Effects of Cutting and Grazing on Andean Treeline Vegetation

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ABSTRACT

Kok, Kasper (Deurningerstraat 36, 7514 BJ Enschede, The Netherlands), Pita A. Verweij (ITC, P.O. Box 6, Enschede, The Netherlands), and Hendrien Beukema (UNEP/DC-PAC, P.O. Box 47074, Nairobi, Kenya). Effects of cutting and grazing on Andean treeline vegetation. Biodiversity and Conservation of Neotropical Montane Forests. 527–539. 1995.—The vegetation of the Andean treeline is described and the impact of human influence on structure and floristic composition analyzed. The study area was located on the western flank of the Central Colombian Cordillera in the northwestern part of Los Nevados National Park between 3400 and 3800 m. The dominant vegetation was a two-layered forest with *Weinmannia mariquitae* and *Miconia* spp. Grazing was extensive, and cutting intensities were classified into limited cutting and clear-cutting. Cleared sites had a regeneration time of at least 5 years. A positive correlation existed between cutting system and grazing intensity. Nine vegetation types were distinguished using TWINSPAN; four of them represented forest without major composition changes, and five represented regenerating forest. An altitudinal range of 400 m included differences in floristic composition. The natural types of forest differed primarily in the presence of different *Miconia* species: *M. latifolia*, *M. psichrophylla*, and *M. bracteolata*; *Weinmannia mariquitae* cover was high in all. The fourth type of natural forest represented remnants of *Polylepis sericea* forest, where *W. mariquitae* and *Miconia* spp. were absent. The five disturbed types were all related to one of the natural forest types dominated by *Weinmannia*. The altitudinal range of important woody species proved useful in predicting vegetation transition after cutting. Cutting at high altitudes led to a lowering of the treeline. Cutting at lower altitudes was limited to the temporal disappearance of trees, after which regeneration of the original forest seemed possible, when grazing intensities were low. High grazing intensities, however, generally led to the creation of pasturelands, independent of altitude. Given the positive correlation between grazing and cutting intensity, chances of regeneration are low, unless the intensity of human disturbance is substantially reduced.

RESUMEN

Kok, Kasper (Deurningerstraat 36, 7514 BJ Enschede, the Netherlands), Pita A. Verweij (ITC, P.O. Box 6, Enschede, the Netherlands), and Hendrien Beukema (UNEP/DC-PAC, P.O. Box 47074, Nairobi, Kenya). Effects of cutting and grazing on Andean treeline vegetation. Biodiversity and Conservation of Neotropical Montane Forests. 527–539. 1995.—En el presente trabajo se describe la vegetación del límite superior del bosque andino y se analiza el impacto de la influencia humana sobre su estructura y composición florística. El área de estudio está localizada en la vertiente occidental de la Cordillera Central colombiana, al noroccidente del Parque Nacional Natural Los Nevados entre los 3400 y 3800 m de altitud. La vegetación predominante en el area es un bosque biestratificado con *Weinmannia mariquitae* y *Miconia* spp. El pastoreo observado en las zonas aledañas es extensivo y las intensidades de tala son clasificadas en tala limitada y tala extendida. Los sitios de muestreo totalmente talados tuvieron un tiempo de regeneración mínimo de 5 años. Los resultados indican una correlación positiva entre el sistema de tala y la intensidad de pastoreo. Haciendo uso del programa de agrupación TWINSPAN se distinguen nueve tipos de vegetación, cuatro de los cuales son bosques sin mayores alteraciones de composición florística, y cinco representan bosques talados en estadios de regeneración. Dentro de un rango altitudinal de 400 m se observaron diferencias en la composición florística. Los tipos de bosque natural difieren principalmente en la presencia de

Biodiversity and Conservation of Neotropical Montane Forests 527–539
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varias especies de *Miconia*: *M. latifolia*, *M. psichrophylla* y *M. bracteolata* con una alta cobertura de *Weinmannia mariquitae* en todos ellos. El cuarto tipo de bosque natural representa restos del bosque de *Polylepis sericea*, en el cual tanto *W. mariquitae* como *Miconia* spp. están ausentes. Los cinco tipos de bosque perturbados están todos relacionados con el bosque natural dominado por *Weinmannia*. El rango de distribución altitudinal de las especies leñosas importantes se consideró un factor útil para predecir la transición de la vegetación después de tala. Las actividades de tala en altas elevaciones ha traido como consecuencia la disminución en el límite superior del bosque. La tala a altitudes menores fue limitada a la remoción temporal de árboles después de la cual la regeneración del bosque pareció posible, cuando las intensidades de pastoreo fueron bajas. Sin embargo, mayores intensidades de pastoreo generalmente llevaron a la creación de pastizales, independientemente de la altitud. Considerando la correlación positiva entre pastoreo e intensidad de tala, las posibilidades de regeneración son bajas, excepto si se disminuye sustancialmente la intensidad de perturbación humana.

Introduction

Low mean temperatures and high radiation values reduce growth of woody species near the treeline to a minimum (Lauer & Klaus, 1975; Grubb, 1977). Regeneration rates consequently are low, so human disturbance has a big impact on forests near the treeline (Janzen, 1973; Ives, 1978; Ewel, 1980; Magee & Antos, 1992). Under natural conditions the location of the treeline is determined by climatic factors (Höllermann, 1978; Stern, 1983). In South America, the treeline is located potentially at an altitude of about 4200 m (Salomons, 1989), but human influence can lower it by as much as a few hundred meters (Hamilton & Perrott, 1981; Corlett, 1984; Lauer, 1988; Uhlig & Uhlig, 1991). Ellenberg (1979), recently followed by Fjeldså (1992) and Laegaard (1992), even stated that grassland vegetation above the treeline in South America (páramo) was created entirely by humans. After tree logging, species of the páramo, which are highly competitive, invade (Hamilton & Perrott, 1981; Corlett, 1987), and pasturelands are maintained by cattle grazing (Stern, 1983; Magee & Antos, 1992).

