Reforestation and Topography Affect Montane Soil Properties, Nitrogen Pools, and Nitrogen Transformations in Hawaii

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ABSTRACT

Land use changes, such as deforestation and reforestation, modify not only the organisms inhabiting affected areas, but also above- and belowground environments. Topography further influences local vegetation and environment. Effects of topography and re-establishment of N-fixing koa (*Acacia koa* A. Gray) trees in +100-yr-old montane grassland on surface soil properties, N pools, and N transformations were assessed using standard and ^{15}N-isotope pool dilution methods. Data were collected for soils on slopes and in drainage bottoms located in grassland, under 9- to 11-yr-old planted koa, and in nearby old-growth koa-ohia (*Metrosideros polymorpha* Gaud.) forest. Soil under planted koa had significantly lower fine soil bulk density and pH than soil in grassland, and had concentrations of total C, total N, and extractable Mg and C/N ratio intermediate between grassland and forest. Topographic position affected pH and concentrations of total C, total N, and extractable P. Ten years after koa trees were re-introduced to grassland, the concentration of soil NH_4^+–N had increased above levels found even in intact forest, and the concentration of NO_3^-–N was intermediate between forest and grassland. Ammonium dominated the inorganic N pools in grassland soil and NO_3^- dominated in forest soil. Under planted koa, NH_4^+ domination was beginning to give way to NO_3^- domination. Soil microorganisms were potentially strong competitors for inorganic N on grassland slopes where they immobilized nearly all the inorganic N that was produced during short- and medium-term field incubations, thus leaving little for plant growth. Re-establishment of koa trees increased soil N availability.

L AND USE CHANGES, such as conversion of forest to grazed grassland, can drastically change plant species composition, and dominant life forms, which in turn markedly affect soils and soil processes (e.g., Neill et al., 1999; Chen et al., 2000; McGrath et al., 2001). Reiners et al. (1994) reported decreased acidity, decreased effective cation exchange capacity (CEC), increased bulk density, decreased soil porosity, greater concentrations of NH_4^+, lower concentrations of NO_3^-, and lower rates of net N-mineralization following conversion of lowland tropical rainforest to pasture grasses. Piccolo et al. (1994) found that soils under pasture grasses had smaller extractable inorganic N pools than forest soils, NH_4^+ dominated the inorganic pools under grasses, and net N-mineralization and net nitrification were slower under grasses. Pasture grasslands created from lowland tropical forests have shown N limitations to plant productivity (Keller et al.,

1993; Parsons et al., 1993; Reiners et al., 1994; Parsons and Keller, 1995).

Re-establishing trees, especially fast-growing N-fixing species, in deforested grassland landscapes can reverse changes in soil structure, chemical properties, and N transformations induced by land use change. Fisher (1995) reported that within 4 yr of planting in abandoned pasture, native Costa Rican trees reduced soil bulk density and increased cation concentrations, and some N-fixing species significantly increased total N concentration. Montagnini and Sancho (1990) found that within 2.5 yr of planting, soils under N-fixing species had greater organic matter content, total N, and exchangeable K and Mg than pasture soils. After 4 yr, net nitrification potentials were greater under plantations of N-fixing species than under non N-fixing species, and that net nitrification rates were comparable with those under older secondary forests (Montagnini and Sancho, 1994). Rhoades et al. (1998) found NO_3^- pools were four times greater and nitrification rates five times faster under N-fixing trees than under pasture grasses. Scowcroft and Jeffrey (1999) reported significantly increased N availability in surface soil as a result of grassland reforestation with koa, a N-fixing tree endemic to Hawaii. Thus, re-establishing tree cover in anthropogenic grasslands can affect soils, but it is not the only factor at work.

Interactions between recovering forest vegetation and physiography can influence changes in soil properties and processes. Studying high elevation grassland in Hawaii, Scowcroft and Jeffrey (1999) showed that soils located in drainage bottoms supported greater amounts of herbaceous biomass and had greater amounts of total N, extractable NH_4^+, P, and Ca than soils on slopes. Similar microrelief influences on spatial variability of vegetation and soil properties have been observed in a number of temperate grassland ecosystems (Barnes and Harrison, 1982; Schimel et al., 1985; Aguilar and Heil, 1988; Burke et al., 1989a, 1989b; Frank et al., 1994; Frank and Groffman, 1998; Corre et al., 2002; Verchot et al., 2002). Typically these studies found that moisture content, total C, N, and P, gross NH_4^+ mineralization and immobilization, N availability, and denitrification potential increased systematically along a gradient from hilltops to drainage bottoms (for opposite effects see Yonker et al., 1988; Turner et al., 1997).

Studies in forested landscapes also have shown topographic effects on soil chemical properties and N transformation, but changes across toposequences are more variable than for grasslands. Silver et al. (1994) found that exchangeable base cation concentrations and pH increased from ridge tops to riparian valleys, while soil

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Abbreviations: APE, atom percent enrichment; asl, above sea level; CEC, cation-exchange capacity; SOM, soil organic matter.

organic matter (SOM), exchangeable acidity, and Fe decreased along the same topographic gradient in a montane wet tropical forest in Puerto Rico. Takyu et al. (2002) reported that total soil C and N, NH_4^+ and NO_3^- pools, and net N mineralization rates decreased downslope in a tropical lower montane forest. In a seasonally dry forest, total soil C and N also decreased downslope, but N pools and net N mineralization rates increased (Raghubanshi, 1992). Garten et al. (1994) reported greater total N concentrations, lower C/N ratios, and greater potential net nitrification in forested valley floors than upslope topographic positions. Greater downslope soil moisture (e.g., Daws et al., 2002) has been correlated with larger soil NO_3^- pools and faster rates of net nitrification and gaseous losses of N (Davidson and Swank, 1986; Groffman et al., 1993; but see Zak et al. [1991] for the opposite).

