Water availability and transpiration behavior of adjacent heath and rain forest stands of the *Selva Alta* in North Peru during the transition from dry to wet period

Disponibilidad de agua del suelo y transpiración de árboles durante la transición del periodo seco al periodo húmedo en dos bosques adyacentes: un chamizal y una selva lluviosa en la Selva alta del Norte del Perú

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Abstract
Stand structure and water balance (soil moisture, canopy transpiration) of a 5-8 m tall heath forest and a 20-35 m tall rain forest were studied at two experimental sites, 1400 m a.s.l. on the Cerro Tambo East slope in Alto Mayo, North Peru, during the transition from the dry to the wet season in September 2000.

Stand structure differed clearly: basal area was 16.6 m^2 ha^{-1} for the heath forest and 50 m^2 ha^{-1} for the rain forest, and biomass 56 t ha^{-1} and 291 t ha^{-1} respectively.

Both heath and rain forest stood on sandy podzols with a 40 and 25 cm thick O-(organic) horizon of peat-like consistence and sandy A/B-(mineral) horizons. In both O- and A-horizon of the rain forest and in the A-horizon of the heath forest the soil moisture did not exceed 0.25 m^3_{H2O} m^{-3}_{soil} even during the wet period. At the end of the dry season, soil moisture had even dropped to a critical level of 0.1 m^3_{H2O} m^{-3}_{soil}. Only the O-horizon of the heath forest possessed a higher soil moisture of 0.4 m^3_{H2O} m^{-3}_{soil} during the wet season and 0.3 m^3_{H2O} m^{-3}_{soil} at the end of the dry season.

Canopy transpiration was low, too. For the rain forest an average of 1.01 kg H_2O m^{-2} d^{-1} was calculated and 0.73 kg H_2O m^{-2} d^{-1} for the heath forest. In both forest types, the canopy transpiration was not affected by the dry season.

Resuming, neither soil moisture nor canopy transpiration are significantly lower in the heath forest than in the rain forest. Hence, the distribution of heath forests at the Cerro Tambo is not restricted to soils of a poor water storage capability. During elongated dry periods, the rain forest might even be at a higher risk of drying out.

Other factors than temporary water shortage have to be evoked to explain the distribution of heath forest patches within rain forests. A possible scheme has been lined out, including factors like geology, nutrient availabilit, and succesion after fire.

Resumen
En este proyecto se estudió la estructura, la flora y el balance hídrico (humedad del suelo y transpiración de la copa) de dos tipos de bosques: un chamizal con una altura de 5-8 m y una Selva tropical de 20-35 m – en dos campos experimentales sobre la pendiente oriental del Cerro Tambo (1400 m s.n.m.) en la región del Alto Mayo (Perú), durante la transición del periodo seco al periodo húmedo en septiembre de 2000.

La estructura de los bosques se definió de forma clara: un área basal de 16.6 m^2 ha^{-1} en el chamizal y un área de 50 m^2 ha^{-1} en la selva alta, y biomasas (troncos) de 56 t ha^{-1} y 291 t ha^{-1} respectivamente. Los dos campos se sitúan sobre suelos podzolicos arenosos con un horizonte orgánico de 40 cm para el chamizal y de 25 cm para la selva, ambos con una consistencia parecida a la de la turba. En los horizontes orgánico y mineral de la selva alta y en el horizonte mineral del chamizal, la humedad del suelo no excedió 0.25 m^3_{H2O} m^{-3}_{soil} incluso durante el periodo húmedo. Al final del periodo seco, la humedad del suelo había descendido a un nivel crítico de 0.1 m^3_{H2O} m^{-3}_{soil}. Solamente en el horizonte orgánico del chamizal se observó una humedad del suelo mayor de 0.4 m^3_{H2O} m^{-3}_{soil} durante el periodo húmedo y de 0.3 m^3_{H2O} m^{-3}_{soil} al final del periodo seco.

La transpiración de la copa puede considerarse baja ya que el promedio calculado para la selva alta fue de 1.01 kg H_2O m^{-2} d^{-1} y de 0.73 kg H_2O m^{-2} d^{-1} para el chamizal. En ambos casos, la transpiración de la copa no se vió sensiblemente afectada durante el periodo seco.

En resumen, ni la humedad del suelo ni la transpiración de la copa eran perceptiblemente más bajas en el chamizal que en la selva alta. Por lo tanto, la distribución de los chamizales sobre el Cerro Tambo no está correlada con suelos de pobre capacidad de conservación del agua. Durante largos períodos secos, la selva alta podría tener un mayor riesgo de secarse.

