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*Paul M. Ramsay and E. R. B. Oxley*

# An Assessment of Aboveground Net Primary Productivity in Andean Grasslands of Central Ecuador





*We estimated the aboveground net primary productivity of 5 seminatural Andean pastures: 2 páramo grassland plots (430 and 512 g/m$^2$/y), 2 plots in cleared montane forest (70 and 110 g/m$^2$/y), and 1 in an intensive agricultural setting (1359 g/m$^2$/y). The páramo and montane forest plots demonstrated very low productivity compared with the lowest altitude plot. The productivity of the montane forest plots was very low because overgrazing had led to the formation of dense* Azorella pedunculata *mats of no pasture value. The inherent productivity of páramo tussock grasses, the dominant plants in the two highest sites, is constrained by the retention of dead leaves, which are periodically burned away by farmers (but probably too frequently for long-term benefit). It is unlikely that montane forest and páramo plots could sustain higher levels of grazing, even with the addition of fertilizer, and efforts would be more appropriately focused on increasing the yields of lower altitude pastures.*

***Keywords:*** *Tropical alpine; fertilizer; cutting; páramo; montane forest; Ecuador.*

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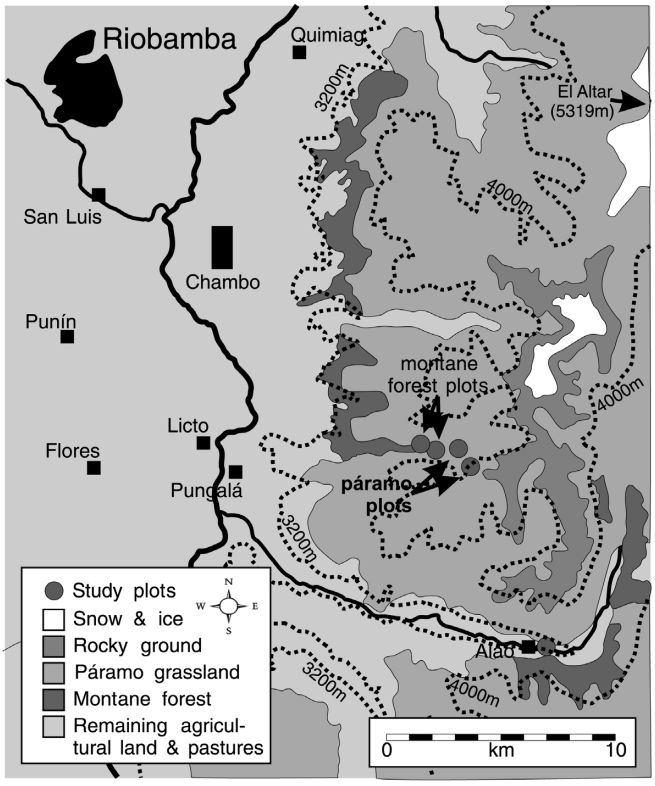



**FIGURE 1** Location of the 5 study sites.

## Introduction

In Ecuador and throughout the northern Andes, the high-altitude grasslands, or páramos, and patches of cleared montane forest are used for extensive livestock grazing and represent a critical element of the rural economy of these highland regions. Fire is commonly used to reinvigorate páramo tussock grasses and kill woody plants in montane forest clearings but often leads to degradation (Acosta-Solís 1984; Brandbyge and Holm-Nielsen 1986; Laegaard 1992; Verweij and Beukema 1992; Ramsay and Oxley 1996; Ramsay 1999). Negative effects of grazing have also been reported (Grubb 1970; Ramsay and Oxley 1996). Low rates of spontaneous primary productivity might explain the vulnerability of these ecosystems.

Although the severity of the high-altitude tropical environment has often led to comparisons with arctic and temperate alpine ecosystems (Bliss 1971; Tieszen and Detling 1983), the tropical montane environment experiences a greater number of degree hours per year (Billings 1973). On this evidence, Smith and Young (1987) suggest that tropical alpine communities may be more productive on a yearly basis than their temperate counterparts, which would confer a greater resilience to agricultural disturbance. However, there have been few published studies of the productivity of (semi-)natural communities from tropical alpine regions of the world (Smith and Young 1987). Nevertheless, estimates of standing biomass and productivity do exist for páramos in Colombia (Cardozo and Schnetter 1976; Tol and Cleef 1994; Hofstede et al 1995a,b) and Venezuela (Smith and Klinger 1985) and for the mountain grasslands of New Guinea (Hnatiuk 1978).

This study investigates standing biomass and productivity for grassland sites in the Andes of central Ecuador, extending along an altitudinal range of nearly 1000 m. Fertilizer was applied to assess the potential for productivity enhancement of these grasslands and cutting regimes were applied to simulate grazing.

