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AGROPRODUCCIÓN

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QUINOA BIOMASS PRODUCTION CAPACITY AND SOIL NUTRIENT DEFICIENCIES IN PASTURES, TREE PLANTATIONS AND NATIVE FORESTS IN THE ANDEAN HIGHLANDS OF SOUTHERN ECUADOR

CAPACIDAD DE PRODUCCIÓN DE BIOMASA DE QUÍNOA Y DEFICIENCIAS DE NUTRIENTES EN SUELOS DE PASTIZALES, PLANTACIONES ARBÓREAS Y BOSQUES NATIVOS EN LOS ALTOS ANDES DEL SUR DEL ECUADOR

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Resumen

En los altos Andes del Ecuador, aunque la agricultura extensiva y el sobrepastoreo tienen impactos negativos en el suelo, aún se desconoce qué práctica reduce más su fertilidad. El crecimiento de quínoa (*Chenopodium quinoa* Willd.) fue evaluado en suelos de bosques nativos (Bn), pastizales (Pa), plantaciones de *Eucalyptus globulus* Labill. (Eg) y *Pinus patula* Schlecht. (Pp). Se aplicó un bioensayo con un diseño de bloques al azar con controles, C; nitrato de amonio, N; superfosfato triple, P; y N+P combinados. En suelos de Pp la mortalidad de quínoa fue del 100 % en N, 88 % en C, 63 % en N+P y 0 % en P. El P fue el que más incrementó el crecimiento. La biomasa de quínoa alcanzó solo 0,1 g/pote, con un contenido de P de 0,7 mg/pote. En los demás suelos, el N+P fue el que más incrementó el crecimiento. La biomasa de quínoa (g/pote) promedió 0,1 en C; 0,4 en N; 1,6 en P y 7,2 en N+P; el contenido de P (mg/pote) promedió 0,9 en C; 0,6 en N; 12 en P y 38 en N+P. En todos los suelos, el PO_4^- fue el elemento primordial deficitario; el K lo fue seguramente en Pp, con toxicidad de Al. Este estudio sugiere que estos suelos no pueden soportar la producción de quínoa sin fertilización combinada esencialmente con P y K. Los suelos de Pp son los que más deficiencias presentaron probablemente debido a una historia de uso más prolongada después del pastoreo y al propio efecto del pino.

Palabras claves: potencial agrícola, deficiencias de nutrientes, suelos volcánicos.

Abstract

In the high Andes of Ecuador, although expanding agricultural practices and overgrazing have had negative impacts on soil fertility, few investigations have been conducted to identify which practices are most likely to reduce fertility. Quinoa (*Chenopodium quinoa* Willd.) was grown in soils from native forests, Nf; pastures, Pa; *Eucalyptus globulus* Labill. plantations, Eg; and *Pinus patula* Schlecht. plantations, Pp. A bioassay study was conducted using a randomized block design with control (C), ammonium nitrate (N), triple superphosphate (P), and combined N and P (N+P) fertilizer treatments. On soils from Pp, quinoa mortality was 100% in N, 88% in C, 63% in N+P and 0% in P; P enhanced growth the most; quinoa biomass attained only 0.1 g/pot and had a P content of 0.7 mg/pot. N+P enhanced quinoa growth the most on soils from Nf, Pa and Eg. Here, quinoa biomass (g/pot) averaged 0.1 in C, 0.4 in N, 1.6 in P and 7.2 in N+P; P content (mg/pot) averaged 0.9 in C, 0.6 in N, 12 in P and 38 in N+P. In all soils, PO_4^- was the principal limiting factor. K deficiencies and Al toxicity probably occurred only in Pp soils. This study suggests that the studied soils cannot support production of quinoa crops without additions of combined fertilizers containing P and K as the principal elements. Pp have the least fertile soils, presumably resulting from a longer history of use after pasturing in addition to the pine effect itself.

Keywords: agricultural potential, nutrient deficiency, volcanic soils.

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1 Introduction

Land-use patterns in the Neotropics in general, and in the Andes in particular, are experiencing a shift towards pasturing for cattle ranching, specifically dairy cattle in the Andean highlands. This shift in land-use patterns responds to changes in unbalanced social structures, market conditions, access to farmland and rural emigration (Jampel, 2016). In Andean Ecuador, the situation is no different from the rest of the region and the local rural economy is largely based on a dairy cattle livelihood, whereas most of the agriculture is dedicated to the production of agro-alimentary goods for export according to massive urban demands within or outside the country (Bretón, 2008; Potthast *et al.*, 2012). Cattle ranching has developed at the expense of Andean montane rainforests and perennially humid páramo grasslands, above the tree line, through slash and burn practices for conversion to pastures. Both types of ecosystems have high biodiversity and produce several ecosystem services, such as water retention and water regulation for the main cities of Ecuador and rural populations (Harden *et al.*, 2013). Not only pastures, but also cultivated lands and tree plantations cause increased streamflow variability and significant reductions in catchment regulation capacity and water yield (Ochoa-Tocachi *et al.*, 2016).

In the Andean highlands of southern Ecuador, steep slopes, high precipitation regimes, water erosion and the lack of proper soil management (which depends exclusively on externalities rather than using and increasing the supply of locally produced and renewable soil fertility resources such as manure, cover crops, compost and optimizing nutrient use efficiency throughout the farm, according to Fonte *et al.* (2012), pasture soils experience progressive degradation linked to soil N and P depletion; after soil degradation pasture lands are ultimately abandoned. On these abandoned pastures, or on natural páramo grasslands, *Pinus patula* Schlecht. is used in monospecific plantations at a wide range of elevations up to 3.400 m.a.s.l. *Eucalyptus globulus* Labill. is also used in plantations, but at lower elevation ranges (maximum upper limit of aprox. 2.800 m.a.s.l.). These two exotic tree species are largely preferred in local forestry plantations because of their fast growth and timber production. However, these plantations, through the effect of their litter, can also cause a decrease in soil pH and soil cation concentrations (Chacón *et al.*, 2009; Farley *et al.*, 2012; Harden *et al.*, 2013).

Within this scenario of land-use patterns in the highlands of Southern Ecuador, a growth response experiment was conducted on soils from pastures, *P. patula* and *E. globulus* plantations, compared to soils of native Andean forests, using quinoa, *Chenopodium quinoa* Willd., as a test crop species, and with fertilization treatments with three fertilizers (N alone, P alone, and a combination of N + P). In Ecuador, quinoa was already used in pre-Inca times, although its cultivation declined in the Andes following the Spanish conquest (circa 1539 AD). Quinoa has been largely replaced by corn as an important staple-crop, but as opposed to corn it is adapted to acid soil conditions generally found in Andean regions (Risi and Galwey, 1989; James, 2009). The specific objectives of this study were:

1. to identify which land-use types (pastures, two tree plantations and native forests) are most likely to reduce soil fertility;
2. to examine which soils from the four land-use types produce the lowest growth of quinoa; and,
3. which soil nutrients are most affected by the four land-use types.