In this study, we examined selected properties and N dynamics of surface soil in montane forest, grassland, and grassland reforested with koa on the mesic windward flank of Mauna Kea, Island of Hawaii. We used standard sampling protocols and analytical procedures to examine soil properties and we used a modification of the ^{15}N isotope pool dilution method to determine short-term N dynamics. The last was used instead of net mineralization and nitrification methods because it allowed us to assess separately the microbially mediated processes of production and consumption that simultaneously regulate N availability. Knowledge of those processes is needed to better understand competition for N between soil microorganisms and plants (Kaye and Hart, 1997). Our main objectives were to determine if vegetation type or topographic position or their interaction affected (i) fine soil bulk density, soil acidity, total C, total N, C/N ratio, and concentrations of extractable P, Ca, and Mg, (ii) size of NH_4^+ and NO_3^- pools, (iii) short-term rates of gross ammonification, gross consumption, gross nitrification, and immobilization, and (iv) intermediate-term rates of net ammonification, net nitrification, and net mineralization.

MATERIALS AND METHODS

Study Sites

Our research was conducted on the northeastern (windward) slopes of Mauna Kea between 1870 and 1990 m above sea level (asl), and between coordinates 155° 19′ 56″ W long., 19° 47′ 53″ N lat. and 155° 19′ 57″ W long., 19° 51′ 13″ N lat. The climate is cool and mesic. Mean daily air temperature ranges from 9 to 14°C and mean daily soil temperature at 10 cm ranges from 10 to 17°C (J. Jeffrey, US Fish and Wildlife Service, personal communication, 1995). Rainfall averages 2000 mm yr^{-1}.

The volcanic-ash-derived soils in our study area were relatively young as evidenced by the presence of primary minerals, including plagioclase feldspar, augite, olivine, and ilmenite and little 1:1 or 2:1 clay (H. Ikawa, U. Hawaii, personal communication, 1989). The acidic Andisols were characterized by variable charge, large amounts of soil organic C (SOC) and noncrystalline minerals, and large capacity to fix P. Soil pH probably exceeded the point of zero variable charge (pH$_0$) and resulted in a net negative charge at all depths (G. Uehara,

U. Hawaii, personal communication, 2003), although the proportion of positively charged sites and anion exchange capacity likely increased as SOM decreased with depth (Sollins et al., 1988). Grassland soil was classified as hydrous, amorphic, isomesic Acrudoxic Hydrudand of the Piihonua series, and forest soil was classified as medial, amorphic, isomesic Typic Hydrudand of the Piha series (C. Smith, USDA Soil Survey, personal communication, 2003). The underlying àà lava flow of the forest was younger than that of the grassland (Wolfe and Morris, 1996), but both belonged to the Laupahoehoe Volcanics Series (Peterson and Moore, 1987) and surface soil to a depth of at least 30 cm was formed in the same Pahala ash deposit that covered both flows (Stearns and Macdonald, 1946).

Grassland and planted-koa portions of our study area lay within upper reaches of Hakalau Forest National Wildlife Refuge. The 2000-ha grassland was the result of logging, burning, pasture development, and cattle grazing that started in the mid 1800s. Only isolated trees and small patches of native plants in steep-sided ravines remained from the former *koa-ohia* forest. Cattle grazing ended shortly after the refuge was created in 1985. The unmanaged old-growth forest portion of our study area lay along the northern edge of the grassland.

Grassland vegetation consisted of perennial introduced pasture species, including, *Pennisetum clandestinum* Chiov., *Anthozanthum odoratum* L., *Holcus lanatus* L., and *Axonopus fissifolius* (Raddi) Kuhlm. *P. clandestinum*, a C_4 grass adapted to cool, fertile sites (Mears, 1970; Wilen and Holt, 1996), dominated drainage bottoms, and the other grasses dominated slopes and ridges. Grass stands were 0.5 m tall and aboveground standing biomass ranged from 7.6 Mg ha^{-1} on slopes to 10 Mg ha^{-1} in drainage bottoms (Scowcroft and Jeffrey, 1999).

Starting in 1987, most koa was planted in corridors that connected old remnant trees. Corridors were three rows wide with 3- to 4-m spacing between rows and between trees within rows. Block plantings had 2.5-m spacing. Crown closure occurred before trees were 7 yr old. Understory vegetation for planted koa sample sites consisted of the same grasses as found in the grassland, but shading significantly reduced their biomass (Scowcroft and Jeffrey, 1999). A nutrient-rich fine koa litter layer accumulated beneath planted koa (Scowcroft and Jeffrey, 1999).

The open-canopy old-growth forest was dominated by native species. Large koa and ohia trees were 15 to 20 m tall and had stem diameters at breast height >1 m. Understory species included *Coprosma rhynchocarpa* A. Gray, *Myrsine lessertiana* A. DC, *Sophora chrysophylla* (Salisb.) Seem., *Ilex anomala* Hook. & Arnott, *Cheirodendron trigynum* (Gaud.) A. Heller, and *Dryopteris wallenchiana* (Spreng.) Hyl. *Erharta stipoides* Labill. was a common grass. Feral pig (*Sus scrofa*) activity, which was absent in grassland and planted koa sites, was extensive and probably influenced N dynamics, although literature about pig effects on soil properties and processes was scarce and inconclusive (Barrett, 1982; Springer et al., 1984; Moody and Jones, 2000).

Experimental Design

We used a 3 by 2 factorial design with five replicates. The three vegetation types were old-growth forest, koa planted in grassland (9–11 yr old at time of sampling), and grassland; the two topographic positions were drainage bottoms and east-to-south facing slopes (90–180° aspect). Five sites were randomly chosen from among 15 prelocated sites per vegetation type and topographic position. Forest sites were distributed across a 0.4-km strip of Piha Forest Reserve between 1870 to 1940 m asl, and they had to have an overstory of koa. Those in grass-

land and under planted koa were distributed across a 3-km strip of the refuge between 1870 and 1990 m asl. Grassland and planted koa sites were paired by locating them within 60 m of each other, and grassland sites were never closer than 15 m to the nearest koa tree to avoid tree roots. This study was not replicated at similar sites in Hawaii, so findings might be different elsewhere.