## Methods

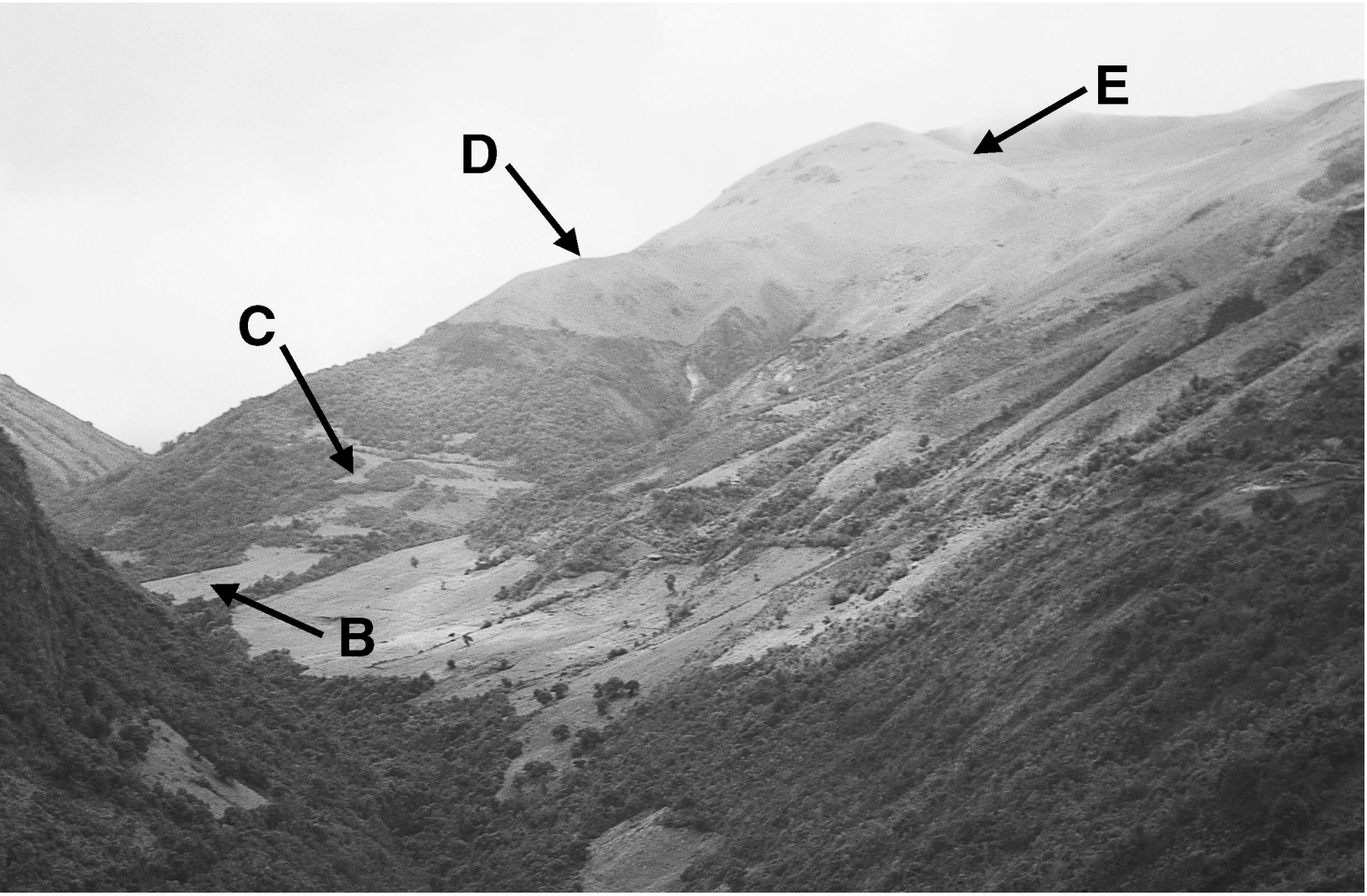
### Study sites

The experiments were carried out in the highland valley systems of Alao (1°53′S, 78°21′W) and Daldal (1°48′S, 78°32′W), about 20–30 km southeast of Riobamba (Figure 1). Five pastures were chosen to cover an altitudinal gradient from 3100 to 4000 m. Ramsay (1992) provides detailed floristic information on these plots.

The lowest plot was located at 3100 m in the valley of Alao. This valley was used for intensive agriculture, including the cultivation of cereals and potatoes. The vegetation of the experimental plot had been intensively grazed from time to time by horses and cattle and

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**FIGURE 2** The upper Daldal Valley, showing the location of the 4 experimental exclosures in cleared montane forest (B and C) and páramo (D and E). Over the course of the experiments, some of the montane forest shown in this photograph, taken on 22 August 1987, was cleared for agriculture. (Photo by Paul M. Ramsay)




consisted of short-cropped grasses (*Dactylis glomerata* L., *Lolium* sp., *Anthoxanthum odoratum* L., *Holcus lanatus* L., and *Elymus* sp.) and other herbaceous elements such as *Trifolium repens* L. There were no signs of cultivation. During the year in which the experiment took place, 1160 mm of precipitation was recorded in Alao (data from Instituto Nacional de Meteorología e Hidrología, Quito).

