SOIL NITROGEN CHANGES, EARLY GROWTH, AND RESPONSE TO SOIL INTERNAL DRAINAGE OF A PLANTATION OF *Alnus jorullensis* IN THE COLOMBIAN HIGHLANDS[1] /

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Resumen

El crecimiento inicial de una plantación de Alnus jorullensis *H. B. K. (=* A. acuminata *H. B. K.) a 2300 msnm en el sur de Colombia fue rápido, alcanzando después de 2 años una altura máxima de 8.0 m y un promedio de 6.2 m en los mejores sitios. Se estimó que en la plantación con una densidad de 1200 árboles/ha, la producción de madera seca fue de 6.4 toneladas/ha.*

El drenaje interno del suelo (orgánico arenoso de origen volcánico) tuvo gran influencia tanto sobre el crecimiento del Alnus *como sobre los cambios de nitrógeno en el suelo. En áreas con buen drenaje el crecimiento del* Alnus *fue mejor que en aquéllas con drenaje deficiente. En áreas pantanosas el* Alnus *sobrevivió pero su crecimiento fue menor. El crecimiento del* Alnus *se correlacionó con el porcentaje de cobertura del pasto kikuyo (*Pennisetum clandestinum *Hochst.) (*$r^2 = 0.93$), sugiriendo que el kikuyo *puede servir como indicador de sitios favorables para la siembra de* Alnus. *El* Alnus *resistió bien la presencia del kikuyo.*

Las raíces tuvieron una gran cantidad de nódulos que a su vez produjeron un inoculum *capaz de inducir la producción de nódulos en plántulas de* Alnus rubra *Bong. cultivadas asépticamente* in vitro.

Por estas características favorables, el Alnus jorullensis *parece ser de un gran potencial para la reforestación en climas húmedos de tierra fría en Centroamérica y Suramérica.*

Introduction

Alnus is one of at least 19 known genera of actinorhizal plants in the world that form root nodules in symbiosis with nitrogen-fixing actinomycetes of the genus *Frankia* (1, 11, 44). Although most alder species are found in temperate regions of the northern hemisphere, several alder species, including *A. jorullensis* H. B. K. are native to the cool tropical highlands of Central and South America where it is often referred to synonomously with *A. acuminata* H. B. K. (18). Alders have been widely planted and they become nodulated in soil, even outside of their native ranges (10).

Estimates of annual nitrogen fixation by alders vary widely because of differences in species, climate, and experimental techniques used by investigators (42). Lawrence (28) estimated that a 5-year-old thicket of *A. sinuata* (Reg.) Rydbert may fix 155 kg/ha of N annually, while Crocker and Major (6) estimated that nitrogen accretion in soil under *A. sinuata* (Regel) Rydb. in areas of receding glaciers in Alaska was 62 kg/ha/yr. *Alnus glutinosa* (L.) Gaertn. was reported to fix nitrogen at an annual rate of 125 kg/ha (45), and Daly (8) calculated that from 155 to 165 kg/ha nitrogen may be added annually to the soil by *A. rugosa* (Du Roi) Sprengle in Quebec. In Oregon, Newton *et al.* (33) found in red alder stands (*A. rubra* Bong.) between 2 and 15 years old, an annual increase of 320 kg/ha N in

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biomass and soil. Such increases in red alder stands were substantiated by the work of Zavitkovski and Newton (47).

Alders have been found to increase growth of associated vegetation (17, 38) as well as to control certain fungal coniferous-root pathogens (19, 32). Alder stands are also thought to increase soil organic matter and to lower bulk density thus increasing soil porosity and water infiltration rates and improving soil hydrologic properties (42). In the northern hemisphere various alder species have been widely planted for soil improvement on minespoils and for stabilization on recent flood deposits and landslide areas (11). Various experiments using nitrogen-fixing alders as nurse crops have demonstrated growth stimulation of associated crop trees (7, 13, 20, 34, 41).

Alders have been used regionally in a number of silvicultural and agrosilvicultural systems in Latin America. Highland farmers in Guatemala have been known to allow scattered alder trees to remain in corn fields to increase crop yields (9). In Costa Rica, upland dairy farmers plant *Alnus acuminata* H. B. K. at wide spacings in pastures to combine a system of wood production with natural fertilization of pasture grass (5). In the Alto Charma region of Andean Venezuela, *A. jorullenis* is the main timber species available to farmers for house construction material (14).