We studied the effects of cutting and grazing on the floristic composition and structure of high-altitude forests as part of a larger project on the impact of humans on vegetation dynamics in the páramo. The objectives of the study were to (1) describe the variation in floristic composition of treeline vegetation in the study area; (2) describe the changes in structure and floristic composition relative to cutting and grazing; (3) analyze and predict the effect of human impact on the present treeline vegetation. Fieldwork was carried out in 1990.

Methods

STUDY AREA

The study was conducted on the western flank of the Central Cordillera in Colombia in Los Nevados National Park (4°35–60′N, 75°10–30′W). Plots covered an altitudinal range of 3400–3800 m. Mean annual precipitation decreases from 1500 mm (at 3400 m) to 1300 mm on the altitudinal gradient. Soil temperature, used as a surrogate measure for the mean annual temperature (Salomons, 1989), ranges from 10.0 to 8.0°C. Agricultural colonization of the park started around 1920 (Verweij & Beukema, 1992). At the time of our study, zonal vegetation consisted of two-layered Andean forest (Cleef et al., 1983) dominated by *Weinmannia mariquitae* and Melastomataceae (mostly *Miconia* spp.), though elements of Andean dwarf forest (*Escallonia myrtilloides, Hesperomeles lanuginosa*) were present in many samples.

HUMAN INFLUENCE

Although the area is located within the borders of a national park, the destructive influence of humans has been present on a large scale. Combined fire events and grazing are common both in the forest and above the treeline (Verweij & Budde, 1992; Verweij & Kok, 1992). The main factors of human influence near the treeline are wood cutting and cattle grazing.

Trees are cut primarily for fuel or to enable expansion of cultivation. Occasionally the forest is cleared for grazing purposes. Two types of wood cutting were distinguished. In the first, limited cutting, occasionally a few big trees or shrubs are removed ("socola"; Verweij & Beukema, 1992), and thus cattle are able to enter the forest. In such cases, changes in floristic composition were small compared with natural forest, and structural differences were therefore negligible. In the second type, clear cutting, most or all trees are cleared, generally for potato cultivation. Normally, cattle are present afterward. In these cases, the remaining trees from the original forest were easily recognizable by their height and were called "residuals."

Grazing intensities were relatively low. We subdivided intensity into three classes based on the number of cow droppings and the presence of small terraces created by cows (cow paths): (1) low (no cow droppings per 100 m^2; no cow paths present); (2) medium (1–3 cow droppings per 100 m^2; no or few cow paths); (3) high (more than three cow droppings per 100 m^2). Grasses are sometimes sown, but it involves a few known species, and the effect on the floristic composition is presumably small (Schmidt & Verweij, 1992). The effect of potato cultivation on floristic composition is present only during the first few years after cultivation (Schmidt & Verweij, 1992). The repeated removal of woody species and tree seedlings to maintain the grassland after clear-cutting ("desmatonar") is a common practice (Verweij & Beukema, 1992).

SELECTION OF PLOTS

A preliminary interpretation of aerial photographs of different years was made, and using a random stratified sample technique areas for sampling were selected. The actual plots were chosen in the field, on the basis of local climatic variations, accessibility, and dissimilarities with the aerial photographs. Plot size was determined depending on species-area curves and varied between 3 m × 3 m for pasturelands and 20 m × 20 m for natural forest. Information was recorded on geomorphology, soils, topography, drainage, vegetation characteristics, and human impact. Topographical conditions were as similar as possible among sites. The typical site was located on a moderate slope (20–30°) between 3400 and 3800 m. Fifty-six samples were made near one of four farms at approximately the same altitude: El Bosque (15 samples), La Sierra (18), La Normandía (21), and El Cortaderal (2).

DATA ANALYSIS

The TWINSPAN clustering technique (Hill, 1979) was used to analyze the vegetation samples. The following eight cover classes were used: 1–2%, 3–5%, 6–15%, 16–25%, 26–35%, 36–55%, 56–75%, and >75%. Clustering of samples was based on the first through fourth levels of divisions as computed by the program. Divisions at a higher level that resulted in the formation of groups smaller than three samples were ignored. Two samples were placed in a separate cluster, on the basis of the presence of the tree *Polylepis sericea. Polylepsis sericea* can be found up to 4300 m, in patches surrounded by páramo vegetation, and could be considered the highest type of forest in the world (Cleef, 1981). The final table contained nine vegetation types. The clustering of species was based on the relative fidelity a species had with respect to a certain vegetation type. Twenty-five sociological groups were formed.

DESCRIPTION OF VEGETATION TYPES

Clusters of samples were divided into two groups: forest types without major floristic changes and disturbed forest types. Floristic composition of all disturbed forest types before cutting could be related to one of the natural types of forest. The type of original vegetation was determined with the use of the following parameters: (1) surrounding vegetation and remnants of original vegetation within the samples; (2) altitude; and (3) location.

In the description of the sample clusters, greatest importance was given to the presence of woody species. In disturbed vegetation types, the presence of grasses and other pasture species was considered important. Remarks about vegetation structure followed Verweij & Beukema, 1992: (1) upper tree layer (11–33 m); (2) lower tree layer (5–10 m); (3) shrub layer (forbs or woody species with a height of 1–5 m); (4) herb layer (forbs or woody species with a height of 11–100 cm); and (5) ground layer (predominantly herbaceous species with a height of 1–10 cm). Nomenclature of communities was based on Cleef et al., 1983.

ALTITUDINAL RANGE OF VEGETATION TYPES

The response of individual tree species to the altitudinal gradient was studied to establish the altitudinal range of the vegetation types recognized. Cover percentages of all trees were used in combination with information about the presence of residuals and surrounding vegetation. Presence of tree species in other than tree layers was not taken into account. Disjunctions in the altitudinal range were extrapolated. In disturbed vegetation types, a distinction was made between invading species, which were absent from the natural forest, and regrowth of species.