The remaining 4 sites were located between 3250 and 4000 m in the valley of the Río Daldal, less than 10 km to the north of Alao (Figure 2). The lower part of the valley was a mosaic of forest and clearings of varying ages, some of the older pastures including species characteristic of improved grasslands. Two plots were sited within this zone, at 3250 and 3450 m. Both plots consisted of short grasses and other herbs, notably *Paspalum* sp., *Holcus lanatus*, *Dactylis glomerata*, *Trifolium repens*, and *Bidens andicola* Kunth, with a substantial cover of *Azorella pedunculata* (Spreng.) M. & C., a mat-forming species. A small herd of approximately 10 cattle grazed the area containing both plots.

Areas above 3650 m in the Daldal Valley were occupied by páramo grassland, dominated by tussock grasses of *Calamagrostis intermedia* (Presl.) Steud. Plots were established at 3750 and 4000 m. In the lower plot, herbs and small, woody plants of *Valeriana microphylla* Kunth and *Lupinus pubescens* Benth. were frequent among the tussocks. Large shrubs were absent from the higher plot, though *Valeriana microphylla* was still common. Cattle and horses grazed extensively on the páramo at low densities. Both páramo plots were subjected to regular agricultural burning, every 2–4 years, to remove dead leaves and to stimulate the production of nutritious, young shoots. The vegetation within the experimental

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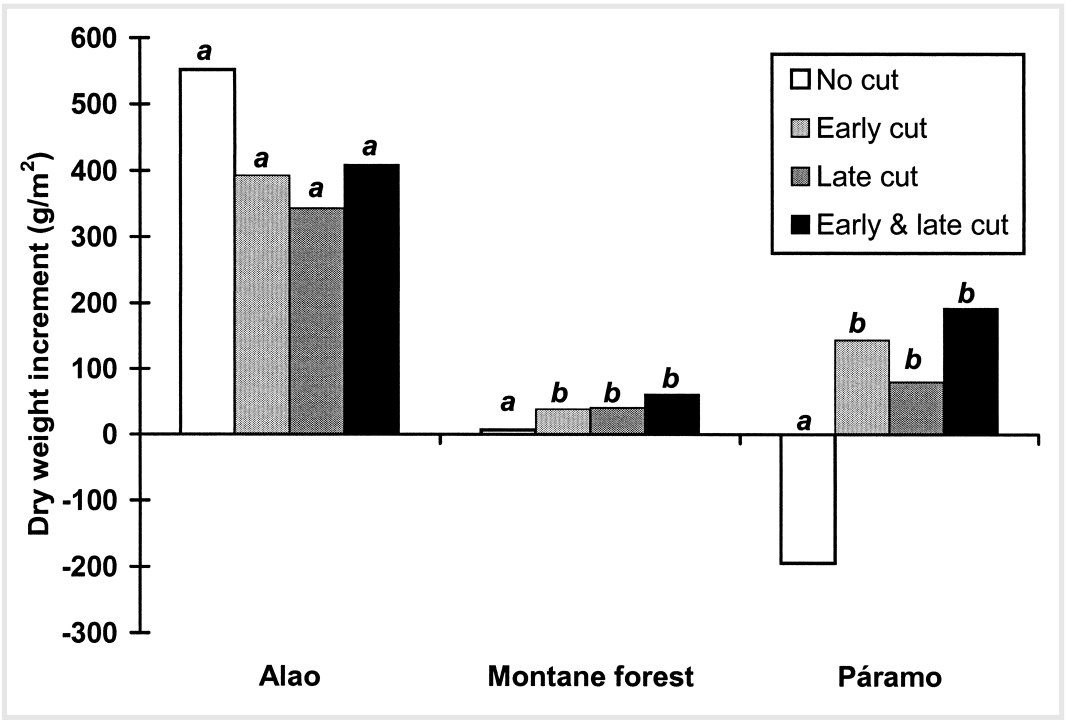



**FIGURE 3** Mean dry weight increments for the cutting treatments for the 3 site groups: Alao, montane forest and páramo. Means sharing a letter within each site group were not separated by a "Student Newman Keuls" (SNK) test.

plots was at the stage where burning would normally be applied and, in both cases, large areas nearby had been burned recently.

### Experimental design

At each of the 5 sites, 10.5 m × 10.5 m-fenced exclosures were constructed, which excluded cattle but did not prevent small mammals such as rabbits and rodents from entering the areas. An unreplicated $2^4$ factorial randomized plot design—all combinations of 2 fertilizers and 2 cutting treatments (16 plots in total)—was employed in each exclosure. The 2 fertilizer treatments (200 kg/ha of nitrogen and 200 kg/ha of potassium plus 100 kg/ha of phosphorus) were used to examine the potential for productivity enhancement with nutrient addition, and the 2 clipping regimes (an early cut at the start of the experiment and a late cut after 70 days) were used to assess whether productivity was stimulated by defoliation. Despite some differences in its effects on vegetation, clipping has been used to simulate grazing in a wide variety of contexts (eg, Clary 1995; Harris et al 1997; Quellet et al 1994), including highland grasslands (Leigh et al 1991; Grant et al 1996).