2 Materials and methods

2.1 Soil sampling and experimental design

Soils of each land-use types were sampled at four separate locations within a wide area of southern Ecuador (Chacón *et al.*, 2015). The four land-use types were second growth native forests (Nf), pastures (Pa), *P. patula* plantations (Pp), and *E. globulus* plantations (Eg) (Figure 1). These land-use types were located in areas of similar elevation, at approximately 3.000 m a.s.l. (Figure 1), and similar annual precipitation regimes (between 1050 and 1700 mm in regions 1 and 2, and between 660 and 1100 mm in regions 3 and 4) (Figure 1). Following a north-south direction, soils change from Histic Andosols in regions 1 and 2, to Dystric Histosols in regions 3 and 4, according to annual rainfall, the influence of volcanic ash or to a lower soil Al and Fe content respectively (Buytaert *et al.*, 2006; Celleri *et al.*, 2007); in either case, these soils developed on pyroclastic materials, lack allophane, have high C and organic

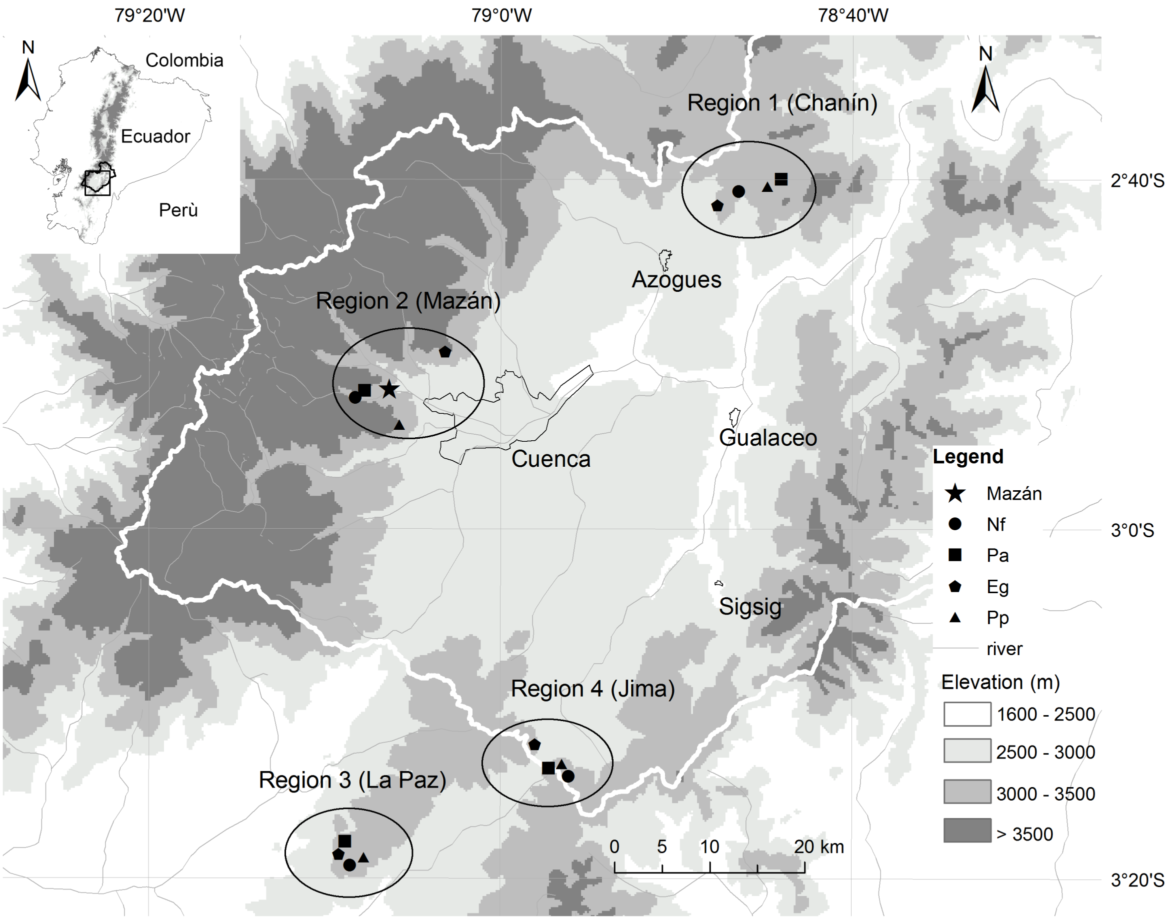

Figure 1. Map of the Paute watershed showing locations of the 4 regions where soils of 4 land-use types were collected. The quinoa experiment was conducted at Mazán. The map is reproduced from Chacón *et al.* (2015).

matter content and low bulk density, and are generally classified as Group 4–Andosols (IUSS Working Group WRB, 2015). In each of the land use types, a 20 m × 20 m plot was established. Within each of the plots, 0.05 m^3 of soil was collected from the first 20 cm of surface soil. Soil samples were transported to a common garden in the Mazán region (Figure 1).

Soil samples were sieved through a 1 cm mesh to remove large non-soil parts. Plastic pots were filled with 4 L of soil. A portion of soil per pot was taken to the laboratory for chemical analyses. A nested randomized block design was established so that each of the four regions corresponded to each of four blocks (Chacón *et al.*, 2015). Within each of the blocks, each of the four land-use types of soils were divided in four sub-units (four pots) and subjected to four treatments (control, N, P, and N+P fertilizers). This design produced 16 randomly distributed combinations of four treatments per block (four blocks = replicates), giving 64 experimental units. Subsequently, six quinoa seeds were planted in each of the pots, and only two germinated seedlings were left to grow. Fertilizer treatments were made once a week during 98 days. N-fertilized soils received weekly additions of 175 mg N as ammonium nitrate (NH_4NO_3). P-fertilized soils received weekly additions of 110 mg P and 65 mg Ca as triple superphosphate [$Ca(H_2PO_4)2H_2O$]. NP-fertilized soils received weekly 87.5 mg N, 55 mg P and 32.5 mg Ca (half of ammonium nitrate and triple superphosphate combined fertilizers) (Chacón *et al.*, 2015).