Se han de incluir otros factores como geología, disponibilidad de nutrientes, las toxicidades y succesion después del fuego para poder explicar la distribución de chamizales dentro de selvas tropicales.

Introduction

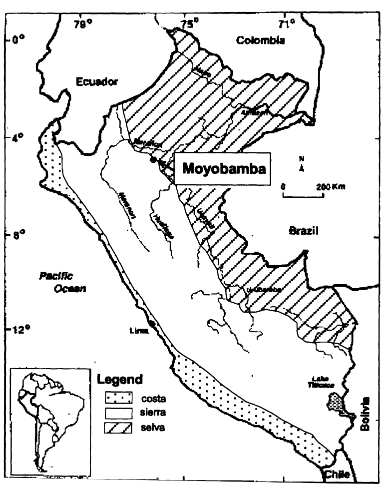


Fig. 1: The Río Mayo drains parts of the northeastern slopes of the Peruvian Andes. Moyobamba is the major city of the upper Río Mayo valley (Alto Mayo), where the study area was located.

There are numerous examples for the occurrence of heath forest islands within tropical rain forests, e.g. *Pandang* and *Keranga* vegetation in Malesia (Specht & Wormersley1979), *Muri* in Guyana (Cooper 1979), *Caatingas* at the Río Negro, Venezuela (Klinge & Medina 1979).
Most authors regard heathland in general as consequences of a low soil nutrient status. In the case of the *Keranga*, *Muri* and *Caatinga amazonica*, the soils often possess a sandy texture and a low CEC, like podzols and arenosols. Besides the poor CEC, the low water storage capacity of such sandy soils might be another limiting factor for tree growth, especially in regions with temporal dry periods.
In the pre-montane zone (1200-1400 m a.s.l.) of the Río Mayo valley (*c.f.* Fig. 1), the pristine vegetation over cretaceous sandstone consists of a mosaic of either 5-8 m tall heath forests with twisted trees or 20-35 m tall well developed rain forests, often forming sharp transitions. There are no obvious signs of anthropogeneous or natural disturbances like landslides or fires that would support the theory of a successional connection of the two forest types. And since regional climate, geology, topography, and altitude are also identical, the reason for the occurrence of such contrasting forests may be related to small scale variation in soil water and/or nutrient availability, since the physiognomy of the heath forest can be understood both as xeromorphic or peinomorphic. The study focused on the question if heath forests in the study area were a

xeromorphic vegetation, adapted to (at least temporal) soil water scarcity, whereas rain forests grew on more favorable soils of the region with good water availability.

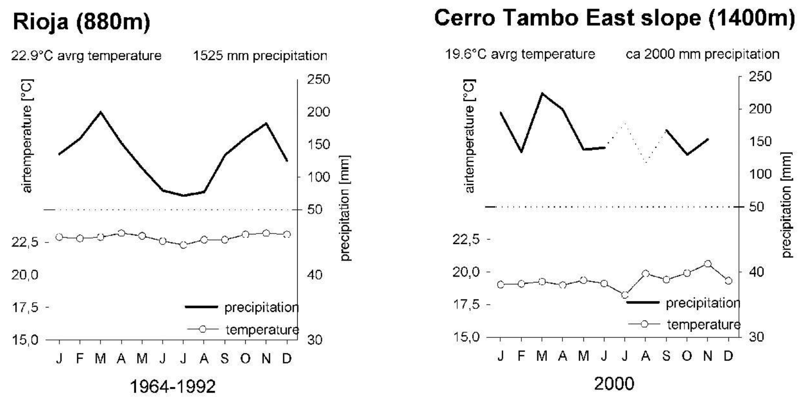


Fig. 2: climate diagrams (left) for Rioja at the bottom of the Río Mayo valley (1964-1992) and (right) the Cerro Tambo East slope at 1400 m a.s.l. (2000; dotted line indicate extrapolated data).

Methods

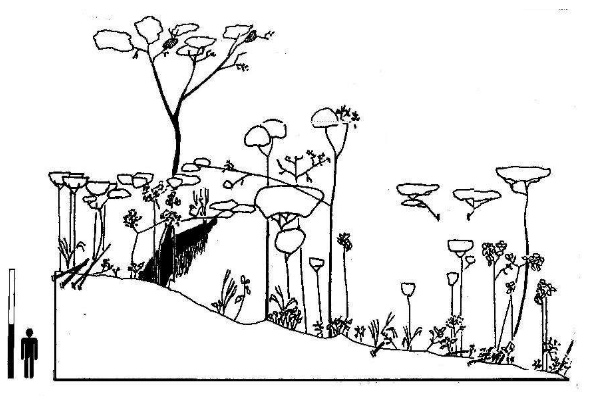
The two experimental sites, one heath forest and one rain forest site, were located 200 m apart on a crest of the Cerro Tambo East slope at an altitude of 1400 m a.s.l.. In the vicinity of the study sites, an automatic weather station (WS1, Delta-T devices) was put up to record the regional climate (*c.f.* Fig. 2).