The experiments were started in the period 13–20 July 1987. The initial clipping treatments were used to estimate the standing biomass. The vegetation was clipped back to ground or tussock pedestal level in the páramo sites and to the level of the *Azorella pedunculata* mats in the montane forest plots. In the páramo sites, much of the harvested material was dead. However, this was not separated from the live material. The word biomass is used here to incorporate these dead leaves still attached to the tussocks but not to include litter on the ground surface. Assessment of belowground productivity was not attempted. Final harvesting was carried out 103–110 days after the experiments were started. Harvested plant material was initially dried at about 65°C in a makeshift oven in Alao to prevent rotting before final drying in Quito at 105°C for 24 hours.

## Results

### Aboveground standing biomass estimates

The standing biomass of the páramo plots was an order of magnitude higher than the others, with 794 g/m$^2$ at 4000 m and 837 g/m$^2$ at 3750 m. The cleared montane forest plots yielded 31 and 42 g/m$^2$ at 3450 and 3250 m, respectively. The páramo and montane forest plots showed similar variability among the eight replicates, 23–34% coefficient of variation. The improved agricultural grassland at 3100 m in Alao varied much more (88%) but at 54 g/m$^2$ had a slightly greater standing crop than the montane forest plots.

### Net aboveground productivity estimates

An analysis of variance was performed on the untransformed biomass increments over the entire experimental period using the higher level interactions as the

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**TABLE 1** Estimated annual aboveground net primary productivity for the 5 exclosure sites. At each altitude, 16 productivity estimates were calculated (including all fertilizer and cutting treatments) and the mean of these values is shown in the "Overall" column. The mean values for fertilized and unfertilized sites are presented, along with those plots that were initially cut and those that were not. The most reliable estimate of spontaneous productivity is given by the final column: those plots that were unfertilized and cut at the start of the experiment.

| | Net annual aboveground productivity ($g/m^2/y$) | | | | | |
|---|---|---|---|---|---|---|
| **Situation of plots** | **Overall (*n* = 16)** | **Fertilized (*n* = 12)** | **Unfertilized (*n* = 4)** | **Initially cut (*n* = 8)** | **Initially uncut (*n* = 8)** | **Unfertilized cut (*n* = 2)** |
| **Alao (3100 m)** | 1503 | 1614 | 1170 | 1420 | 1586 | 1359 |
| **Montane forest (3250 m)** | 154 | 192 | 43 | 214 | 95 | 110 |
| **Montane forest (3450 m)** | 93 | 117 | 23 | 122 | 64 | 70 |
| **Páramo (3750 m)** | 243 | 269 | 168 | 578 | 91 | 430 |
| **Páramo (4000 m)** | 128 | 73 | 295 | 548 | 292 | 512 |

error term. Transformation of the data did not reduce their variability, and there was no correlation between variance and sample dry weights. There were significant interaction effects between altitude and fertilizer treatments and cutting regimes. Multiple range tests defined complex groups of means corresponding to 3 site types, each with its own distinct vegetation: páramo sites dominated by tussock grasses, cleared montane forest sites dominated by mats of *Azorella,* and the improved agricultural grassland at Alao dominated by coarse grasses.

Cutting did not affect yields in the 3100 m improved grassland plot, but yields of the uncut plots on the other sites were significantly lower than the corresponding cut plots (Figure 3). In fact, the uncut páramo plots showed a negative yield compared with the yields at the start of the experimental period. It is this differential response of the uncut plots that was responsible for the interaction between altitudes and cutting regime. Removal of the early and late cut treatments from the analysis did not alter the significant differences between altitudinal groups (páramo, montane forest, and improved grassland; $P < 0.001$), and there was no difference between the remaining cutting treatments ($P = 0.195$). However, the site interactions with fertilizer treatment disappeared, leaving a simple difference between fertilizer regimes ($P = 0.019$): the NPK (nitrogen-phosphorus-potassium) treatment was more productive than the others in all of the plots but was particularly evident in the lowest altitude plot (Figure 4).

Table 1 extrapolates the dry weight increments measured over the experimental period to a yearly base. Overall, the lowest site (improved grassland) was much more productive than the rest. The productivity estimates for remaining sites were an order of magnitude lower. The addition of fertilizer stimulated production at the four lowest sites. Although the upper páramo site showed depressed yield with fertilizer (73 compared with 295 $g/m^2$), this relates to the high variability of the initial standing biomass in this site more than the effect of fertilizer per se. Comparing only initially cut plots (to remove the initial biomass effect), this highest site also shows an increase in yield with addition of NPK (Figure 4). The initial cut stimulated yields in the montane forest and páramo pastures (Table 1). This represented roughly a doubling of productivity at 3 of these sites and a fivefold increase in the lowest páramo site. The production in the improved pasture in Alao was not increased by this early cut since it was already grazed close to the ground at the start of the experiment.

