *et al.* 2000, Schmidt-Lebuhn *et al.* 2006; Romoleroux pers. communication). In contrast to other regions, both species are apparently always coexisting in central Ecuador and form mixed populations mainly dominated by hybrids (Romoleroux pers. communication). Recent genetic data (Ploch, pers. comm.) did not reveal any conclusive evidence of the taxonomic status of the Papallacta populations. For practical reasons and due to a lack of more detailed studies, I subsume here all trees of these populations including possible hybrids under *P. pauta* in accordance with Lauer *et al.* (2001).

The majority of the forest stands in the area are mixed with other tree species such as *Gynoxys* spp., *Escallonia myrtilloides*, *Solanum stenophyllum* and *Hesperomeles obtusifolia* var. *microphylla*. *Gynoxis acostae* is the most common of these species in the study area and even forms monospecific forests – mainly at the upper treeline at 4100 m. This forest type has not been described in the vegetation survey by Lauer *et al.* (2001), obviously due to the low accessibility of these stands. As suggested by Lægaard (1992), I could observe a lower adult mortality after fire in comparison to *P. incana* and *P. pauta*. Consequently, genuine *G. acostae* forests might be a consequence of the fire regime. Therefore, *G. acostae* was included into the study on post-fire regeneration (chapter 5). This composite is a tree up to 12 m in height (own data) and has entire leaves with glossy upper and a white-pubescent lower surface. The inflorescences are aggregated into corymbs and characterized by peripheral yellow ligulate flowers. Each inflorescence produces between 20 and 30 seeds of 2-4 mm in length with a short pappus. In addition, vegetative regeneration through root suckers as well as resprouting from the stem base after fire have been reported (Brandbyge and Holm Nielsen 1991, Lægaard 1992)

I started with an inventory of the understorey and herbaceous vegetation in the *Polylepis* stands described in chapter 2 and recorded 153 species of vascular plants. There were pronounced differences to the species composition reported by Lauer *et al.* (2001) as only plots below the closed canopy were investigated and species of the open paramo are absent. Species numbers per 100-m² study plot ranged between 15 and 51 species (mean = 26.5, N = 46), which is in line with data on Bolivian *Polylepis* forest (16-43 species, mean = 29.3; Fernández Terrazas and Stahl 2002). A species list is provided in the appendix of this study.

DESCRIPTION OF THE FOREST STANDS

P. incana stands

Ten *P. incana* forest remnants from the Páramo de Papallacta were included into the study (Stands 1-9 and 19; Figure 1). Details on soil properties and stand structure of forests 1-9 are given in chapter 2. Forest 19 is situated in the proximity of forest 6 and is expected to show comparable soil and stand conditions. Data on grazing intensities and stand history refer to interviews with the landowners. However, due to the lack of fencing the actual grazing intensity within a given forest patch depended on fodder availability rather than on the overall cattle loads.

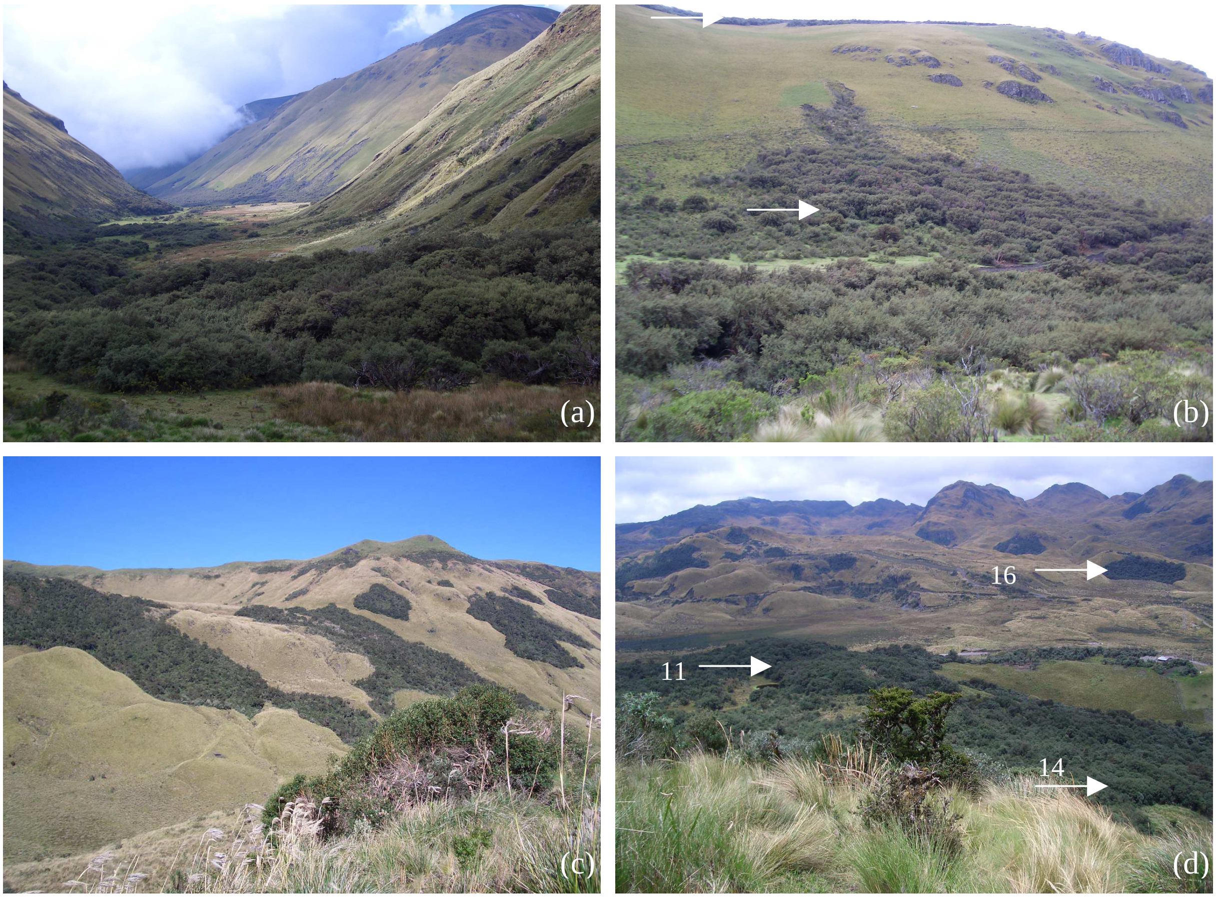

Figure 8. (a) Forest 19, *P. incana*. (b) Forest 6 (below) and forest 8 (on the top), *P. incana*, note the different green scales on the slope that indicate recovery time after burning events. (c) Forest 13, *P. pauta*. (d) Panorama showing the forests 14, 11 and 16, *P. pauta*. Stand numbers refer to Figure 1.

Forests 1 and 4 are part of the Itulcachi estate and are grazed by moderate animal loads (0.15 animals per ha). Forest 1 (34 ha; Figure 2a) is the most spatially extensive forest which occurs along the river Carihuaycu at altitudes between 3600 and 3700 m asl. The forest area was heavily reduced through the construction of a new road to Papallacta and a water pipeline. There were no signs of burning in this forest but some parts of the stand were thinned. Forest 4 extends from the river Carihuaycu to an altitude of about 4000 m. The lower parts are formed by *P. incana*, whereas at the upper part above 3800 m there is a transition to *P. pauta* forest. At the river, the forest has also been disturbed in the course of construction work for a water pipeline. In both forests, I established study plots and transects described in chapters 2 and 3.

Near the village of Paluguillo at altitudes between 3600 and 3700 asl, *P. incana* grows in a linear forest remnant along the river Quebrada Alpatola (forest 2, 1 ha). This forest is privately owned and fenced-off. According to an interview with the owner, grazing was ceased in 2000, but cow paths and dung were still visible. The stand has a remarkable number of old trees. This area is described in chapters 2 and 3.

The forest stands 3 and 6 (Figure 8b) belong to the largest forest remnants along the river Quebrada Encañada river, which extends over about 70 ha at altitudes between 3500 and 3700 m asl. It runs through the land of Itulcachi, Inga Alto and Inga Bajo, and the studied parts are grazed at an intensity of 0.15 animals per ha. In the lowest part of Quebrada Encañada there is a continuous transition of the predominantly monospecific *Polylepis* forests to a species rich “Ceja andina” forest (Lauer *et al.* 2001). In this zone, the forest was partly transformed into meadowland following clear-cutting and charcoal production (Figures 2b, d). The establishment of a new access road in 2001 accelerated this process. In the course of charcoal production, a couple of sites within the forest suffered from high-intensity wildfires. In addition, in many parts forest edges are affected by burning. The forest is included in chapters 2 and 3. Three of the burned areas were selected for the permanent plots described in chapter 5.

Forest 5 is a small remnant (3 ha) located within Inga Bajo land at the entrance of the valley Pucahuaycu. It is one of the few examples of forests on the slopes which are most commonly deforested – presumably due to fire. The area is grazed at an animal load of 0.17 per ha and is studied in chapters 2 and 3.

In forest 7 and 9, small areas at the lower border of *G. acostae* forests (5 and 8 ha) are populated with *P. incana* between 3900 and 4000 m asl. Although the stands that are on Itulcachi land are grazed at low intensities (0.15), they are heavily affected by cattle trampling. In both stands, I additionally found small numbers of *P. pauta* trees and hybrids. Forests 7 and 9 are analysed in chapters 2 and 3.

Forest stand 8 (17 ha; Figures 8b, 9a) represents the highest forest remnant of *P. incana* in the study area and consists of a mixture of old trees of *P. incana* and *Gynoxis acostae* (50% each). The forest forms part of the Inga Alto land and is moderately grazed at an intensity of 0.44 animals per ha, but only a few animals really climb up that high. At the lower forest border, some trees show clear signs of burning, whereas the upper limit is characterized by a continuous transition to the surrounding cushion and grass vegetation. Thus, this treeline was taken as the natural upper distribution limit of the species. The forest is analysed in chapters 2 and 3 and, due to its location at the presumed upper treeline, it was chosen for the establishment of the permanent plots in chapter 4.

Forest 19 (9 ha; Figure 8a) occupies the highest site among the *P. incana* stands growing along the river Quebrada Encañada. It ends at 3700 m asl forming an abrupt boundary with the tussock vegetation. As part of the Inga Bajo land, it is grazed at 0.17 animals per ha. It was studied in the course of the transect analysis presented in chapter 3.

***Polylepis pauta* forests**

P. pauta forests are found exclusively in the Páramo de Papallacta *sensu stricto*. I studied 9 forest stands (Forest 10-18). Forests 10 and 13 form part of a system of forest patches (30 ha overall; Figures 8c and 9b) located in the upper part of the Carihuaycu valley on Itulcachi land at altitudes between 3800 m and 4100 m asl. Grazing intensity was 0.15 animals per ha, but I scarcely observed cows in the upper parts. Especially at forest boundaries on the slopes, there are numerous burnt trees. The upper treeline of these forests is easily accessible. I therefore chose this stand for the establishment of the permanent plots described in chapter 4 as well as in chapters 2 and 3.

Forests 11 and 14 are owned by a family in El Tambo and are situated at altitudes between 3800 and 4050 m asl (Figure 8d). The lower parts of the forests are subjected to grazing by cattle, horses, lamas and goats at low animal loads (0.13 animals per ha). Most recently the family began to produce small amounts of charcoal. The forest is therefore becoming increasingly more fragmented. The upper treeline of this forest is formed by rocky outcrops and is barely accessible due to the density of the stand. These stands have been incorporated into the analyses presented in chapter 2 and 3.

Forest number 12 is the lowest continuous *P. pauta* forest in the study area located at about 3700 m asl. The stand is surrounded by species-rich upper montane rainforest formations and is privately owned by a family in El Tambo. The grazing intensity is high (1.25 animal per ha) due to the silvipastural system applied, but some parts of the original forest are fenced-off and protected. Thus, the forest could be used for the establishment of study plots and transects such as those described in chapters 2 and 3.

Figure 9. (a) Forest interior of stand 8; *P. incana* with a species-rich herbaceous stratum dominated by *Valeriana* spp. (b) Forest interior of stand 10; *P. pauta*. Stand numbers refer to Figure 1.

Forests 15, 16 and 18 are located in the Cayambe-Coca reserve between 3850 and about 4000 m asl (Figure 8d). Forest 15 comprises an area of 8 ha. Although cows had never been observed in these forests, the stand had suffered heavy trampling by ungulates. Therefore, the stand was included into the analysis of trampling in chapters 2 and 3. Stands 16 and 18 were considered for the establishment of transects along the forest edge. There were no signs of grazing by cattle, but I found twigs browsed by wild ungulates – presumably white-tailed deer. The upper treelines in these stands were marked by steep rocks.

Forest 17 is a stand of about 9 ha which was disturbed during construction of an oil pipeline. The upper limit of the forest is formed by rocks. Here, the forest mainly consists of *G. acostae*. Many parts along the pipeline lane have been burned, which caused a high mortality in *P. pauta* but not in *G. acostae*. In some parts of the forest, I found single individuals of *P. incana*. This forest is part of the transect analysis presented in chapter 3.

2 IMPACT OF ALTITUDE AND CATTLE TRAMPLING ON *POLYLEPIS* REGENERATION ALONG A TREELINE IN SOUTH-AMERICA

Together with Nadine Katrin Rühr, Karsten Wesche and Isabell Hensen

Plant Ecology (accepted)

ABSTRACT

Regeneration failure is considered to be an important factor in treeline formation. However, little is known about the impacts of altitude and anthropogenic disturbance on regeneration patterns along tropical treelines. The study focused on the reproductive traits of two *Polylepis* species in the Páramo de Papallacta in Ecuador along an altitudinal gradient, and involved varying intensities of cattle trampling within each altitudinal level. We analysed flowering, fruit set, seed viability, germination, and seedling establishment as well as stand structure of *Polylepis incana* and *P. pauta*. The number of *P. incana* inflorescences and seedlings per m² showed a marginally significant decrease with increasing altitude. In addition, mean tree height was significantly lower at higher altitudes, while stem number increased. The number of *P. pauta* inflorescences also decreased significantly upslope. In both forest types trampling was found to have a positive impact on seedling abundance, presumably due to the removal of the litter layer. Sapling establishment was rare inside the forest stands at all altitudes and grazing levels, which suggests that the investigated species mainly rejuvenate in forest gaps. We consequently observed a low proportion of narrow stems within all investigated forests. Our results highlight the importance of regeneration to treeline formation. The position of the upper treeline in Ecuador coincides with reproductive failure at about 4100 m for *P. incana,* and at about 4200 m for *P. pauta*. Forest borders below this altitude are rather caused by present and past land use. However, there was no evidence that moderate cattle grazing influences the regeneration of both treeline species negatively.