The Andean alder or aliso (*Alnus jorullensis* H. B. K.) is native to humid areas of the central and eastern sierras of the Colombian Andes at elevations between 2 000 and 3 250 m (36). Andean alder does well in zones with annual precipitation averaging between 2 000 and 3 000 mm and with an average temperature of 18°C, ranging between 5° and 24°C. The alder's rapid growth, straight bole, natural pruning, useful wood, and nitrogen-fixing capability make it an ideal species for plantation culture (39).

In Colombia, *A. jorullenis* has been extensively planted in the watersheds of the cities of Manizales and Armenia. Peace Corps volunteers in the Manizales region used the alder for establishing farm woodlots on heavily eroded sites and for direct seeding of landslide areas. Also in Manizales an experimental plantation interplanting *A. jorullensis* with a *Cedrela* species has been established to evaluate the effect of the interplanted alder on *Cedrela* growth (35).

Several decades of plantation work with the alder in Caldas, Colombia have resulted in the development of some silvicultural treatments for the species in that zone (36, 39). Tree heights of 35 m and diameters at breast height of 79 cm have been noted for alder and height growth of 25 m in 10 years in Colombia is possible (36). Common tree associates of Andean alder in native forests of Colombia include species of *Cedrela, Juglans, Tabebuia, Nectandra,* and *Ocotea* (36).

Tree legumes are prevalent in many tropical ecosystem (2, 24) and a number of nodulated tree legumes are used for reforestation in the lowland tropics (15). We observed *Frankia*-nodulated *Alnus* and *Myrica* to occur commonly in the Colombian highlands, though these and other actinorhizal (*Frankia*-nodulated) trees are not common in tropical lowlands (11). Various genera of nitrogen-fixing tree legumes have traditionally been incorporated into the agricultural systems of the lower and middle elevation neotropics, such as the use of species of *Inga, Albizia,* and *Erythrina* as shade trees for coffee and cacao plantations and in pastures. However, only the non-leguminous, nitrogen-fixing *Alnus* has been used to any great extent in silvicultural and agro-silvicultural systems in the cool highlands of Colombia. Actinorhizal plants seem to be equally efficient in fixing dinitrogen as legumes (43). Consequently, actinorhizal woody plants such as *Alnus* may be important contributors to the nitrogen economy of some highland forestry and agricultural systems, much as tree legumes are at lower elevations for site amelioration and improvement of soil productivity.

Future intensive reforestation efforts in Colombia will undoubtedly be directed toward humid zones where there are high potentials for loss of soil N due to nitrate leaching and denitrification. Nitrogen fixation will become an increasingly desirable characteristic in tree crops in order to avoid high fertilizer costs and to maintain site productivity. In cool highland areas the use of alder, either in rotation with *Pinus* or *Eucalyptus* or in mixed planting systems, should be investigated as a possible technique to maintain site productivity. In addition, since human population and intensive land use in many parts of Colombia are concentrated in highland areas, techniques using alder in agro-forestry systems may prove to be sustainable methods for increasing food and fiber production while expanding the amount of tree cover on deforested upland areas of the Andes.

The objectives of this study were to measure the growth of *Alnus jorullensis* plantations at the Merenberg Nature Reserve at various spacings and to determine changes in soil nitrogen concentration in alder plantation soils.

Materials and methods

A three-quarter ha area at the Merenbert Nature Reserve was planted in May of 1981 with *Alnus jorullensis* The Merenberg Reserve is located in the Andean highlands of southern Colombia approximately 80 km East of the city of Popayan The area lies at latitude 2°15' North and longitude 76°10' West and is situated on the eastern slopes of the central sierra of the Colombian Andes at an elevation of 2 300 m