(n=4)	Native forest			Pasture			Eucalyptus plantation			Pine plantation		
pH	5.2	(9)	**ab**	5.6	(3)	**a**	5.5	(6)	**a**	4.9	(3)	**b**
% SOM	39.9	(68)	**a**	30.1	(47)	**a**	29.7	(66)	**a**	36.6	(18)	**a**
NO_3^- (mg/kg)	3.9	(86)	**a**	5.0	(59)	**a**	3.0	(50)	**a**	6.6	(47)	**a**
NH_4^+ (mg/kg)	42.3	(74)	**ab**	19.8	(33)	**b**	25.6	(42)	**ab**	46.1	(16)	**a**
PO_4^- (mg/kg)	8.9	(58)	**a**	6.7	(128)	**a**	3.3	(2)	**a**	6.3	(51)	**a**
ECEC (cmol/kg)	19.1	(78)	**a**	8.6	(29)	**a**	7.9	(17)	**a**	7.1	(16)	**a**
K (cmol/kg)	0.8	(118)	**a**	0.3	(17)	**a**	0.5	(65)	**a**	0.2	(20)	**a**
Ca (cmol/kg)	12.1	(124)	**a**	6.0	(43)	**ab**	4.2	(47)	**ab**	0.9	(55)	**b**
Mg (cmol/kg)	1.6	(86)	**a**	0.9	(31)	**ab**	1.0	(41)	**a**	0.2	(26)	**b**
Al (cmol/kg)	4.0	(151)	**ab**	1.0	(53)	**b**	1.9	(61)	**ab**	5.3	(24)	**a**
Fe (cmol/kg)	0.063	(180)	**a**	0.002	(89)	**b**	0.004	(122)	**b**	0.054	(73)	**a**

Table 1. Comparison of soil properties before bioassay with quinoa. In parentheses: CV in %. Different letters represent significant differences at $P \leq 0.05$. Table is reproduced from Chacón *et al.* (2015).

2.2 Laboratory and data analyses

The two quinoa plants per pot were harvested and washed, taken to the laboratory and oven dried at 50°C for 72 hours. Plants were weighed for dry biomass. Analyses of total N, P, K, Ca and Mg in plant tissues followed an acid-hydrogen peroxide digestion procedure (Allen, 1989). For the soil samples, NH_4^+-N and NO_3^--N were extracted with KCl 2*M* and analyzed according to Maynard and Kalra *et al.*, (1993). Exchangeable cations were extracted with $BaCl_2$ 0.1*M* and analyzed according to Hendershot *et al.*, (1993). The effective cation exchange capacity was calculated by adding all cations. PO_4^--P was extracted by the method of Bray II and analyzed according to McKeague (1978). The percent soil organic matter was estimated by loss on ignition (Grimshaw, 1989). Soil pH was determined with a glass electrode from a 1:2 soil:water solution.

A nested ANOVA and a Tukey means comparison test were used for all variables after normality of data was confirmed. All statistical analyses were done using SAS (SAS Institute, 2008).

3 Results and discussion

3.1 Comparison of soil properties

In the initial soil samples from the four land-use types across four regions, statistically significant differences were found for the soil variables that are linked to the pH. The Al concentration in pine soils places Al in these soils at the toxic levels (>60 %) reported by Cochrane T. T. y P. A. Sanchez (1982), while Ca can be seen as deficient compared to the other soils (Tables 1 and 2). This pattern is associated with differences in pH, and the general low base status of pine soils in the Ecuadorian Andes and under *Pinus patula* plantations in the same region as this study (Farley and Kelly, 2004; Chacón *et al.*, 2009). However, this pattern is different in the other soils. Generally, the lower pH values and higher ECEC and cation concentrations found in native forest soils are not consistent with the higher pH values and lower ECEC and cation concentrations found in pasture and eucalyptus soils. The effect of soil organic matter, through its humic and fulvic acids, and the effect of a higher Al and Fe content in native forest soils may have decreased soil pH, although the higher base status of these soils probably offers a truer assessment of their fertility (Table 2).

Table 2. Comparison of final soil properties after conclusion of bioassays with quinoa (this study) and corn (Chacón *et al.*, 2015). Soils from both bioassays were analyzed separately but combined for this table because values and statistical significance were nearly identical (n = 8).