3 POTENTIAL LATERAL EXPANSION OF *POLYLEPIS* FOREST FRAGMENTS IN CENTRAL ECUADOR

Together with Karsten Wesche and Isabell Hensen

Forest Ecology and Management (in press)

ABSTRACT

High-Andean forests formed by *Polylepis* are among the most endangered forest types in South America and effective strategies are urgently required to facilitate their conservation. The remaining forest stands are presently distributed in discontinuous patches which usually form abrupt boundaries with the adjacent grassland vegetation. Mechanisms of natural regeneration in this transition zone between forest and grass paramo are still poorly understood. The present study investigates the establishment of seedlings, saplings and vegetative shoots along edges of *Polylepis incana* and *P. pauta* forests in the Páramo de Papallacta, central Ecuador. For each species, we analysed 18 transects of 20 m in length, which traversed the edge zone, and sampled 10 subplots of 2 × 2 m each. Differences between subplot positions were analysed using a repeated measures ANOVA. In addition, we determined correlations of altitude and grazing parameters of the *P. incana* transects with regeneration data. Seedling numbers of both species were significantly higher in the forest interior than in the exterior, presumably due to less extreme climatic conditions and a more continuous seed rain. Sapling and ramet numbers, however, showed a clear maximum at the forest boundary, which indicates that favourable light conditions are required for sapling and ramet establishment. The importance of vegetative reproduction increased towards *P. incana* stands at higher altitudes, because the overall number of seedlings and saplings decreased significantly with increasing altitude. Sexual regeneration is limited at the upper distribution limit of the species, which we ascribe to extreme climatic conditions. In *P. pauta* stands, in contrast, there was no effect of altitude. Grazing by ungulates did not affect the recruitment of saplings or vegetative shoots in the investigated *Polylepis* stands, but trampling resulted in a significant increase in the abundance of *P. incana* seedlings. Our results show that boundaries of *Polylepis* stands are zones of high natural recruitment. Fire is expected to be the most

relevant factor for the formation of edges at lower altitudes, as the use of fire strongly affects the reproductive boundary zone of the remaining *Polylepis* forests, whereas grazing at moderate animal loads does not lead to any severe consequences for these forest communities. We conclude that stands below the upper treeline would expand continuously towards the exterior if human impact ceased, and that the present patchy distribution of *Polylepis* is as a result of anthropogenic influence and not of natural site conditions.

4 IMPACT OF SOWING, CANOPY COVER AND LITTER ON SEEDLING DYNAMICS OF TWO *POLYLEPIS* SPECIES AT UPPER TREELINES IN CENTRAL ECUADOR

Together with Juan Enrique Iglesias, Karsten Wesche and Isabell Hensen

Journal of Tropical Ecology (in press)

ABSTRACT

Failure of reproduction is hypothesised as being a main reason for the formation of upper treelines but, as yet, there is little evidence of such. This study investigates the effects of experimental sowing, canopy cover and litter depth on seedling emergence and survival of *Polylepis incana* and *Polylepis pauta* at the upper distribution limit of the species in the Páramo de Papallacta, central Ecuador. We established 18 study plots located at the interior, the edge and the exterior of the closed forest at the upper treeline and analysed seedling dynamics for one year following experimental sowing in four different litter treatments. In *P. pauta*, sowing significantly increased seedling number, which was more pronounced within and at the edge of the forest than outside. In contrast, there was no impact of sowing on seedling emergence in *P. incana*. In both species, seedling numbers were significantly higher in the forest interior than outside and higher in the treatments with the litter layer removed. First-year seedling survival and mean growth rate per month were low in both species. Log-linear models did not reveal significant interactions between survival and canopy cover or litter removal. Our data show that seedling recruitment is limited at the upper treeline, presumably due to extreme climatic conditions, which indicates the relevance of sexual regeneration for treeline formation in central Ecuador.

5 POST-FIRE TREE SEEDLING DYNAMICS IN HIGH-ALTITUDE *POLYLEPIS* (ROSACEAE) FORESTS OF CENTRAL ECUADOR

Together with Silvia Salgado, Karsten Wesche and Isabell Hensen

Biotropica (submitted)

ABSTRACT

Fire is considered as the main reason for the discontinuous, patchy distribution of high-montane tropical forests growing below the upper limit of tree occurrence, but there is little quantitative evidence so far. This study compared seedling recruitment of the tree species *Polylepis incana* and the coexisting *Gynoxis acostae* in burned and unburned forest stands in the Páramo de Guamaní, central Ecuador. Two years after fire, the density of *P. incana* saplings was higher than that of *G. acostae* which, in contrast, produced a higher number of ramets. A sowing experiment revealed a lower overall seedling emergence of both species in the burned than in the unburned plots. However, regardless of burning, experimental sowing increased the seedling number significantly, which rules out climatic constraints for seedling emergence in this altitude. Seedlings of *P. incana* were significantly more abundant than those of *G. acostae*. Log-linear models showed interactions between seedling survival, burning and litter for *P. incana*, but not for *G. acostae*, indicating a higher survival of *Polylepis* seedlings after burning. Our data imply that single fire events lead to a lower seedling emergence due to limited seed availability after canopy and seed bank burning. We conclude that fire as opposed to climate is the main reason for forest boundaries below the upper distribution limit of the tree species, and that artificial sowing could facilitate the restoration of burned *Polylepis* forests. Predominant clonal growth may explain the high percentage of *G. acostae* in the remaining Ecuadorian *P. incana* stands.

6 SYNTHESIS

ENVIRONMENTAL INFLUENCES ON REGENERATION

This study provides evidence that regeneration of both *Polylepis* species is influenced by altitude, canopy cover and litter depth. I found an inverse relationship between altitude and numbers of inflorescences, seedlings and saplings in *P. incana* and of inflorescences in *P. pauta*. In contrast to available data on many temperate treelines (Tranquillini 1979, Holm 1994), no impact of altitude on seed quality was found for any of the studied species. Seedling number is clearly higher below the closed canopy, which, at the upper distribution limit of the species, can be ascribed to the less extreme conditions in the forest interior along with seed rain effects. In contrast, saplings (generative individuals between 0.05 and 1.3 m in height) and ramets show a completely different pattern, as both prevailed at the forest edge. Finally, litter layer proved to significantly affect seedling emergence and survival. A thick litter layer decreases seedling number, and such was confirmed in all parts of the study. However, at burned sites, where the litter layer had been destroyed completely, experimental litter addition led to a higher seedling emergence, and in unburned conditions and greenhouse experiments an artificial litter layer did not have a significant impact.

The variables of altitude, canopy and litter include sets of abiotic environmental factors that, in addition to all else, proved to influence the life stages of the study species differently. Within a field study, these factors cannot be disentangled, which might be one of the main limitations for any research on treeline ecology and perhaps be the reason as to why no fundamental mechanism for treeline formation has, as yet, been agreed upon. However, my data provide evidence of the most relevant ecological filters affecting the different life stages of a *Polylepis* individual.

The mean soil and atmospheric temperatures measured at the upper distribution limit of *P. pauta* of 5.4 and 5.9°C respectively coincide with the temperature range of 5-7°C proposed as a climatic threshold for treeline formation by Körner and Paulsen (2004). My data did not confirm the lower mean temperatures of 4.8°C at treeline in the Páramo de Papallacta reported by Bendix and Rafiqpoor (2001), but are similar to those recently reported from Bolivia (Hoch and Körner 2005). The climatic constraints proposed for adult tree growth also apply to central Ecuador as shown by a decrease in mean height and mean canopy diameter with altitude in the studied forest stands. In addition, thermal limitations may equally affect the processes of flowering, germination and seedling growth. The correlations of regeneration traits and altitude given in chapters 2 and 3 indicate a decline in inflorescence number as well as seedling and sapling density to zero at an altitude of about 4100 m asl in *P. incana*. In the *P. pauta* stands, regeneration failure concerning the number of inflorescences was determined at about 4200 m asl. In both species, this is the altitude of the present upper treeline. Moreover, experimental sowing at the upper distribution limit of the species did not or only barely increased the seedling numbers and germination was clearly lower than those determined using the same seedlings stock at lower altitudes. Thus, limitations of germination may also be attributed to low temperatures. My data therefore support the hypothesis of Körner and Paulsen (2004) that mean growing season temperature determines the position of any treeline. However, the fact that sexual regeneration also responds to thermal conditions is in clear contrast to data presented for other *Polylepis* species by Byers (2000) from Peru and Hoch and Körner (2005) from Bolivia. These authors found sufficient seedling numbers at the upper treeline, which was also reflected by a stand structure with a high ratio of young trees. Although quantitative data are not given in these studies, the findings indicate either marked idiosyncratic differences between the *Polylepis* species or between the treelines studied, and further quantitative research on the regeneration at tropical treelines is needed to obtain a more comprehensive picture.

The decrease in seedling abundance along transects from the interior through the edge to the exterior is at least in part also a consequence of extreme climate at the forest exterior as sowing at the upper treeline did not substantially change this pattern and hence rules out mere seed rain effects. However, theses differences cannot be attributed to mean temperatures, as these are lower within the forest stands in comparison to the forest exterior. In contrast, extreme climatic conditions and frost occur clearly less frequently in the forest interior. Hence, seedling cohorts are affected by temperature extremes although mean temperatures exceed the threshold of 5°C. As the diurnal temperature changes are most pronounced at the soil surface, the seedling life stage with < 5 cm in height suffers particularly from climatic extremes. This demonstrates that seedlings may be relevant for tropical treeline formation as is equally proposed for temperate treelines (Wardle 1985, Wardle and Coleman 1992, Cuevas 2000, Dullinger *et al.* 2004). The increased seedling occurrence in the less extreme conditions below the canopy show a facilitation effect of existing forest stands on seedling recruitment. Even single trees or groups of trees may facilitate successful seedling establishment at high altitudes (Miller and Halpern 1998). Moreover, artificial shelter by rocks or plastic tubes as well as shading proved to increase seedling survival in high-Andean forests (Smith 1977, Renison *et al.* 2002a, Bader *et al.* in press)

Saplings and ramets show a completely different pattern along forest edges, which indicates a less pronounced sensitivity to extreme temperature conditions. Sapling number on the one hand depends on a sufficient seedling bank. Nevertheless, saplings predominate at the forest edge where radiation conditions are more conducive for development. This is in line with the results on stand structure, which revealed a diameter distribution typical for shade-intolerant tree species with a clear lack of stems in the narrower diameter classes, regardless of altitude or anthropogenic influence. In addition, sapling number is clearly higher in burned *P. incana* patches where the canopy cover had previously been destroyed. The number of vegetative ramets is also higher at the forest edge indicating a positive impact of light conditions on ramet growth. Moreover, the formation of ramets is promoted at the forest boundary as soil contact and rooting is more likely for horizontally growing and lower branches. Thus, the studied *Polylepis* species mainly establish under favourable light conditions, which has also been reported for Bolivian and Argentinean species (Hensen 1993, Enrico *et al.* 2003). Similar patterns have been described for other species of Ecuadorian treelines (Bader *et al.* in press).

Litter is known to act as a physical barrier for seedlings (Facelli and Picket 1991, Kitajima and Fenner 2000, Ellsworth *et al.* 2004, Rotundo and Aguiar 2005), which applies in particular to small seeded species, such as *P. incana* and *P. pauta* (mean seed length about 3 mm), which have less resources to penetrate through a deep litter layer with the radicula (Molofsky and Augspurger 1992, Peterson and Facelli 1992). In addition, small seeds are more easily shaded, which might impede germination processes (Kitajima and Fenner 2000). In the studied *Polylepis* species, a litter layer with > 4 cm depth leads to a total collapse in seedling number. However, artificial litter addition scarcely affected seedling emergence, which might be attributed to insufficient depth and density of the litter applied. This is supported by sowing experiments in the greenhouse with different depths of litter layer, which in accordance to Renison and Cingolani (1998) did not reveal significant differences among litter treatments (data not shown). On the contrary, seedling emergence and survival are significantly higher after litter addition in the burned plots. This highlights the positive impact of litter layer below a critical depth, which is most pronounced under dry conditions (Fowler 1986, Hamrick and Lee 1987, Eckstein and Donath 2005); *i.e.* after burning.

I found no evidence for interspecific competition between seedlings and herbaceous plants as proposed by Smith (1977). There is no correlation of herbaceous vegetation cover and seedling number. However, due to the fact that I removed the litter layer together with the herbaceous stratum in the sowing experiments and that artificial litter addition did not influence seedling number, this conclusion could not be tested experimentally, which calls for further research.

In summary, only the upper treeline might be attributed to environmental factors. In contrast, forest boundaries below this altitude did not show recruitment limitations, which provides quantitative evidence supporting the hypothesis of Lægaard (1992) and Lauer *et al.* (2001) that these are caused by human influence.