The Merenbert Reserve lies on the upper slopes of and ancient volcano, el Volcan Merenberg, which last erupted approximately 50 000 years ago (27), and the parent material of the upper soil layers is probably wind-deposited volcanic ash from the nearby Puracé Volcano which has erupted within the last few centuries The mean annual temperature of the farm is 15°C with temperatures never falling below 5°C. Mean annual precipitation on the Reserve for the years 1976 through 1982 averaged 1956 mm. The Merenberg region typically experiences two wet and two relatively dry seasons each year with the principal dry season occurring between December and February and a lesser dry season falling between July and September. Apart from rainfall, the area receives a large amount of mist and fog, and insolation during much of the year is quite low for a site near to the equator

The experimental site was chosen because it contained the least topographic variability (with slopes ranging from 10 to 30°) within the area designated to be reforested in 1981 The soil in the top 20 cm is an organic sandy loan (30% organic matter) with a bulk density of 0.9 g/cc and a pH of 5.2 The soil varies from being very poorly drained (depth to gleying of 15 to 25 cm) in the lower portions of the field to somewhat poorly drained (depth to gleying of 45 to 60 cm) in the upper parts of the field. The very poorly drained downslope are was generally defined by a ground cover of mosses, ferns, and sedges with islands of kikuyo grass (*Pennisetum clandestinum* Hochst.), an introduced pasture species, on better drained rises. The somewhat poorly drained upslope region was covered predominately with kikuyo grass with pockets of mosses and ferns in swales and other wet spots. The area of the experiment had been covered by highland hardwood forest (dominated by *Quercus humboltdii* Bonpl., *Billia columbiana* Planch & Lind., *Ficus* spp., *Weinmania* spp, and *Ocotea* spp.) until the late 1940s, when it was cleared, burned, and converted to pasture The area had been in cattle pasture until 2 months before planting.

Alnus jorullensis seedlings were grown from seed collected in Colombia at La Selva farm above Manizales, Caldas. Seed was germinated in the state nursery in Villamaría, Caldas and grown for 4 months. Seedlings of approximately 4 cm in height were then transported in moist peat moss to the Merenberg nursery At Merenberg the small seedlings were planted in 7 x 12 cm black polyethylene bags containing local forest soil. The containers were inoculated with crushed nodules from established alders in the Merenberg nursery to insure adequate nodulation, and the seedlings were grown to a 20 to 25 cm height (8 months after germination) before planting on the experimental site.

In April of 1981, the site was prepared for planting by removing aboveground vegetation on areas 70 cm square for each seedling and by thoroughly chopping the soil down to a depth of 15 to 20 cm Site preparation was done with machetes and an 18 x 22 cm pick hoe for breaking ground Trees were planted in the center of these "plateos" the following month. "Plateos" were weeded at 3, 12, and 24 months after planting. There was 100% survival of the alder despite the fact that in the first 3 months after planting many trees stood in pools of water in the concavity resulting from site preparation.

Tree plantings were organized in a randomized complete block design with 5 replications of 3 spacings (Figure 1). Trees were planted with rows offset, giving a staggered rather than a linear configuration across rows. The 3 spacings in 0.03 ha plots were: (1) 5.0 x 5.0 m, giving a density of 400 alder trees/ha; (2) 2.5 x 5.0 m, giving a density of 800 alder trees/ha; and (3) alder planted with 2.5 m between rows and alternating within row spacings of 2.5 and 5.0 m, giving a density of 1 200 alder trees/ha. The blocks were located across the principal slope with 2 blocks positioned on the lower slope, which was very poorly drained, and the remaining 3 blocks on the upper and middle slopes, which had better drainage Swales occurred on the slope, resulting in drainage variation across the slope in some of the middle slope blocks (Figure 1). The plantation site was mapped for dominant ground cover before tree establishment.

Alder tree height and diameter measurements were taken 2 years after planting Height measurements were taken to the nearest tenth of a meter using an 8 m measuring pole, and diameter measurements were taken with a caliper at 30 cm above ground. There was one staggered row of border trees within each plot which was excluded from statistical analysis. An ANOVA was performed to determine the variation in