Stand structure and flora of both sites were documented and a transect was drawn (*c.f.* Fig. 3). Basal area was 16.6 m ha^{-1} in the heath forest and 50 m ha^{-1} in the rain forest; stem biomass 56 t ha^{-1} and 291 t ha^{-1} (Ogawa 1965, using regressions of comparable monsoon forests).

In the heath forest, the most abundant trees belonged to the Clusiaceae, Melastomataceae, Araliaceae, Chrysobalanaceae and Theaceae. Highly abundant and apparently vital was *Humiria balsamifera* (Humiriaceae). The rain forest tree spectrum consisted mostly of Moraceae, Euphorbiaceae (highly abundant: *Pera* (valde) *officinalis*), Sapotaceae, Lauraceae and also Melastomataceae.

At both sites, soil moisture was measured in a depth of 25 cm (organic horizon) and 50 cm (mineral horizon) using Theta probes (ML2, Delta-T devices). To estimate canopy transpiration, xylem flux sensors with a constant heat dissipitation were inserted into 15 trees each site (Granier 1985). Soil moisture and tree transpiration data were continuously recorded in 30 min intervals from the beginning of September until mid December 2000. Transpiration was scaled up to the stand on a daily basis.

Fig.: 3: Transect (left) near the heath forest and (right) near the rain forest study site. Transect length is 20 m, the meter steps are 2 m.. Tress in the rain forest reach easily 25 m, trees in the heath forest seldom 10 m.