ANTHROPOGENIC INFLUENCES ON REGENERATION

Many studies on grazing regimes in the world have demonstrated the detrimental impact of ungulates on forest ecosystems (*e.g.* Ammer 1996, Kuiters and Slim 2002, Danell *et al.* 2003, Husheer *et al.* 2003, Rooney and Waller 2003, Cierjacks and Hensen 2004, Palmer *et al.* 2004). Negative consequences of grazing on regeneration and stand structure have also been reported for *Polylepis* forests in Bolivia and Argentina (Kessler 1995, Hensen 2002, Teich *et al.* 2005). However in central Ecuador, I found no evidence of negative effects of cattle grazing on seedling, sapling or ramet numbers. This can be explained by the feeding strategy (browsers vs. grazers) of the ungulates involved in the existing grazing regime (Gordon 2003). Cattle are known to consume a rather low percentage of woody plants – even at high stocking rates (Mayer *et al.* 2003). In accordance with Lægaard (1992), browsing ("feeding on above-ground biomass of woody plants other than stripping bark"; Danell *et al.* 2003) was observed, albeit rarely, and may be rather attributed to wild ungulates such as white-tailed deer than to cattle (pers. obs.). Additionally, there is no correlation between dung counts and regeneration traits. Consequently, this study failed to show any interactions between grazing parameters and stand structure. In contrast, seedling numbers are significantly higher in trampled areas, leaving a reduction in litter depth as the only remaining cause (Olson-Rutz *et al.* 1996, Yates *et al.* 2000) and as such was proved experimentally in the sowing experiments. Thus, the existing grazing regime in the study area is at a sustainable level both in terms of animal load and livestock. Neither the opening of vegetation in the course of grazing (Verweij and Budde 1992) nor the impact of herbivory affect treeline position, as is described for other ecosystems (Cairns and Moen 2004). This is presumably due to a sufficient fodder supply from the grass paramo surrounding the forest patches, which obviously prevents the trees from being browsed. In addition, triterpenes and flavonoids might decrease the palatability of the study species. Recent plans to introduce goats into the forested areas have raised concerns, as this may lead to similar degradation as described for forests in Bolivia (Kessler 1995, Hensen 2002).

In contrast to other regions in South America (Kok *et al.* 1995, Aucca and Ramsay 2005), the use of *Polylepis* forests for fuel wood has not been relevant over the last few decades, as the energy supply for heating and cooking, even in poorer households, relies on gas (Gustavo Mosquera, Fundación Antisana, pers. comm.). This is a consequence of low gas prices and of the remoteness of the *Polylepis* forests. *Polylepis* wood is nearly exclusively used in small amounts for fencing. Therefore woodcutting did not lead to a decrease in forest cover in former times. More recently however, there has been an increasing demand of *Polylepis* charcoal in the capital, and the construction of new roads in the study area has helped to accelerate wood exploitation for this purpose. However, the cautious grazing regime and the absence of large scale cutting activities in the last 40 years might be the main reasons why the forest cover of high-Andean forests in central Ecuador is considerably high in comparison to Bolivia or Argentina.

As neither grazing nor woodcutting have played a major role in stand history and only the uppermost distribution limit of the forest proved to be environmentally driven, burning is suggested to be the most important factor responsible for the discontinuous forest distribution at lower altitudes. The sowing experiments in burned forest patches provide evidence that single fire events cause a clearly lower seedling number. In the case of *P. incana*, this has to be attributed to a reduced seed supply from the canopy and the soil seed bank after burning due to the fact that sowing significantly increased seedling numbers without showing an interaction with burning (Chapter 5). In contrast, sowing after burning in *P. pauta* did not have an effect on seedling number and overall seedling counts were much lower than in *P. incana*, which can be explained by the extreme climatic conditions occurring at the study plots situated between 3900 and 4050 m asl (see appendix). Despite these additional climatic effects, the overall pattern of seedling emergence is similar in *P. incana* and *P. pauta*, which corresponds to findings from other forest ecosystems after burning (Kennard *et al.* 2002). In addition, both *Polylepis* species show a high adult mortality and limited resprouting capacity after burning. Consequently, the recovery rates of *Polylepis* that nearly exclusively rely on sexual regeneration are expected to be rather low although seedling survival and growth rate may increase due to more favourable light conditions and nutrient availability after burning (Kennard and Gholz 2001). Fire intervals of 5-10 years are probably too short to allow for the natural expansion of the forest stands, as even at lower altitudes intervals of up to 9 years are required for long-term persistence of woody plants (Hoffman 1999). Hence, although this study cannot directly show any correlation between the observed distribution pattern and the existing fire regime, there is some evidence that fire interrupts recruitment, and most notably, generative regeneration. The reproductive edge zone, which is characterized by a high proneness to fire (Cochrane and Lawrence 2002), is particularly affected by burning. Saplings and ramets are most probably destroyed by bunch grass fires reaching temperatures of up to 600°C at the top of the tussocks (Ramsay 1992). This was also reported by Kessler (2000). In addition, high fire frequencies are known to prevent seedling and sapling establishment (Peterson and Reich 2001). Thus, the lateral expansion of the stands at lower altitudes is impeded, which leads to a stabilization of the patchy distribution pattern. I therefore conclude that the scattered forest distribution below the upper distribution limit of the species is at least in part a consequence of the fire regime. In addition, the high ratios of *G. acosta*, which shows a vigorous resprouting capacity after burning, might indicate a transition of species composition toward a higher ratio of sprouters in the remaining Andean forests; as is equally shown for other forest ecosystems (*e.g.* Cushman and Wallin 2002, Calvo *et al.* 2003, Ivanauskas *et al.* 2003, Tryterud 2003). In summary, this study highlights the importance of fire for the typical distribution pattern of *Polylepis* forests in central Ecuador, which is in accordance with other studies on tropical-alpine treelines (Kessler 1995, Horn *et al.* 2001, Renison *et al.* 2002b, Holtmeier 2003, Spehn *et al.* 2005). Due to the nonexistent effect of silvipastural use, interactions of fire and grazing as shown for other forest ecosystems (Kessler 1995, Kramer *et al.* 2003) will not be relevant in the studied *P. incana* and *P. pauta* forests.

RECOMMENDED REFORESTATION AND CONSERVATION ACTIVITIES

The conclusions of this study raise implications for management activities, which should aim at conserving these highly endangered forest ecosystems that host a wide variety of rare plant and animal species (*e.g.* Fernández Terrazas and Ståhl 2002, Fjeldså 2002, Yensen and Tarifa 2002). In order to compensate for forest losses in the last five years, I recommend a community-based forestry approach which comprises both reforestation and conservation measures in the area. Similar projects have led to significant improvements in Bolivia and Peru (Ibisch 2002, Aucca and Ramsay 2005). In addition, the forests might have potential in terms of carbon sequestration projects due to their relatively high rates of biomass accumulation at high altitudes (Fehse et el. 2002). Any project in the area should consider the collaboration with the Fundación Antisana, a non-governmental organization, that has been working for more than 10 years on conservation in the Páramo de Papallacta.

Figure 25. (a) Community work of the farmer association Itulcachi for the establishment of permanent plots. (b) Member of the farmer association Inga Alto planting *P. incana* saplings.

Reforestation with *P. incana*, *P. pauta* and other native species will be the most time-consuming activity within a potential project. In Ecuador, *Polylepis* saplings are only produced in a few nurseries, and it will be necessary to establish at least two further village nurseries with an overall yearly production of 20 000 saplings. Saplings of *P. incana* and *P. pauta* can be most easily raised from seeds. The areas for reforestation should be chosen based on documents on land use planning and land allocation already existing at the Fundación Antisana. The lower and medium parts of the slopes between 3500 and 3900 m asl are the most promising zones for reforestation, due to high growth rates at this altitude in comparison to the upper distribution limit of the species (In *P. incana*: 0.22 cm/mo at 3600 m vs. 0.14 cm/mo at 4000 m asl; chapters 4 and 5). In addition, impact of fire is expected to be less severe at valley bottoms than on the mid and upper slopes (Renison *et al.* 2006). According to the findings of this study and experience with reforestation activities in Argentina (Renison *et al.* 2002a), shelter from extreme climatic conditions will be important, which could be achieved by planting in the proximity of existing forest stands or by protection of young sapling with rocks or plastic tubes. The recommended density for planting one-year-old saplings is at three individuals per 3 × 3 m squared (van Voss *et al.* 2001, Alarcón and Segovia 2001). Plantations are subsequently thinned to about 1100 individuals per ha, which is a typical stand density of natural forest stands in the area (Chapter 2). The described nursery output will be sufficient for reforestation of 6 ha per year. According to an estimated labour requirement of about 200 working-days for planting and maintenance (Lamprecht 1989), this is the area that can be managed by the farmer associations themselves without additional labour from external sources (Fundación Antisana, pers. comm.).

Forest conservation measures should include the fencing of cattle pastures. Although the existing grazing regime itself does not lead to negative consequences for stand structure and forest regeneration, it is accompanied by burning of the grass paramo in order to provide palatable fodder for the animals. The establishment of grazing zones can make burning of forest remnants unnecessary. In addition, a sustainable silvipastural system, which joins forest conservation with increased cattle production and supplements already existing approaches, could be explored testing different animal loads and stem densities. As cattle do not browse on *Polylepis*, *Polylepis* forests provide protection from wind and a palatable herbaceous flora to cattle, while cattle trampling enhances seedling establishment removing the thick litter layer.

However, a definite cessation of burning activities in the short-term seems rather unlikely. Therefore, the establishment of firebreaks around the forest patches seems to be a promising activity. The studied *Polylepis* species show a high capacity of natural regeneration both sexually and by layering, under appropriate conditions. These conditions are best met at the forest border (Chapter 3). The establishment of firebreaks will protect the regeneration zone at the forest edge against the influence of fire. Moreover, the removal of plant material in this zone will improve the contact of fallen seeds with the soil, which is mandatory for successful germination.

These potential activities should be accompanied by a range of capacity and awareness building activities together with the local population in the villages of the Páramo de Papallacta, as changes of the existing land use practices will only be achieved through a high level of ownership and participation by the land users (Morris 1985, 1997; Bubb *et al.* 2004, Aucca and Ramsay 2005). A very important activity aimed at ensuring the success of reforestation and forest conservation measures will be the establishment of village regulations, which specify the commitment of the villagers to forest conservation (*e.g.* fire prevention) and project participation. In addition, alternative income possibilities should be elaborated on in order to compensate for the potential reduction in income from present land use on the plateau. The establishment of home gardens and eco-tourism, which have been successfully applied in other regions of Ecuador, might be promising activities in the area.

A couple of activities have already been implemented in the course of this study (Figure 25). Based on these experiences, it will be easy to establish a fruitful cooperation with the local population for a more efficient conservation of the *Polylepis* forests in the Páramo de Papallacta.

CONCLUSION

The focus on regeneration of the present study provides a detailed knowledge about the dynamic processes in the studied forest ecosystems. My data give rise to a complex pattern of partly interrelated human and environmental factors influencing different life stages of the studied *Polylepis* species (summarized for *P. incana* in figure 26).

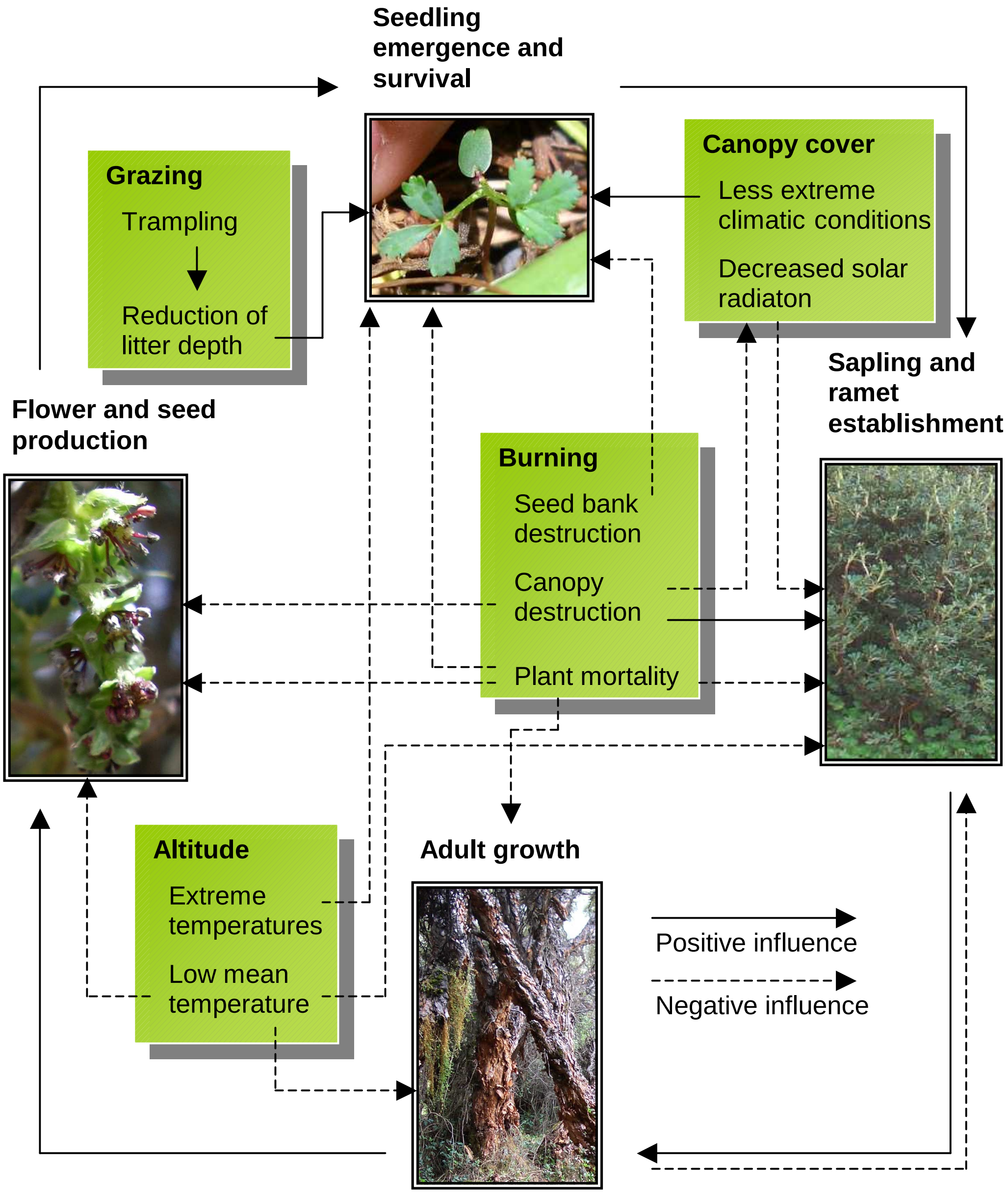

Figure 26. Environmental and human factors influencing the life stages of *P. incana*.