CHANGES IN STRUCTURE AND DIVERSITY

Structural changes were analyzed as per Verweij and Beukema (1992). Species were classified into nine groups that represent different growth forms or taxonomic groups. Vascular plants were classified as (1) trees, woody species with a height >5 m; (2) shrubs, woody species with a height ≤5 m; (3) herbs; (4) Gramineae; (5) climbers, woody or herbaceous species that have adaptations for climbing; (6) ferns; and (7) orchids. This last group was treated separately because orchids' extreme sensitivity to disturbance makes them suitable as an indicator group. Nonvascular plants were classified as (8) bryophytes or (9) lichens.

Results and Discussion

FLORISTIC COMPOSITION

The floristic data set included 75 families, with 189 genera and 294 identified vascular plant species, 20 genera with 23 identified bryophyte species, and four genera with four identified lichen species. The most important families of vascular plants in terms of number of genera were Compositae (33 genera, 69 species), Gramineae (16, 19), Ericaceae (9, 11), and the fern family Polypodiaceae (11, 16). Important genera were *Miconia* (Melastomataceae, nine species); *Mikania* (Compositae, nine); *Pentacalia* (Compositae, five); *Baccharis* (Compositae, five); and *Lachemilla* (Rosaceae, five). A list of the plant species mentioned here is given in Appendix A, following the nomenclature of Rangel et al. (1983), completed with information from a checklist of the Herbario Nacional de Bogotá (COL).

DESCRIPTION OF VEGETATION TYPES

A synoptic vegetation table is presented in Table I. A maximum of three species per sociological group was included: a dominant species (present with more than 25% cover in every sample) and a maximum of two characteristic species (unique for the vegetation type).

VEGETATION TYPES OF THE NATURAL FOREST

Four of the recognized vegetation types represent forest types that were not disturbed heavily: types A, B, C, and D (the *Polylepis sericea* forest) (Table I).

Type A

Type A included upper Andean forest of *Escallonia myrtilloides*, *Weinmannia mariquitae*, and *Miconia latifolia*. Six samples were taken at altitudes between 3645 and 3750 m and represent the uppermost type of two-layered forest. This type is considered a transition between Andean dwarf forest type 3d, with *Hesperomeles lanuginosa* and *Miconia* spp., and Andean forest type 4b, with *Weinmannia mariquitae* and *Miconia* spp. as distinguished by Cleef et al. (1983). Some big trees were selectively removed approximately 50 years ago. Grazing intensity was very low.

The well-developed higher tree layer was dominated by *Weinmannia mariquitae* and *Escallonia myrtilloides* together with *Hesperomeles lanuginosa*. The lower tree layer was dominated by *Miconia latifolia*, *M. ochracea*, in association with *Oreopanax ruizianum*, and the diagnostic species *Miconia* sp. The shrub layer was dominated by the same species. Characteristic elements of the inconspicuous herb layer were the wet elements (Cleef et al., 1983) *Neurolepis* sp. and *Myrrhiodendron glaucescens*. Bryophytes covered large parts of the soil and tree stems; most abundant was *Porotrichodendron superbum*.

Type B

Type B was Andean forest of *Weinmannia mariquitae* and *Miconia psichrophylla*. The majority of the eight samples were taken in an altitudinal range of 3520 to 3570 m. This type is comparable to Andean forest type 4b (Cleef et al., 1983). Some big trees were cut at least 50 years ago. Evidence of cows entering the forest was absent.

The high tree layer was well developed, up to 22 m, and was dominated by *Weinmannia mariquitae* and the diagnostic trees *Myrcianthes* sp. and *Hedyosmum bonplandianum*. The dense lower tree layer was dominated by the *Miconia* species *M. psichrophylla* and *M. tinifolia* together with *Vallea stipularis* and *Oreopanax ruizianum*. The shrub layer was dominated as well by *Miconia* spp., but, unlike type A, small individuals of other trees such as *Saurauia* sp. and *Hedyosmum bonplandianum* were important. The bamboo *Chusquea spadicea* accounted for half of the cover of the shrub layer. Herb and ground layer were characterized by a high variety of species; the most important were the herbs *Nertera granadensis* and *Myrrhiodendron glaucescens* and the bryophyte *Prionodon densus*. Samples were characterized furthermore by a high number of orchids.

Type C

Type C consisted of lower Andean forest of *Weinmannia mariquitae* and *Miconia bracteolata*. This group of eight samples included all five of the samples representing the socola cutting system. The altitudinal range was very small (3370–3420 m) and was significantly lower than that of type B. It can be considered a second variety of the Andean forest type 3d (Cleef et al., 1983). Most samples were subject to a higher grazing pressure than were those of type B.

Though absent in some samples (presumably removed by cutting), *W. mariquitae* was the principal component of the higher tree layer, together with *M. tinifolia*. The dense lower tree layer was characterized by *M. bracteolata*, diagnostic for the lowest forest type, accompanied by *Sessea crassivenosa* and *Saracha quitoensis*. The shrub layer was dominated