Due to the differential response of plots that were initially uncut, the best estimates of the spontaneous productivity of the 5 areas are given by the plots that were cut at the start of the experiment, with no fertilizer added. The improved pasture at 3100 m produced an estimated 1359 $g/m^2/y$. The 2 montane forest plots, at 110 and 70 $g/m^2/y$, yielded 10 to 20 times less than the Alao plots. The páramo plots produced 430 and 512 $g/m^2/y$.

## Discussion

The 5 exclosure sites fall into 3 distinct groups, both in terms of their initial standing biomass and their net aboveground productivity: the improved agricultural grassland (3100 m), the montane forest clearings (3250 and 3450 m), and the páramo grasslands (3750 and 4000 m).

The improved agricultural pasture at Alao, with a spontaneous productivity of almost 1400 $g/m^2/y$, is comparable to boreal mountain forest and semiarid savanna productivity (Rodin et al 1975). These plots were intensively grazed before the start of the experiment; this explains the initial low standing biomass and the fact that there was no difference between cut and uncut plots in subsequent productivity—they were all cut or grazed close to the ground at the start.

The pastures in cleared montane forest showed very low productivity levels: 70 and 110 $g/m^2/y$ is more consistent with desert vegetation (Rodin et al 1975), semidesert (Lieth 1975), and tundra (Wielgolaski et al 1981) than with mountain grasslands elsewhere. The standing biomass was also very low. These findings are surprising because these pastures were only about

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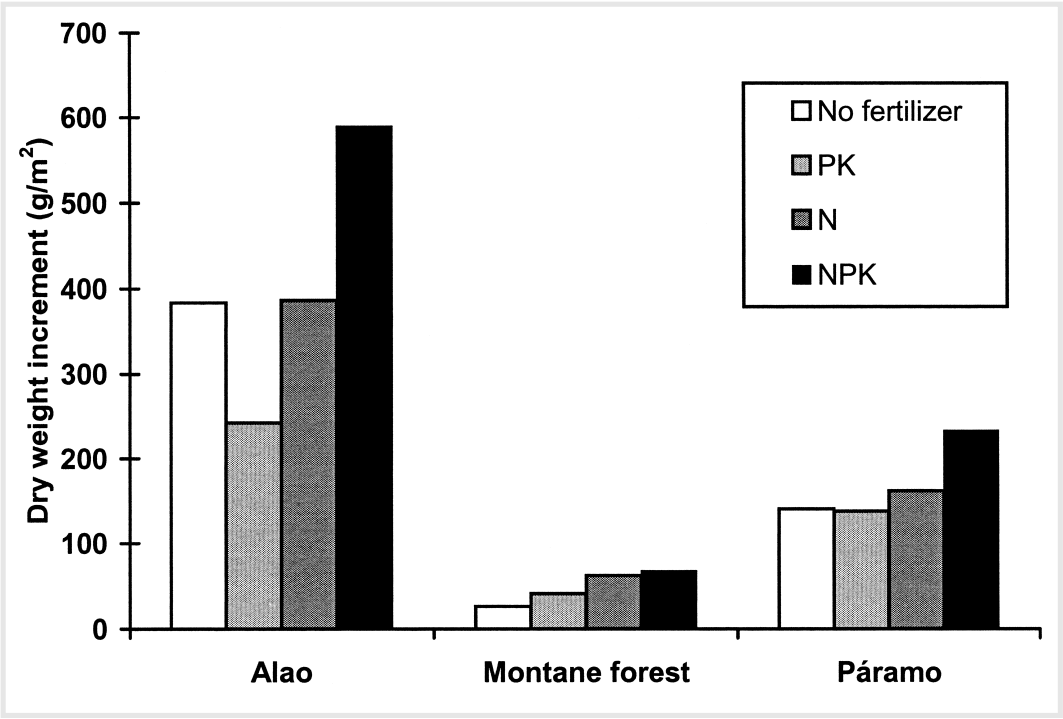



**FIGURE 4** Mean dry weight increments for the 4 fertilizer treatments in Alao, the montane forest, and the páramo plots. Only data for initially cut plots are shown.

1–2°C cooler than the Alao site, which is 10–20 times more productive. Overgrazing appears to be the most likely explanation for the low productivity of the montane forest pastures. *Azorella pedunculata* formed a dense mat of unpalatable rosettes at ground level, and relatively few palatable plants were available to grazing animals (contrasting with the herbaceous mat reported by Hofstede et al [1995a] for a Colombian páramo). Harvesting the *Azorella* mat itself would have destroyed the vegetation completely, and so this plant is not included in the low productivity figures presented here. Clearly, the inclusion of *Azorella* would certainly increase the overall annual productivity estimates for these plots, but it is of no forage value to livestock. Grubb et al (unpublished manuscript) reported the dominance of a similar mat of the same *Azorella* species in intensively grazed sheep pastures at 4050 m on Volcán Antisana, Ecuador, and the suppression of shoots of other species as *Azorella* surrounded them. Once established, it becomes difficult for other species to compete effectively with *Azorella*. Here is the problem for farmers of these pastures: too little grazing and the clearing would revert to forest once more; too much grazing and a mat of *Azorella* forms, reducing forage productivity to very low levels.