Altitude and burning are the most important factors that affect the life cycles of *P. incana* and *P. pauta* negatively. At high altitudes, the regeneration patterns are determined by thermal conditions, whereas at lower altitudes regeneration outside the closed canopy is exclusively hampered by the current burning regime, which leads to the discontinuous distribution of forest stands in the area.

The temperature range at the upper treeline in the study area supports the hypothesis that low mean temperatures hamper the growth of adult trees, saplings and ramets and are thus the main cause for the current upper treeline (growth limitation sensu Körner 1998). In contrast, the seedlings of *P. incana* and *P. pauta* proved to be particularly sensitive to temperature extremes. Failure of seedling recruitment was frequently ruled out as a principle mechanism in treeline formation (Körner 1998, Körner 2003b: "It is not obvious, why many high-alpine plant species should be able to establish seedlings, and trees should not."). However, many studies have shown that seedling emergence and survival is limited at higher altitudes (Wardle 1985, Cuevas 2000, Germino *et al.* 2002, Holtmeier 2003, Smith *et al.* 2003), which could now also be shown for tropical treeline species such as *P. incana* and *P. pauta* in the Páramo de Papallacta. It seems plausible that if the adult tree is not capable of growing, there is also no selection pressure for the evolution of special adaptations for a successful seedling establishment above treeline. This may be the reason why in many treeline species regeneration failure is observed. What ever the case may be, poor seedling recruitment at the treeline contributes to the maintenance of the current treeline position, as upslope establishment of seedlings and population expansion is not possible. Further studies will be needed to provide more long-term observations on treeline dynamics in order to quantify mortality and recruitment rates at all life stages. Based on this information, it will be possible to develop models on treeline populations and to calculate fluctuations of treeline position in relation to regeneration parameters.

REFERENCES

ABE, M., J. IZAKI, H. MIGUCHI, T. MASAKI, A. MAKITA, AND T. NAKASHIZUKA 2002. The effects of *Sasa* and canopy gap formation on tree regeneration in an old beech forest. *J. Veg. Sci.* 13: 565–574.

AGEE, J.K. 1999. Fire effects on landscape fragmentation in Interior West forests. In Rochelle, J.A., L.A. Lehmann, and J. Wisniewski (Eds.). *Forest fragmentation, wildlife and management implications*, pp. 43–60. Brill, Leiden.

ALARCÓN, D., AND P. SEGOVIA 2001. *Propuesta de plan de manejo de la cuenca alta de la quebrada La Encañada*. Camaren–Iedeca, Ecuador.

AMMER, C. 1996. Impacts of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *For. Ecol. Manage.* 88: 43–53.

ARCOS, C., E.E. GARECA, I.I. MARTÍNEZ, AND R. CASTRO 2006. Germinación de semillas de *Polylepis besseri* Hieron. bajo diferentes tipos de suelo y cantidades de luz generados por *Eucalyptus* spp. y *Pinus* spp. In Ojeda, P., M. Guardamino, C. Aucca, J. Cahil, and H. Arnal (Eds.). *II Congreso de ecología y conservación de bosques de* Polylepis. *Libro de resumenes. Mayo 2006*, p. 104. Universidad Mayor de San Simón, American Bird Conservancy, Cusco.

AUCCA, C., AND P.M. RAMSAY 2005. Management of biodiversity and land use in southern Peru. *Mountain Res. Dev.* 25: 287–289.

AUGSPURGER, C.K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *J. Ecol.* 72: 777–795.

BACH, C.E., D. KELLY, AND B.A. HAZLETT 2005. Forest edges benefit adults, but not seedlings, of the mistletoe *Alepis flavida* (Loranthaceae). *J. Ecol.* 93: 79–86.

BADER, M.Y., I. VAN GELOOF, AND M. RIETKERK in press. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecol.*

BELLINGHAM, P.J., AND C.N. ALLAN 2003. Forest regeneration and the influences of white-tailed deer (*Odocoileus virginianus*) in cool temperate New Zealand rain forests. *For. Ecol. Manage.* 175: 71–86.

BENDIX, J., AND M.D. RAFIQPOOR 2001. Studies on the thermal conditions of soil at the upper treeline in the Páramo de Papallacta (Eastern Cordillera of Ecuador). *Erdkunde* 55: 257–276.

BENÍTEZ-MALVIDO, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rainforest. *Conserv. Biol.* 12: 380–389.

BONFIL, C., AND J. SOBERÓN 1999. *Quercus rugosa* seedling dynamics in relation to its re-introduction in a disturbed Mexican landscape. *Appl. Veg. Sci.* 2: 189–200.

BRANDBYGE, J., AND L.B. HOLM NIELSEN 1991. *Reforestación de los Andes ecuatorianos con especies nativas*. CESA, Quito.

BRUSH, S. 1982. The natural and human environment of the central Andes. *Mountain Res. Dev.* 2: 19–38.

BUBB, P., I. MAY, L. MILES, AND J. SAYER 2004. *Cloud forest agenda*. UNEP-WCMC, Cambridge.

BULLOCK, J.M. 2000. Gaps and seedling colonization. In Fenner, M. (Ed.). *Seeds. The ecology of regeneration in plant communities*, pp. 375–396. CABI Publishing, Wallingford.

BURTON, P.J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-central British Colombia. *Silva Fennica* 36: 329–352.

BYERS, A.C. 2000. Contemporary landscape change in the Huascarán National Park and buffer zone, Cordillera Blanca, Peru. *Mountain Res. Dev.* 20: 52–63.

CABIDO, M., AND A. ACOSTA 1985. Estudio fitosociológico en bosques de *Polylepis australis* Bitt. (“Tabaquillo”) en las Sierras de Córdoba, Argentina. *Documents Phytosociologiques N.S.* 9: 385–400.

CABRERA, H.M., F. RADA, AND L. CAVIERES 1998. Effects of temperature on photosynthesis of two morphologically contrasting plant species along an altitudinal gradient in the tropical high Andes. *Oecologia* 114: 145–152.

CAIRNS, D.M., AND J. MOEN 2004. Herbivory influences treelines. *J. Ecol.* 92: 1019–1024.

CAIRNS, D.M., AND J.D. WALDRON 2003. Sigmoid wave transitions at alpine treeline. *Geogr. Annaler* 85: 115–126.

CALVO, L., S. SANTALLA, E. MARCOS, L. VALBUENA, R. TÁRRAGA, AND E. LUIS 2003. Regeneration after wildfire in communities dominated by *Pinus pinaster*, an obligate seeder, and in others dominated by *Quercus pyrenaica*, a typica resprouter. *For. Ecol. Manage.* 184: 209–223.

CAMARERO, J.J., AND E. GUTIÉRREZ 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Clim. Change* 63: 181–200.

CAPRILES, J.M., AND E. FLORES BEDREGAL 2002. The economic, symbolic, and social importance of the „Keñua“ (*Polylepis* spp.) during prehispanic times in the Andean highlands of Bolivia. *Ecotropica* 8: 225–231.

CÁRDENAS, P.A. 2000. Estudio preliminar del desarrollo de *Polylepis tarapacana* en el Parque Nacional Sajama, Bolivia. In Herzog, S.K., J. Cahill, and F. Sagot (Eds.). *I Congreso* *internacional de ecología y conservación de bosques de* Polylepis. *Resumenes. 28 de Agosto al 1° de Septiembre de 2000*, p. 59. Universidad Mayor de San Simón, Cochabamba.

CATALANO, S., P.L. CIONI, M. MARTINOZZI, V. DE FEO, AND I. MORELLI 1995. Chemical investigation of *Polylepis incana* (Rosaceae). *Biochem. Sys. Ecol.* 23: 105–107.

CHEN, J., J.F. FRANKLIN, AND T.A. SPIES 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Applications* 2: 387–396.

CHEN, J., J.F. FRANKLIN, AND T.A. SPIES 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol. Applications* 5: 74–86.

CHEPSTOW-LUSTY, A., M.B. BUSH, M.R. FROGLEY, P.A. BAKER, S.C. FRITZ, AND J. ARONSON 2005. Vegetation and climate change on the Bolivian Altiplano between 108,000 and 18,000 yr ago. *Quaternary Res.* 63: 90–98.

CIERJACKS, A., AND I. HENSEN 2004. Variation of stand structure and regeneration of Mediterranean holm oak along a grazing intensity gradient. *Plant Ecol.* 173: 215–223.

CIERJACKS, A., N.K. RÜHR, K. WESCHE, AND I. HENSEN 2005. Reproduction, stand structure and the impact by cattle on *Polylepis* species along an altitudinal gradient in the Páramo de Papallacta, Ecuador. *Verh. Ges. Ökol.* 35: 231.

CIERJACKS, A., N.K. RÜHR, K. WESCHE, AND I. HENSEN accepted. Impact of altitude and cattle trampling on *Polylepis* regeneration along a treeline in South-America. *Plant Ecol.*

CIERJACKS, A., K. WESCHE, AND I. HENSEN in press a. Potential lateral expansion of *Polylepis* forest fragments in central Ecuador. *For. Ecol. Manage.*

CIERJACKS, A., J.E. IGLESIAS, K. WESCHE, AND I. HENSEN in press b. Impact of sowing, canopy cover and litter on seedling dynamics of *Polylepis* species at upper treelines in central Ecuador. *J. Trop. Ecol.*

CLAPPERTON, C.M., M. HALL, P. MOTHES, M.J. HOLE, J.W. STILL, K.F. HELMENS, P. KUHRY, AND A.M.D. GEMMEL 1997. A younger Dryas icecap in the Ecuatorial Andes. *Quaternary Res.* 47: 13–28.

COCHRANE, M.A., AND W.F. LAURANCE 2002. Fire as large-scale edge effect in Amazonian forests. *J. Trop. Ecol.* 18: 311–325.

COLMENARES, M. 2002. *Estudio del crecimiento de* Polylepis sericea *Wedd. en el páramo venezolano.* Universidad de los Andes, Mérida.

CORLETT, R.T. 1987. Post-fire succession on Mt. Wilhlem, Papua New Guinea. *Biotropica* 19: 157–160.

CRISSMAN, C.C. 2003. *La agricultura en los páramos: Estrategías para el uso del espacio.* Contribuciones para el desarrollo sostenible de los Andes (CONDESAN) 1, Lima.

CROW, T.R. 1992. Population dynamics and growth pattern for a cohort of northern red oak *Quercus rubra* seedlings. *Oecologia* 91: 192–200.

CUEVAS, J.G. 2000. Tree recruitment at the *Nothofagus pumilio* alpine treeline in Tierra del Fuego, Chile. *J. Ecol.* 88: 840–855.

CUSHMAN, S.A., AND D.O. WALLIN 2002. Separating the effects of environment, spatial and disturbance factors on forest community structure in the Russian Far East. *For. Ecol. Manage.* 168: 201–215.

DANELL, K., R. BERGSTRÖM, L. EDENUIS, AND G. ERICSSON 2003. Ungulates as drivers of tree population dynamics at module and genet levels. *For. Ecol. Manage.* 181: 67–76.

DULLINGER, S., T. DIRNBÖCK, AND G. GRABHERR 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *J. Ecol.* 92: 241–252.

ECKSTEIN, R.L., AND T.W. DONATH 2005. Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species. *J. Ecol.* 93: 807–816.

ELLENBERG, H. 1958. Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. *Umschau*: 645–648, 679–681.

ELLENBERG, H. 1979. Man´s influence on tropical mountain ecosystems in South America. *J. Ecol.* 67: 401–416.

ELLENBERG, H. 1996. Páramos und Punas der Hochanden Südamerikas heute großenteils als potentielle Wälder anerkannt. *Verh. Ges. Ökol.* 25: 17–23.

ELLSWORTH, J.W., R.A. HARRINGTON, AND J.H. FOWNES 2004. Seedling emergence, growth, and allocation of Oriental bittersweet: effects of seed input, seed bank, and forest floor litter. *For. Ecol. Manage.* 190: 255–264.

ENRICO, L., G. FUNES, AND M. CABIDO 2003. Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina. *For. Ecol. Manage.* 190: 301–309.

EVERARD, D.A., J.J. MIDGLEY, AND G.F. VAN WYK 1995. Dynamics of some forests in the KwaZulu-Natal, South Africa, based on ordination and size-class distribution. *S. Afr. J. Bot.* 61: 283–293.

FACELLI, J.M., AND S.T.A. PICKETT 1991. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.* 57: 1–33.

FEHSE, J., N. AGUIRRE, C. PALADINES, R. HOFSTEDE, AND J. SEVINK 1999. *La productividad de cuatro bosques secundarios en la sierra del Ecuador.* Proyecto ECOPAR, Quito.

FEHSE, J., R. HOFSTEDE, N. AGUIRRE, C. PALADINES, A. KOOIJMAN, AND J. SEVINK 2002. High altitude tropical forests: a competitive carbon sink? *For. Ecol. Manage.* 163: 9–25.

FENNER, M. 2000. *Seeds: the ecology of regeneration in plant communities.* CABI Publishing, Wallingford.

FERNÁNDEZ TERRAZAS, E. AND B. STÅHL 2002. Diversity and phytogeography of the vascular flora of the *Polylepis* forests of the cordillera de Cochabamba, Bolivia. *Ecotropica* 8: 163–182.

FJELDSÅ, J. 2002. Key areas for conserving the avifauna of *Polylepis* forests. *Ecotropica* 8: 125–131.

FJELDSÅ, J., AND M. KESSLER 1996. *Conserving the biological diversity of* Polylepis *woodlands of the highland of Peru and Bolivia. A contribution to sustainable natural resource management in the Andes.* Nordeco, Copenhagen.