Soil Sampling and Analysis

Undisturbed core samples (AMS Extendible Split Core Sampler, 4.8 cm i.d., AMS Inc., American Falls, ID) were obtained from the top 15 cm of soil at each site to determine fine soil (<2 mm) bulk density (oven-dry basis). Dry weight and volume of fine soil was determined by adjusting for dry weight and volume of rock fragments (measure by water displacement) caught on a 2-mm sieve. Composite bulk samples were collected and sieved (2 mm) for determination of pH, total C, total N, and extractable P, Ca, and Mg. Soil pH was measured in a 1:2 soil/water slurry. Total C and N were measured with a LECO C&N 2000 Analyzer (LECO Corp., St. Joseph, MI). Samples were combusted at 1350°C. Mehlich-3 solution was used to extract P, Ca, and Mg (Mehlich, 1984), and concentrations were determined with a Thermo Jarrell-Ash inductively coupled plasma spectrometer (Thermo Jarrell-Ash, Grand Junction, CO).

Nitrogen-15 Protocols

A modification of the ^{15}N stable isotope pool dilution method was used to measure rates of gross N transformations (Davidson et al., 1991; Hart et al., 1994; Stark and Hart, 1996). We used disturbed soil samples instead of intact cores because rocks in the forest soil blocked insertion of the syringe needle and prevented uniform distribution of ^{15}N labeled solutions. Composite bulk soil samples ($n \approx 3$) to a depth of 15 cm were collected from each site, sieved (<2 mm), and mixed thoroughly. Approximately 100 g of soil (o.d. equivalent) was weighed into each of six resealable plastic bags per site. One bag of soil was used to determine initial concentrations of NH_4^+–N and NO_3^-–N. Four bags of soil were used to determine gross NH_4^+ and NO_3^- transformation rates during 2-d field incubations. The sixth bag was used to determine net ammonification and nitrification during 20- to 30-d field incubation by the buried bag technique (Hart et al., 1994).

We labeled NH_4^+ and NO_3^- pools by using a syringe to dribble about one third of the amendment volume over the surface of each bagged soil sample, mixing the soil, and then repeating the process until the entire volume had been added. Two bags of soil were each amended with 10 mL of ($^{15}NH_4)_2SO_4$ (99.9 atom% ^{15}N) solution to determine gross ammonification and microbial consumption of NH_4^+. Two other bags of soil were each amended with 10 mL of $K^{15}NO_3$ (99.3 atom% ^{15}N) solution to determine gross nitrification and microbial consumption of NO_3^-. Concentrations of ^{15}N solutions varied according to expected initial sizes of native NH_4^+ and NO_3^- pools, which were estimated from preliminary samples taken 1 to 2 wk before actual sampling. Atom percent enrichments (APE) of NH_4^+ pools ranged from 46 to 57% using NH_4^+ solution concentrations of 80 μg ^{15}N mL^{-1} for forest bottom and planted koa soils and 40 μg ^{15}N mL^{-1} for forest slope and grassland soils. With the exception of soil in forest drainage bottoms, APEs of NO_3^- pools ranged from 40 to 76% using NO_3^- solution concentrations of 80 μg ^{15}N mL^{-1} for forest soils, 10 μg ^{15}N mL^{-1} for planted koa soils on the slope, 30 μg ^{15}N mL^{-1} for planted koa soils in drainage bottoms, and 15 μg ^{15}N mL^{-1} for grassland soils. The APE of NO_3^- pools in forest drainage

bottoms was only 20% due to very large NO_3^- pools. Amendments raised absolute gravimetric soil water contents by 10% to between 1.06 and 1.32 kg kg^{-1}.

One of each pair of $^{15}NH_4^+$– and $^{15}NO_3^-$–labeled bags were sealed, returned to site, buried 10 cm below ground, and incubated about 2 d before being extracted with KCl solution. One bag of unlabeled soil was buried on site and incubated for 20 to 30 d before being extracted. The two other labeled bags of soil and the unlabeled bag of soil were extracted immediately—within 10 min of adding the label. Extractions were done in the field using 15-g aliquots of soil (o.d. equivalent). Aliquots were put into specimen cups containing 75 mL of 2 M KCl solution. The cups were sealed, shaken by orbital shaker for 1 h, and shipped to Honolulu where they were vacuum filtered the next day using preleached and dried Whatman 42 paper (Whatman International Ltd., Maidstone, UK), and the filtrates frozen until colorimetric analyses and diffusions could be done. Ammonium concentrations were determined by the indophenol blue method (Keeney and Nelson, 1982) and NO_3^- concentrations by the Cd-reduction method (Mulvaney, 1996). Concentrations were blank corrected to adjust for contaminants on filter paper and in extracting solutions. Thereafter, remaining extracts were diffused over 6 d onto acidified filter paper disks (Whatman 1) using the methods of Stark and Hart (1996). Atom percent NH_4^+–^{15}N and NO_3^-–^{15}N enrichment were determined by isotope-ratio mass spectrometry (ANCA-SL Stable Isotope Analysis System, Europa Scientific, Cincinnati, OH) at the Stable Isotope Laboratory, Utah State University, Logan, UT.

The ^{15}N stable isotope pool dilution experiment was done twice. In April 1999, we made a preliminary run to make sure field sampling and extract processing protocols were workable; only one sample site per combination of vegetation type and topographic position was used. In October 1999, we ran the full experiment (five replicates per treatment combination).

Calculations and Statistical Analysis

Rates of gross NH_4^+–N and NO_3^-–N transformations and net ammonification and nitrification were calculated using the equations of Hart et al. (1994) and Stark (2000). Atom percent enrichment values for diffused samples were corrected for background and contaminant N using Eq. [2] and [3] described by Stark and Hart (1996). The natural abundance atom% ^{15}N was assumed to be 0.3663% in all calculations. The t_0 data for labeled and unlabeled soils were used to estimate the fraction of added ^{15}N that was recoverable (Hart et al., 1994; Stark, 2000), and initial pool size calculations were adjusted for incomplete recovery. Net N mineralization was defined as net ammonification plus net nitrification. We encountered negative rates of gross NO_3^- consumption, especially for drainage bottom soils under forest cover. Others have reported negative NO_3^- immobilization rates (Verchot et al., 2001; Wang et al., 2001; Carmosini et al., 2002). These negative rates were theoretically impossible and were probably due to heterogeneity between aliquots used to estimate initial NO_3^- pool sizes, even though they were drawn from sieved well-mixed bulk soil samples. Negative rates of consumption were not included in the analyses.

