Tree Growth History, Stand Structure, and Biomass of Premontane Forest Types at the Cerro Tambo, Alto Mayo, Northern Peru

Historia del Crecimiento Arbóreo, Estructura Vertical, y Biomasa de Diferentes Tipos de Bosque Premontanos en el Cerro Tambo, Alto Mayo, al Norte del Perú,

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Abstract
Tree growth and biomass accumulation were studied for two structurally contrasting premontane forest types occuring from 1200 -1600 m a.s.l. at the Cerro Tambo, Region Alto Mayo in Peru. The premontane vegetation at the Cerro Tambo consists of a mosaic of poor heath forests and well developed premontane rain forests. Within each forest type, the variation in species composition and aboveground biomass is small compared to the dramatic differences between the heath forests and the rain forests. Mosaic type heath forest establishment in a zone with potential dense rain forest cover could be a result of rare recurring natural fires on a secular scale. This may trigger a series of successional stages which leads to irreversible deterioration of site quality under current conditions. In order to test this hypothesis, information on stand structure, tree growth rates, and tree age was obtained for describing the growth dynamics of the contrasting forests and for detecting presence or absence of stand growth depression within the life span of old growth individuals. Tree ring analysis of 106 trees from sites along an altitudinal gradient showed that all forests of the Cerro Tambo area are characterized by low annual tree growth rates. Heath forests and tall rain forests show pronounced difference in growth rates. Heath forests are young and no individuals older than 45 years were found. In contrast, tall rain forests trees of more than 150 years in age were found. We conclude that heath forests are most likely successional stages after fairly recent disturbance, probably by natural fires. A linear positive increase in tree growth in all forest plots and a further increase in the past two decades may be attributed to a combined effect of the increasing atmospheric CO_2 concentration and a recent increase in atmospheric deposition of nutrients.

Resumen
Las transiciones abruptas entre el bosque lluvioso de alta montaña a lo largo grandes islas de chamizales bajo condiciones locales idénticas de geología, topografía y clima es común en el área del Cerro Tambo. La alteración por los derrumbes es insignificante. La influencia de la presencia humana puede excluirse debido a la lejanía. Los chamizales tipo mosaico establecidos cerca a una zona cubierta con potencial bosque lluvioso denso podrían ser el resultado de la alteración natural. La única alteración creíble en esta área podría ser los incendios. Ninguna evidencia de fuego directa se ha encontrado (carbón de leña), pero la vegetación natural puede arder fácilmente y una observación en las áreas intervenidas muestra que los incendios se provocan por sí mismos durante la estación seca. La frecuencia de incendios naturales podría ser baja y en una escala esporádica. Los incendios también pueden activar una serie de fases

sucesorias que llevan a la deterioración irreversible de la calidad del lugar bajo las condiciones actuales. Bien podría ser, que estos eventos, - aún esporádicos -, lleven a cambios sustanciales en las propiedades del suelo, en el rebrote de árboles y la recuperación de estos bosques lluviosos altos puede tomar de décadas a siglos. Todos los bosques del área del Cerro Tambo, se caracterizan por las proporciones anuales de crecimiento arbóreo muy bajas. Los chamizales y los bosques lluviosos altos no muestran ninguna diferencia en las proporciones de crecimiento. Los chamizales son jóvenes y ningún especímen mayor a 45 años fue encontrado. En contraste, en los bosques lluviosos altos se encontraron árboles de más de 150 años de edad. Concluimos que los chamizales pueden ser una fase sucesional después de una reciente alteración, lo más probable los incendios naturales.

Introduction

Abrupt transitions from tall rain forest to large islands of low heath forest under identical local conditions of geology, topography, and climate are commonly found in the Cerro Tambo Region of the Alto Mayo Valley, Northern Peru (Fig. 1).

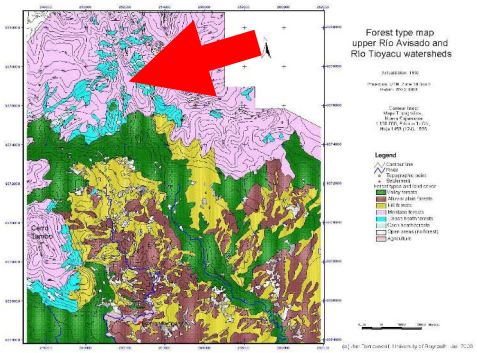

Fig.1. Heath forest islands (blue) within tall montane rain forests (magenta). Forest map from Dempewolf (2000).