FOWLER, N.L. 1986. Microsites requirements for germination and establishment of three grass species. *Amer. Midl. Natur.* 115: 131–145.

FRAVER, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conserv. Biol.* 8: 822–832.

GEHLHAUSEN, S.M., M.W. SCHWARTZ, AND C.K. AUGSPURGER 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecol.* 147: 21–35.

GERMINO, M.J., W.K. SMITH, AND A.C. RESOR 2002. Conifer seedling distribution and survival in an alpine treeline ecotone. *Plant Ecol.* 162: 157–168.

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

GOLDSTEIN, G., F.C. MEINZER, AND F. RADA 1994. Environmental biology of a tropical treeline species *Polylepis sericea*. In Rundel, P.W., A.P. Smith, and F.C. Meinzer (Eds.). *Tropical Alpine Environments: Plant form and function,* pp. 129–151. Cambridge University Press, Cambridge.

GORDON, I.J. 2003. Browsing and grazing ruminants: are they different beasts? *For. Ecol. Manage.* 181: 13–21.

GRUBB, P.J. 1970. The impact of man on the Cerro Antisana, Ecuador. *J. Appl. Ecol.* 7: 7–8.

HAMRICK, J.L., AND J.M. LEE 1987. Effects of soil surface topography and litter cover on germination, survival and growth of musk thistle. *Amer. J. Bot.* 74: 451–457.

HARPER, K.A., AND S.E. MACDONALD 2002. Structure and composition of edges next to regenerating clearcuts in the mixed wood boreal forest. *J. Veg. Sci.* 13: 535–564.

HARPER, K.A., S.E. MACDONALD, P.J. BURTON, J. CHEN, K.D. BROSOFSKE, S.C. SAUNDERS, E.S. EUSKIRCHEN, D. ROBERTS, M.S. JAITEH, AND P. ESSEEN 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conserv. Biol.* 19: 1–15.

HÄTTENSCHWILER, S., AND W.K. SMITH 1999. Seedling occurrence in alpine treeline conifers: a case study from the central Rocky Mountains, USA. *Acta Oecol.* 20: 219–224.

HENSEN, I. 1993. *Vegetationsökologische Untersuchungen in* Polylepis-*Wäldern der Ostkordillere Boliviens.* Diss. Univ. Göttingen.

HENSEN, I. 1995. Die Vegetation von *Polylepis*-Wäldern der Ostkordillere Boliviens. *Phytocoenologia* 25: 235–277.

HENSEN, I. 2002. Impacts of anthropogenic activity on the vegetation of *Polylepis* woodlands in the region of Cochabamba, Bolivia. *Ecotropica* 8: 183–203.

HEWITT, N., AND M. KELLMAN 2004. Factors influencing tree colonization in fragmented forests: an experimental study of introduced seeds and seedlings. *For. Ecol. Manage.* 187: 39–59.

HOCH, G., AND C. KÖRNER 2003. The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia* 135: 10–21.

HOCH, G., AND C. KÖRNER 2005. Growth, demography and carbon relations of *Polylepis* trees at the world highest treeline. *Functional Ecol.* 19: 941–951.

HOFFMANN, W.A. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecol.* 80: 1354–1369.

HOFSTEDE, R.G.M. 1995a. The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant and Soil* 173: 111–132.

HOFSTEDE, R.G.M. 1995b. *Effects of burning and grazing on a Colombian páramo ecosystem.* Dissertation, University of Amsterdam.

HOFSTEDE, R.G.M. 2001. El impacto de las actividades humanas sobre el páramo. In Mena Vásconez, P.M., G. Medina, and R.G.M. Hofstede (Eds.). *Los páramos del Ecuador. Particularidades, problemas y perspectivas,* pp. 161–185. Abya Yala/Proyecto Páramo, Quito.

HOLM, S.-O. 1994. Reproductive patterns of *Betula pendula* and *B. pubescens* along a regional altitudinal gradient in northern Sweden. *Ecography* 17: 60–72.

HOLTMEIER, F.K. 2003. Mountain timberlines. Ecology, patchiness, and dynamics. *Advances in Global Change Res.* 14:1–369.

HORN, S.P., L.M. KENNEDY, AND K.H. ORVIS 2001. Vegetation recovery following a high-elevation fire in the Dominican Republic. *Biotropica* 33: 701–708.

HUGHES, J.W., AND D.A. BECHTEL 1997. Effect of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. *Can. J. For. Res.* 27: 2088–2096.

HUSHEER, S.W., D.A. COOMES, AND A.W. ROBERTSON 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *For. Ecol. Manage.* 181: 99–117.

IBISCH, P.L. 2002. Evaluation of a rural development project in Southwest Cochabamba, Bolivia, and its agroforestry activities involving *Polylepis besseri* and other native species – a decade of lessons learned. *Ecotropica* 8: 205–218.

IUCN 2006. *2006 IUCN Red list of threatened species*. www.iucnredlist.org. Downloaded on 10 October 2006.

IVANAUSKAS, N.M., R. MONTEIRO, AND R.R. RODRIGUES 2003. Alterations following a fire in a forest community of Alto Rio Xingu. *For. Ecol. Manage.* 184: 239–250.

JOBBÁGY, E.G., AND R.B. JACKSON 2000. Global controls of forest line elevation in the northern and southern hemispheres. *Global Ecol. Biogeogr.* 9: 253–268.

JØRGENSEN, P.M., AND S. LEÓN-YÁNEZ (eds.) 1999. Catalogue of the vascular plants of Ecuador. *Monogr. Syst. Bot. Missouri Bot. Gard.* 75: 1–1182.

JULES, E.S., AND B.J. RATHKE 1999. Mechanisms of reduced *Trillium* recruitment along edges of old-growth forests. *Conserv. Biol.* 13: 784–793.

KEEVER, C. 1973. Distribution of major forest species in south-eastern Pennsylvania. *Ecol. Monogr.* 43: 303–327.

KELLMAN, M. 2004. Sugar maple (*Acer sacharum* Marsh.) establishment in boreal forest: results of a transplantation experiment. *J. Biogeogr.* 31: 1515–1522.

KENNARD D.K., AND H.L. GHOLZ 2001. Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest. *Plant and Soil* 234: 119–129.

KENNARD, D.K., K. GOULD, F.E. PUTZ, T.S. FREDERICKSEN, AND F. MORALES 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *For. Ecol. Manage.* 162: 197–208.

KERR, M.S. 2003. *A phylogenetic and biogeographic analysis of Sanguisorbae (Rosaceae), with emphasis on the pleistocene radiation of the high Andean genus* Poylepis. Diss. Univ. of Maryland.

KESSLER, M. 1995. *Polylepis*-Wälder Boliviens: Taxa, Ökologie, Verbreitung und Geschichte. *Dissertationes Botanicae* 246: 1–303.

KESSLER, M. 2000. Observations on a human-induced fire event at a humid timberline in the Bolivian Andes. *Ecotropica* 6: 89–93.

KESSLER, M. 2002. The “*Polylepis* problem“: where do we stand? *Ecotropica* 8: 97–110.

KESSLER, M., AND P. DRIESCH 1993. Causas e historia de la destrucción de bosques Altoandinos en Bolivia. *Ecología en Bolivia* 21: 1–18.

KITAJIMA, K., AND M. FENNER 2000. Ecology of seedling regeneration. In Fenner, M. (Ed.). *Seeds. The ecology of regeneration in plant communities*, pp. 331–359. CABI Publishing, Wallingford.

KOK, K., P.A. VERWEIJ, AND H. BEUKEMA 1995. Effects of cutting and grazing on Andean treeline vegetation. In Churchill, P., H. Balslev, E. Forero, and J.L. Luteyn (Eds.). *Biodiversity and conservation of neotropical montane forests. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21-26 June 1993*, pp. 527–539. The New York Botanical Garden, New York.

KÖRNER, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115: 445–459.

KÖRNER, C. 2003a. *Alpine plant life. Functional plant ecology of high mountain ecosystems*. Second edition. Springer, Berlin.

KÖRNER, C. 2003b. Carbon limitation in trees. *J. Ecol.* 91: 4–17.

KÖRNER, C., AND J. PAULSEN 2004. A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* 31: 713–732.

KRAMER, H., AND A. AKCA 1995. *Leitfaden zur Waldmesslehre*. Third edition. Sauerländer´s Verlag, Frankfurt am Main.

KRAMER, K., T.A. GROEN, AND S.E. VAN WIEREN 2003. The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE. *For. Ecol. Manage.* 181: 205–222.

KREMSATER, L., AND F.L. BUNNELL 1999. Edge effects: theory, evidence and implication to management of western North American forests. In Rochelle, J.A., L.A. Lehmann, and J. Wisniewski (Eds.). *Forest fragmentation, wildlife and management implications*, pp. 117–139. Brill, Leiden.

KUITERS, A.T., AND P.A. SLIM 2002. Regeneration of mixed deciduous forest in Dutch forest-heathland, following reduction of ungulate densities. *Biol. Conserv.* 105: 65–74.

KUPFER, J.A., AND J.R. RUNKLE 2003. Edge-mediated effects on stand dynamic processes in forest interiors: a coupled field and simulation approach. *Oikos* 101: 135–146.

LÆGAARD, S. 1992. Influence of fire in the grass páramo vegetation of Ecuador. In Balslev, H. and J.L. Luteyn (Eds.). *Páramo; An Andean ecosystem under human influence*, pp. 151–170. Academic Press, London.

LAMBRECHT, H. 1989. *Silviculture in the tropics.* Gesellschaft für Technische Zusammenarbeit, Eschborn.

LAUER, W., M.D. RAFIQPOOR, AND I. THEISEN 2001. Physiogeographie, Vegetation und Syntaxonomie der Flora des Páramo de Papallacta (Ostkordillere Ecuador). *Erdwissenschaftliche Forschung* 19: 1–209.

LAURANCE, W.F.L., V. FERREIRA, J.M. RANKIN-DE MERONA, S.G. LAURANCE, R.W. HUTCHINGS, AND T.E. LOVEJOY 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conserv. Biol.* 12: 460–464.

LI, Q., AND K. MA 2003. Factors affecting establishment of *Quercus liaotungensis* Koidz. under mature mixed oak forest overstory and in shrubland. *For. Ecol. Manage.* 176: 133–146.

LUKEN, J.O., AND N. GOESSLING 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *Am. Midl. Natur.* 133: 124–130.

MAYER, A.C., V. STÖCKLI, C. HUOVINEN, W. KONOLD, B.L. ESTERMANN, AND M. KREUZER 2003. Herbage selection by cattle on sub-alpine wood pastures. *For. Ecol. Manage.* 181: 39–50.

MCKAY, D.B. 1972. The measurement of viability. In Roberts, E.H. (Ed.). *Viability of seeds.* Chapman and Hall Ltd, London.

MEINERS, S.J., S.T.A. PICKETT, AND S.N. HANDEL 2002. Probability of tree seedling establishment changes across a forest-old field edge gradient. *Am. J. Bot.* 89: 466–471.

MENA VÁSCONEZ, P.M. 1995. Las areas protegidas con bosque montano en el Ecuador. In Churchill, P., H. Balslev, E. Forero, and J.L. Luteyn (Eds.). *Biodiversity and conservation of neotropical montane forests. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21-26 June 1993*, pp. 627–635. The New York Botanical Garden, New York.

MENOYO, E. 2004. *Colonización micorrícica de* Polylepis australis *Bitt. en relación a sitios con distinta carga de ganado.* Univ. Nacional de Córdoba.

MIEHE, G., AND S. MIEHE 1994. Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia* 24: 53–110.

MILLER, E.A., AND C.B. HALPERN 1998. Effect of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *J. Veg. Sci.* 9: 265–282.

MOLOFSKY, J., AND C.K. AUGSPURGER 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecol.* 73: 68–77.

MORI, A., E. MIZUMACHI, T. OSONO, AND Y. DOI 2004. Substrate-associated seedling recruitment and establishment of major conifer species in an old-growth subalpine forest in central Japan. *For. Ecol. Manage.* 196: 287–297.

MORRIS, A. 1985. Forestry and land-use conflicts in Cuenca, Ecuador. *Mountain Res. Dev.* 5: 183–196.

MORRIS, A. 1997. Afforestation projects in highland Ecuador: patterns of success and failure. *Mountain Res. Dev.* 17: 31–42.

NARUKAWA, Y., AND S. YAMAMOTO 2002. Effects of dwarf bamboo (*Sasa* sp.) and forest floor microsites on conifer seedling recruitment in a subalpine forest, Japan. *For. Ecol. Manage.* 163: 61–70.

NETO, C.C., A.J. VAISBERG, B. ZHOU, D.G.I. KINGSTON, AND G.B. HAMMOND 2000. Cytotoxic triterpene acids from the Peruvian medicinal plant *Polylepis racemosa*. *Planta med.* 66: 483–484.

OESTERHELD, M., AND O.E. SALA 1990. Effects of grazing on seedling establishment: the role of seed and safe-site availability. *J. Veg. Sci.* 1: 353–358.

OJEDA F., F.G. BRUN, AND J.J. VERGARA 2005. Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. *New Phytol.* 168: 155–165.

OLSON-RUTZ, K.M., C.B. MARLOW, K. HANSEN, L.C. GAGNON, AND R.J. ROSSI 1996. Recovery of a high elevation plant community after packhorse grazing. *J. Range Manage.* 49: 541–545.

PALMER, S.C.F., R.J. MITCHELL, A.M. TRUSCOTT, AND D. WELCH 2004. Regeneration failure in Atlantic oakwoods: the roles of ungulate grazing and invertebrates. *For. Ecol. Manage.* 192: 251–265.

PEREIRA DE SOUZA, R.P., AND I.F.M. VÁLIO 2001. Seed size, seed germination, and seedling survival of Brazilian tropical tree species differing in successional status. *Biotropica* 33: 447–457.

PETERSON, C.J., AND J.M. FACELLI 1992. Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. *Am. J. Bot.* 79: 1209–1216.