		Native forest				Pasture				Eucalyptus plantation				Pine plantation			
	C	5.1	(11)	**bc**	*a*	5.5	(3)	**a**	*a*	5.4	(5)	**ab**	*ab*	4.5	(3)	**c**	*ab*
pH	N	4.7	(13)	**ab**	*a*	4.8	(8)	**a**	*b*	4.8	(6)	**a**	*c*	4.3	(6)	**b**	*b*
	P	5.1	(12)	**ab**	*a*	5.6	(3)	**a**	*a*	5.5	(5)	**a**	*a*	4.7	(3)	**b**	*a*
	NP	4.8	(11)	**ab**	*a*	5.1	(6)	**a**	*b*	5.1	(8)	**a**	*bc*	4.5	(8)	**b**	*ab*
	C	39.1	(67)	**a**	*a*	29.8	(43)	**a**	*a*	30.3	(64)	**a**	*a*	38.4	(20)	**a**	*a*
% SOM	N	39.5	(66)	**a**	*a*	30.4	(44)	**a**	*a*	30.2	(64)	**a**	*a*	38.6	(22)	**a**	*a*
	P	37.9	(64)	**a**	*a*	30.6	(45)	**a**	*a*	30.4	(23)	**a**	*a*	38.4	(23)	**a**	*a*
	NP	39.4	(63)	**a**	*a*	29.9	(44)	**a**	*a*	30.4	(62)	**a**	*a*	38.6	(22)	**a**	*a*
	C	22.9	(65)	**ab**	*c*	14.3	(92)	**b**	*c*	25.4	(109)	**ab**	*c*	38.8	(42)	**a**	*bc*
NO_3	N	354.9	(65)	**a**	*a*	310.8	(48)	**a**	*a*	275.7	(62)	**a**	*a*	287.9	(58)	**a**	*a*
mg/kg	P	10.1	(98)	**b**	*c*	3.8	(66)	**b**	*c*	3.6	(82)	**b**	*d*	21.9	(39)	**a**	*c*
	NP	114.9	(101)	**a**	*b*	116.8	(94)	**a**	*b*	81.1	(95)	**a**	*b*	89.3	(70)	**a**	*b*
	C	25.2	(84)	**ab**	*b*	12.2	(52)	**b**	*bc*	12.2	(63)	**b**	*bc*	33.1	(38)	**a**	*c*
NH_4	N	325.0	(78)	**a**	*a*	194.8	(89)	**a**	*a*	189.9	(63)	**a**	*a*	326.7	(36)	**a**	*a*
mg/kg	P	31.2	(88)	**a**	*b*	11.0	(37)	**bc**	*c*	9.8	(53)	**c**	*c*	23.1	(50)	**ab**	*c*
	NP	114.1	(143)	**ab**	*b*	33.9	(91)	**b**	*b*	30.6	(68)	**b**	*b*	134.8	(36)	**a**	*b*
	C	9.4	(68)	**a**	*b*	7.2	(127)	**ab**	*b*	3.1	(95)	**b**	*b*	7.4	(58)	**ab**	*b*
P	N	11.2	(82)	**a**	*b*	7.4	(124)	**a**	*b*	3.7	(106)	**a**	*b*	6.8	(44)	**a**	*b*
mg/kg	P	263.9	(98)	**a**	*a*	106.1	(115)	**a**	*a*	115.8	(97)	**a**	*a*	128	(51)	**a**	*a*
	NP	127.8	(83)	**a**	*a*	38.2	(91)	**b**	*a*	39.7	(109)	**b**	*a*	70.3	(38)	**ab**	*a*
	C	29.9	(97)	**a**	*a*	12.9	(128)	**a**	*a*	13.5	(150)	**a**	*a*	6.8	(23)	**a**	*a*
ECEC	N	17.6	(74)	**a**	*a*	12.4	(115)	**a**	*a*	7.3	(21)	**a**	*a*	6.6	(21)	**a**	*a*
cmol/kg	P	30.1	(95)	**a**	*a*	18.3	(101)	**ab**	*a*	11.7	(95)	**ab**	*a*	7.9	(18)	**b**	*a*
	NP	26.9	(99)	**a**	*a*	11.7	(104)	**ab**	*a*	11.2	(113)	**ab**	*a*	7	(22)	**b**	*a*
	C	0.4	(67)	**a**	*a*	0.3	(20)	**ab**	*a*	0.5	(72)	**a**	*a*	0.2	(17)	**b**	*a*
K	N	0.4	(38)	**a**	*a*	0.3	(23)	**ab**	*a*	0.4	(67)	**a**	*a*	0.2	(21)	**b**	*a*
cmol/kg	P	0.4	(49)	**a**	*a*	0.2	(17)	**b**	*ab*	0.4	(73)	**a**	*a*	0.2	(46)	**b**	*a*
	NP	0.3	(40)	**a**	*a*	0.2	(18)	**a**	*b*	0.3	(73)	**a**	*a*	0.2	(47)	**a**	*a*
	C	24.0	(128)	**a**	*a*	10.7	(154)	**a**	*a*	10.3	(194)	**a**	*a*	0.8	(55)	**b**	*bc*
Ca	N	12.4	(114)	**a**	*a*	9.9	(146)	**a**	*a*	3.9	(44)	**a**	*a*	0.8	(40)	**b**	*c*
cmol/kg	P	25.3	(118)	**a**	*a*	16.2	(115)	**a**	*a*	8.6	(130)	**a**	*a*	2.5	(37)	**b**	*a*
	NP	21.8	(128)	**a**	*a*	9.4	(133)	**a**	*a*	8.1	(159)	**a**	*a*	1.3	(33)	**b**	*ab*
	C	3.7	(150)	**b**	*a*	0.9	(51)	**b**	*a*	1.7	(70)	**b**	*a*	5.3	(25)	**a**	*a*
Al	N	3.3	(139)	**b**	*a*	1.3	(59)	**b**	*a*	1.8	(54)	**b**	*a*	5	(30)	**a**	*a*
cmol/kg	P	2.7	(144)	**b**	*a*	0.8	(55)	**b**	*a*	1.6	(70)	**b**	*a*	4.7	(28)	**a**	*a*
	NP	3.2	(138)	**b**	*a*	1.1	(50)	**b**	*a*	1.9	(66)	**b**	*a*	5	(30)	**a**	*a*

SOM = Soil Organic Matter. ECEC = Effective Cation Exchange Capacity.
C =Control. N = Ammonium-nitrate fertilizer.
P = Triple super phosphate fertilizer. NP =Combined N-P fertilizers.
Numbers in parentheses are CV (%). Different bold letters represent significant differences between land use types (horizontally) at $P \leq 0.05$. Different italic letters represent significant differences between treatments (vertically) at $P < 0.01$.

Nutrient depletion at a critical level was found for high elevation volcanic soils in northern Ecuador; a minimum soil PO_4^- level of 12 ppm is generally required for adequate growth of agricultural products (Espinosa, 1992). Except for soils in the P and NP-fertilizer treatments, all soils fall below these levels, with native forest soils having a higher PO_4^- content, and pasture and eucalyptus soils having a lower PO_4^- content in the C- and NP-treatments. Thus, the soils used in the experiments reported here can all be considered as PO_4^- deficient. Evidence suggests that PO_4^- levels decrease when PO_4^- is fixed by reactions with Fe and Al in acid soils (Smethurst, 2010). Pine soil PO_4^- content was no different from the other soils in spite of a lower pH. PO_4^- availability in pine soils may be also related to mycorrhizal activity, which can enhance the weathering rates of PO_4^- from the bound PO_4^- pools (Allen, 1991).

The lack of statistical differences, especially in the N-treatment, implies that all soils responded similarly to N additions (Table 2), and that the differences in initial NH_4^+-N and NO_3^--N values are less important in determining specific differences among the four land-use type soils. The only clear pattern, probably very variable in time, is that pine and native forest soils tend to have higher amounts of NH_4^+-N and NO_3^--N than pasture and eucalyptus soils. This trend is clearer if we add together NH_4^+-N and NO_3^--N values. Increased availability of N and PO_4^- has been reported in other coniferous forests, although N deficiencies can appear in second or more rotations (Crous *et al.*, 2011). In initial soil samples NH_4^+-N was the dominant form in all soils. However, after the bioassay, NO_3^--N was considerably increased and NH_4^+-N decreased, suggesting that nitrification had occurred, perhaps caused by some form of incubation process in the bioassay pots. N mineralization experiments with volcanic soils in Costa Rica (Montagnini and Sancho, 1994) also revealed enhanced nitrification in incubations.

In normal conditions, nitrification in our soils should be limited by the acidic pH found more generally in pine soils. Further evidence is the predominance of NH_4^+-N over NO_3^--N in pine soils in the N- and NP-treatments, whereas NH_4^+-N and NO_3^--N values were equivalent in native forest soils, and NO_3^--N had become predominant in pasture and eucalyptus soils. This highlights the potential for N mineralization in native forest soils, and the role of higher pH values in pasture and eucalyptus soils, as well as the problem of lower pH in pine soils. However, N mineralization during the bioassay in this study was not significant because the sum of NH_4^+-N and NO_3^--N was similar to the sum of initial soil values. Therefore, in natural conditions, we confirmed the patternsvseen elsewhere showing that nitrification is inhibited by acidic soil conditions and by the amount of available NH_4^+-N, which is the principal control for nitrification in most humid tropical ecosystems (Vitousek *et al.*, 2010).