Fig.2. Tall rain forest on the flanks and heath forests on top of a mountain ridge near the Cerro Tambo peak, Peru. The photo is taken at 1170 m a.s.l. (5.7216°S / 77.2604° W) 26.03.99

In this tropical montane area over cretaceous sandstone formations with moderate topography, disturbance by landslides is very marginal and restricted to steep canyon walls (Fig.2). Recent and historic anthropogenous influence can be excluded due to the remote location. Historically the lowland terraces of the Alto Mayo were inhabited by a few Aguaruna tribes but the montane region was visited for occasional hunting only. The sparse macro-fauna has no impact on the forest distribution.

The differences in forest structure at the Cerro Tambo are quite striking. While the rain forest vegetation have a closed canopy with tree heights of more than 30 m, the heath forests are shrubs or small trees of up to 4 (max. 8 m) with grasses and herbs in the understorey. Heath forests exhibit both xeromorphic structures as well as peinomorphic features, both supposedly pointing toward increased competition for water and nutrient resources.

A detailed study of soils (Dempewolf, 2000; Börner 2001) showed that variation in soil structure and composition could not explain the current vegetation distribution. In a subsequent eco-physiologically oriented study of the vegetation water use and mineral nutrition by Mette (2001) it turned out, that both vegetation types did neither differ much in water consumption, which was low, nor in the nutritional status of plants which was also low but not critical. However it was

found that under conditions of an extended dry season, the rain forest was more susceptible to water stress and drought damage and that soil water storage was more critical. During the study of Mette (2001), the seasonal drought broke just a few days before the soil water storage in the rain forest became completely depleted. However, in drier years, the critical point of irreversible drought damage could be reached. It was observed that during the dry season man made slow burning forest fires maintain themselves for several days until the next rainfall, demonstrating the potential for spatially limited fire disturbance in these montane rain forests.

Fig. 3. Tree disc of *Ocotea* sp. (Lauraceae), 157 years old, from a tall rain forest site at the Cerro Tambo.

The question remained open, what the cause of the peculiar distribution pattern of both forest types was. It was suspected that natural disturbances must cause the occurance of heath forests and that the disturbances must occur spatially irregular. Nothing could be said at this point about temporal patterns of disturbance, since the age of the forest types was not known and successional stages were not obvious due to the lack of transitional stages. Since fire and exceptional drought are both known disturbance factors in forests, we investigated the climatic history, the stand and tree age and the growth patterns over time of both vegetation types.

It was hypothesized, that

(1) Climatic data must indicate coincidence of extended dry seasons at maximum stand lifetime for existing heath forests if drought matters
(2) Spatially limited but massive disturbance like fire must be reflected in stands by contemporal tree establishment (similar maximum age of older individuals).
(3) Growth patterns in old stands must show systematic differences between stand type if edaphic preconditions matter (site quality)

Material and Methods

Climate data from long term weather stations in the Alto Mayo valley and four own weather stations along an altitudinal gradient were analysed. Forest structure, forest composition and soil properties were studied on sites along an altitudinal gradient for heath forest stands and tall rain forest stands. Tree age was analyzed at cross-sectional discs of 106 trees. Annual tree ring formation (Worbes 1989) is present in most woody species of the area. This is most likely caused by the pronounced seasonality in precipitation (Fig. 4). Tree growth ceases during the dry season (Detienne 1989). Sesonal tree ring formation was confirmed in a blind test on discs of several tree species from a helicopter landing site in the area which had a confirmed age of 31 years and was abandoned after a one day use for setting up a trigonometric point in the forest.

Climate

The monthly precipitation sum in the Alto Mayo region may fall to critical levels below 100 mm month^{-1} in some years. Several extended periods of such conditions in the region were recorded at two stations in the Alto Mayo valley over the past fourty years with the most pronounced drought occuring in 1961 (Fig. 5). While tall rain forest and heath forests tolerate short droughts, the vegetation and organic soil matter dries out to critical levels during such times.