SAS Proc Mixed procedures (Version 8.1, SAS Institute Inc., Cary, NC) were used to analyze treatment effects on soil properties, N-pool sizes, and rates of gross and net N transformations. The two-parameter Box-Cox transformation (Draper and Smith, 1998, p. 290) was used to equalize variance where needed. Multiple pairwise comparisons (Tukey HSD test, α set at 0.05) were used to determine significant differences among factor level means or, where interactions were

significant, among the six possible combinations of vegetation type and topographic position. Least squares means presented in this paper were backtransformed as necessary to original units using the smearing estimator (Duan, 1983).

RESULTS AND DISCUSSION
Soil Properties

After koa was re-established in grassland, many properties of surface soil began reverting to levels associated with forest cover, and some properties were also affected by topographic position. Soil bulk density and pH was significantly greater in grassland than under forest or planted koa ($p = 0.02$ and $p = 0.01$, respectively) (Table 1). Topographic position did not affect bulk density, but soils on slopes were significantly less acid ($p = 0.01$) than those in drainage bottoms. Vegetation–position interactions were not significant.

The rapid changes that we observed in bulk density and pH after re-establishment of trees in grassland might be the norm for the tropics (Reiners et al., 1994; McGrath et al., 2001). Rhoades and Binkley (1996) observed rapid acidification of a lowland Typic Hydrudand after establishment of tree plantations on abandoned sugarcane land in Hawaii; the N-fixing tree, *Albizia falcataria* (L.) Fosberg, produced the greatest pH decline, from 5.9 to 4.6 in just 8 yr. Binkley and Richter (1987) postulated that net acidification beneath N-fixing species was possible only if NO_3^- leaching accompanied greater proton generation during nitrification. At our sites, N-fixation by planted koa and high potential for NO_3^- leaching due to high rainfall (2000 mm yr^{-1}) might have contributed to the decline in pH in planted koa.

Forest soil had significantly greater total C and N concentrations, and significantly lower C/N ratios than grassland soil ($p \leq 0.01$); under planted koa values were intermediate (Table 1). Zou and Bashkin (1998) reported similar changes as secondary plant communities developed on abandoned low elevation caneland in Hawaii. Bashkin and Binkley (1998) reported net accumulation of 11 Mg C ha^{-1} in the top 15 cm of soil 10 to 13 yr after afforestation of lowland Hawaii caneland with *Eucalyptus saligna* Sm. Our data did not indicate an accumulation of C following afforestation with koa; planted koa and grassland soils both contained approximately 116 Mg C ha^{-1}. However, when topographic position was taken into account, we found that, 9 to 11 yr after planting, 6.2 Mg C ha^{-1} had accumulated in surface soil under koa on slopes while 5.6 Mg C ha^{-1} had disappeared under koa in drainage bottoms. The disappearance of C from the surface soil in drainage bottoms was probably offset by C accumulation in tree litter in the O horizon as indicated by Scowcroft and Jeffrey (1999) who measured 8.8 Mg koa litter ha^{-1} under planted koa in drainage bottoms and 3.3 Mg ha^{-1} on slopes. Parfitt et al. (1997) found that soil C lost after conversion of pasture to tree plantation in New Zealand was offset by C accumulation in tree litter.

Soils in drainage bottoms had significantly greater concentrations of C and N than on slopes ($p = 0.01$ for C and $p = 0.02$ for N). Topographic position did not significantly affect C/N ratios ($p = 0.38$). Vegetation–topography interactions were not significant for C, N, or C/N.

Concentrations of extractable base cations and P were affected mainly by vegetation type (Table 1). Although forest soil had more than twice the concentrations of base cations than planted koa or grassland soils, base cation concentrations under planted koa had risen to levels that were intermediate between mature forest and grassland. Extractable P under planted koa was still close to grassland levels, and both had only one-half the concentration found in forest soil.

Soil Nitrogen Pool Sizes

Re-introducing N-fixing koa trees to grassland markedly influenced the size of NH_4^+ and NO_3^- pools. Ammo-

Table 1. Average bulk density, pH, total C and N, C/N ratio, concentrations of Mehlich-3 extractable P, Ca, and Mg, and gravimetric soil water contents in March and October 1999 for surface soil (0–15 cm) from east-facing slopes and drainage bottoms under old-growth forest, 9 to 11-yr-old *Acacia koa* planted in grassland, and grassland at 1950-m elevation in and next to Hakalau Forest National Wildlife Refuge, Island of Hawaii.

Topographic position	Vegetation type	Bulk density†	pH‡	Total			Mehlich 3-extractable			Water content	
				C	N	C/N	P	Ca	Mg	Mar '99	Oct '99
		Mg m⁻³		— g kg⁻¹ —			— mg kg⁻¹ —			— kg kg⁻¹ —	
Slope (S)	Forest (F)	0.41§	5.6a	212ab	15ab	15	5.7b	1967a	347ab	1.00e	1.15ab
	Planted koa (P)	0.41	5.4ab	182b	11b	18	5.1b	604c	199ab	1.25d	1.07b
	Grassland (G)	0.44	5.7a	158b	8b	19	3.6b	590c	117b	1.21d	1.02b
Bottom (B)	Forest	0.37	5.2b	280a	18a	16	15.8a	1857ab	302ab	1.62a	1.26a
	Planted koa	0.36	5.4ab	227ab	15ab	16	5.5b	1009bc	367a	1.35c	1.08b
	Grassland	0.48	5.6a	179b	10b	18	6.1b	526c	166ab	1.53b	1.13b
		Comparison of factor levels¶ and significance of interaction terms									
Factor											
Vegetation type (V)		F P G	F P G	F P G	F P G	F P G	F P G	F P G	F P G	F P G	F P G
Topographic position (T)		S B	S B	S B	S B	S B	S B	S B	S B	S B	S B
Interaction (V × T)		NS#	NS	NS	NS	NS	*	NS	NS	***	NS

* Significant at the 0.05 probability level
*** Significant at the 0.001 probability level.
† Fine soil bulk density (<2 mm).
‡ pH determined in 1:2 water.
§ Means within a column followed by the same lowercase letter are not significantly different (Tukey HSD test, α set at 0.05); when no lowercase letters are given, values are not statistically different.
¶ Factor levels, which are denoted by uppercase letters, joined by underlines are not significantly different (Tukey HSD test, α set at 0.05).
\# NS = not significant.