TABLE I

Synoptic table of 56 vegetation samples of intact and cut Andean forest

Vegetation type*	Ad1	A	D	B	C	Cd	Ad2	Bd	Ad3
Mean altitude (m)	3623	3670	3700	3580	3397	3480	3614	3601	3750
Location (farm name)†	S	S	B	B	N	N	N	B	S
Cutting system‡	C	N	L	N	L	C	C	C	C
Grazing intensity§	L/M	N	N/L	N	N/L	M	H	M/H	H
Potato cultivation‖	P	N	N	N	N	R	R	P	N
Removal of woody species	No	No	No	No	No	No	No	Yes	Yes
Species#									
Gaultheria strigosum									
Vaccinium floribundum	■	O							
Miconia cf. *ochracea*									
Miconia latifolia	□	□							
Miconia sp.									
Neurolepis sp.	O	□							
Polylepis sericea									
Dictyonema glabratum			■						
Rhynchospora sp.									
Myrrhiodendron glaucescens	□	□	□	□					
Frullania sp. 1									
Hedyosmum bonplandianum				●					
Weinmannia mariquitae									
Hydrocotyle gunnerifolia									
Oreopanax ruizianum	□	■	O	■	□				
Mikania sp.									
Lathyrus sp.				●	●				
Monnina sp.									
Pilea sp. 1					●				
Relbunium hypocarpium									
Polypodium aff. *funckii*	□	□	□	□	□	□	O	O	O
Miconia psichrophylla									
Miconia tinifolia									
Polypodium monosorum		O	O	■	□	□			
Miconia bracteolata									
Lasiocephalus patens					●	●			
Baccharis floribunda									
Buddleja sp.						□			
Ranunculus geranioides									
Sessea crassivenosa					■	■	●		
Paspalum bonplandianum									
Lolium perenne									
Juncus bufonius						■	□		
Oxalis cf. *lotoides*									
Rubus compactus	□	□	●	●	□	□	□	●	O
Anthoxanthum odoratum									
Rumex acetosella					O	■	■	■	
Conyza uliginosa									
Baccharis latifolia								●	
Nertera granadensis									
Porotrichodendron superbum	□	□	O	■	■	■	■	O	□
Hesperomeles lanuginosa									
Escallonia myrtilloides	■	□	O		O	□	□		●
Miconia salicifolia									
Agrostis haenkeana	O					□	■		■
Lachemilla orbiculata									
Geranium sibbaldioides									
Gnaphalium colombianum	□		O			□	□	□	■
Tibouchina andreana	■							■	
Hypericum laricifolium									
Gynoxys tolimensis	□								■
Festuca sublimis									
Lucilia kunthiana									■

*Natural forest (type A–D), disturbed forest (types Ad1 to Ad3, B2, and Cd).
†B, el Bosque; N, la Normandía; S, la Sierra.
‡C, clear-cutting; L, limited cutting; N, no cutting.
§H, high L, low; M, medium; N, no.
‖P, in the past; N, no visible traces; R, recently.
#The first species in each group is dominant (occurs with a high cover mainly in the indicated vegetation types); the second and third species are characteristic (mostly occur with a low cover and do not occur in other vegetation types). ■ high probability, cover >10%; □ high probability, cover <10%; ● medium probability, cover < 10%; O probability, cover < 10%.

by seedlings of *M. psichrophylla* and *Vallea stipularis*, both not present in the tree layers, together with the shrub *Monnina* sp. Pasture species were present in some of the samples; the most common were the grasses *Dactylis glomerata* (sown) and *Anthoxanthum odoratum* and the herb *Rumex acetosella*.

Type D

Type D was *Polylepis sericea* dwarf forest. The two sample plots, at an altitude of approximately 3700 m, were taken in relics of larger stands of *P. sericea* forest. At present, *Polylepis* forest is rare in the study area. Its composition equals Andean dwarf forest type 12g as described by Cleef et al. (1983). Grazing traces were absent.

There was one tree layer consisting of two species: *P. sericea* and *Myrsine dependens*; most other woody species were absent. The shrub layer was dominated by *Chusquea spadicea*. The species-poor herb layer mainly consisted of *Myrrhiodendron glaucescens*. The dense ground layer was dominated by liverworts (*Lepicolia pruinosa* and *Frullania* sp. 2).

VEGETATION TYPES OF DISTURBED FOREST

Five of the recognized vegetation types (Ad1, Ad2, Ad3, Bd, and Cd) represent disturbed forest.

Type Ad1

Type Ad1 consisted of six samples of totally cut upper Andean forest with *Tibouchina andreana*, *Escallonia myrtilloides*, and *Miconia* cf. *ochracea*. The natural forest was type A, indicated by the similarity in species composition and similar location. The altitudinal range of 3570–3645 m was somewhat lower. Floristic composition (but not structure) of the shrubby regrowth resembled Andean dwarf forest type 3a, with *Gynoxys* spp., *Pentacalia andicola*, and *Hesperomeles lanuginosa* as distinguished by Cleef et al. (1983). The forest was completely cut about 25 years ago, to cultivate potatoes. Cow grazing was at a low to medium-high level without grasses sown.

Trees were absent. The shrub layer was dominant and consisted of a high number of different species, most of which were also present in the tree layer of type A. The dominant species was *Tibouchina andreana*, a species absent from the natural forest. Other important species were *Escallonia myrtilloides*, *Miconia latifolia*, *M.* cf. *ochracea*, *Weinmannia mariquitae*, *Hesperomeles lanuginosa*, *Hypericum laricifolium*, *Gynoxys tolimensis*, and *Pentacalia andicola*. The herb layer was poorly developed compared with other disturbed types. The ground layer was not dominated by grasses and herbs, because of the absence of severe grazing. Here, liverworts exhibited a high cover percentage; most important were *Plagiochila* spp. and *Trichocolea* cf. *tomentosa*, both dominant in the natural forest.

Type Ad2

Type Ad2 was seven samples of partly cut upper Andean forest with *Hesperomeles lanuginosa* and *Sessea crassivenosa*. The high cover of residual *Hesperomeles lanuginosa* suggested an original forest of type A. Residuals *Sessea crassivenosa* and *Buddleja* sp. were not present in type A and seem to be location-specific. The shrub layer included scarce regrowth of *Escallonia myrtilloides* and the invading *Hypericum laricifolium*, which reflected a high affinity with type A. The altitudinal range (3590–3640 m) confirmed this hypothesis. The presence of *Agrostis haenkeana* indicates similarities to meadow type 8c (Cleef et al., 1983). Some of the trees were cut approximately 50 years ago, then potatoes were cultivated for many years, and finally grasses were sown. A high grazing intensity exists at present as in the past. Because of similar human influence, the floristic composition resembles type Cd (see below). There are no diagnostic species; differences with type Cd are found mainly in the absence of species.

The higher tree layer was absent. The lower tree layer consisted of a few scattered medium-high trees, mostly dying. The most common species were *Hesperomeles lanuginosa*, *Sessea crassivenosa*, and *Escallonia myrtilloides*. The herb layer was well developed, though average height was reduced. Important species were sown grasses together with pasture species such as *Agrostis haenkeana* and *Paspalum bonplandianum*. The ground layer was less developed than in other disturbed types; the pasture species *Lachemilla orbiculata* was most important. Climbers and orchids were almost completely absent. Ferns were scarce, except for *Elaphoglossum* spp. and *Polystichum* aff. *muricatum*. *Syrropodon* spp. was an abundant bryophyte genus that was rare in the natural forest plots, although more frequently found by Wolf (1993).