The annual productivity estimates for the páramo plots were 168 and 295 g/m$^2$/y, similar to those reported for some tundra ecosystems and about one quarter that of mountain steppe (Lieth 1975; Rodin et al 1975; Wielgolaski et al 1981). They are in accordance with values recorded by Hnatiuk (1978) in the tropical alpine grasslands of New Guinea of 128–442 g/m$^2$/y. They also correspond to Hofstede et al's (1995b) estimates for the productivity of tussock grasses in Colombian páramo with different management regimes (198–308 g/m$^2$/y). Higher net aboveground productivity has been reported for giant rosette plants dominating some páramos: 700 g/m$^2$/y for *Espeletia timotensis* in Venezuela (Monasterio 1986) and 1500 g/m$^2$/y for *Espeletia grandiflora* in Colombia (Sturm and Abouchaar 1981). In the desert páramo at high altitudes in Venezuela, consisting mostly of *Espeletia* giant rosette plants, productivity was lower at just 160 g/m$^2$/y (Lamotte et al 1989). In the Central Andes, rainfall is much lower and Mann (1966) estimated the gross annual primary productivity of dry and humid puna vegetation in Peru at 0.3 and 8 g/m$^2$/y, respectively.

The páramo plots yielded the highest standing biomass values in this study of 794 g/m$^2$ and 837 g/m$^2$. Tropical alpine grasslands have the highest ratio of aboveground to belowground biomass of all vegetation (Smith and Klinger 1985), and the estimates for these Ecuadorian plots are consistent with reports from elsewhere. Acosta-Solís (1984) recorded 435 g/m$^2$ in an Ecuadorian páramo. Smith and Klinger (1985) measured aboveground biomass between 436 and 628 g/m$^2$ in a Venezuelan páramo. Colombian páramos appear to support a higher standing phytomass than the Ecuadorian and Venezuelan páramos—estimates from Colombia range

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from 735–3486 g/m$^2$/y (Cardozo and Schnetter 1976; Hofstede and Witte 1993; Tol and Cleef 1994; Hofstede et al 1995a,b). Despite very low rates of productivity, the dry and humid punas of Peru exhibit relatively high standing biomasses of 200 and 700 g/m$^2$, respectively (Mann 1966). Hnatiuk (1978) reported aboveground living biomass estimates between 436 and 628 g/m$^2$ in tropical alpine tussock grassland in New Guinea.

Most of the aboveground standing biomass in the páramo plots consisted of dead leaves within *Calamagrostis intermedia* grass tussocks. These dead leaves may perform useful functions in insulating living leaves from cold and high fire temperatures (Laegaard 1992; Ramsay and Oxley 1996; Ramsay 2001), storing nutrients within the plant (Tol and Cleef 1994) and discouraging herbivory by lowering the overall palatability of the plant (Schmidt and Verweij 1992). However, these dead leaves also almost certainly inhibit photosynthesis and thus productivity. Farmers burn away this dead material periodically, and the páramo sites examined in this study were nearing a condition when burning would be applied (though its application is somewhat erratic). All of the initially uncut plots in the páramo showed a loss in weight over the course of the experiment, suggesting that biomass was being lost rather than gained. This may be related to the buildup of dead leaves in the tussocks, and cutting back páramo tussock grasses stimulated production in the experimental plots. On this evidence, it would seem that the local agricultural practice of burning is well founded. However, the measured rates of biomass increase after cutting would need to be sustained for at least 3–5 years to accumulate the standing material harvested at the start of the study. This is slightly longer than the 2–4-year burning frequency in these pastures. Furthermore, it is unlikely that the tussocks would be able to sustain their initial rate of production because the self-shading effect would return as leaves build up once more and, after the initial productivity gain following the fire, immobilization of nutrients takes place rapidly (Hofstede 1995). In addition, fire would be expected to cause more damage to the grasses than clipping due to high temperature damage within surviving plant tissues. Ramsay and Oxley (1996) demonstrated high rates of mortality in grass tillers that survived a fire near one of the present páramo study areas, and Verweij (1995) has estimated that complete recovery of *Calamagrostis* tussocks takes about 10 years in the páramo of the Colombian Cordillera Central. Therefore, although a short-term benefit may result from páramo burning, in the longer term, the practice seems unsustainable. This has been recognized by some groups of farmers themselves in the Ecuadorian páramos (Medina et al 1997).