Generally, N concentrations (and PO_4^- concentrations) in our sample soils was limited because soil productivity was generally decreased. The low PO_4^- availability might be limiting N mineralization from organic matter (Munevar and Wollum, 1977). Percent SOM was high, statistically comparable in the samples, and unaffected by any of the treatments. In montane tropical soils the decay of humus in the mineral soil is slow (Jenny, 1950) because of low temperatures, low pH, water-logging and litter quality, which results in high SOM accumulation (Oades *et al.*, 1989). Nevertheless, changes of a few percent in soil organic matter can have important effects on the soil nutrient status and on plant nutrition, which was shown in Andisols from the lower montane rain forest zone in southern Ecuador (Davidson *et al.*, 1999). In this study, SOM in native forest and pine soils averaged 39.9 % and 36.6 % respectively as opposed to 29.9 % found in pasture and eucalyptus soils. The humus-rich (high SOM) Andisols contain high amounts of humic acid (Nanzyo *et al.*, 1993). This may explain the low pH found in native forest and pine soils compared to pasture and eucalyptus soils. Under cultivation, carbon and organic matter is lost (Ewel *et al.*, 1991) which may explain the loss of SOM in pasture and eucalyptus soils, since it is very likely that cultivation had been the previous land use of these soils (Chacón *et al.*, 2009). However, in pine soils SOM may have accumulated because of low decomposition rates due to the litter's high lignin content (Taylor *et al.*, 1989). Comparing native forest and pine soils, fertility may be largely dependent upon the quality and not the quantity of SOM, which would cause different mineralization rates due to different types of litter inputs to the forest floor. Except for Ca, Al, pH and the limitations of N and P, the other soil properties measured in this study tend to reflect the characteristics of volcanic ash derived soils rather than the effects of the current vegetation as shown elsewhere (Chacón *et al.*, 2015).

Table 3. Percent mortality of quinoa after bioassay on soils from four land-use types and under four fertilizer treatments.

	C	N	P	NP	Total
Native forest	0	50	0	0	18.8
Pasture	0	0	0	25	6.3
Eucalyptus globulus	0	0	0	0	0
Pinus patula	87.5	100	0	62.5	62.5
Total	28.1	37.5	0	21.9	

C = control,
N = ammonium-nitrate fertilizer,
P = triple super phosphate fertilizer,
NP = combined N-P fertilizers, n = 8 (4 blocks x 2 plants / pot).

3.2 Fertilizer treatment effects on soil properties

The effects of N additions are reflected in the pattern seen for soil pH. Whether in the N- or combined NP-treatments, pH values were always significantly lower in all soils except in native forest soils. We interpret this as the result of H+ released during nitrification of NH_4^+-N from the ammonium nitrate fertilizer (Table 2). All N-fertilizers are largely converted to NO_3^- thus acidifying the soil (Wild, 1989; Oskarsson *et al.*, 2006). In the P-treatment, NH_4^+-N content was always higher than NO_3^-, suggesting that PO_4^- increased N mineralization from organic matter, but the amounts of P added were too low to produce significant differences (Table 2). In volcanic soils from Colombia, sampled from similar elevations as in this study, additions of large quantities of $Ca(H_2PO_4)_2.H_2O$ increased N mineralization rates by enhancing the use of soil carbon by microorganisms (Munevar and Wollum, 1977). Ammonium, ammonium nitrate, urea (Finck, 1982) and poultry manure have been considered as acidifying fertilizers. We can conclude that fertilizer applications in the studied soils should include PO_4^- and Ca as well, in order to increase pH and to enhance SOM mineralization.

Findings suggest that these soils depend more upon inorganic fertilization rather than natural P mineralization. In fact, fertilizer experiments in soils taken from the highlands of northern Ecuador (Espinosa, 1992) have also found PO_4^- increments and enhanced yields of agricultural crops. In Costa Rica, inorganic P fertilization increased the mineralization of organic P as opposed to the reduction of the P pools through organic additions (Paniagua *et al.*, 1995). There was a pattern of increased pH in soils that received P additions, more visible in eucalyptus and pine soils than in native forest and pasture soils. Soil pH in the P-treatment was always higher than in the control treatment, but was lower than the pH measured in initial soils samples (Tables 1 and 2). This is most likely the effect of the amounts of Ca present in the triple-superphosphate utilized as P-fertilizer rather than PO_4^- alone. The use of lime can alleviate Al toxic levels by neutralizing soil acidity in volcanic ash soils (Shoji *et al.*, 1993). In Costa Rican acid soils, $CaSO_4$ and $CaCO_3$ reduced Al toxicity; the latter also raised pH values, although neither fertilizer had significant effects on K and Mg (López and González, 1987). The additions of Ca in this study had no significant effects on the soil concentrations of other cations suggesting that the level of Ca added was low, although sufficient to raise soil pH and to lower Al content in pine soils.

3.3 Quinoa growth, biomass and the effects of fertilizer treatment

The overall quinoa mortality was generally distributed as N (38 %) >C (28 %) >NP (22 %) >P (0 %) (Table 3). Quinoa 100 % survival occurred only in eucalyptus soils and in the P-treatment across the four land-use types. In a few cases, only one of two quinoa seedlings survived per pot. Only one seedling survived in pine soils under control and N-P treatments in only one block. In the other soils and treatments where mortality was present, the two plants per pot died (Table 3). The negative effect of

Table 4. Quinoa biomass and quinoa nutrient content after bioassay on soils from four land-use types and under four fertilizer treatments (n = 4, unless specified left of each mean).