Type Ad3

Six samples were taken of type Ad3, totally cut upper Andean forest with *Hypericum laricifolium* and *Gynoxys tolimensis*. This vegetation type was located very close to the treeline, at an altitude of 3725–3775 m. The natural forest was of type A. Regeneration strongly resembled the páramo community of *Hypericum laricifolium* as described by Verweij & Budde (1992) and Cleef et al. (1983), in both the páramo and cut sites close to the treeline. Regeneration time was 15 years. Woody species were regularly removed, but time since the last desmatonar activity was at least five years. Grazing intensity was high, though no grasses were sown. The near absence of pasture species implies that grazing pressure has been lower in the past.

Trees were absent. The shrub layer was well developed. The dominant species were *Hypericum laricifolium* and *Gynoxys tolimensis*. Few species from the forest regenerated. Some regrowth of *Hesperomeles lanuginosa*, *Escallonia myrtilloides*, and *Miconia latifolia* was observed, and *M. salicifolia* was present. The poorly developed herb layer was composed of species that are known from the páramo flora. Most important were the tussock grass *Festuca sublimis* and the herbs *Lucilia kunthiana* and *Hypochaeris sessiliflora*. Several grazing indicators were notably absent. *Taraxacum officinale*, *Trifolium repens*, and *Plantago australis* were expected but not recorded, as they are present in grazed sites in the páramo. The absence of *Anthoxanthum odoratum*, *Rumex acetosella*, and *Veronica serpyllifolia* is explained by the absence of potato cultivation. Bryophytes covered a high percentage of the area but were mainly represented by *Porotrichodendron superbum* and the genus *Syrropodon*. Co-dominant in the ground layer were the pasture species *Lachemilla orbiculata* and *Agrostis haenkeana*.

Type Bd

Seven samples were taken of type Bd, totally cut Andean forest with *Tibouchina andreana* and *Baccharis latifolia*. The original forest corresponded with type B, on the basis of the presence of *Vallea stipularis* (residual in three samples) and the similarity in location. The altitude varied between 3600 and 3730 m. Comparable invasion of *Baccharis* spp. was reported by Seibert (1983) of the treeline in Peru. Regeneration time was relatively short, ranging from 6 to 30 years. Afterward, the majority of the woody species were removed regularly until recently. Potatoes were presumably cultivated in the past. Grazing intensity at present is medium, but the presence of pasture species suggests a grazing history. Probably no grasses were sown.

The number of species was very low. Trees were absent, except for *Vallea stipularis*. The shrub layer covered a relatively high percentage. The dominant species were *Tibouchina andreana* and *Baccharis latifolia*, both absent from the natural forest. The same dominance of a few species (especially *Anthoxanthum odoratum*) held for the dense herb layer. The ground cover was low and made up of *Lachemilla orbiculata*. Bryophytes were almost completely absent. The numbers of ferns, climbers, and orchids were likewise low.

Type Cd

Six samples were taken of type Cd, partly cut Andean forest with *Sessea crassivenosa* and *Miconia bracteolata*. The natural forest was determined to be type C with the aid of residuals present, although the mean altitude (3480 m) was slightly higher. Some of the trees were cut about 25 years ago, after which potatoes were cultivated. Several herbs that are indicator species after potato cultivation (Verweij & Budde, 1992) were still present. A high number of residuals were present, in terms of both abundance and number of species. At present the grazing intensity is medium. The presence of fences and sown grasses implies a higher grazing intensity in the past.

The higher tree layer was absent. The lower tree layer was composed of scattered individuals of a limited number of residuals of which *Sessea crassivenosa*, *Hesperomeles lanuginosa*, and *Buddleja* sp. were most important. The shrub layer was poorly developed and dominated by the diagnostic *Baccharis floribunda* and *Miconia salicifolia*, together with regrowth of *M. psichrophylla*, *M. tinifolia*, *Vallea stipularis*, and *Escallonia myrtilloides*. Most species that are characteristic for the understory of natural forest (e.g., *Plagiochila* spp. and *Hydrocotyle gunnerifolia*) were absent. The herb layer dominated because of sowing activities; pasture species such as the grasses *Anthoxanthum odoratum*, *Dactylis glomerata*, and *Lolium perenne* and the herbs *Trifolium repens* and *Taraxacum officinale* were present. The ground layer was strongly dominated by *Nertera granadensis*. The number of climbers and bryophytes was low; the number of orchids (mainly *Odonthoglossum* spp.) and ferns (*Polypodium* spp.) was remarkably high.

ALTITUDINAL RANGE OF VEGETATION TYPES

The following altitudinal ranges were established for the natural forest types (Fig. 1a): 3600–3800 m, type A; 3450–3700 m, type B; 3350–3550 m, type C; 3700–3800(–4300?) m, type D. Altitudinal ranges for the disturbed vegetation types (Fig. 1b) were 3750–3800 m, type Ad3; 3600–3750 m, type Ad1, Ad2, or Bd; and 3350–3600 m, type Cd

Floristic differences between natural vegetation types were caused primarily by altitude, though an overlap of at least 100 m was found. A second factor could be the geographical position, because the three types were located near different farms. Occurrence of *Miconia* cf. *ochracea*, *M. latifolia*, and *Baccharis latifolia* may be geographically restricted. Most other tree species occurred at all locations. The *Polylepis sericea* forest occurred at the same altitude as type A. Further investigations are needed of this type of forest.