Table 2. Mean NH_4^+–N and NO_3^-–N concentrations in surface soil (0–15 cm), by topographic position and vegetation type between December 1998 and October 1999.†

Topographic position	Vegetation type	Ammonium			Nitrate		
		Dec '98	Mar '99	Oct '99	Dec '98	Mar '99	Oct '99
		mg N kg^{-1}					
Slope (S)	Forest (F)	17.4‡	5.9b	3.6	18.4abc	34.5a	9.3b
	Planted koa (P)	23.3	26.2ab	5.7	4.3c	3.7c	1.7b
	Grassland (G)	12.8	12.4ab	2.6	1.0c	0.2c	0.1b
Bottom (B)	Forest	20.1	10.9ab	5.2	30.7a	32.7ab	30.1a
	Planted koa	26.6	32.0a	8.7	23.5ab	20.6b	9.4b
	Grassland	19.3	11.7ab	3.6	6.9bc	3.8c	0.5b
		Comparison of factor levels§ and significance of interaction terms					
Factor							
Vegetation type (V)		F P G	P F G	P F G	F P G	F P G	F P G
Topographic position (T)		S B	S B	S B	S B	S B	S B
Interaction (V × T)		NS¶	NS	NS	NS	*	NS

* Significant at the 0.05 probability level.
† Means were based on sample sizes of n = 3 for Dec. 1998 data and n = 5 for the other dates.
‡ Means within a column that are followed by the same lowercase letter are not statistically different (Tukey HSD test, α set at 0.05); when no lowercase letters are given, values are not statistically different.
§ Factor levels, which are denoted by uppercase letters, joined by underlines are not significantly different (Tukey HSD test, α set at 0.05).
¶ NS = not significant.

nium pools were significantly greater under planted koa than under forest or grassland (Table 2). Nitrate pools were consistently greatest under forest, intermediate under planted koa, and least under grassland.

Vegetation type also affected relative size of NH_4^+ and NO_3^- pools with NO_3^- comprising 56 to 82% of the combined NH_4^+ + NO_3^- pools under forest, 29 to 42% under planted koa, and 8 to 20% under grassland. Nitrate has been found to be the dominant form of inorganic N in forests and NH_4^+ the dominant form in grasslands of the Amazon Basin (Piccolo et al., 1994; Verchot et al., 1999) and Costa Rica (Reiners et al., 1994). Davidson et al. (1990) and Stienstra et al. (1994) hypothesized that N-limited systems are characterized by greater extractable NH_4^+ than extractable NO_3^-. If true, the hypothesis suggests that plants and microorganisms in our forest soils were not N limited, while those in grassland and planted koa soils were N limited. Indeed, variable charge soils like those in the present study might be typically N deficient (Fox, 1980).

Topographic position did not significantly affect size of NH_4^+ pools, but did affect size of NO_3^- pools—significantly larger pools occurred in drainage bottoms than on slopes (Table 2). Down slope transport of this mobile ion (Silver et al., 1994), or enhanced nitrification in wetter drainage bottoms (Venterea et al., 2003) might account for the larger NO_3^- pools. Vegetation–topography interactions were not significant for either ion.

Gross Nitrogen Transformations

Gross N transformation rates were elevated under planted koa compared with grassland, but not significantly so (Fig. 1). Lack of significance probably reflects the high variability within vegetation types and topographic positions. Although gross ammonification and gross NH_4^+ immobilization did not differ among vegetation types (or between topographic positions) in our study, vegetation (and topographic position) had a significant effect on gross NH_4^+ consumption, mainly due to effects on gross nitrification (data not shown). Con-

sumption under forest averaged 10 mg NH_4^+–N kg^{-1} d^{-1}, which was significantly greater ($p < 0.01$) than the 5.8 mg NH_4^+–N kg^{-1} d^{-1} measured under grassland. Ammonium consumption under planted koa occurred at an intermediate rate (8 mg NH_4^+–N kg^{-1} d^{-1}) that did not differ statistically from either mature forest or grassland. Gross NH_4^+ consumption was significantly greater ($p = 0.03$) in drainage bottoms than on slopes (9.0 and 6.8 mg N kg^{-1} d^{-1}, respectively).

Vegetation type (and topographic position) significantly affected gross nitrification (Fig. 1). Nitrification was significantly faster under forest than under either planted koa or grassland ($p = 0.02$ and < 0.01, respectively), and significantly faster in drainage bottoms than
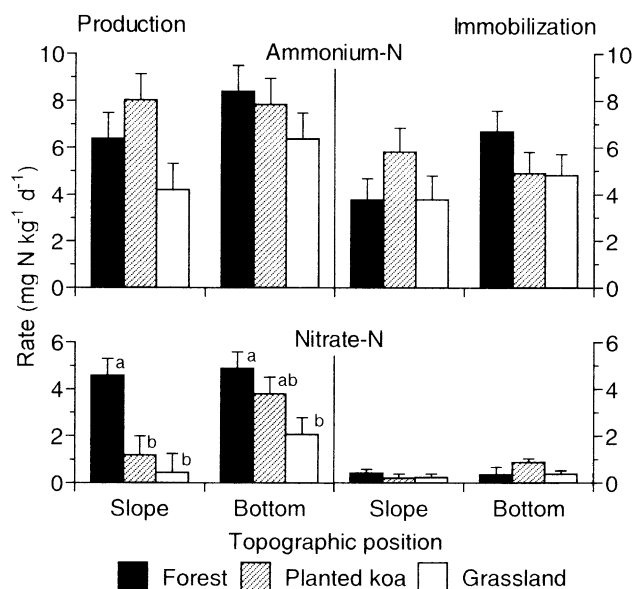