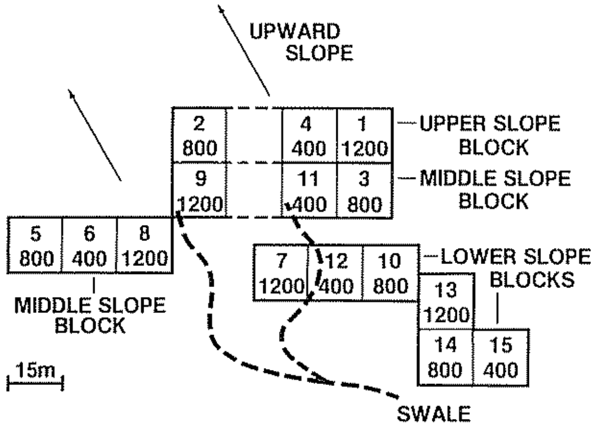

Fig. 1. Schematic diagram of plot layout on the site. The upper number represents ranking of mean alder height growth. The lower number is density of *A. jorullensis* plantings in a plot. Irregular blocking is due to rough terrain.

2-year alder height associated with blocks, spacing, and block by spacing interaction. Means and standard deviations of alder height and an alder volume indes (D^2H = diameter at 30 cm squared times tree height) were determined by plot and were ranked in descending order by mean alder height. Mean alder height was plotted against % kikuyo cover in each plot. Also, after 2 years a stem analysis was done on 4 randomly-selected entire alder tree stems from each of the 6 plots with mean tree heights exceeding 4.9 m by measuring diameters at 1-m intervals. A volume estimate for 2-year alder growth was made using Smalien's Formula (23), and an estimate of 2-year dry tonnage of stemwood biomass was made using and average value for dehydrated specific gravity of 0.338 g/cc for *A. jorullensis* as reported by Rojas *et al.* (36).

Prior to tree planting, soil samples were collected by taking 4 cores with a soil probe in each block. Cores were taken to a depth of 20 cm and were divided into 5-cm depth increments. The soil was immediately air dried at the Merenberg Reserve and was transported to the University of Illinois in Urbana where the samples were sieved through a 2-mm mesh prior to total nitrogen determination using a micro-Kjeldahl procedure (31). After 2 years, soil samples were again taken around one randomly selected alder tree in each spacing plot. Cores were taken with a soil probe adjacent to the alder stem and at 10, 25, 50, 75, and 100 cm distances at a randomly selected stem azimuth for each sample. The cores were again taken to a depth of 20 cm, divided into 5-cm increments, air dried at the Merenberg Reserve, and transported to Urbana, Illinois for total nitrogen analysis. Nitrogen concentrations at the various distance by depth combinations from alder stems were combined for the 3 better drained upslope blocks and for the 2 poorly drained downslope blocks. These 2-year concentrations were compared with soil nitrogen concentrations from corresponding depths and drainage class prior to tree planting using a t-test for comparing means of unequal sample sizes (40).

Nodulated *Alnus jorullensis* plants from the plantation were brought to Urbana, Illinois and fresh nodules from these plants were ground in a Virtis homogenizer in a phosphate buffer solution at pH 7.0. The ground nodular suspension was filtered through cheesecloth and used to inoculate aseptically grown *Alnus rubra* seedlings on Hoagland's agar slants according to the method described in Knowlton and Dawson (26). Nodulated seedlings were assayed for nitrogenase activity using an acetylene reduction method of Dawson and Gordon (12).

Results

Analysis of variance showed significant differences in alder height and D^2H means associated with spacing, blocks, and their interaction. The significant difference associated with spacing is probably the result of the spacing effect being confounded with an effect due to drainage, since plots at the wider spacings often were in the wettest areas.

A ranking of spacing plots by mean alder height shows increasing alder growth with better soil drainage (Table 1). The poorest alder growth occurred in the most poorly drained areas which were covered with mosses and ferns. Two-year tree heights ranged from a maximum of 8 m in the best drained plots to a minimum average of slightly under 2 m in the wettest areas. Examination of Table 1 reveals an apparent lack of spacing effect on alder growth. The fastest growing alder plot with a density of 1 200 trees/ha was estimated to have produced 6.5 dry metric tons of stemwood/ha after its first 2 years of growth.

Fitting mean alder height with percentage kikuyo cover (Figure 2) further illustrates the strong influence drainage seems to have upon alder growth. The r^2 value for this simple linear regression is 0.83, indicating a strong positive correlation between percentage of kikuyo grass and alder height growth. The linear equation provided the best fit of the regression line, compared with quadratic or logarithmic fits as is manifest in Figure 2. Kikuyo grass is intolerant of poor soil drainage.