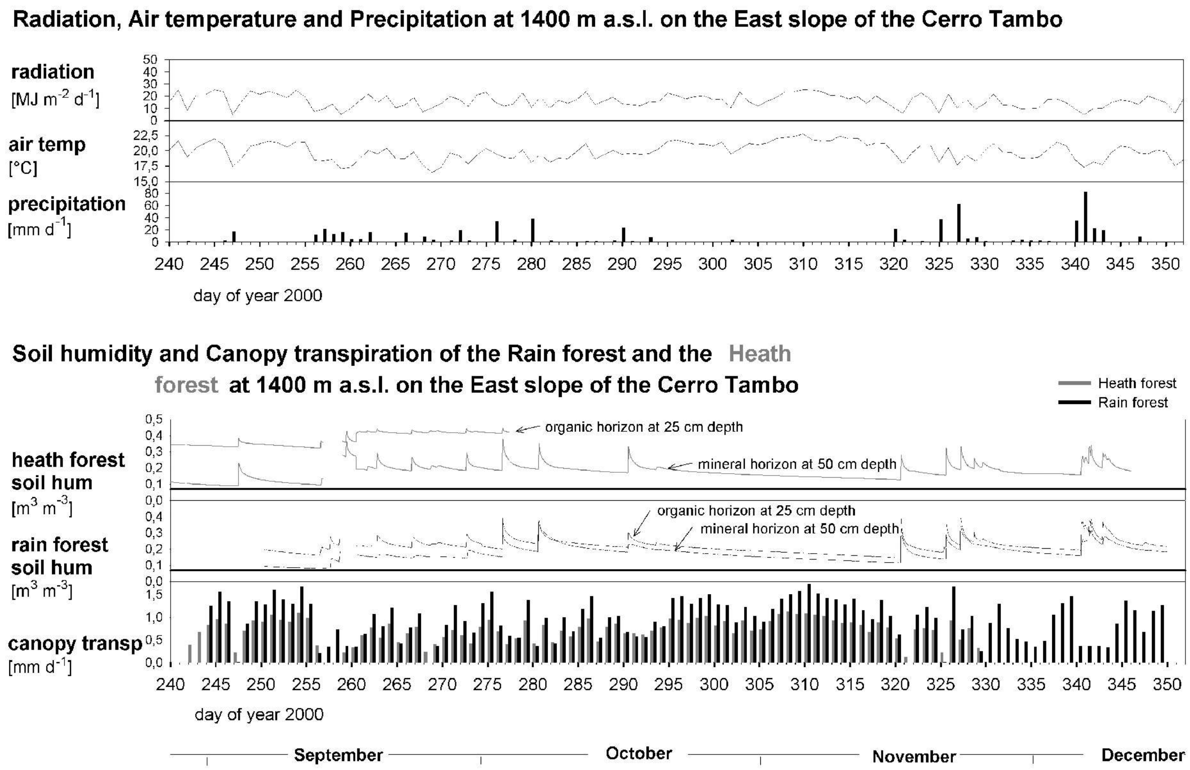


Results / Discussion

As shown in Fig. 4, the initial rains that broke the dry period began on day 256 (September 13). After this day, the soil moisture level in heath and rain forest rose again. On day 255, the soil moisture of the mineral horizon was 0.10/ 0.08 m^3_{H2O} m^{-3}_{soil} in the heath/ rain forest - close to the estimated limit of plant available soil water at 0.07 m^3_{H2O} m^{-3}_{soil} (KA4, AG Boden 1995). On day 264, after a week of rain, the soil moisture of the mineral horizon was 0.20/ 0.15 m^3_{H2O} m^{-3}_{soil} respectively.
The soil moisture of the peat-like organic horizons did never drop to 0.1 m^3_{H2O} m^{-3}_{soil}. For the rain forest was measured 0.16 m^3_{H2O} m^{-3}_{soil} on day 255 (end of dry season) and 0.23 m^3_{H2O} m^{-3}_{soil} on day 264 (beginning of wet season), for the heath forest 0.32 m^3_{H2O} m^{-3}_{soil} and 0.42 m^3_{H2O} m^{-3}_{soil}, respectively. The organic horizon may be an important water storage, especially in the heath forest.
If the low soil moisture level at the end of the dry season was a stress factor for the plants, it would show in a decreased transpiration. The opposite was the case: the canopy transpiration of both heath and rain forest dropped (!) with the beginning of the wet season. This has to be interpreted as an effect of the reduced light offer during the rain-clouded days. The low soil moisture at the end of the dry season did not limit the transpiration.
The absolute canopy transpiration was very low and did not differ much between heath forest and rain forest: in average 0.73 kg H_2O m^{-2} d^{-1} in the heath forest and 1.01 kg H_2O m^{-2} d^{-1} in the rain forest. One should be aware that the abundant undergrowth of the heath forest contributed an undetermined amount to the total stand transpiration.
Canopy transpiration for a (lowland) rain forest is usually given with 3-4 mm day^{-1} (Jordan & Kline 1977, Larcher 1994). But even when comparing our estimated transpiration with more recent results from OREN et al. (1996), < 2 mm day^{-1}, the studied heath and rain forest still have to be a vegetation that is adapted to the constant low water availability of the sandy soils of the region. This theory seems to be further supported by the fact, that –to our astonishment– another unexpected dry period occurred between mid October and mid November 2000 (day 291-321),

when rainfall was supposed to be high (*c.f.* Fig. 2). The risk of water scarcity is not restricted to the dry season from May to August and December.

Fig. 4: (up) Climate parameters: radiation, airtemperature and precipitation as recorded at the automatic weather



station at 1400 m a.s.l. on the Cerro Tambo East slope and
(down) soil moisture and canopy transpiration as measured for the heath forest and rain forest study side on the Cerro Tambo East slope

Based on the results, the initial question if the heath forests on the Cerro Tambo were a xeromorphic counterpart of the rain forest, growing on the most adverse soils in terms of water scarcity, has to be denied. During elongated dry periods (perhaps in El Niño years) it is even rather the rain forest that is at risk of drying out.

In Tab. 1, we tried to gather the presented results together with further investigations that were not mentioned here (Dempewolf 2000 unpubl., Börner 2000 unpubl., Mette 2001, unpubl., Dietz 2002 in prep), into a scheme that lines out probable factors that determine the distribution of heath and rain forests in the Cerro Tambo region.

The basic assumption was that heath forests grow on adverse soils, poor in water storage and nutritient mineral stock. As the heath forest matures and becomes denser, rain forest species might invade and eventually take over. In favorable soils rain forest might quickly follow another type of pioneer vegetation. The distribution of heath forests would represent the distribuition of fires in the past, and the ratio heath forest: rain forest cover might be stable fire-dependent equilibrium.

Tab. 1: Summary of important factors for the distribution of heath forest and rain forest: geology, soil parameters, soil moisture (vs) transpiration, nutrient stocks and availability, toxic substances; and a hypothesis of succession after fire.