Fig. 1. Effects of vegetation type and topographic position on average (+1 SE) gross rates of production and immobilization of NH_4^+–N and NO_3^-–N in surface soils (0–15 cm). Differences among means were significant only for NO_3^-–N production; bars capped by a common lowercase letter were not significantly different (Tukey HSD test, α set at 0.05).
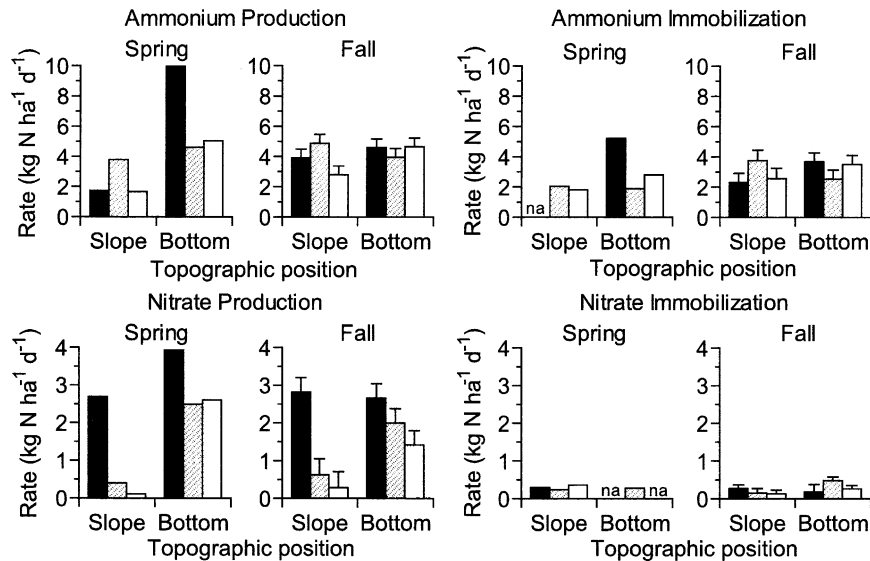
Fig. 2. Rates (area basis, +1 SE) of gross production and immobilization of NH_4^+–N and NO_3^-–N as measured in spring (April) and fall (October) 1999 by the ^{15}N pool dilution method in disturbed surface soils (0–15 cm), by vegetation type and topographic position. Data for April are based on one sample per combination of vegetation and topographic position, hence no error bars are shown. Fill patterns denoting vegetation type are the same as shown in Fig. 1.

on slopes ($p = 0.02$). Corre et al. (2002) also reported a significant topographic effect on nitrification in temperate grassland soils, but opposite our findings. Gross NO_3^- immobilization was slow (Fig. 1), and differences among vegetation types and between topographic positions were not significant ($p = 0.37$ and 0.16, respectively). Nitrate immobilization might have been stimulated by addition of $^{15}NO_3^-$ label, especially in grassland soil on slopes where the additions exceeded ambient concentrations by an order of magnitude. If true, then we speculate that, unlike our measured rates, actual NO_3^- immobilization rates were probably not different from zero.

The effects of vegetation type and topographic position on rates N transformations were similar in both spring and fall 1999, although spring data were unreplicated (Fig. 2). Ammonium production exceeded immobilization and NO_3^- immobilization was a small fraction of production in both seasons. Gross NH_4^+ immobilization was an order of magnitude greater than NO_3^- immobilization in both time periods, which was similar to findings of Bengtsson et al. (2003) for a temperate deciduous forest. Nitrification was greater in forest soil than in planted koa or grassland soil. Nitrification was also greater in drainage bottoms than on slopes both in spring when water contents were generally above field capacity and in fall when water contents were near field capacity. Gross nitrification was weakly and positively correlated with soil moisture ($r^2 = 0.323$); even at moisture contents of 1.6 kg kg^{-1} gross nitrification exceeded 7 mg N kg^{-1} d^{-1}. In contrast, Corre et al. (2002) found greater rates of gross nitrification on drier upper slopes of Northeastern U.S. grassland and attributed it to better aeration due to lower soil moisture.

The assumption that N transformations occur less rapidly in weathered volcanic ash soils with large amounts of amorphous materials (Broadbent et al., 1964; Monreal et al., 1981) was not supported by our data, although our use of disturbed soil may have increased rates. In-

stead we found that rates of gross production and immobilization (Fig. 1 and 2) were generally within the range of rates reported for temperate and lowland tropical forests and grasslands (summarized by Hart et al., 1994; Barrett and Burke, 2000; Verchot et al., 2001; Carmosini et al., 2002; Compton and Boone, 2002; Bengtsson et al., 2003). Only gross NO_3^- immobilization was slower than most reported rates.

Relative Contributions of Production, Consumption, and Immobilization

Vegetation and topographic position affected relative competitiveness of nitrifiers for NH_4^+, microbial preferences for NH_4^+ and NO_3^-, and potential N limitations to growth of organisms. Ammonium consumption exceeded production, except on slopes under planted koa where consumption accounted for 93% of production (Table 3). Immobilization accounted for 60 to 90% of NH_4^+ production. Neither vegetation type nor topographic position significantly affected ratios of NH_4^+ consumption/production or ratios of NH_4^+ immobilization/production, and vegetation–topography interactions were not significant.

The ratio of gross NO_3^- production to gross NH_4^+ consumption was affected by vegetation type and topographic position, and there was significant vegetation–topography interaction ($p = 0.02$). Nitrifiers were strong competitors with heterotrophs for NH_4^+ in forest soil where they accounted for approximately 50% of the NH_4^+ consumed (Table 3). Nitrifiers were significantly less competitive in planted koa and grassland soils, especially on slopes where they accounted for only 10 to 15% of NH_4^+ consumption ($p < 0.01$ in both cases). Under planted koa, nitrification accounted for a significantly greater fraction of NH_4^+ consumption in drainage bottoms than on slopes ($p = 0.05$).