		Native Forest					Pasture					*Eucalyptus globulus*				*Pinus patula*				
Total g/pot	**C**	n=3	0.2	(99)	**a**	*a*		0.02	(34)	**ab**	*b*	0.03	(87)	**ab**	*b*	n=1	0.01	—	**b**	*a*
	N	n=2	1.2	(133)	**a**	*a*		0.02	(40)	**b**	*b*	0.05	(77)	**ab**	*b*		—	—	—	—
	P		1.7	(112)	**ab**	*a*		1.6	(81)	**ab**	*a*	1.7	(38)	**a**	*a*		0.1	(62)	**b**	*a*
	NP		7.7	(107)	**a**	*a*	n=3	5.4	(90)	**a**	*a*	8.4	(107)	**a**	*a*	n=2	0.1	(90)	**a**	*a*
Total N mg/pot	**C**	n=3	4	(103)	**a**	*a*		0.4	(31)	**a**	*b*	0.8	(109)	**a**	*c*	n=1	0.3	—	**a**	*a*
	N	n=2	48.3	(132)	**a**	*a*		0.7	(47)	**a**	*b*	1.9	(81)	**a**	*c*		—	—	—	—
	P		26.6	(110)	**a**	*a*		22	(77)	**a**	*a*	26.8	(45)	**a**	*b*		3.2	(65)	**a**	*a*
	NP		252.3	(90)	**a**	*a*	n=3	193	(76)	**a**	*a*	255	(88)	**a**	*a*	n=2	3.9	(113)	**a**	*a*
Total P mg/pot	**C**	n=3	0.2	(112)	**a**	*a*		0.02	(25)	**b**	*b*	0.03	(84)	**ab**	*b*	n=1	0.03	—	**ab**	*a*
	N	n=2	1.8	(134)	**a**	*a*		0.03	(78)	**a**	*b*	0.06	(101)	**a**	*b*		—	—	—	—
	P		17.2	(123)	**a**	*a*		8.3	(82)	**ab**	*a*	10.3	(47)	**ab**	*a*		0.7	(68)	**b**	*a*
	NP		37.8	(115)	**a**	*a*	n=3	24.7	(106)	**a**	*a*	30	(94)	**a**	*a*	n=2	0.5	(108)	**a**	*a*
Total K mg/pot	**C**	n=3	7.7	(116)	**a**	*a*		0.6	(28)	**ab**	*b*	1.3	(111)	**ab**	*b*	n=1	0.1	—	**b**	*a*
	N	n=2	85.7	(136)	**a**	*a*		0.7	(86)	**b**	*b*	1.4	(75)	**ab**	*b*		—	—	—	—
	P		89.2	(125)	**a**	*a*		64.3	(87)	**ab**	*a*	83.6	(70)	**a**	*a*		1.3	(56)	**b**	*a*
	NP		165.5	(102)	**a**	*a*	n=3	122.2	(76)	**a**	*a*	358	(109)	**a**	*a*	n=2	1.4	(125)	**a**	*a*
Total Ca mg/pot	**C**	n=3	2.7	(110)	**a**	*a*		0.4	(41)	**ab**	*b*	0.5	(83)	**ab**	*b*	n=1	0.03	—	**b**	*a*
	N	n=2	25.6	(132)	**a**	*a*		0.6	(107)	**a**	*b*	1	(94)	**a**	*b*		—	—	—	—
	P		25.7	(101)	**a**	*a*		28.1	(77)	**a**	*a*	28.5	(36)	**a**	*a*		1.6	(59)	**b**	*a*
	NP		121.2	(96)	**a**	*a*	n=3	118.4	(71)	**a**	*a*	99.5	(94)	**a**	*a*	n=2	1	(94)	**a**	*a*
Total Mg mg/pot	**C**	n=3	3.4	(140)	**a**	*a*		0.2	(45)	**ab**	*b*	0.5	(106)	**ab**	*b*	n=1	0.02	—	**b**	*a*
	N	n=2	31.1	(138)	**a**	*a*		0.3	(73)	**a**	*b*	0.8	(88)	**a**	*a*		—	—	—	—
	P		22.9	(122)	**a**	*a*		17.8	(91)	**ab**	*a*	24.9	(62)	**a**	*a*		0.8	(66)	**b**	*a*
	NP		115.1	(115)	**a**	*a*	n=3	75.5	(102)	**a**	*a*	86.5	(101)	**a**	*a*	n=2	0.6	(112)	**a**	*a*

Total = stem + leaf + root.
Biomass data are the sum of the actual plant production in each of the pots.
C = control,
N = ammonium-nitrate fertilizer,
P = triple super phosphate fertilizer,
NP = combined N-P fertilizers.
Numbers in parentheses are CV (%). Different bold letters represent significant differences between land-use types (horizontally) at $P \leq 0.05$. Different italic letters represent significant differences between treatments (vertically) at $P < 0.01$.

Pinus patula plantations soils is clearly shown by quinoa mortality in all treatments (control included), except in the P-treatment. Quinoa died in the control (25 %) and N (50 %) treatments of native forest soils, suggesting an effect of lower soil pH, which was reduced with Ca additions in the P and NP-treatments (Table 3). In pasture soils, quinoa mortality was 25 % in the NP-treatment, although there was no mortality in the N- or other treatments, and might be explained by the accidental loss of one plant (grasshopper damage) rather than a soil problem (Table 3). Quinoa mortality was significantly decreased by P additions, P more than NP perhaps because of an acidifying effect of the N fertilizer according to Oskarsson *et al.*, (2006). Mortality was increased by N additions in pine soils to the point where all quinoa plants died in the N-treatment and none in the P-treatment with respect to control soils, suggesting a stronger P limitation and perhaps a lower pH, K and Ca as principal factors controlling mortality in pine soils. This also suggests that quinoa is more sensitive to soil nutrient deficiencies than corn (Chacón *et al.*, 2015) (Table 4). This mortality, as well as the higher coefficients of variation for native forest soil nutrients have reduced the number of statistically significant differences in quinoa biomass production, and nutrient contents, among the four land-use type soils. Generally, quinoa growth responded to P and NP-fertilizers in soils excluding those from the pine plantations (Tables 2, 3 and 4). There was no response in the N-treatment and growth was very similar to the one found in control soils. The combined effect of N and P significantly increased corn and quinoa biomasses. Thus, N and P are limiting in these soils, but P is the primary limiting factor. The same is true for nutrient contents (Table 4).

The very low biomasses produced by all control soils indicate a loss of agricultural potential through the reduction of soil fertility, which has lead to fertilization dependency to sustain crop production. For example, experiments with potatoes on Ecuadorian Andisols required P applications every cycle to obtain adequate yields (Espinosa, 1992). Quinoa growth started to be consistently poorer in pine soils just as growth began to respond to fertilization in the other soils. This suggests that pine soils are further limited by soil factors other than N or P limitation alone.

It is not proven that N and P supply was limited in pine soils because of the generally higher amounts of N and P present in these soils when compared to pasture and eucalyptus soils. The trends seen for increased quinoa biomass and nutrient contents were too small to be statistically significant. Specifically, the contents of P, K, Ca and Mg increased with P additions as opposed to N additions. One hypothesis is that P concentrations regulate Ca and Mg uptake by controlling the efflux pump in crops (Blevins, 1994). At low P concentrations, effluxes of Mg and Ca were reported from roots in wheat and tall fescue crops (Reinbott and Blevins, 1991). In pine soils, the effect of Ca in the P-fertilizer treatment was to reduce soil acidity, and perhaps Al toxicity, and is likely to have improved quinoa growth, although we cannot separate it from the direct effect of P. However, pine soil deficiencies, especially K and Ca, were not eliminated to attain better growth. We can observe large increases of K content in quinoa, with the P- and NP-treatments in pasture and eucalyptus soils (Table 4).