	Open heath forest	Dense heath forest	Rain forest

Status				
Vegetation Stem biomass (t ha^{-1})	< 10	10-50	+> 250	
Height (m)	< 5	5-10	> 20	
Family spectrum	Clusiaceae, Araliaceae, Chrysobalanaceae, Melastomataceae, Humiriaceae, Theaceae, ...		Moraceae, Euphorbiaceae, Lauraceae, Sapotaceae, ...	
Geology (?)	Quartzitic sandstone (slow weathering)			Loose sandstone (fast weathering)
Soil Depth	--	-	+	+
Thickness of org. horizon	0	++	+/0	0
Water storage capacity	-	+/0	0	+
Transpiration	? (--)	-	-	?
Nutrient stocks*	-	-	-	+
Availability** (esp. N)	-	-	0	+
Toxic substances (e.g. Al in soil, phenoles in litter, ...)	?	?	?	?
Dynamics				
Fire capability	++	0/ +	-	-
Regrowth after fire (???)	Heath forest stock			Rain forest stock
Succession (???)	pioneer-veg. itself (?), *Pteridium* (?) => open heath forest	Open heath forest => dense heath forest	Dense heath forest => rain forest	pioneer veg. => rain forest
Key factor (???)	Adverse soil conditions (water storage and nutrient stocks)	Thickening organic horizon and more undergrowth improve water storage	An increasingly foreslike microclimate and enhanced decomposition lead to intrusion of rain forest species	Good soil conditions from the beginning (water storage and nutrient stocks)
Time span of succession (yrs, ???)	< 3	20-40	>> 100	30-60

* soils were analyzed for N, Ca, Mg, K and P
** leaves were analyzed for N, Ca, K, Mg and P

? data base insecure
??? hypothesis

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References

AG Boden 1995. *Bodenkundliche Kartieranleitung* 4. Aufl... – Stuttgart

Börner, A. 2000. *Classification of premontane tropical forests at the eastern slope of the Andes in the Rio Avisado watershed, Alto Mayo Region, Northern Peru.* www.uni-bayreuth.de/ obg/ diplomarbeit_annett.pdf

Cooper, A. 1979.:Muri and white savannah in Guyana, Surinam and french Guinea. - In: Specht, R.L. ed. 1979a. - pp. 471-481

Dempewolf, J. 2000. *Classification of montane rain forests on the eastern slopes of the Peruvian Andes, in the Rio Avisado and Rio Tioyacu watersheds*. www.uni- bayreuth.de/ obg/ Diplomarbeit_Jan.pdf

Dietz, J. 2002, in prep. *Distribution of Forest Types and their Variation in Structure and Biomass with Topography on the Southern Flanks of the Cordilliera Cahuapanas, Alto Mayo, Peru.*

Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. - *Ann. Sci. For.* **42(2)**: 81-88

Jordan, C.F. & J.R. Kline 1977. Transpiration of trees in a tropical rainforest. - *Journal of applied Ecology* **14**: 853-860

Klinge, H. & E. Medina 1979. Rio Negro caatinga and campinas, Amazonas states of Venzuela and Brazil. - In: Specht, R.L. ed. 1979b. - pp. 483-488

Larcher, W. 1994.: *Ökophysiologie der Pflanzen*. - Stuttgart

Mette, T. 2001. *Stand structure and water use of two contrasting premontane forests of the Cerro Tambo, Alto Mayo, North Peru.* www.uni-bayreuth.de/obg/diplomarbeit_ tobi.pdf

Ogawa, H., Y. Kyolji, K. Ogino, T. Kira 1965. Comparative ecological studies on three main forest vegetation in Thailand. - *Nature and life in Southeast Asia* **4**: 49-80

Oren, R., Zimmermann, R., Terborgh, J. 1996. Transpiration in upper Amazonia floodplain and upland forests in response to drought-breaking rains. - *Ecology* **77**: 968-973

Specht, R.L. 1979a.: Heathlands and related shrublands of the world. – In: Specht, R.L. ed. 1979b. - pp. 1-18

Specht, R.L. 1979b. Heathlands and related shrublands 1. Descriptive studies. – In: Goodall, D.W. ed. in chief.: *Ecosystems of the world Vol. 9A*.. – Amsterdam

Specht, R.L. 1981. Heathlands and related shrublands 2. Analytical studies. – In: Goodall, D.W. ed. in chief.: *Ecosystems of the world Vol. 9B*.. – Amsterdam

Specht, R.L. & J.S. Wormersley 1979. Heathlands and related shrublands of Malesia with particular reference to Borneo and New Guinea.. – In: Specht, R.L. ed. 1979b. - pp 321-338