VEGETATION CHANGE UNDER HUMAN INFLUENCE

On the basis of altitudinal position of vegetation types, the effects of cutting and grazing at different altitudes were the following (Fig. 2). Independent of the grazing intensity, forest close to the treeline was converted to a vegetation type that resembles the subpáramo (type Ad3), though some woody species that originate from the forest were present. In combination with a low to medium grazing intensity and potato cultivation, forest of type A between 3600 and 3750 m was converted to vegetation type Ad1. Most tree species showed substantial regrowth, and the floristic composition was comparable to that of the original forest. In addition, some woody and herbaceous species originating from the páramo invaded. Cutting at this altitude, at least temporarily, creates areas where páramo species can extend to an altitude of 3600 m. Grazing at this altitude had a major influence on species composition. Regrowth of woody species was inhibited, and several herbaceous species that dominate the herb and ground layer were introduced (type Ad2). Particularly sensitive to grazing were: *Weinmannia mariquitae*, *Oreopanax ruizianum*, *Vallea stipularis*, and the genus *Miconia*. *Hesperomeles lanuginosa*, *Escallonia myrtilloides*, and *Saracha quitoensis* appeared better adapted to the effects of cattle grazing.

Forest of type B at the same altitude was converted to a vegetation type that is species-poor and dominated by a few invading species, partially from the páramo (type Bd). Regrowth of tree species was lacking, because of the repeated removal of woody species and high grazing intensity. Cutting of this type of forest at altitudes below 3600 m probably results in a vegetation type that has affinity with type Cd, although floristic composition of the tree and shrub layer may be different.

Cutting, combined with potato cultivation, of type C forest resulted in a vegetation type that resembles the original forest (type Cd), with regrowth of most forest species. Regrowth was less abundant than observed after the cutting of type A. Species originating from the páramo were absent.

GRAZING INTENSITY AND THE INTERACTION WITH CUTTING

Grazing intensity was low in comparison with the páramo of the same area. There was a maximum of 5 cow droppings per 100 m^2, compared with a maximum of 42 per 100 m^2 (Verweij & Budde, 1992), and animals were observed rarely. Grazing intensity depended largely on the cutting system practiced; natural stands of forest were never visited by cattle even if isolated sites were surrounded by pasturelands. Limited cutting was followed by either low-intensity grazing, when trees were cut, or medium-intensity grazing, when shrubs were removed. Cows were present when clear-cutting was practiced. If the aim was potato cultivation or wood collection, grazing intensities were medium; otherwise they were high.

STRUCTURE AND DIVERSITY

In Figure 3, the groups of herbs and grasses were lumped, as their reaction to disturbance proved similar. The groups of the bryophytes, climbers, orchids, ferns, and lichens were also lumped, as they showed a common preference for the forest. Two aspects were of interest: changes in the total number of species and changes in the number of species per growth form.

The total number of species was smallest (33–40) in the *Polylepis* dwarf forest. In two-layered forest types, the number of species increased initially with the degree of disturbance. In natural forest types there were 53 ± 5 and 54 ± 10 species for types A and B, respectively. In samples of type C, where socola was practiced, a mean of 63 ± 9 species was found, and under medium grazing intensities (type Cd) the number increased to 75 ± 9 species, with maximum values of 86 and 88 species. A higher grazing intensity, in combination with clear-cutting, resulted in a decrease of the total number of species, with a minimum in type Bd (36 ± 11 species).

In natural forest all structural groups were represented in every sample with two or more species. The tree layer was dominant (4–10 species), but the diversity of bryophytes (5–11 species), climbers (4–17), and orchids (2–7) was high. After cutting in combination with a medium grazing intensity (type Cd) most structural groups were present with a smaller number, except for the diversity of herbs and grasses, which increased enormously. Up to 50 different species were recorded versus 11 to 21 species per sample in the natural forest. Total cutting combined with high-intensity grazing (types Bd and Ad3) resulted in the almost complete disappearance of five structural groups: trees, climbers, orchids, ferns, and lichens. The total number of species consisted of four struc-