As for soil properties, the differences in quinoa biomass production and nutrient content are better observed between the group of native forest, pasture and eucalyptus soils and of pine soils alone, which always produced lower biomasses and nutrient contents, and an thus be considered to have lower productivity and fertility than all the other soils. Eucalyptus soils produced higher quinoa biomass in the P-treatment, suggesting a further P limitation for this species in these soils as opposed, for example, to corn (Chacón *et al.*, 2015). Quinoa K, Ca and Mg contents, similar in native forest, pasture and eucalyptus soils, were generally higher than the one produced on pine soils in the P-treatment, suggesting that K, Ca and Mg supply to quinoa was equivalent in all soils except for pine soils, and highlights the lower K, Ca and Mg contents in pine soils. Because quinoa had 100 % mortality in the N-treatment on pine soils, quinoa biomass, N, Ca and K contents after growth on pasture soils were significantly lower than in native forest soils, evidence that may indicate that N is more limiting in pasture soils than in the other soils.

Apart from the identified nutrient limitations to growth such as P for all soils (except perhaps pine soils), N specifically in pasture soils, and K and Ca coupled with a lower pH in pine soils, the magnitude of growth responses to nutrient enrichment, especially among native forest, pasture and eucalyptus soils is linked to the fact that all land-use types were subjected to past impacts that have lowered soil fertility (Chacón *et al.*, 2009), and to the different nutrient requirements of quinoa. The assessment of specific nutrient limitations to plant growth varies depending on the species selected. Quinoa seemed more sensitive to nutrient limitations than corn (Chacón *et al.*, 2015), however, quinoa is reported to grow in the Andes from sea level to 3.800 m.a.s.l., in marginal areas with poor (Risi and Galwey, 1989), acid soils (pH = 4.5 in Cajamarca, Peru), both sandy or clayey soils (Mujica, A, 1994), where N influences the growth of quinoa. Evidence from this study suggests that despite the fact that quinoa can adapt to severe climatic conditions, soils of southern Andean Ecuador are currently not able to support the production of this crop without additions of combined fertilizers containing P, N, K and Ca as the principal elements. Corn remains an easier crop to grow (Chacón *et al.*, 2015), in terms of soil requirements, and this may largely explain why it has replaced quinoa as a major Andean crop, as historic land-use effects have generally reduced soil fertility.

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Bibliography

Allen, M. F. 1991. The ecology of mycorrhizae. Cambridge.

Allen, S. 1989. Analysis of vegetation and other organic materials. **Chemical analysis of ecological materials.** Allen, D. (Ed.). Blackwell, Oxford. pages 46-61.

Blevins, D.G. 1994. Uptake, translocation, and function of essential mineral elements in crop plants. **Physiology and determination of crop yield.** Boote, K. J., J. M. Bennett, T. R. Sinclair y G. M. Paulsen (Eds.). Madison, EE.UU. pages 259-275.

Bretón, V. 2008. From agrarian reform to ethnodevelopment in the highlands of Ecuador. **Journal of Agrarian Change.** 8:583-617. doi: 10.1111/j.1471-0366.2008.00181.x

Buytaert, W., J. Deckers y G. Wyseure. 2006. Description and classification of nonallophanic Andosols in south Ecuadorian alpine grasslands (páramo). **Geomorphology.** 73:207-221. doi: 10.1016/j.geomorph.2005.06.012

Celleri, R., P. Willems, W. Buytaert y J. Feyen. 2007. Space-time rainfall variability in the Paute basin, Ecuadorian Andes. **Hydrological Processes.** 21:3316-3327. doi:10.1002/hyp.6575

Chacón, G., D. Gagnon y D. Paré. 2009. Comparison of soil properties of native forests and *Pinus patula* plantations, and pastures in the Andean highlands of southern Ecuador: land-use history or recent vegetation effects? **Soil Use and Management.** 25:427-433. doi:10.1111/j.1475-2743.2009.00233.x

Chacón, G., D. Gagnon y D. Paré. 2015. Soil agricultural potential in four common Andean land use types in the Highlands of Southern Ecuador as revealed by a corn bioassay. **Agricultural Sciences.** 6(10):1129-1140. doi: 10.4236/as.2015.610108

Cochrane, T. T. y P. A. Sanchez. 1982. Land resources, soils and their management in the Amazon region: a state of knowledge report. **Proceedings of the international conference on Amazonian agriculture and land-use research.** S. Hecht (Ed). Cali, Colombia, CIAT series 03E-3(82):137-209.

Crous, J. W., A. R. Morris y M. C. Scholes. 2011. Changes in topsoil, standing litter and tree nutrient content of a *Pinus patula* plantation after phosphorus and potassium fertilization. **European Journal of Forest Research.** 130:277-292. doi: 10.1007/s10342-010-0430-z

Davidson, R., D. Gagnon e Y. Mauffette. 1999. Growth and mineral nutrition of the native trees *Pollalesta discolor* and the N-fixing *Inga densiflora* in relation to the soil properties of a degraded volcanic soil of the Ecuadorian Amazon. **Plant and Soil.** 208:135-147. doi:10.1023/A:1004549216198

Espinosa, J. 1992. Phosphorus diagnosis and recommendations in volcanic ash soils. **PDSS Proceedings. TropSoils Bulletin.** 92:109-115.

Ewel, J. J., M. J. Mazzarino y C. W. Berish. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. **Ecological Applications.** 1:289-302. doi: 10.2307/1941758

Farley, K. A. y E. F. Kelly. 2004. Effects of afforestation of a páramo grassland on soil nutrient status. **Forest Ecology and Management.** 195:281-290. doi:10.1016/j.foreco.2003.12.015

Farley, K. A., L. L. Bremer, C. P. Harden y J. Hartsig. 2012. Changes in carbon storage under alternative land uses in biodiverse Andean grasslands: implications for payment for ecosystem services. **Conservation Letters.** 0:1-7. doi/10.1111/j.1755-263X.2012.00267.x

Finck, A. 1982. Fertilizers and fertilization: introduction and practical guide to crop fertilization. Verlag Chemie, Weinheim, Germany.

Fonte, S. J, S. J. Vanek, P. Oyarzun, S. Parsa, D. C. Quintero, I. M. Rao y P. Lavelle. 2012. Pathways to agroecological intensification of soil fertility management by smallholder farmers in the Andean Highlands. **Advances in Agronomy.** D. L. Sparks, (Ed.). Burlington: Academic Press. 116:125-184.