Fig. 4. Climate diagram of Rioja (880 m) in the Alto Mayo

Fig. 5. Monthly sum of precipitation from 1959 to 1984 for two meteorological stations at Moyobamba and Rioja in the Alto Mayo valley, Northern Peru.

Drought events at the eastern slopes of the Andes and the subsequent occurance of natural fires could be due to El Niño events. El Niño events at the Pacific coast are supposed to lead to drought effects in the following years along the Eastern Andes. The sea surface temperature of the South Pacific tropical current as a proxy for El Niño events (ENE) in Peru increased slightly from 1959 until recent with several positive deviations indication major ENE (Fig. 6a). Annual precipitation in the Alto Mayo region varied from less than 1000 mm to 2400 mm over the same time period but showed no clear temporal trend (Fig. 6b). Contrary to common assumption, no correlation was found between ENE and years with low precipitation for the Alto Mayo valley.

Fig. 6a. Mean Sea surface temperature deviation (SST) of the South Pacific tropical current from 1958 until 1998.

Fig. 6 b. Annual precipitation in the Alto Mayo valley, measured at Moyobamba (data mising for 1984 and 1984 due to terrorist problems).

Study sites ranged along a transect with varying slopes but similar geology from 1202 to 1570 m a.s.l. with four tall rain forests, two dense, and three open heath forests. Forest cover is much lower in open heath forests. Basal area in one of the open heath forests was surprisingly high with 27 m^2 ha^{-1} (Table 1). Biomass of the tall rain forests (Ogawa et. Al.1965) is significantly higher than in the heath forests and reaches 300 t ha^{-1} (Fig.7) while stem density is higher in most heath forests. Based on the inventory data we suspected that either biomass accumulation (i.e. growth) is lower in the heath forests than in the tall rain forest or that growth rates are comparable but heath forests are significantly younger than tall rain forests and probably exposed to more frequent and significant disturbance.

Stand age and growth rates

Mosaic type heath forests in a zone with potential dense rain forest cover could be the result of natural disturbance. A plausible disturbance in this area are fires, but no direct fire evidence (charcoal) has been found so far in soils. However, natural vegetation can be burnt easily and observation in intervened areas shows that fires maintain themselves during the dry season. The natural fire frequency could be low and on a secular scale. Fires may also trigger a series of successional stages which lead to irreversible deterioration of site quality under current conditions. It might well be, that these events, - while rare -, lead to substantial changes in the soil properties for tree regrowth and the recovery to tall rain forest may take decades to centuries.

			Vegetation cover at 1.2 m	Slope %	Basal area [m ²/ha]
		m.a.s.l			
Tall rain forest	T2	1412	92	52	51
Tall rain forest	T3	1570	92	0	
Tall rain forest	HLC06	1495	84	80	31
Tall rain forest	HLC07	1437	94	36	22
Dense heath fores	T5	1406	82	26	17
Dense heath fores	HLC04	1406	90	80	12
Open heath forest	HLC05	1404	33	73	9
Open heath forest	HLC09	1226	37	29	27
Open heath forest	HLC10	1202	47	44	

Table 1. Site and stand structure paramenters of nine study sites in the Cerro Tambo region, Peru.

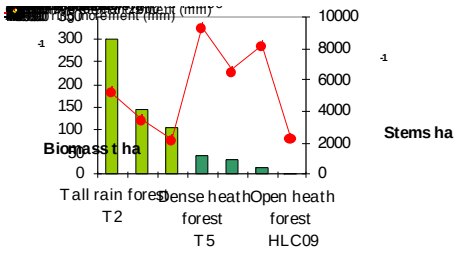

Fig. 7. Biomass and stem density of seven study sites in the Cerro Tambo region, Peru.

Fig. 8. Growth dynamics of trees in a dense heath forests (left) and a open heath forest (right) in the Cerro Tambo region, Peru. Cumulative stem growth (top) and mean annual tree ring width (bottom) with standard deviation (bars) are shown.