PETERSON, D.W., AND P.B. REICH 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecol. Applications* 11: 914–927.

PODWOJEWSKI, P., AND N. GERMAIN 2005. Short-term effects of management on the soil structure in a deep tilled hardened volcanic-ash soil (cangahua) in Ecuador. *Eur. J. Soil Sci.* 56: 39–51.

PUGH, J., AND F.O. SARMIENTO 2004. Selling the public on sustainable watershed conservation. *Bul. Latin Am. Res.* 23: 303–318.

PURCELL, J., AND A. BRELSFORD 2004. Reassessing the causes of decline of *Polylepis*, a tropical subalpine forest. *Ecotropica* 10: 155–158.

QUINN, G.P., AND M.J. KEOUGH 2002. *Experimental design and data analysis for biologists.* Cambridge University Press, Cambridge.

RADA, F., A. AZOCAR, B. BROCENO, J. GONZALEZ, AND C. GARCIA-NUNEZ 1996. Carbon and water balance in *Polylepis sericea*, a tropical treeline species. *Trees* 10: 218–222.

RAMSAY, P.M. 1992. *The páramo vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes.* Diss. Univ. of Wales.

RENISON, D., AND A.M. CINGOLANI 1998. Experiencias en germinación y reproducción vegetativa aplicados a la reforestación con *Polylepis australis* (Rosaceae) en las Sierras Grandes de Córdoba, Argentina. *AgriScientia* 15: 47–53.

RENISON, D., A.M. CINGOLANI, AND D. SCHINNER 2002a. Optimizing restoration of *Polylepis australis* woodlands: when, where and how to transplant seedlings to the mountains? *Ecotropica* 8: 219–224.

RENISON, D., A.M. CINGOLANI, AND R. SUAREZ 2002b. Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en las montañas de Córdoba, Argentina. *Rev. Chil. Hist. Nat.* 75: 719–727.

RENISON, D., A.M. CINGOLANI, R. SUAREZ, E. MENOYO, C. COUTSIERS, A. SOBRAL, AND I. HENSEN 2005. The restoration of degraded mountain woodland: Effects of seed provenance and microsite characteristics on *Polylepis australis* seedling survival and growth. *Restor. Ecol.* 13: 129–137.

RENISON, D., I. HENSEN, AND A.M. CINGOLANI 2004. Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina. *For. Ecol. Manage.* 196: 327–333.

RENISON, D., I. HENSEN, R. SUÁREZ, AND A.M. CINGOLANI 2006. Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? *J. Biogeogr.* 33: 876–887.

REPUBLIC OF ECUADOR 2000. *National communication. Climate change.* Gráficas Ibéricas, Ecuador.

RESTREPO, C., AND A. VARGAS 1999. Seeds and seedlings of two neotropical montane understory shrubs respond differently to anthropogenic edges and treefall gaps. *Oecologia* 119: 419–426.

ROMOLEROUX, K. 1996. *Rosaceae. Flora of Ecuador 56.* Aarhus University Press, Aarhus.

Rooney, T.P., and D.M. Waller 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.* 181: 165–176.

Rotundo, J.L., and M.R. Aguiar 2005. Litter effects on plant regeneration in arid lands: a complex balance between seed retention, longevity and soil-seed-contact. *J. Ecol.* 93: 829–238.

Rundel, P.W., A.C. Gibson, G.S. Midgley, S.J.E. Wand, B. Palma, C. Kleier, and J. Lambrinos 2003. Ecological and ecophysiological patterns in a pre-altiplano shrubland of the Andean Cordillera in northern Chile. *Plant Ecol.* 169: 179–193.

Sanford, N.L., R.A. Harrington, and J.H. Fownes 2003. Survival and growth of native and alien woody seedlings in open and understory environments. *For. Ecol. Manage.* 183: 377–385.

Sarmiento, F.O. 2000a. Breaking mountain paradigms: Ecological effects of human impacts in managed Tropandean landscapes. *Ambio* 29: 423–431.

Sarmiento, F.O. 2000b. Restoration of Andean forests for conservation and development. In Price, M.F., and N. Butt (Eds.). *Forests in sustainable mountain development: a state of knowledge report for 2000*, pp.59–70. CABI Publishing, Wallingford.

Sarmiento, F.O. 2002. Impulsores de cambio de paisaje: Dinámica de las líneas de árboles en la montología neotropical. *Ecotrópicos* 15.

Sarmiento, F.O., and L.M. Frolich 2002. Andean cloud forest treelines. *Mountain Res. Dev.* 22: 278–287.

Sarmiento, G. 1986. Ecological features of climate in high tropical mountains. In Monasterio, M., and F. Vuilleumier (Eds.). *High tropical biogeography*, pp. 11–45. Oxford University Press, Oxford.

Schmidt-Lebuhn, A.N., M. Kessler, and M. Kumar 2006. Promiscuity in the Andes: a phylogenetic analysis of the genus *Polylepis* (Rosaceae) based on morphology and AFLP data. *Syst. Bot.* 31: 547–559.

Segovia, P. 2002. *Informe Páramo de El Inga Bajo.* Camaren-Iedeca, Ecuador.

Segovia- Salcedo, M.C., H.E. Ballard, and A. Narváez 2000. Phenetic studies of *Polylepis* in Ecuador. In Herzog, S.K., J. Cahill, and F. Sagot (Eds.). *I Congreso internacional de ecología y conservación de bosques de* Polylepis*. Resumenes. 28 de Agosto al 1° de Septiembre de 2000*, p. 66. Universidad Mayor de San Simón, Cochabamba.

Segura, A.M., M. Holmgren, J.J. Anabalón, and E.R. Fuentes 1998. The significance of fire intensity in creating local patchiness in the Chilean matorral. *Plant Ecol.* 139: 259–264.

Simpson, B.B 1979. A revision of the genus *Polylepis* (Rosaceae: Sanguisorbeae). *Smithsonian Contributions to Botany* 43: 1–62.

SIMPSON, B.B. 1986. Speciation and specialisation of *Polylepis* in the Andes. In Monasterio, M., and F. Vuilleumier (Eds.). *High tropical biogeography*, pp. 304–316. Oxford University Press, Oxford.

SMITH, A.P. 1977. Establishment of seedlings of *Polylepis sericea* in the páramo (alpine) zone of the venezuelan Andes. *Bartonia* 45: 11–14.

SMITH, A.P., AND T.P. YOUNG 1987. Tropical alpine plant ecology. *Annual Rev. Ecol. Sys.* 18: 137–158.

SMITH, W.K., M.J. GERMINO, T.E. HANCOCK, AND D.M. JOHNSON 2003. Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology* 23: 1101–1112.

SPEHN, E.M., M. LIBERMAN, AND C. KÖRNER (Eds.) 2005. *Land use change and mountain biodiversity*. CRC Press, Boca Raton.

STEVENS, G.C., AND J.F. FOX 1991. The causes for treeline. *Annual Rev. Ecol. Sys.* 22: 177–191.

SVEINBJORNSSON, B. 2000. North American and European treelines: external forces and internal processes controlling position. *Ambio* 29: 388–395.

TEICH, I., A.M. CINGOLANI, D. RENISON, I. HENSEN, AND M. GIORGIS 2005. Do domestic herbivores retard *Polylepis australis* woodland recovery in the mountains of Córdoba, Argentina? *For. Ecol. Manage.* 219: 229–241.

THE R FOUNDATION FOR STATISTICAL COMPUTING 2006. *R version 2.3.1.*

TRANQUILLINI, W. 1979. Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. *Ecological Studies* 31: 1–137.

TROLL, C. 1959. Die tropischen Gebirge – Ihre dreidimensionale klimatische und pflanzengeographische Zonierung. *Bonner Geogr. Abh.* 25: 1–93.

TRYTERUD, E. 2003. Forest fire history in Norway: from fire-disturbed pine forests to fire-free spruce forests. *Ecography* 26: 161–170.

ULLOA, C., AND P.M. JØRGENSEN 1993. *Arboles y arbustos de los Andes del Ecuador.* AAU Reports, Aarhus.

UNEP-WCMC 2004. *United Nations Environment Programme, World Conservation Monitoring Center.* http://www.unep-wcmc.org. Cited 1 Oct 2005.

VAN VOSS, O.H., N. AGUIRRE, AND R.G.M. HOFSTEDE 2001. *Sistemas forestales integrales para la sierra del Ecuador.* Abya Yala, Quito.

VELEZ, V., J. CAVELIER, AND B. DEVIA 1998. Ecological traits of the tropical treeline species *Polylepis quadrijuga* (Rosaceae) in the Andes of Colombia. *J. Trop. Ecol.* 14: 771–787.

VERA, M.L. 1995. Efecto de la altitud en la fenología de la floración en especies arbustivas del norte de España. *Lagascalia* 18: 3–14.

VERWEIJ, P.A., AND P.E. BUDDE 1992. Burning and grazing gradients in páramo vegetation: Initial ordination analyses. In Balslev, H. and J.L. Luteyn (Eds.). *Páramo; An Andean ecosystem under human influence*, pp. 177–195. Academic Press, London.

VESK, P.A., AND M. WESTOBY 2001. Sprouting ability across diverse disturbances and vegetation types worldwide. *J. Ecol.* 92: 310–320.

VUILLE, M., AND R.S. BRADLEY 2000. Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophys. Res. Letters* 27: 3885–3888.

WALTER, H., AND E. MEDINA 1969. Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subalpinen und alpinen Stufe in den Anden Venezuelas. *Berichte der Deutschen Botanischen Gesellschaft* 82: 275–281.

WARDLE, P. 1985. New Zealand timberlines. 2. A study of forest limits in the Crow Valley near Arthur's Pass, Canterbury. *New Zealand J. Bot.* 23: 235–261.

WARDLE, P., AND M.C. COLEMAN 1992. Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand J. Bot.* 30: 303–314.

WESCHE, K. 2002. The high-altitude environment of Mt. Elgon (Uganda,Kenya): Climate, vegetation, and the impact of fire. *Ecotropical Monographs* 2: 1–253.

WEST, A.G., J.J. MIDGLEY, AND W.J. BOND 2000. Regeneration failure and potential importance of human disturbance in a subtropical forest. *Appl. Veg. Sci.* 3: 223–232.

WEYENBERG, S.A., S.E. FRELICH, AND P.B. REICH 2004. Logging versus fire: How does disturbance type influence the abundance of *Pinus strobus* regeneration? *Silva Fennica* 38: 179–194.

WHELAN, R.J. 1995. *The ecology of fire.* Cambridge University Press, Cambridge.

WILLE, M., H. HOOGHIEMSTRA, R.G.M. HOFSTEDE, J. FEHSE, AND J. SEVINK 2002. Upper forest line reconstruction in a deforested area in northern Ecuador based on pollen and vegetation analysis. *J. Trop. Ecol.* 18: 409–440.

WINCKELL, A., C. ZEBROWSKI, AND M. SOURDAT 1997. *Geografía básica del Ecuador. Tomo IV Geographía física. Las regiones y paisajes del Ecuador, vol II.* Centro Ecuatoriano de Investigación Geográfica, Quito.

YATES, C.J., D.A. NORTON, AND R.J. HOBBS 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: Implications for restoration. *Aust. Ecol.* 25: 36–47.

YENSEN, E. & T. TARIFA 2002. Mammals of Bolivian *Polylepis* woodlands: Guild structure and diversity patterns in the world's highest woodlands. *Ecotropica* 8: 145–162.

APPENDIX

SPECIES LIST

The list gives all vascular plant species found in the forest stands described in chapter 2. It contains a total of 56 families and 153 taxa. Species names refer to Jørgensen and León-Yánez (1999).

Pteridophyta
Aspleniaceae
    Asplenium castaneum Schtdl. ex Cham.
    Asplenium sessilifolium Desv.
Blechnaceae
    Blechnum schomburgkii (Klotzsch) C. Chr.
Dennstaedtiaceae
    Hypolepis bogotensis H. Karst
    Hypolepis crassa Maxon
    Hypolepis spec.
Drypteridaceae
    Cystopteris fragilis (L.) Bernh.
    Polystichum orbiculatum (Desv.) J. Rémy and Fée
Equisetaceae
    Equisetum bogotense Kunth
Grammitidaceae
    Melpomene pseudonutans (H. Christ and Rosenst.) A.R. Sm. and R.C. Moran
    Terpsichore heteromorpha (Hook and Grev.) A. R. Sm.
Lomariopsidaceae
    Elaphoglossum lingua (C. Presl) Brack.
    Elaphoglossum muscosum (Sw.) T. Moore
    Elaphoglossum ovatum (Hook. and Grev.) T. Moore
Lycopodiaceae
    Huperzia linifolia (L.) Trevis.
    Huperzia crassa (Humb. and Bonpl. Ex Willd) Rothm.
Ophioglossaceae
    Botrychium virginianum (L.) Sw.
    Ophioglossum crotalophoroides Walter
Polypodiaceae
    Campyloneurum amphostenon (Kunze ex Klotzsch) Fée
    Polypodium mindense Sodiro
    Polypodium monosorum Desv.
    Polypodium murorum Hook.
Pteridaceae
    Pityrogramma ebenea (L.) Proctor
Thelypteridaceae
    Thelypteris rigescens (Sodiro) A. R. Sm.
    Thelypteris spec.

Spermatophyta – Angiospermae
Amaryllidaceae
    Bomarea multiflora (L. f.) Mirb.
Apiacea
    Azorella pedunculata (Spreng.) Math. and Const.
    Bowlesia lobata Ruizand Pav.
    Daucus montanus Humb. and Bonpl. ex Spreng.
    Hydrocotyle bonplandii A. Rich.
    Hydrocotyle spec.
    Niphogeton dissecta (Benth.) J.F. Macbr.
Araliaceae
    Oreopanax spec.
Asclepiadaceae
    Cyanchum spec.
Asteraceae
    Aetheolaena heterophylla (Turcz.) B. Nord.
    Aetheolaena involucrata (Kunth) B.Nord
    Ageratina azangaroensis (Sch. Bip. Ex Wedd.) R.M.King and H.Rob.

