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 hypotheses. 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\textsubscript{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. 2004).
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).


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](image)

*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. paauta* 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](image-url)  
*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 Guíñiz 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](image-url)

*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 circumpolarly 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](image)

*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.

![Forest Stand Images](image1.png)

*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.