Our data indicated that vegetation type and topographic position influenced microbial preferences for

Table 3. Average ratios of (i) gross consumption of NH_4^+ to gross ammonification, (ii) NH_4^+ immobilization to gross ammonification, (iii) gross nitrification to gross NH_4^+ consumption, and (iv) NO_3^- immobilization to gross nitrification in surface soil (0–15 cm) in fall, by topographic position and vegetation type.

Topographic position	Vegetation type	NH_4^+ Consum./ NH_4^+ Prod.	NH_4^+ Immob./ NH_4^+ Prod.	NO_3^- Prod./ NH_4^+ Consum.	NO_3^- Immob./ NO_3^- Prod.
Slope (S)	Forest (F)	1.36†	0.62	0.54a	0.11
	Planted koa (P)	0.94	0.82	0.13b	0.74
	Grassland (G)	1.21	0.99	0.10b	1.59
Bottom (B)	Forest	1.40	0.79	0.44a	0.06
	Planted koa	1.22	0.68	0.43a	0.74
	Grassland	1.12	0.77	0.32ab	0.21
		Comparison of factor levels‡ and significance of interaction terms			
Factor					
Vegetation type (V)		<u>F P G</u>	<u>F P G</u>	<u>F P</u> G	<u>F P G</u>
Topographic position (T)		<u>S B</u>	<u>S B</u>	S B	<u>S B</u>
Interaction (V × T)		NS§	NS	*	NS

* Significant at the 0.05 probability level.
† Means within a column that are followed by the same lowercase letter are not statistically different (Tukey HSD test, α set at 0.05); when no lowercase letters are given, values are not statistically different.
‡ Factor levels, which are denoted by uppercase letters, joined by underlines are not significantly different (Tukey HSD test, α set at 0.05).
§ NS = not significant.

NH_4^+ and NO_3^-. In forest soil and in grassland soil in drainage bottoms, microorganisms seemed to prefer NH_4^+ over NO_3^-. Ratios of NH_4^+ immobilization to NH_4^+ production were 4 to 13 times greater than ratios of NO_3^- immobilization to NO_3^- production (Table 3). Vitousek and Matson (1988) found that recovery of ^{15}N in microbial biomass was greater when label was added as $^{15}NH_4^+$ than as $^{15}NO_3^-$. Under planted koa, the two ratios were nearly identical, which suggested that the N fixer induced a change in either microbial preferences for the ion species or the composition of microbial populations (Jones and Richards, 1977; Grayston et al., 2001).

Our data also suggested that organisms growing on grassland slopes were potentially N limited and that planting koa potentially alleviated the limitation. All of the NH_4^+ and NO_3^- produced on grassland slopes were immobilized (Table 3). This situation might have been due to stimulation of consumption by addition of labeled solutions (Davidson et al., 1991; Corre et al., 2002) or not. If non N-fixing plants compete with soil microorganisms for inorganic N, as Kaye and Hart (1997) hypothesized, then plants might have difficulty meeting their N requirements. Even if plants were better competitors for NO_3^- than microorganisms (Kaye and Hart, 1997), the amount of NO_3^- available in grassland was very low (Table 2), especially on slopes. By planting koa on those slopes, NH_4^+ and NO_3^- production were, within 12 yr, increased to levels where they exceeded consumption, thus relieving potential N limitation to productivity.

Net Nitrogen Transformation Rates

Net N transformation rates provide data for assessing the effects of vegetation and topography on relative amounts of N available for plant uptake after microbial needs have been met. Vegetation type, but not topographic position, had a marginally significant ($p = 0.052$) effect on rates of net ammonification, calculated as the difference between gross NH_4^+ production and gross consumption (Table 4). Net ammonification for forest soil was more negative than for planted koa and grass-

Table 4. Average net ammonification, nitrification, and mineralization (net ammonification plus net nitrification) in surface soil (0–15 cm), by topographic position and vegetation type.

Topographic position	Vegetation type	Net ammonification		Net nitrification		Ammonification plus nitrification	
		^{15}N†	Std‡	^{15}N§	Std‡	^{15}N	Std‡
		mg N kg^{-1} d^{-1}					
Slope (S)	Forest (F)	−1.98¶	−0.09b	4.48a	2.00ab	1.58	1.91ab
	Planted koa (P)	0.67	0.28a	0.06b	0.83bc	0.87	1.11bc
	Grassland (G)	−0.55	−0.05b	0.21b	0.26c	0.23	0.21c
Bottom (B)	Forest	−3.15	−0.12b	5.57a	2.93a	2.37	2.81a
	Planted koa	−0.86	−0.15b	3.29ab	1.84ab	1.19	1.68ab
	Grassland	−0.37	−0.08b	1.69ab	1.05bc	1.32	0.97bc
		Comparison of factor levels# and significance of interaction terms					
Factor							
Vegetation type (V)		<u>F P G</u>	<u>F P G</u>	<u>F P G</u>	<u>F P G</u>	<u>F P G</u>	<u>F P G</u>
Topographic position (T)		<u>S B</u>	S B	S B	S B	<u>S B</u>	S B
Interaction (V × T)		NS††	*	NS	NS	NS	NS

* Significant at the 0.05 probability level.
† Net ammonification = gross ammonification minus gross consumption.
‡ Net rates determined using 25-d field incubations of unamended, disturbed soil.
§ Net nitrification = gross nitrification minus gross consumption.
¶ Means within a column that are followed by the same lowercase letter are not statistically different (Tukey HSD test, α set at 0.05); when no lowercase letters are given, values are not statistically different.
# Factor levels, which are denoted by uppercase letters, joined by underlines are not significantly different (Tukey HSD test, α set at 0.05).
†† NS = not significant.

land soils. Consumption exceeded production (negative rates) except on slopes under planted koa. Net nitrification, which was calculated as gross nitrification minus gross NO_3^- immobilization, was significantly affected by vegetation type ($p < 0.01$) and topographic position ($p = 0.02$), and interaction was not significant ($p = 0.41$) (Table 4). Accumulation of NO_3^- was greatest in forest soil and least in grassland soil. Drainage bottoms showed greater NO_3^- accumulation than slopes, which suggested that enhanced net nitrification rather than mass downslope transport of this mobile ion might account for larger NO_3^- pools in drainage bottoms (Table 2). Nitrate production and immobilization were virtually identical on slopes under planted koa, which resulted in net nitrification near zero. Net N mineralization rates that were based on gross N transformations were positive in all instances (Table 4), which suggested that inorganic N was available for plant uptake, although on grassland slopes the amounts were small. Neither vegetation type nor topographic position significantly affected net mineralization ($p = 0.68$ and 0.50, respectively).