  - *Ageratina pichinchensis* (Kunth) R.M.King and H.Rob.
  - *Baccharis macrantha* Kunth
  - *Bacharis odorata* Kunth
  - *Bacharis padifolia* Hieron.
  - *Barnadesia arborea* Kunth
  - *Cotula mexicana* (DC.) Cabrera
  - *Diplostephium hartwegii* Hieron.
  - *Diplostephium rupestre* (Kunth) Wedd.
  - *Diplostephium* spec.
  - *Gnaphalium pensylvanicum* Willd.
  - *Gynoxis acostae* Cuatrec.
  - *Gynoxis buxifolia* (Kunth) Cass.
  - *Gynoxis hallii* Hieron.
  - *Monticalia myrsinites* (Turcz.) C. Jeffrey
  - *Munnozia senecionidis* Benth.
  - *Pentacalia arbutifolia* (Kunth) Cuatrec.
  - *Pentacalia andicola* (Turcz.) Cuatrec.
  - *Sigesbeckia jorullensis* Kunth
  - *Taraxacum officinalis* Weber
- Berberidaceae
  - *Berberis pichichensis* Turcz.
- Bignoniaceae
  - *Eccremocarpus longiflorus* Ruiz and Pav.
- Boraginaceae
  - *Moritzia lindenii* (A. DC.) Gürecke
  - *Plagiobothrys linifolius* (Lehm.) Johnst.
- Brassicaceae
  - *Cardamine jamesonii* Hook.
- Bromeliaceae
  - *Puya clava-herculis* Mez.and Sodiro
  - *Puya* spec.
- Campanulaceae
  - *Centropogon* spec.
- Caryophyllaceae
  - *Arenaria* spec.
  - *Cerastium mollissimum* Poir.
  - *Cerastium* spec.
  - *Stellaria recurvata* Willd ex Schltdl.
- Cyperaceae
  - *Carex pichinchensis* Kunth
  - *Uncinia phleoides* (Cav.) Pers.
  - *Uncinia* spec.
- Elaeocarpaceae
  - *Vallea stipularis* L. f.
- Ericaceae
  - *Ceratostema alatum* (Hoerold) Sleumer
  - *Pernettya prostrata* (Cav.) DC.
  - *Vaccinium floribundum* Kunth
- Euphorbiaceae
  - *Dysopsis glechomoides* (A. Rich.) Müll. Arg.
- Fabaceae
  - *Otholobium brachystachyum* (Spruce ex Diels) J.W.Grimes
  - *Trifolium pratense* L.
  - *Trifolium repens* L.
  - *Vicia andicola* Kunth
- Gentianaceae
  - *Gentianella rapunculoides* (Willd. ex Schult.) J.S. Pringle
- Geraniaceae
  - *Geranium hirtum* Willd. ex Spreng.
  - *Geranium reptans* Kunth
  - *Geranium sibbaldoides* Benth.
- Grossulariaceae
  - *Escallonia myrtilloides* L. f.
  - *Ribes andicola* Jancz.
- Haloragaceae
  - *Gunnera magellanica* Lam.
- Hypericaceae
  - *Hypericum quitense* R.Keller
- Juncaceae
  - *Luzula gigantea* Desv.
- Lamiaceae
  - *Clinopodium nubigenium* (Kunth) Kuntze
  - *Prunella vulgaris* L.
- Loganiaceae
  - *Buddleja pichichensis* Kunth
- Melastomataceae
  - *Brachyotum ledifolium* (Desv.) Triana
  - *Miconia latifolia* (D.Don.) Nandin
  - *Miconia salicifolia* (Bonpl. ex Nandin) Nandin
- Onagraceae
  - *Fuchsia vulcanica* André
  - *Oenothera epilobiifolia* Kunth
- Orchidaceae
  - *Aa maderoi* Schltr.
- Oxalidaceae
  - *Oxalis lotoides* Kunth

Passifloraceae
- *Passiflora* spec.

Piperaceae
- *Peperomia rotundata* Kunth
- *Peperomia* spec.

Plantaginaceae
- *Plantago lanceolata* L.
- *Plantago* spec.

Poaceae
- *Aira caryophyllea* L.
- *Brachypodium distachyon* (L.) P. Beauv.
- *Calamagrostis intermedia* (J.Presl.) Steud.
- *Cortaderia nitida* (Kunth) Pilg.
- *Dactylis glomerata* L.
- *Elymus cordilleranus* Davidse and R.W. Pohl
- *Festuca* spec.
- *Holcus lanatus* L.
- *Lolium perenne* L.
- *Poa annua* L.
- *Poa* spec.
- *Vulpia bromoides* (L.) Gray

Polygalaceae
- *Monnina crassifolia* (Bonpl.) Kunth
- *Monnina obtusifolia* Kunth
- *Monnina* spec.

Polygonaceae
- *Muehlenbeckia tamnifolia* (Kunth) Meisn.
- *Rumex acetosella* L.
- *Rumex obtusifolius* L.

Ranunculaceae
- *Ranunculus peruvianus* Pers.

Rosaceae
- *Acaena elongatum* L.
- *Acaena ovalifolia* Ruiz and Pav.
- *Geum peruvianum* Focke
- *Hesperomeles obtusifolia* (Pers.) Lindl var. *microphylla*
- *Lachemilla andina* (L. M. Perry) Rothm.
- *Lachemilla aphanoides* (Mutis ex L. f.) Rothm.
- *Lachemilla hirta* (L. M. Perry) Rothm.
- *Lachemilla holosericea* (L. M. Perry) Rothm.
- *Lachemilla orbiculata* (Ruiz and Pavon) Rydb.
- *Polylepis incana* Kunth
- *Polylepis pauta* Hieron.
- *Rubus coriacaeus* Poir.
- *Rubus glabratus* Kunth

Rubiaceae
- *Galium aparine* L.
- *Galium hypocarpium* (L.) Endl. ex Briseb.
- *Galium pseudotrifolium* Dempster and Ehrend
- *Galium* spec.

Scrophulariaceae
- *Calceolaria crenata* Lam.
- *Sibthorpia repens* (L.) Kuntze

Solanaceae
- *Solanum andreanum* Baker
- *Solanum columbianum* Dun.
- *Solanum stenophyllum* Dun.

Tropaeolaceae
- *Tropaeolum pubescens* Kunth

Urticaceae
- *Urtica leptophylla* Kunth
- *Urtica urens* L.

Valerianaceae
- *Valeriana ascendens* Turcz.
- *Valeriana microphylla* Kunth
- *Valeriana plantaginea* Kunth
- *Valeriana rumicoides* Wedd.

Violaceae
- *Viola dombeyana* DC.

POST-FIRE SEEDLING DYNAMICS IN *P. PAUTA*

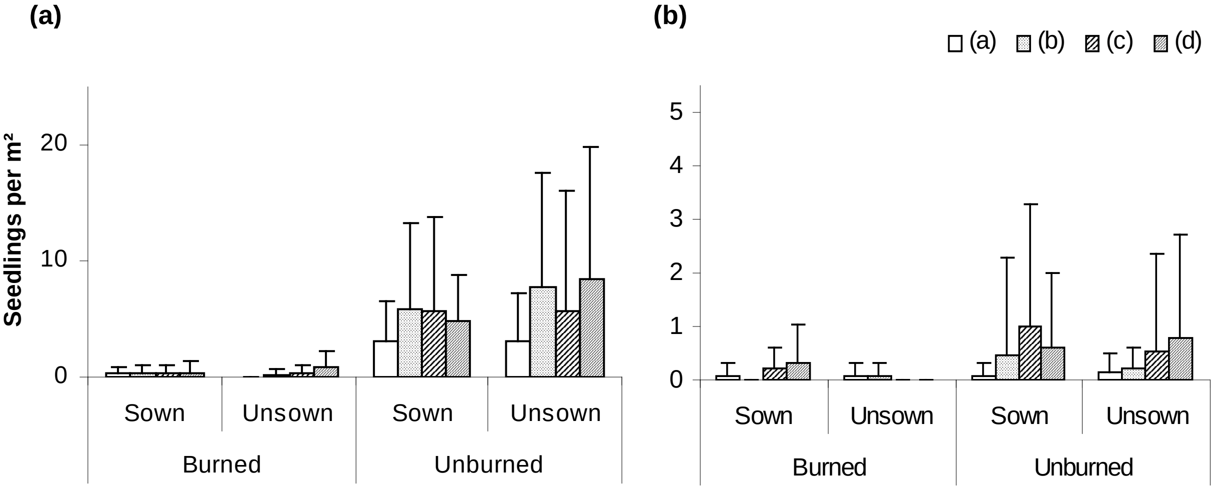

Figure 26. Seedling numbers of *P. pauta* (a) and *G. acostae* (b) in different litter treatments, with and without sowing, in burned and unburned conditions (Means of 15 subplots nested within 3 blocks; error bars: standard deviation; litter treatment (a), (b), (c) and (d) as described in chapter 5). Study plots located in forest at altitudes between 3861 and 4032 m asl in forest stands 14, 17 and 18.

Table 25. Multifactor ANOVA for the seedling numbers of *P. pauta* and *G. acostae*.

	df	SS	F-ratio	P
Error Block				
Residuals	2	998.4		
Error Block × Burning				
Burning	1	952.0	2.61	0.247
Residuals	2	2255.4		
Error Block × Burning × Sowing				
Sowing	1	10.8	0.49	0.523
Sowing × Burning	1	14.7	0.67	0.460
Residuals	4	88.1		
Error Block × Burning × Sowing × Litter				
Litter	3	99.0	2.69	0.069
Litter × Burning	3	70.1	1.91	0.156
Litter × Sowing	3	25.91	0.71	0.558
Litter × Burning × Sowing	3	18.4	0.50	0.686
Residuals	24	294.0		
Error Block × Burning × Sowing × Litter × Species				
Species	1	853.3	11.46	0.002
Species × Burning	1	710.5	9.54	0.004
Species × Sowing	1	20.83	0.28	0.600
Species × Litter	3	61.7	0.28	0.842
Species × Burning × Litter	3	44.9	0.20	0.895
Species × Burning × Sowing	1	14.7	0.20	0.660
Species × Litter × Sowing	3	22.9	0.10	0.958
Species × Burning × Sowing × Litter	3	10.3	0.05	0.987
Residuals	32	2382.3		
Error within residuals	384	2711.6		

PUBLICATIONS OF THIS STUDY

PUBLICATIONS IN PEER REVIEWED JOURNALS

CIERJACKS, A., J.E. IGLESIAS, K. WESCHE, AND I. HENSEN in press. Impact of sowing, canopy cover and litter on seedling dynamics of *Polylepis* species at upper treelines in central Ecuador. *J. Trop. Ecol.*

CIERJACKS, A., N.K. RÜHR, K. WESCHE, AND I. HENSEN accepted. Impact of altitude and cattle trampling on *Polylepis* regeneration along a treeline in South-America. *Plant Ecol*.

CIERJACKS, A., S. SALGADO, K. WESCHE, AND I. HENSEN submitted. Post-fire tree seedling dynamics in high-altitude *Polylepis* (Rosaceae) forest of central Ecuador. *Biotropica*.

CIERJACKS, A., K. WESCHE, AND I. HENSEN in press. Potential lateral expansion of *Polylepis* forest fragments in central Ecuador. *For. Ecol. Manage*.

CONTRIBUTIONS TO CONFERENCES

British Ecological Society Annual Meeting, University of Oxford, UK, 5 – 7 September 2006

WESCHE, K., **A. CIERJACKS,** A. YOSEPH, AND I. HENSEN. Reproduction of tree species at tropical-alpine treelines in Ecuador and Ethiopia. (Talk)

II congreso de ecología y conservación de bosques de Polylepis, Cusco, Peru, May 2006

CIERJACKS, A., I. HENSEN, AND K. WESCHE. Impactos de la altura y de la intervención humana sobre la regeneración de *Polylepis* spp. en la cordillera oriental de los Andes Ecuatorianos. *Libro de Resumenes*: 44. (Talk)

IGLESIAS, J.E., **A. CIERJACKS,** S. LEON-YANEZ, AND H. NAVARRETE. Germinación de *Polylepis incana* Kunth y *Polylepis pauta* Hieron., en vivero y en el límite altitudinal del bosque. *Libro de Resumenes*: 106. (Poster)

SALGADO, S., **A. CIERJACKS,** AND S. LEON-YANEZ. Impacto de la quema sobre la regeneración de especies de *Polylepis pauta* Hieron., *Polylepis incana* Kunth, en los Páramos de Papallacta e Itulcachi, en las provincias de Napo y Pichincha, Ecuador. *Libro de Resumenes*: 36. (Talk)

XXIX Jornadas ecuatorianas de biología, Manta, Ecuador, 24 – 26 November 2005

IGLESIAS, J.E., **A. CIERJACKS,** S. LEON-YANEZ, AND H. NAVARRETE. Germinación de *Polylepis incana* Kunth y *Polylepis pauta* Hieron. en vivero y en el límite altitudinal del bosque. *Resumenes*: 41. (Talk)

SALGADO, S., **A. CIERJACKS,** AND S. LEÓN-YÁNEZ. Impacto de la quema sobre la regeneración de especies de *Polylepis pauta* Hieron., *Polylepis incana* Kunth, en los Páramos de Papallacta e Itulcachi, en las provincias de Napo y Pichincha, Ecuador. *Resumenes*: 42. (Talk)

III congreso de conservación de la biodiversidad de los Andes y de la Amazonía, Loja, Ecuador, 14 – 17 November 2005

SALGADO, S., **A. CIERJACKS,** AND S. LEÓN-YÁNEZ. Impacto de la quema sobre la regeneración de especies de *Polylepis pauta* Hieron., *Polylepis incana* Kunth, en los Páramos de Papallacta e Itulcachi, en las provincias de Napo y Pichincha, Ecuador. *Resumenes del III congreso de conservación de la biodiversidad de los Andes y de la Amazonía*: 111. (Talk)