Nodules were formed on most aseptic *Alnus rubra* seedlings after inoculation with ground nodules from

Table 1. Ranking of plots by mean *Alnus* height.

	Topographic position	% Kikuyo cover	Density (stems/ha)	No. of trees	Mean tree height (m) mean ± sd	Range (m)	D^2H* (dm^3) mean ± sd
1.	Upper slope	100	1 200	19	6.22 ± 0.91	4.8 – 8.0	24.9 ± 12.4
2.	Upper slope	100	800	12	6.08 ± 0.86	5.2 – 7.9	38.8 ± 19.0
3	Middle slope	100	800	12	5.43 ± 1.47	1.1 – 7.3	20.5 ± 14.5
4.	Upper slope	100	400	6	5.25 ± 0.41	4.8 – 6.0	16.6 ± 6.8
5	Middle slope	72	800	12	5.23 ± 0.82	3.7 – 6.7	15.5 ± 8.1
6	Middle slope	100	400	6	4.93 ± 1.22	3.1 – 6.5	14.4 ± 8.4
7.	Lower slope w/rise	60	1 200	19	4.39 ± 1.26	2.0 – 6.0	10.9 ± 7.0
8.	Middle slope	92	1 200	19	4.34 ± 1.05	2.4 – 6.0	10.2 ± 9.7
9	Middle slope w/swale	100	1 200	19	4.24 ± 1.08	2.4 – 6.0	8.8 ± 4.7
10	Lower slope w/rise	52	800	12	3.76 ± 1.23	2.0 – 6.0	6.8 ± 6.2
11	Middle slope w/swale	48	400	6	3.28 ± 1.32	1.5 – 5.0	5.4 ± 6.2
12	Lower slope	12	400	6	2.97 ± 1.08	2.2 – 5.1	4.2 ± 4.5
13	Lower slope	12	1 200	19	2.49 ± 0.84	1.3 – 5.0	2.4 ± 3.2
14	Lower slope	0	800	12	2.48 ± 0.71	1.5 – 3.5	2.3 ± 1.9
15.	Lower slope	0	400	6	1.95 ± 0.47	1.2 – 2.4	0.9 ± 0.6

* Diameter for D^2H measured at 30 cm above ground

the *A. jorullenis* plantation. Nitrogen fixation was evidenced by the greening of nodulated seedlings on N-free Hoagland's agar slants, and by the ability of intact nodules to reduce acetylene to ethylene.

Soil nitrogen concentration in the relatively better drained upslope area increased significantly after 2 years in the superficial 20-cm soil layer at distances from 50 to 100 cm from alder stems (Table 2). Within 50 cm of tree stems, soil N seemed to increase slightly over preplanting levels, but the increases were not statistically significant. Only at the base of alder stems in the top 10 cm did there seem to be a decrease in soil N, but this decrease was not significant. Soil N at the 50 to 100 cm distance from stems seemed to increase most in the surficial soil layer (0 to 10 cm) while closer to alder stems this trend did not exist. Soil N concentrations in the very poorly drained downslope area decreased at all depths around the alder trees with no consistent pattern of nitrogen change evident in this region (Table 3).

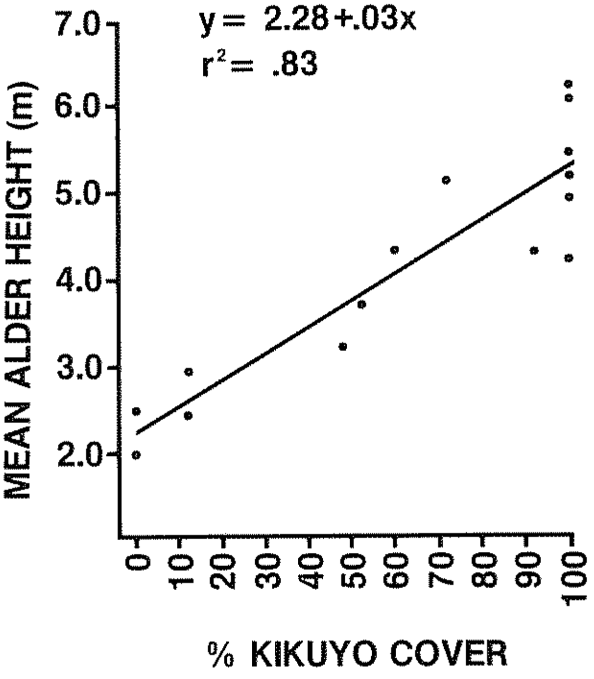

Fig 2. Relationship between mean *A. jorullensis* height and % kikuyo ground cover