Net rates determined by 30-d buried-bag field incubations closely paralleled net rates estimated by ^{15}N stable isotope pool dilution (Table 4). For net ammonification, topographic position, and vegetation–topography interaction were significant ($p \leq 0.01$), although rates were close to zero. Soils on slopes under planted koa had significantly greater net ammonification (0.28 mg N kg^{-1} d^{-1}) than all other locations. Rates for other locations were negative and differences among them were not significant. The interaction effect was not significant for net nitrification, but effects of both vegetation type and topographic position were significant ($p < 0.01$ in both cases). Net nitrification was greatest for forest soil, intermediate for planted koa soil, and least for grassland soil. Net nitrification in drainage bottoms was nearly double that on slopes ($p < 0.01$). Like net nitrification, net N mineralization showed significant vegetation type and topographic position effects, but no significant interaction effect. Forest soil had greater net N mineralization than either planted koa ($p = 0.02$) or grassland soils ($p < 0.01$), and planted koa soil had greater mineralization than grassland soil ($p = 0.05$). Net N mineralization was significantly greater in drainage bottoms than on slopes ($p < 0.01$).

Net accumulation of NO_3^-, especially in drainage bottoms, might contribute to leaching losses from surface soil. The soils we studied have large amounts of amorphous materials, which become dominant at depths >50 cm (H. Ikawa, Univ. Hawaii, personal communication, 1989). These amorphous materials, hydrated Fe and Al oxides, and organic matter have an abundance of pH-dependent, positively charged sites for adsorption of anions (Uehara and Gillman, 1981). Nitrate leached from surface soil, which has a net negative charge (Balasubramanian and Kanehiro, 1978), might be retained on positively charged exchange sites in lower horizons (Matson et al., 1987) where deeper rooted species than grasses could get it.

Factors Potentially Influencing Nitrogen Transformations

The methods we used probably affected N transformation rates, thus invalidating their use in a budgetary

manner, but not their use in comparing vegetation and topographic effects. The use of disturbed soil samples rather than intact soil cores for measuring gross and net N transformations might have resulted in overestimation of rates (Cabrera and Kissel, 1988; Schimel et al., 1989; Sierra, 1992). We examined this possibility by comparing rates in our forest study area with rates reported by Riley and Vitousek (1995). They used intact soil cores to estimate rates for the top 9 cm of several rainforest soils that were located at around 1150 m asl and in various stages of development in Hawaii. We adjusted their rates to account for cooler temperature at our sites, as follows. Assuming (i) that Q_{10} for microbial activity is 2 (Townsend et al., 1995), (ii) that the lapse rate is 6.4°C per 1000 m elevation (Juvik and Nullet, 1994), and (iii) that our study area is 780 m higher elevation (5°C cooler), then rates of ammonification and nitrification observed by Riley and Vitousek (1995) should be about two-thirds what they were at 1150 m elevation (compare Hart and Perry, 1999). Adjusted rates of gross ammonification ranged from 0.11 to 0.36 g N m^{-2} d^{-1} and rates of gross nitrification ranged from 0.01 to 0.07 g N m^{-2} d^{-1}. In comparison, rates of gross ammonification for an equivalent 9-cm thick layer of topsoil in our forest site, averaged 0.23 and 0.28 g N m^{-2} d^{-1} and rates of gross nitrification averaged 0.17 and 0.16 g N m^{-2} d^{-1} for slopes and drainage bottoms, respectively. Thus, our use of disturbed soil probably increased rates of nitrification but not ammonification. In contrast, Schimel et al. (1989) reported that ammonification was stimulated by soil disturbance, probably due to release of labile organic N from disrupted soil aggregates, while nitrification increased <6%.

Adding ^{15}N label raised soil moisture and added substrate. Although soil water contents were at or slightly above field capacity (90–140 kg kg^{-1}; H. Ikawa, Hawaii, personal communication, 1989) after labeled solutions were added, we cannot rule out some loss of NO_3^- due to denitrification. Such losses would cause overestimation of gross NO_3^- consumption. Adding NH_4^+ and NO_3^- might have stimulated consumers, but the close correspondence between net rates determined by buried bag and ^{15}N pool dilution methods seems to argue against such stimulation.

For the above reasons we do not represent our rates as actual field rates. They are for comparative purposes to evaluate potential effects of vegetation type and topographic position on gross N transformations. Our use of mixed soils might have confounded effects of vegetation type. Grassland soils probably had better structure than forest soils, which were subject to intermittent feral pig-rooting, and if so, then disruption of the former might have increased rates of N transformation more than disruption of the latter.

CONCLUSIONS

Re-establishing koa in high-elevation grassland produced changes in physical and chemical properties of surface soil within 10 yr of planting. The speed with which soil properties reverted to those found under

forest cover depended on the property. Whereas soil bulk density and acidity had recovered completely, extractable P was still very close to grassland levels, and total C and N, C/N ratio, and extractable base cations showed intermediate recoveries. Nitrogen forms and their transformation rates were, in most cases, in intermediate stages of recovery, which supported the notion that grassland establishment brought N limitation to plants and soil microorganisms, especially on slopes, and that re-establishing koa was a means of removing it. Topographic position affected some surface soil properties and gross rates of NO_3^- but not NH_4^+ transformations.

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