35. Annual Conference of the GfÖ, Regensburg, 19 – 23 September 2005

CIERJACKS, A., N.K. RÜHR, K. WESCHE, AND I. HENSEN. Reproduction, stand structure and the impact of trampling by cattle on *Polylepis* species along an altitudinal gradient in the Páramo de Papallacta, Ecuador. *Verh. Ges. Ökol.* 35: 231. (Talk)

18. Annual Conference of the GFÖ – Section Plant Population Biology, Potsdam, 04 – 08 May 2005

CIERJACKS, A., N.K. RÜHR, K. WESCHE, AND I. HENSEN. Reproduction, stand structure and the impact of trampling by cattle on *Polylepis* species along an altitudinal gradient in the Páramo de Papallacta, Ecuador. *Progress in plant population biology*: 63. (Poster)

RÜHR, N.K., **A. CIERJACKS,** K. WESCHE, I. HENSEN, H. PFANZ, AND G. ASCHAN. Impact of altitude on seed production and quality of *Polylepis incana* in the Páramo de Papallacta, Ecuador. *Progress in plant population biology*: 86. (Poster)

Ecología y conservación de bosques montanos, Córdoba, Argentina, 10 February 2005

CIERJACKS, A. Regeneración de *Polylepis incana* y *P. pauta* en la Cordillera Oriental de los Andes Ecuatorianos. *Ecología y conservación de bosques montanos*: 6. (Talk)

IGLESIAS, J.E., **A. CIERJACKS,** S. LEON-YANEZ, AND H. NAVARRETE. Germinación de *Polylepis incana* Kunth y *Polylepis pauta* Hieron, en vivero y en la zona de bosques de altura. *Ecología y conservación de bosques montanos*: 17. (Poster)

SALGADO, S., **A. CIERJACKS,** AND S. LEÓN-YÁNEZ. Impacto de la quema sobre la regeneración de especies de *Polylepis pauta* Hieron., *Polylepis incana* Kunth. y *Gynoxys acostae* Cuatrec, en los páramos de Papallacta e Itulcachi. *Ecología y conservación de bosques montanos*: 19. (Poster)

ERKLÄRUNG ÜBER DEN PERSÖNLICHEN ANTEIL AN DEN PUBLIKATIONEN

Die folgende Auflistung gibt einen Überblick über meinen persönlichen Anteil an den hier zusammengestellten Publikationen mit Co-Autorenschaft:

IMPACT OF ALTITUDE AND CATTLE TRAMPLING ON *POLYLEPIS* REGENERATION ALONG A TREELINE IN SOUTH-AMERICA

Datenerhebung: Felderhebung: 100%

Bodenanalyse: Durch Nadine Rühr

Keimfähigkeitsanalyse: 50% in Zusammenarbeit mit Nadine Rühr

Datenanalyse: 100%

Schriftliche Umsetzung: 90% (Korrekturen durch Isabell Hensen und Karsten Wesche)

POTENTIAL LATERAL EXPANSION OF *POLYLEPIS* FOREST FRAGMENTS IN CENTRAL ECUADOR

Datenerhebung: 100%

Datenanalyse: 100%

Schriftliche Umsetzung: 90% (Korrekturen durch Isabell Hensen und Karsten Wesche)

IMPACT OF SOWING, CANOPY COVER AND LITTER ON SEEDLING DYNAMICS OF TWO *POLYLEPIS* SPECIES AT UPPER TREELINES IN CENTRAL ECUADOR

Datenerhebung: Einrichtung der Dauerflächen, Anfangs- und Abschlusserhebung: 100%

Aussaat: 50% in Zusammenarbeit mit Juan Iglesias

Flächenmonitoring: 10% in Zusammenarbeit mit Juan Iglesias

Datenanalyse: 100%

Schriftliche Umsetzung: 95% (Korrekturen durch Isabell Hensen und Karsten Wesche)

POST-FIRE TREE SEEDLING DYNAMICS IN HIGH-ALTITUDE *POLYLEPIS* (ROSACEAE) FORESTS OF CENTRAL ECUADOR

Datenerhebung: Einrichtung der Dauerflächen, Anfangs- und Abschlusserhebung: 100%

Aussaat: 50% in Zusammenarbeit mit Silvia Salgado

Flächenmonitoring: 10% in Zusammenarbeit mit Silvia Salgado

Datenanalyse: 100%

Schriftliche Umsetzung: 95% (Korrekturen durch Isabell Hensen und Karsten Wesche)

Halle (Saale), den

Unterschrift:

CURRICULUM VITAE

Name: Arne Cierjacks

Geburtsdatum und -ort: 4.4.72 in Karlsruhe
Geschlecht: männlich
Staatsangehörigkeit: deutsch
Familienstand: verheiratet, 3 Kinder
Anschrift: Treskowstr. 25
13165 Berlin
Tel. +49-30-44 34 11 06
Email: arne.cierjacks@gmx.de

Aus- und Weiterbildung

Ab 10/2003	**Martin-Luther-Universität Halle-Wittenberg** Promotion in Biologie im Rahmen des Forschungsvorhabens „Mechanismen der Regeneration von Gehölzen tropisch-alpiner Waldgrenzen“.
01 – 12/2001	**Seminar für ländliche Entwicklung (SLE) an der Humboldt-Universität zu Berlin** Aufbaustudium mit folgenden Schwerpunkten: Projektmanagement Monitoring & Evaluierung Teamarbeits-, Moderations- und Präsentationstechniken
04/1993 – 10/2000	**Freie Universität Berlin** Studium der Biologie und Biochemie. Diplomarbeit: *Auswirkungen silvipastoraler Nutzung auf Regeneration und Bestandsstruktur einer mediterranen Waldgesellschaft in Südostspanien.* Prädikat: sehr gut. Studienschwerpunkte: Botanik, Bodenkunde, Tropenökologie, Genetik an Nutzpflanzen, Molekularbiologie.
02/1992 – 03/1993	**Städtisches Klinikum Karlsruhe** Zivildienst.
06/1991	**Gymnasium Neureut** Allgemeine Hochschulreife.

Berufserfahrung (Angestellter)

10/2003 – 10/2006	**Martin-Luther-Universität Halle-Wittenberg** Wissenschaftlicher Mitarbeiter für das Forschungsvorhaben „Mechanismen der Regeneration von Gehölzen tropisch-alpiner Waldgrenzen“ im ecuadorianischen Projektteil.
06/2002 – 12/2003	**Umweltbundesamt/Deutscher Evangelischer Kirchentag, Fulda** Mitarbeiter zum Aufbau eines Umweltmanagement- und Indikatorensystems für die Großveranstaltung.
04/1998 – 03/2001	**Freie Universität Berlin, Institut für Systematische Botanik und Pflanzengeographie** Tätigkeit als studentische Hilfskraft mit Lehraufgaben. Schwerpunkte: Pflanzenökologie und Systematik.
10/1998 – 09/1999	**Freie Universität Berlin, Zentrales Projekttutorienprogramm** Studentische Hilfskraft. Organisation einer einjährigen universitären Veranstaltungsreihe zum Thema „Nachhaltige Nutzung der tropischen Feuchtwälder in Ecuador, Bolivien und Peru“.
	Eigene Schwerpunkte: tropische Forstwirtschaft, Agroforstsysteme, Biodiversität.

Freiberufliche Tätigkeiten

10/2005	**Deutsche Welthungerhilfe e.V.** Erstellung eines Projektvorschlags für den Namha Nationalpark, Nordlaos, zum Tropenwald-Programm der Europäischen Kommission.
04 – 10/2005	**Deutscher Evangelischer Kirchentag, Fulda** Weiterführung des Umweltmonitoring zum Evangelischen Kirchentag 2005 in Hannover.
04 – 10/2003	**Bundesamt für Strahlenschutz/Newscope GbR, Gilching** Aufbau einer Datenbank zum Verhalten transuraner Radionuklide in Waldökosystemen im Rahmen des Forschungsvorhabens „FASSET – Framework for Assessment of Environmental Impact“.
04 – 10/2002	**Bundesamt für Strahlenschutz/Newscope GbR, Gilching** Entwicklung einer Datenbank zur Aufnahme von Radionukliden durch Nutzpflanzen im Rahmen des Projekts St.Sch 4222.
02 – 06/2002 und 02/2003	**Seminar für Ländliche Entwicklung** Dozent im Rahmen des Lehrmoduls Monitoring und Evaluierung, Redaktion von Hausveröffentlichungen.

07 – 10/2001	**United Nations Volunteers (UNV)/Seminar für ländliche Entwicklung, Berlin/Otavalo, Ecuador** Evaluierung eines Ressourcenschutzprojekts in Ecuador. Entwicklung eines Evaluierungssystems für UNV.
10/2000 – 04/2001	**C+S Consult, Berlin** Baumgutachten, Biotoptyp- und Avifauna-Kartierungen im Berliner Raum.

Ausgewählte Studienpraktika

04 – 06/1997	**Universidad austral de Chile, Valdivia, Chile** Forschungspraktikum zum Thema „Degradation des Bodens und der Vegetation des Valdivianischen Regenwaldes“.
09 – 10/1997	**Phytobacter GmbH, Wallmow, Mecklenburg-Vorpommern** Forschungspraktikum im Bereich Bodenmikrobiologie. Untersuchung der Auswirkungen von Pflanzenschutzmitteln auf Bodenbakterien.
09 – 10/1994	**Agrargenossenschaft Brodowin, Biosphärenreservat Schorheide-Chorin** Hofpraktikum auf dem Biobetrieb.

Halle (Saale), den

Unterschrift:

Veröffentlichungen

CIERJACKS, A., J.E. IGLESIAS, K. WESCHE, AND I. HENSEN in press. Impact of sowing, canopy cover and litter on seedling dynamics of *Polylepis* species at upper treelines in central Ecuador. *J. Trop. Ecol.*

CIERJACKS, A., N.K. RÜHR, K. WESCHE, AND I. HENSEN accepted. Impact of altitude and cattle trampling on *Polylepis* regeneration along a treeline in South-America. *Plant Ecol*.

CIERJACKS, A., S. SALGADO, K. WESCHE, AND I. HENSEN submitted. Post-fire tree seedling dynamics in high-altitude *Polylepis* (Rosaceae) forest of central Ecuador. *Biotropica*.

CIERJACKS, A., K. WESCHE, AND I. HENSEN in press. Potential lateral expansion of *Polylepis* forest fragments in central Ecuador. *For. Ecol. Manage*.

CIERJACKS, A., UND H. DIEFENBACHER in press.: Umwelt-Controlling bei Großveranstaltungen – ein Pilotprojekt des Deutschen Evangelischen Kirchentages. *Zeitschrift für angewandte Umweltforschung*.

CIERJACKS, A., UND H. DIEFENBACHER 2006. Vom Recyclingpapier bis zur Nullemission – Umweltmanagement beim Deutschen Evangelischen Kirchentag. In Altner, G., H. Leitschuh-Fecht, G. Michelsen, U.E. Simonis, und E.U. v. Weizsäcker, (Hrsg.). *Jahrbuch Ökologie 2007*, pp. 174–182. Verlag C.H. Beck. München.

CIERJACKS, A., AND I. HENSEN 2004. Variation of stand structure and regeneration of mediterranean holm oak along a grazing intensity gradient. *Plant Ecol.* 173: 215–223.

CIERJACKS, A., I. HENSEN, AND P. SANCHEZ 2002. Effects of grazing on the species composition in a holm oak forest community of south-eastern Spain (*Adenocarpo decorticantis-Quercetum rotundifoliae* Rivas Martínez 1987). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 123: 447–461.

CIERJACKS, A. 2005. *Umweltkennzahlen. Ergebnisse aus dem Umweltcontrolling für die Jahre 2004 und 2005.* Deutscher Evangelischer Kirchentag, Fulda.

CIERJACKS, A., UND B. ALBERS 2004. Zusammenstellung und Auswertung von radio-ökologischen Messdaten zum Transfer Boden/Pflanze unter Berücksichtigung der lokalen Variabilität in Deutschland. St.Sch.-Nr. 4220. In Bergler, I., C. Bernhard, R. Gödde, A. Löbke-Reinl, und A. Schmitt-Hannig (Hrsg.). *Strahlenschutzforschung Programmreport 2002*, pp. 81–86. BfS-Reihe "Strahlenschutz und Gesundheit" Nr. 4.

CIERJACKS, A., UND B. ALBERS 2004. Zusammenstellung und Auswertung von radio-ökologischen Messdaten zum Transfer Boden/Pflanze unter Berücksichtigung der lokalen Variabilität in Deutschland. *Schriftenreihe Reaktorsicherheit und Strahlenschutz* 642: 1–53.

CIERJACKS, A., UND H. DIEFENBACHER 2003. Wenn man auf Papphockern sitzen bleibt – Öko-Controlling bei Kirchentagen; Ergebnisse eines Pilotprojekts. *Kirchentag aktuell* 4: 7.

ANTEZANA, I., A. CIERJACKS, M. HEIN, G. JIMÉNEZ, Y A. RÜTH 2001. Diseño y verificación de un marco metodológico para la evaluación de proyectos del Servicio de Voluntarios de las Naciones Unidas (VNU). Evaluación del proyecto Randi-Randi en Ecuador. *Schriftenreihe des Seminars für Ländliche Entwicklung* 191: 1–283.

CIERJACKS, A., T. FLÄMIG, M. HEIN, A. RÜTH, UND A. WULF (Hrsg.) 2001. Entwicklungspolitische Diskussionstage 2001. *Schriftenreihe des Seminars für Ländliche Entwicklung* 190: 1–142.

CIERJACKS, A. 2001. Quo vadis Entwicklungszusammenarbeit? Die "Entwicklungspolitischen Diskussionstage" in den Hackeschen Höfen. *Humboldt* 5/6: 8.

EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass diese Arbeit nicht bereits zu einem früheren Zeitpunkt der Naturwissenschaftlichen Falkultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg oder einer anderen wissenschaftlichen Einrichtung zur Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Im Übrigen erkläre ich, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den

Unterschrift:

Arne Cierjacks