Discussion

Alder Tree Growth

Growth of *A. jorullensis* in the better-drained plots on the upper slopes is extremely rapid. Although the alder does not occur naturally in the immediate area of Merenberg, its early height growth and abundant nodulation suggest that the species may be well adapted for more extensive use in reforestation in the region. An actinorhizal *Myrica* species occurs naturally at Merenberg and may be a source of *Frankia* propagules, explaining the abundant nodulation of *Alnus* at this locale. Several 5-year-old alder trees in the Merenberg botanical garden have reached heights of 15 m with 15 cm dbh's and have produced a seed crop.

Alder on the better "somewhat poorly drained" sites had three times the height growth of alder on the

Table 2. Mean change in total soil N around the stems of *A. jorullensis* on the somewhat poorly drained upslope site (mg N/kg air-dried soil sample). Mean values are for 9 plantation soil samples minus the mean value (n = 12) for soil N concentration at corresponding depth prior to planting.

Soil depth (cm)	Distance from alder stem (cm)						Initial soil N concentration mean ± sd
	0	10	25	50	75	100	
0 – 5	–112	223	162	864**	930**	657**	1 661 ± 276
5 – 10	–101	110	302	536**	740**	581**	1 071 ± 314
10 – 15	87	187*	321**	308**	408**	394**	706 ± 108
15 – 20	22	32	69	309*	200*	222*	666 ± 185

** Significantly different from mean N concentration at corresponding soil depth prior to plantation establishment (α = 0.01).

* Significantly different from mean N concentration at corresponding soil depth prior to plantation establishment (α = 0.05).

Table 3. Mean change in total soil N around the stems of *A. jorullensis* on the very poorly drained downslope site (mg N/kg air-dried soil sample). Mean values are for 6 plantation soil samples minus the mean value (n = 8) for soil N concentration at corresponding depth prior to planting.

Soil depth (cm)	Distance from alder stem (cm)						Initial soil N concentration mean ± sd
	0	10	25	50	75	100	
0 – 5	–550**	–329	–337	–463**	–278*	–101	1 784 ± 304
5 – 10	–844**	–581*	–617**	–795**	–371	–546**	1 750 ± 382
10 – 15	–742**	–529**	–565**	–550**	–281**	–543**	1 459 ± 420
15 – 20	–471*	–349	–466*	–451*	–355	–428	1 180 ± 528

** Significantly different from mean N concentration at corresponding soil depth prior to plantation establishment (α = 0.01).

* Significantly different from mean N concentration at corresponding soil depth prior to plantation establishment (α = 0.05).

very poorly drained sites. Although *Alnus jorullensis* naturally occurs on wet sites along streams and around swamps, the species grows best on well-drained sites as long as soil moisture is not limiting. This situation may be analagous to that found with *A. glutinosa* in the British Isles (29) where alder grows best on upland sites but is limited in occurence to streamsides and wetlands because of extreme sensitivity of germinating seedlings to desiccation. Although alder growth on the lower slopes of the experimental plantation is evidently limited by poor aeration, the trees have grown at least 1 m per year and have suffered no mortality.

Alder's ability to become established on boggy sites may be useful. In the cool Merenber region where high precipitation is coupled with low evaporative potential, *Sphagnum* filled boggy pasture land often is found adjacent to fairly well-drained forest lying on the same terrain. The poorly aerated conditions of the pasture may be the result of the loss of the evapotranspirative tree cover which allowed for a buildup of *Sphagnum* and other mosses. The mosses seem to hold water on the site resulting in saturated soil conditions and the exclusion of many tree species and preferred pasture grasses. Since alder trees are able to survive these poorly drained soils, they may lower soil moisture content over time through evapotranspiration. If this is the case, then planting of alder trees may be a low cost means for converting wet sites to more productive wood and forage sites.