All of the experimental exclosures showed that the application of fertilizer increased yields, at least in the short term. The NPK treatment gave significantly better results than the others, particularly in the improved pasture at 3100 m, and there appears to be scope for boosting productivity in these improved, lower altitude pastures by fertilizer additions. The productivity gains in the montane forest and páramo pastures were relatively modest, however, and fertilizing these areas would not be economically viable. In the montane forest, the dominance of the *Azorella* mat overshadows other considerations. In the páramo, the characteristic climate of "summer every day, winter every night" is probably the key factor in determining the productivity of the plants that live there. Körner (1989) found evidence that tropical alpine plants keep their growth rates under control, and Ramsay (1992) lent further support to this hypothesis with evidence suggesting genetic control on the growth of some Ecuadorian tussock grass species under greenhouse conditions.

These data suggest that efforts to increase the productivity of Andean pastures in central Ecuador should be concentrated in the lower altitude grasslands. These are characterized by higher spontaneous productivity and show potential for higher yields with nutrient additions. The extensive páramo grasslands and the montane forest clearings do not respond well to fertilizer applications, have generally low spontaneous productivity, and appear ecologically fragile to current agricultural management practices (Luteyn 1999). There may be some merit in a detailed study of the ecology of *Azorella pedunculata* in montane forest clearings and its response to grazing intensity. Nevertheless, the productivity of the grazing livestock themselves is impaired at higher altitudes by physiological stress and the need to travel longer distances and forage for more time to meet their nutritional requirements (Schmidt and Verweij 1992).

## Conclusion

Pastures in páramo and cleared montane forest patches demonstrated relatively low productivity. It is unlikely that these pastures could sustain more intensive use by farmers, and there is evidence that, in both cases, current use may be unsustainable: the productivity of the montane forest plots had been adversely affected by the dominance of a dense mat-forming species, apparently a consequence of overgrazing, and the current rates of páramo burning appeared too frequent to allow full recovery of the vegetation between fires. Without burning, the productivity of the dominant tussock grasses in the páramo would be reduced to very low levels by self-shading. On the other hand, the lowest altitude plot in this study produced a high yield of biomass, and this was boosted by the addition of nutrients. There is potential here to increase productivity and stocking rates without the damaging consequences that would result from increases at higher altitudes.