Analysis of tree growth and biomass accumulation showed that heath forests are young and all trees on the open and dense heath forest plots turned out to be less than 40 years old (Fig.8). The only tree individual which was found to be several years older showed a significant tree growth depression between 1960 and 1962 followed by high increments in the next years. Growth rates were then low, but between 1 and 1.5 mm year-1 with not much inter-annual variation. A increasing tree growth trend over the last four decades was found in all heath forests plots.

Tall rain forest trees reach much higher age with a 157-year old *Ocotea* sp. (Fig. 3.) being the oldest individual found from tree disk analysis. However, older individuals of probably twice this age are likely but not yet confirmed since tree cores from much larger trees in the same area have not yet been analysed for age. Tree age and annual growth varied more in tall rain forests between individuals compared to heath forests. Mean growth rates for the tall rain forest stands ranged from 0.5 to almost 2.0 mm year-1 and showed a larger inter-annual variability compared to heath forests.

Tall rain forest growth at the Cerro Tambo shows variation, but no sign of major disturbances in tree growth for the past 150 years. Temporal dynamics of tree growth rates for the last four decades in the studied forest stands were not much different between heath forests and tall rain forests. However, superimposed on a small positive linear trend in tree ring width increase over the entire observation time of the past 150 years, an additional recent increase in tree growth in all plots was found after ca. 1985. This increasing trend can be best demonstrated by the growth patterns of the study plot with the longest record at the Cerro Tambo (Fig. 9).

We have no obvious explanation for this positive growth effect based on site properties or climatic records in the region (cf. Fig. 6a and b). Since the tree ring width in all plots has not been geometrically corrected for tree dimension actually a systematic decrease in ring with was expected under steady growth conditions for older tree individuals. The increasing trend will be even stronger if geometric correction will be applied.
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Fig. 9. Mean annual stem radius increment for trees of a tall rain forest site at 1570 m a.s.l. at the Cerro Tambo, Peru. The time series ranges from 1920 until 2000 (n=9).

It seems less likely that only the increase in atmospheric CO_2 promotes the observed growth increase, since the increase of approx. 30 ppm in global CO_2 concentration over the past 15 years does physiologically not justify an observed >30 % increase in carbon allocation to stems. The higher CO_2 availability may be responsible for the positive linear long term trend observed.

For the recent positive shift in growth it is probable that an increase in nutrient deposition, either by long distance transport or locally from the rural development activities in the neighbouring Alto Mayo valley has lead to a better nutrient availability in these ecosystems. From soil analysis it was clear that all forest types are stocking on poor soils and that especially the N and Mg, P, K supply is low (Demewolf 200, Boerner 2001). Consequently, all stands will react positively to an improvement in nutrient supply. The Carretera Marginal has opened the Alto Mayo valley in 1977 to traffic. Intensive agricultural activities, including the application of industrial fertilizers for rice cultivation, started in the early eighties. The agricultural area of the Alto Mayo valley and the Carretera Marginal are less than 20 km direct line away from the Cerro Tambo.
Tree growth rates in the Alto Mayo rgeion decrease with increasing altitude (Fig 11).The studied tall montane rain forests and heath forests at the Cerro Tambo show a significantly lower growth

than forests of the lowlands. The hill areas of the Alto Mayo region vary in growth rates. This variation is caused by different edaphic soil properties. In general, the higher thermal regime in the lowlands and the significantly better nutrient supply on alluvial soils are responsible for high growth rates.

Conclusions

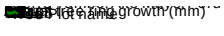

Fig. 10. Annual mean radial tree ring growth for six study sites at the Cerro Tambo, Peru.

Fig. 11. Annual radial increment of trees of the Alto Mayo region, Peru.

All forests of the Cerro Tambo area are characterized by low annual tree growth rates. Heath forests and tall rain forests show pronounced difference in growth rates. Heath forests are young and no individuals older than 45 years were found. In contrast, tall rain forests trees of more than 150 years in age were found. We conclude that heath forests are most likely successional stages after fairly recent disturbance, probably by natural fires. This needs to be confirmed by direct evidence. A linear positive increase in tree growth in all forest plots and a further increase in the past two decades may be attributed to a combined effect of the increasing atmospheric CO_2 concentration and a recent increase in atmospheric deposition of nutrients.

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