Grimshaw, H. M. 1989. Analysis of soil. **Chemical analysis of ecological materials.** S. E. Allen y A. Stewart, (Eds.). Blackwell, Oxford. pages 7-45.

Harden, C. P., J. Hartsig, K. A. Farley, J. Lee y L. L. Bremer. 2013. Effects of land-use change on water in Andean páramo grassland soils. **Annals of the Association of American Geographers.** 103: 375-384. doi: 10.1080/00045608.2013.754655

Hendershot, W. H., H. Lalande y M. Duquette. 1993. Soil reaction and exchangeable acidity. **Soil sampling and methods of analysis.** Carter, M. R. (Ed.). Lewis Publishers, EE.UU., pages 141-145.

IUSS Working Group WRB. 2015. World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. **World Soil Resources Reports No. 106.** FAO, Rome.

James, L.E.A. 2009. Chapter 1: Quinoa (Chenopodium *quinoa* Willd.): Composition, chemistry, nutritional, and functional properties. **Advances in Food and Nutrition Research.** 58:1-31. doi:10.1016/S1043-4526(09)58001-1

Jampel, C. 2016. Cattle-based livelihoods, changes in the taskscape, and human-bear conflict in the Ecuadorian Andes. **Geoforum.** 69:84-93. doi:10.1016/j.geoforum.2016.01.001

Jenny, H. 1950. Causes of the high nitrogen and organic matter content of certain tropical forest soils. **Soil Science.** 69:63-69. doi: 10.1097/00010694-195001000-00005

López, M. A. y M. González. 1987. Efecto de dos fuentes de calcio sobre la fertilidad de tres suelos ácidos de Costa Rica. **Agronomía Costarricense.** 11:1-15.

Maynard, D. G. y Y. P. Kalra. 1993: Nitrate and exchangeable ammonium nitrogen. **Soil sampling and methods of analysis.** Carter, M. R. (Ed). Lewis Publishers, EE.UU. pages 25-38.

McKeague, J. A. 1978. Manuel de méthodes d'échantillonage et d'analyse des sols. **Comité Canadien de Pédologie.** Ottawa, Canada.

Montagnini, F. y F. Sancho. 1994. Net nitrogen mineralization in soils under six indigenous tree species, an abandoned pasture and a secondary forest in the Atlantic lowlands of Costa Rica. **Plant and Soil.** 162:117-124. doi: 10.1007/BF01416097

Mujica, A. 1994. Esquema de la resistencia duradera de la quinua (*Chenopodium quinoa* Willd). **Memorias del primer taller sobre resistencia duradera en cultivos alto andinos de Bolivia, Colombia, Ecuador y Perú.** 30:105-111.

Munevar, F. y A. G. Wollum. 1977. Effects of the addition of phosphorus and inorganic nitrogen on carbon and nitrogen mineralization in Andepts from Colombia. **Soil Science Society of American Journal.** 41:540-545. doi:10.2136/sssaj1977.03615995004100030023x

Nanzyo, M., R. Dahlgren y S. Shoji. 1993. Chemical characteristics of volcanic ash soils. **Volcanic ash soils: genesis, properties and utilization.** Shoji, S., Nanzyo, M. y Dahlgren, R. (Eds). Elsevier, Amsterdam. pages 145-187.

Oades, J. M., G. P. Guillman y G. Uehara. 1989. Interactions of soil organic matter and variable-charge clays. **Dynamics of soil organic matter in tropical ecosystems.** Coleman, D. C., Oades, J. M. y Uehara, G. (Eds). NifTAL Project. Honolulu. pages 69-95.

Ochoa-Tocachi, B. F., W. Buytaert, B. De Bièvre, R. Célleri, P. Crespo, M. Villacís, C. A. Llerena, L. Acosta, M. Villazón, M. Guallpa, J. Gil-Ríos, P. Fuentes, D. Olaya, P. Viñas, G. Rojas y S. Arias. 2016. Impacts of land use on the hydrological response of tropical Andean catchments. **Hydrological Processes.** doi: 10.1002/hyp.10980

Oskarsson, H., A. Sigurgeirsson, y K. Raulund-Rasmussen. 2006. Survival, growth, and nutrition of tree seedlings fertilized at planting on Andisol soils in Iceland: Six-year results. **Forest Ecology and Management.** 229:88-97. doi: 10.1016/j.foreco.2006.03.018

Paniagua, A. M., J. Mazzarino, D. Kass, L. Szott y C. Fernandez. 1995. Soil phosphorus fractions under five tropical agro-ecosystems on a volcanic soil. **Australian Journal of Soil Research.** 33:311-320. doi: 10.1071/SR9950311

Potthast, K., U. Hamer, y F. Makeschin. 2012. In an Ecuadorian pasture soil the growth of Setaria sphacelata, but not of soil microorganisms, is co-limited by N and P. **Applied Soil Ecology.** 62:103-114. doi:10.1016/j.apsoil.2012.08.003

Reinbott, T. M. y D. G. Blevins. 1991. Phosphate interaction with uptake and leaf concentration of magnesium, calcium, and potassium in winter wheat seedlings. **Agronomy Journal.** 83:1043-1046. doi: 10.2134/agronj1991.00021962008300060021x

Risi, J. C., y N. W. Galwey. 1989. The pattern of genetic diversity in the Andean grain crop quinoa (Chenopodium *quinoa* Willd). I. Associations between characteristics. **Euphytica.** 41:147-162. doi: 10.1007/BF00022424

SAS Institute Inc. 2008. SAS/STAT® 9.2 User's Guide. Cary, NC: SAS Institute Inc.

Shoji, S., M. Nanzyo, y R. Dahlgren. 1993. Productivity and utilization of volcanic ash soils. **Volcanic ash soils: genesis, properties and utilization.** Shoji, S. Nanzyo, M., y Dahlgreen, R. (Eds). Elsevier. pages 209-251.

Smethurst, P. J. 2010. Forest fertilization: trends in knowledge and practice compared to agriculture. **Plant and Soil.** 335:83-100. doi: 10.1007/s11104-010-0316-3

Taylor, B. R. D. Parkinson y W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. **Ecology.** 70:97-104. doi:10.2307/1938416

Vitousek, P. M., S. Porder, B. Z. Houlton y O. A. Chadwick. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen?phosphorus interactions. **Ecological applications.** 20:5-15. doi: 10.1890/08-0127.1

Wild, A. 1989: Mineral nutrients in tropical ecosystems: a soil scientist's view. **Mineral nutrients in tropical forest and savanna ecosystems.** Proctor, J. (Ed.). British Ecological Society, Blackwell Scientific Publications, Oxford. pages 441-456.