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## REFERENCES

***Acosta-Solís M.*** 1984. *Los Páramos Andinos del Ecuador.* Quito: Publicaciones Científicas MAS.
***Billings WD.*** 1973. Arctic and alpine vegetations: similarities, differences and susceptibility to disturbance. *Bioscience* 23:697–704.
***Bliss LC.*** 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2:405–438.
***Brandbyge J, Holm-Nielsen LB.*** 1986. *Reforestation of the High Andes with Local Species.* Aarhus, Denmark: University of Aarhus.
***Cardozo H, Schnetter ML.*** 1976. Estudios ecológicos en el Páramo de Cruz Verde, Colombia. III. La biomasa de tres asociaciones vegetales y la productividad de *Calamagrostis effusa* (H.B.K.) Steud. y *Paepalanthus columbiensis* Ruhl. en comparación con la concentración de clorofila. *Caldasia* 11:85–91.
***Clary WP.*** 1995. Vegetation and soil responses to grazing simulation on riparian meadows. *Journal of Range Management* 48:18–25.
***Grant SA, Torvell L, Common TG, Sim EM, Small JL.*** 1996. Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle. *Journal of Applied Ecology* 33:1267–1280.
***Grubb PJ.*** 1970. The impact of man on the páramo of Cerro Antisana, Ecuador. *Journal of Applied Ecology* 58:7B–8B.
***Harris CA, Blumenthal MJ, Kelman WM, McDonald L.*** 1997. Effect of cutting height and cutting interval on rhizome development, herbage production and herbage quality of *Lotus pedunculatus* cv. Grasslands Maku. *Australian Journal of Experimental Agriculture* 37:631–637.
***Hnatiuk RJ.*** 1978. The growth of tussock grasses on an equatorial high mountain and on two sub-Antarctic islands. *In:* Troll C, Lauer W, editors. *Geoecological Relations between the Southern Temperate Zone and the Tropical Mountains*. Wiesbaden, Germany: Franz Steiner, pp 152–190.
***Hofstede RGM.*** 1995. *Effects of Burning and Grazing on a Colombian Páramo Ecosystem* [PhD thesis]. Amsterdam: University of Amsterdam.
***Hofstede RGM, Chilito EJ, Sandovál EM.*** 1995b. Vegetative structure, microclimate, and leaf growth of a páramo tussock grass species, in undisturbed, burned and grazed conditions. *Vegetatio* 119:53–65.
***Hofstede RGM, Mondragón MX, Rocha CM.*** 1995a. Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. I. Aboveground vegetation. *Arctic and Alpine Research* 27:1–12.
***Hofstede RGM, Witte HJL.*** 1993. An evaluation of the use of the dry-weight-rank and the comparative yield biomass estimation methods in páramo ecosystems research. *Caldasia* 17:11–14.
***Körner C.*** 1989. The nutritional status of plants from high altitudes: a worldwide comparison. *Oecologia* 81:379–391.
***Laegaard S.*** 1992. Influence of fire in the grass páramo vegetation of Ecuador. *In:* Balslev H, Luteyn JL, editors. *Páramo: An Andean Ecosystem Under Human Influence.* London: Academic Press, pp 151–170.
***Lamotte M, Garay I, Monasterio M.*** 1989. Les grands traits du fonctionnement d'un écosystème tropical d'altitude. *Società Italiana di Ecologia Atti* 3:61–66.
***Leigh JH, Wood DH, Slee AV, Holgate MD.*** 1991. The effects of burning and simulated grazing on productivity, forage quality, mortality and flowering of 8 sub-alpine herbs in Kosciusko National Park. *Australian Journal of Botany* 39:97–118.
***Lieth H.*** 1975. Primary production of the major vegetation units of the world. *In:* Leith H, Whittaker RH, editors. *Primary Productivity of the Biosphere.* Berlin: Springer, pp 203–215.
***Luteyn JL.*** 1999. *Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature.* New York: The New York Botanical Garden.
***Mann GF.*** 1966. *Bases Ecológicas de la Explotación Agropecuaria en la América Latina.* Washington, DC: Departmento de Asuntos Científicos, Unión Panamericana.
***Medina G, Recharte J, Suárez E, Bernal F.*** 1997. *Informe Final del Proyecto: Perspectivas para la Conservación de los Páramos en Ecuador*. Quito: Ecociencia & The Mountain Institute, Programa Andino.
***Monasterio M.*** 1986. Adaptive strategies of *Espeletia* in the Andean desert páramo. *In:* Vuilleumier F, Monasterio M, editors. *High Altitude Tropical Biogeography.* Oxford: Oxford University Press, pp 49–80.
***Quellet JP, Boutin S, Heard DC.*** 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the arctic. *Canadian Journal of Zoology* 72:1426–1435.
***Ramsay PM.*** 1992. *The Páramo Vegetation of Ecuador: The Community Ecology, Dynamics and Productivity of Tropical Grasslands in the Andes* [PhD thesis]. Bangor: University of Wales.
***Ramsay PM.*** 1999. Landscape mosaics in the High Andes: the role of fire in páramo communities. *In:* Ková Ṗ editor. *Nature and Culture in Landscape Ecology: Experiences for the 3rd Millennium.* Prague: The Karolinum Press, pp 192–199.
***Ramsay PM.*** 2001. Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community. *In:* Ramsay PM, editor. *The Ecology of Volcán Chiles: High-Altitude Ecosystems on the Ecuador–Colombia Border.* Plymouth: Pebble & Shell, pp 101–111.
***Ramsay PM, Oxley ERB.*** 1996. Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio* 124:129–144.
***Rodin LE, Bazilevich NI, Rozov NN.*** *1975*. Productivity of the world's main ecosystems. *In: Productivity of World Ecosystems: Proceedings of a Symposium.* Washington DC: National Academy of Sciences (NAS), pp 13–26.
***Schmidt AM, Verweij PA.*** 1992. Forage intake and secondary production in extensive livestock systems in páramo. *In:* Balslev H, Luteyn JL, editors. *Páramo: An Andean Ecosystem Under Human Influence.* London: Academic Press, pp 197–210.
***Smith AP, Young TP.*** 1987. Tropical alpine plant ecology. *Annual Review of Ecology and Systematics* 18:137–158.
***Smith JMB, Klinger LF.*** 1985. Aboveground : belowground phytomass ratios in Venezuelan páramo vegetation and their significance. *Arctic and Alpine Research* 17:189–198.
***Sturm H, Abouchaar A.*** 1981. Observaciones sobre la ecología del páramo andino de Monserrate. *Caldasia* 13:223–256.
***Tieszen LL, Detling JK.*** 1983. Productivity of grassland and tundra. *In:* Lange OL, Nobel PS, Osmond CB, Ziegler H, editors. *Physiological Plant Ecology. IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence.* Berlin: Springer, pp 173–203.
***Tol GJ, Cleef AM.*** 1994. Above-ground biomass structure of a *Chusquea tessellata* bamboo páramo, Chingaza National Park, Cordillera Oriental, Colombia. *Vegetatio* 115:29–40.
***Verweij PA.*** 1995. *Spatial and Temporal Modeling of Vegetation Patterns* [PhD thesis]. Amsterdam: University of Amsterdam.
***Verweij PA, Beukema H.*** 1992. Aspects of human influence on upper-Andean forest line vegetation. *In:* Balslev H, Luteyn JL, editors. *Páramo: An Andean Ecosystem Under Human Influence.* London: Academic Press, pp 171–175.
***Wielgolaski FE, Bliss LC, Svoboda J, Doyle G.*** 1981. Primary production of tundra. *In:* Bliss LC, Heal OW, Moore JJ, editors. *Tundra Ecosystems: A Comparative Analysis.* Cambridge: Cambridge University Press, pp 187–225.

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