The results of this experiment suggest that kikuyo grass may be a useful indicator plant for a good alder site. This exotic grass is widespread over most of the Colombian highlands and is a dominant ground cover in many pasturelands. We have observed in Colombia that sites with volcanic soils lacking kikuyo invariably have drainage that is too poor for the establisment of trees.

While kikuyo grass may indicate the best sites for alder growth, the presence of the grass generally increases the costs of tree plantation establishment owing to the highly competitive nature of the grass (36) *Eucalyptus globulus* Labill. the principal hardwood planted in the Colombian highlands, is notoriously intolerant of grass competition (16), and much of the cost of *Eucalyptus* establishment is the result of kikuyo control The alder is more tolerant of kikuyo competition than in *Eucalyptus*. Although two weedings are recommended for establishment of alder in kikuyo (34), we have observed in previous work with *A jorullensis* that the species can become adequately established in kikuyo with only one weeding. This ability to tolerate weed competition is important because campesinos often do not carefully follow recommended maintenance practices with small tree plantations

It is fortuitious that *A. jorullensis* grows well in kikuyo grass because an important use of this tree species is in agri-silvicultural systems in which alder is cultivated at wide spacings in pastures Interplanting alder in pasture has been carried out for decades in parts of Costa Rica (22) We have observed in some farms above Manizales, Caldas, that farmers somewhat passively follow this practice by leaving volunteer alders that grow in their pastures when cleasing their fields of other volunteer trees Also. kikuyo under partial alder shade continues to produce throughout the dry season while the open-field kikuyo does not, which may be due in part to moisture inputs from condensation and drip during misty weather (personal communication from John Beer of CATIE, Turrialba, Costa Rica, 1981). Furthermore, tree cultivation in pastures diversifies and expands a farm economy via production of fuelwood and timber

Apart from its beneficial effect on pasture grass, alders have been found to support greater volume and variety of understory plants than stands of other timber species (42). We have observed in the Manizales region that understory vegetation in alder plantations is much greater and more varied than under plantations of conifers or *Eucalyptus* This abundant understory may be due to increased nitrogen fertility, increased dripping of water condensed from mists on the alders, or abundant light penetration permitted by the relatively open alder canopy.

Nitrogen Accretion

A dense mat of heavily-nodulated roots was observed near the soil surface within 1 m of alder trees in the better-drained plots. Aseptically grown *Alnus rubra* seedlings inoculated with ground nodules from this plantation produced nodules that were effective in reducing acetylene to ethylene, indicating nitrogenase activity of *Frankia* originating from this plantation The existence of large-diameter roots at 1 m from tree stems in the better-drained plots suggest that alder roots were extensive. However, roots were not totally excavated to determine their extent. The zone of greatest soil nitrogen accretion was in the concentric zone from 50 to 100 cm around alder stems. Various researchers have found evidence for the importance of roots in nitrogen cycling. Hansen and Dawson (20) found localized regions of soil N accretion confined to the zone of greatest early root growth around 2-year-old *A. glutinosa* in northern Wisconsin Root mortality was found to be the most important cycling mechanism for nitrogen in a southern Appalachian forest soil (21), and Zavitkovski and Newton (47) estimated that 60% of soil nitrogen added in a stand of *A. rubra* came from within the soil

The absence of significant net nitrogen accretion within 50 cm of alder stems, despite many heavily-nodulated roots there, might be explained by the effects of site preparation In the process of removing the ground cover vegetation during site preparation, part of the N-rich top horizon was also removed. Chopping the soil probably resulted in a mixing of the upper soil horizon with lower horizons, while undoubtedly increasing soil aeration at the planting site and increasing activities of microorganisms, including nitrifiers Improved aeration may have led to accelerated decomposition of roots of kikuyo grass with subsequent addition to soil N, but it also might have promoted nitrification. Although nitrification rates are usually low in acidic soils with pH's around 5 0 or below (25), Bollen and Lu (3) found high rates of nitrification in strongly acidic soil under red alder in coastal Oregon. Once formed, nitrates could have been leached through the coarse texture soil Significant increases at the 10 to 15 cm depth close to alder stems (Table 2) suggest that leached nitrates may have accumulated in that zone Ponding also occured in the depressions created by soil chopping for seedling planting This could have accelerated nitrate leaching in the site-prepared zone closest to the alder stems and reduced nitrogenase activity of nodules