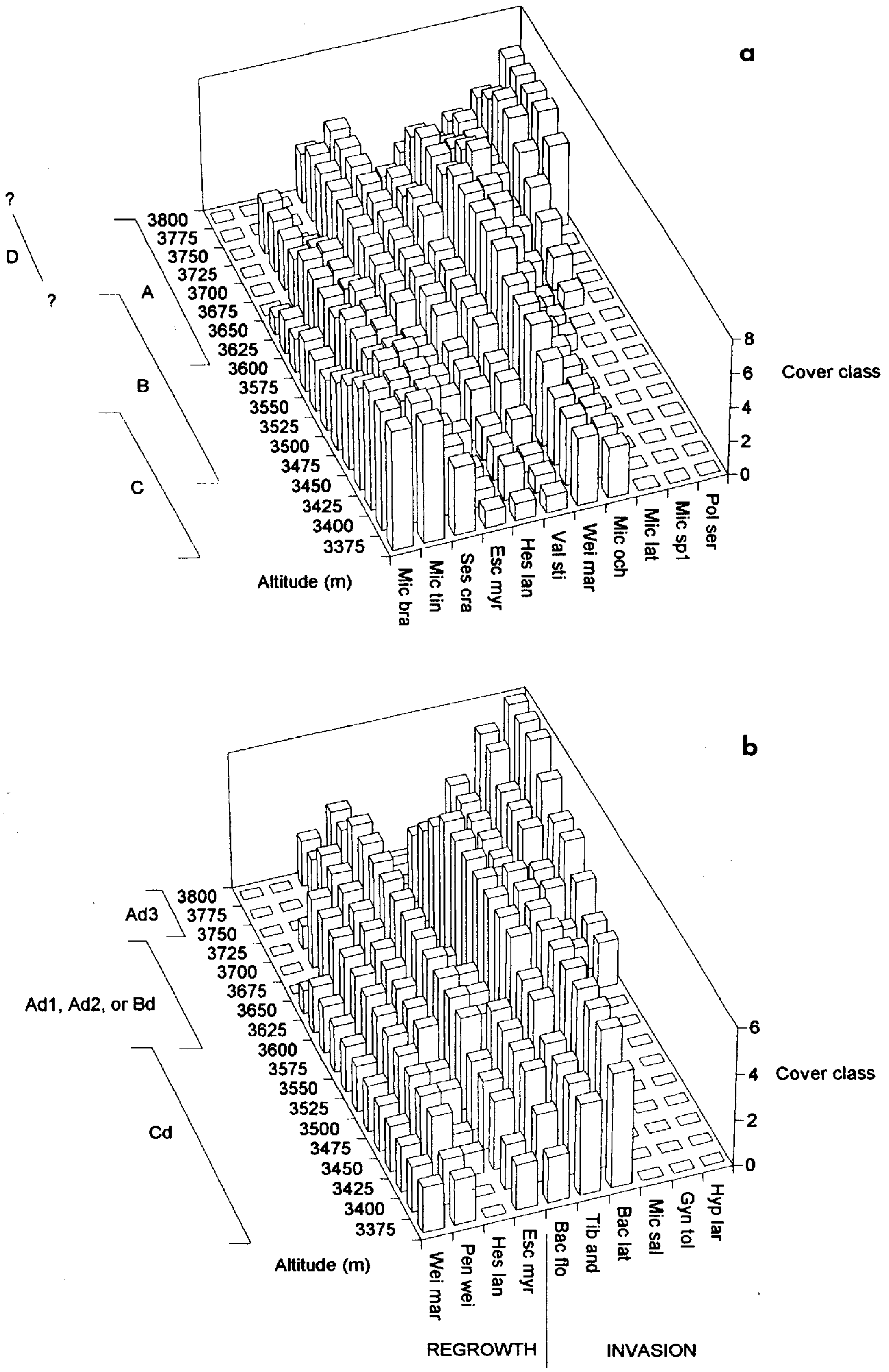

Figure 1. Cover percentage of the most important woody species along the altitudinal gradient. **(a)** Natural forest types (A–D). **(b)** Disturbed vegetation types (Ad1 to Ad3, Bd, and Cd); regrowth of other woody species including different *Miconia* species was observed only in type Ad1. Based on data from 56 samples. Disjunctions were interpolated. Cover classes: 1, 0–2%; 2, 3–5%; 3, 6–15%; 4, 16–25%; 5, 26–35%; 6, 36–55%; 7, 56–75%; 8, >75%.

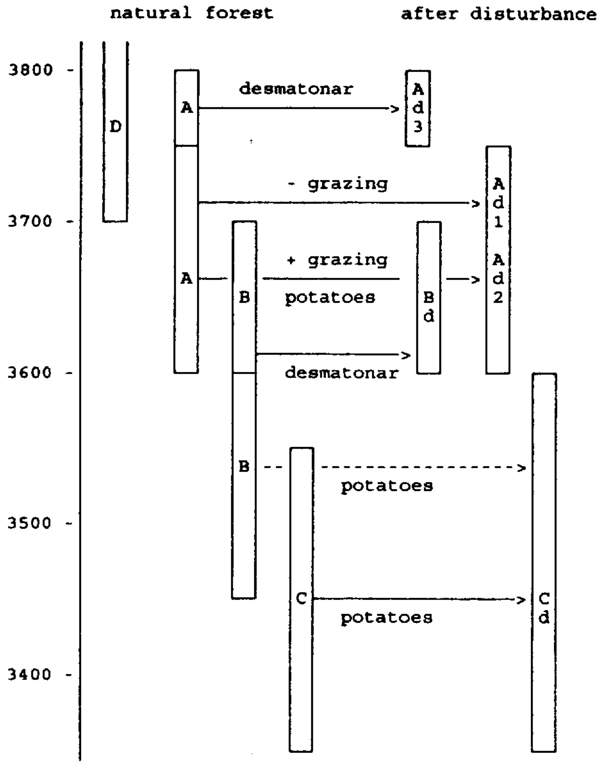

FIGURE 2. Relational diagram showing the effects of altitude (in meters) and presence (+) or absence (–) of grazing and cutting on floristic composition. Regeneration in natural forest is not included. Letters indicate natural forest (type A–D) or disturbed forest (types Ad1 to Ad3, Bd, and Cd). The dashed line indicates that floristic composition of tree and shrub layer of the vegetation type after disturbance may differ from the indicated type.

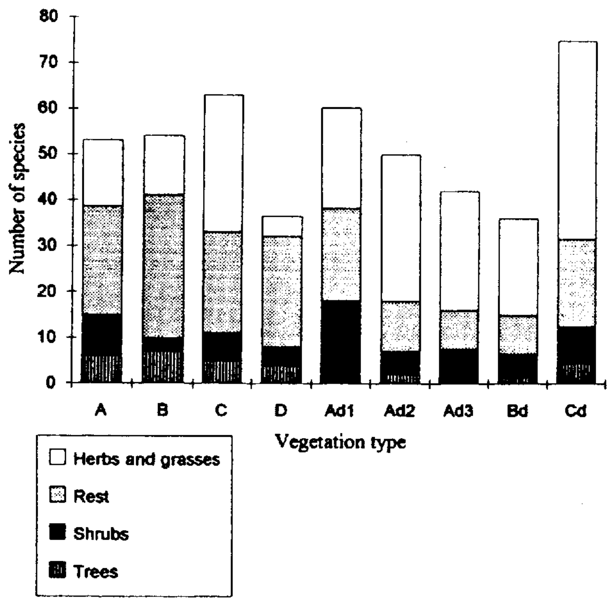

FIGURE 3. Mean number of species per structural group, in nine vegetation types as distinguished by TWINSPAN. Trees = species with >10 cm dbh; shrubs = woody species in shrub layer; rest = orchids, ferns, bryophytes, lichens, and climbers. Vegetation type: natural forest (type A–D), disturbed forest (types Ad1 to Ad3, Bd, and Cd).

tural groups; shrubs were abundant (5–9 species), and herbs and grasses were represented by 17–27 species. The number of bryophytes was low (2–5). Where clear-cutting was not followed by high-intensity grazing (type Ad1), the number of shrubs was exceptionally high (13–19 species). Compared with the natural forest, however, the decrease in diversity of climbers and orchids is noteworthy; it indicates that substantial regenération of woody species is no assurance for the regrowth of species that depend on trees or a forest environment.

CHANCES OF RECOVERY

An important question is, What are the chances of recovery of recently cut forest toward the original vegetation? Will artificially created meadows eventually disappear, or will sprouting of tree seedlings be inhibited permanently? Most investigators favor eventual meadow disappearance. Stern (1983) stated that only constant removal of seedlings can keep meadows free of woody plants; Ellenberg (1979) found that *Trifolium repens* and *Lolium perenne* meadows can be maintained only if enough fertilizer is supplied and tree species are removed; Magee and Antos (1992) mentioned five causes for inhibition of seedling regrowth, but they stated that ultimately all meadows will convert to forest. Nevertheless, the opposite view is encountered as well; Beaman (1962) and Lauer and Klaus (1975) argued that grazing prevents regrowth and that, even without the presence of animals, the strongly competitive grasses slow down the recovery process. Even limited cutting can lead to the accidental opening of forest, followed by the creation of pasturelands (Stern, 1983). According to these opinions, regeneration of forest in the study area is possible only if grazing ceases. Because that option seems only theoretical, we conclude that the treeline in the study area is permanently lowered, unless drastic actions are taken. Solutions such as alternative fuel sources (e.g., charcoal) or restricting grazing to certain, less vulnerable areas (as proposed by Egziabher, 1988) are urgently required.

Conclusion

Floristic composition of the treeline vegetation showed high variation over a small (400 m) altitudinal range in a limited geographical area, in particular with regard to species of *Miconia*. Vegetation structure did not change over the 400-m gradient, and five structural layers were present in all forest types, except the *Polylepis* forest, which lacked a higher tree layer.

Limited cutting had little influence on floristic composition. Vegetation composition and structure remained similar to undisturbed sites. The type of regrowth after clear-cutting, however, was primarily dependent on altitude when grazing intensity was low and regeneration of forest was possible. Cutting at altitudes close to the treeline led to a domination of shrubs and herbs that belong to the páramo flora. The effect of cutting at lower altitudes was limited to the temporal removal of trees, after which regeneration of the original forest seemed possible. Medium or high grazing intensities invariably led to the creation of pasturelands independent of altitude.

Given the high correlation between grazing and cutting intensity, chances for treeline vegetation to regenerate are low. Only substantial changes in the intensity of human disturbance could prevent a further lowering of the treeline.

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Appendix A: Plant Species and Authors for the Vascular Plants

Vascular plants
Actinidiaceae
Saurauia sp.
Araliaceae
Oreopanax ruizianum Cuatr.
Chloranthaceae
Hedyosmum bonplandianum Kunth. ex H.B.K.
Compositae
Baccharis floribunda
Baccharis latifolia (R.&P.) Pers.
Conyza uliginosa (Benth.) Cuatr.
Gnaphalium colombianum Hiern.
Gynoxys tolimensis Cuatr.
Hypochaeris sessiliflora H.B.K.
Lasiocephalus patens (H.B.K.) Cuatr.
Lucilia kunthiana (H.B.K.) Hiern.
Mikania sp.
Pentacalia andicola Turcz.
Taraxacum officinale Weber
Cunoniaceae
Weinmannia mariquitae Szyszyl.
Cyperaceae
Rhynchospora sp.
Eleocarpaceae
Vallea stipularis Mutis ex L.f.
Ericaceae
Vaccinium floribundum H.B.K.
Escalloniaceae
Escallonia myrtilloides L.f.
Fabaceae
Trifolium repens L.
Geraniaceae
Geranium sibbaldioides Benth.
Gramineae
Agrostis haenkeana Hitchc.
Anthoxanthum odoratum L.
Chusquea spadicea Pilger
Dactylis glomerata L.
Festuca sublimis Pilger
Lolium perenne L.
Neurolepis sp.
Paspalum bonplandianum Fluegge
Guttiferae
Hypericum laricifolium Juss.
Juncaceae
Juncus bufonius L.
Loganiaceae
Buddleja sp.
Melastomataceae
Miconia bracteolata (Bonpl.) D.C.
Miconia latifolia (Don.) Naud.
Miconia cf. *ochracea* Naud.
Miconia psichrophylla Naud.
Melastomataceae (*cont'd*)
Miconia salicifolia (Bonpl.) Naud.
Miconia tinifolia Naud.
Miconia sp.
Tibouchina andreana Cogn.
Myrsinaceae
Myrsine dependens (R.&P.) Spreng. F.
Myrtaceae *Myrcianthes* sp.
Orchidaceae
Odonthoglossum spp.
Oxalidaceae
Oxalis aff. *lotoides* H.B.K.
Papilionidae
Lathyrus sp.
Polygalaceae
Monnina sp.
Polygonaceae
Rumex acetosella L.
Polypodiaceae
Elaphoglossum spp.
Polypodium aff. *funckii* Mett.
Polypodium monosorum Desv.
Polystichum aff. *muricatum* (L.) Fee
Ranunculaceae
Ranunculus geranioides H.B.K. ex D.C.
Rosaceae
Hesperomeles lanuginosa R.&P.
Lachemilla orbiculata (R.&P.) Rydb.
Polylepis sericea Wedd.
Rubus compactus Benth.
Rubiaceae
Nertera granadensis (L.f.) Druce
Relbunium hypocarpium (L.) Hemsl.
Scrophulariaceae
Veronica serpyllifolia L.
Solanaceae
Saracha quitoensis (Hook.) Miers
Sessea crassivenosa Bitter.
Umbelliferae *Hydrocotyle gunnerifolia* Wedd.
Myrrhiodendron glaucescens (Benth.) Coult. & Rose
Urticaceae *Pilea* sp.
Mosses
Porotrichodendron superbum (Tayl.) Broth.
Prionodon densus (Hedw.) C. Müll.
Syrropodon spp.
Hepatics
Frullania sp. 1
Frullania sp. 2
Lepicolia pruinosa (Tayl.) Spruce
Plagiochila spp.
Trichocolea cf. *tomentosa* (Sw.) Gott.;
Lichens
Dictyonema glabratum (Spreng.) D. Hawksw.

Note: Following the nomenclature of Rangel et al., 1983.