Nitrates also could have been lost from the chopped "plateos" by denitrification. Denitrification occurs when nitrates are present in a water-saturated soil with an available energy source When the supply of oxygen in soil is not adequate to meet the requirements of aerobic microorganisms, denitrifying microorganisms utilize the nitrates in place of oxygen as hydrogen acceptors and volatile dinitrogen gas is lost in the process (4). With an abundant energy source, owing to the high organic matter content of the soil, and with water saturation caused by precipitation, high rates of denitrification could have occurred at the planting site. Even when the soil was not water saturated, denitrification could have occurred in anaerobic microsites present in the soil resulting from low oxygen potentials caused by active root respiration and microbial activity (46).

Another possibility for low N accretion near the upslope alder stems after 2 years is that much fine root activity of these large trees migrated away from the root collar. Near the alder stems were large, suberized roots with large, older nodules. It is possible that N was added here in the first year of tree growth when fine root activity would have been greatest, but that much of this N had subsequently been removed from the soil as a result of ammonification, nitrification, leaching, and denitrification.

Although less soil nitrogen accretion was expected on the very poorly drained lower slopes of the plantation because of the slower alder growth, the losses of N were surprising, and we have no precise explanation for them. It seems possible that loss of nitrogen in surface runoff or due to denitrification may have been significant in these areas. Making direct measurements of denitrification based on the inhibition by acetylene of N_2O reduction during denitrification, Ryden and Lund (37) estimated N losses as high as 3.60 kg/ha/day after rains, and annual nitrogen losses of up to 233 kg/ha in irrigated vegetable crop lands in California. In the Merenberg area with a stable year around temperature and considerable precipitation, it seem possible that levels of denitrification of such a magnitude could also have occurred. This could explain the losses in soil N found after 2 years in the very poorly drained parts of the plantation.

The largest annual N contribution estimated for red alder in the coastal range of Oregon, an enviroment not unlike that of the wet highland Andes, is 320 kg/ha in the top 60 cm of soil and in the standing biomass based on stands 2 to 15 years olds (33). This research suggests that *A. jorullensis* might be a similarly prodigious contributor of nitrogen to highland tropical ecosystems where alder growth, nitrogen fixation, and nitrogen accretion in soil are not limited by poor drainage. By averaging the values for changes in soil N concentration for the top 20 cm of soil within 1 m of alder stems on the better-drained upslope plots (Table 2), using the corresponding soil bulk density value of 0.9 g/cc, and assuming a density of 1 200 trees/ha, a rough estimate of 279 kg/ha of annual soil N increase can be derived. Additional sampling of soil and plant nitrogen contents will be necessary to accurately determine soil nitrogen accretion rates in these plantations.

Summary

Early growth of *Alnus jorullensis* H. B. K. (= *A. acuminata* H. B. K.) in a plantation at 2 300 m in elevation in southern Colombia was very rapid with maximum individual tree heights of 8 m, and maximum average heights of 6.2 m in the best plot after 2 years. Stemwood production in a plot with a density of 1 200 trees/ha was estimated to be 6.4 dry metric tons/ha after 2 years.

Internal drainage of the volcanically-derived organic sandy loam soil influenced both alder growth and soil nitrogen changes. Alder growth was greatest on upper slope soils with better drainage. On very poorly drained lower slopes, alder survived well, but grew slowly. Alder height growth was strongly linearly correlated with percentage of kikuyo grass (*Pennisetum clandestinum* Hochst.) cover ($r^2 = 0.83$) suggesting that kikuyo may be a useful indicator of a good alder site. Alder was also quite tolerant of kikuyo competition. Trees were heavily nodulated, and nodules produced an inoculum capable of inducing effective nodules on aseptically-grown *A. rubra* Bong.

Because of these favorable features, *A. jorullensis* seems to have potential for use in similar moist highland areas of South and Central America.

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