Carbon and Nitrogen Dynamics of a Subtropical Savanna Ecosystem: Consequences of Increased Woody Plant Abundance

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ABSTRACT

The abundance of woody plants has increased in recent history in many grassland and savanna ecosystems throughout the world. Woody plants involved in this successional process are often capable of N_2-fixation, such as *Prosopis glandulosa*. The biogeochemical consequences of grassland invasion by N_2-fixing woody plants may include increased belowground carbon storage and increased N_2O emissions from the soils, both of which may have the potential to influence atmospheric chemistry and climate.

At the Texas Agricultural Experiment Station LaCopita Research Area in the Rio Grande Plains of southern Texas, soil samples were collected under mesquite trees at 0-10 cm and 10-20 cm depths. The mesquite trees were harvested and age was determined for each tree by counting its rings. The soil samples were analyzed for organic carbon and total nitrogen using combustion/gas-chromatography. Regressions were developed for nutrient concentrations and nutrient mass/area vs. tree age.

Soil organic carbon and total nitrogen concentrations and mass/area increased significantly with tree age. In the closed canopy woodlands, soils are accumulating total nitrogen at a rate of 2.96 $g/m^2/yr$ and organic carbon at a rate of 35.84 $g/m^2/yr$. The increase of nutrients beneath *Prosopis* canopies suggest that the soils are temporarily sequestering a significant quantity of carbon and nitrogen from the atmosphere, and therefore influencing carbon and nitrogen dynamics of this subtropical ecosystem.

INTRODUCTION

The abundance of woody plants has increased in recent history in many grassland and savanna ecosystems throughout the world (Archer 1994). Woody plants involved in this successional process are often capable of N_2-fixation, such as *Prosopis glandulosa* (mesquite) in the southwestern USA (Johnson & Mayeaux 1990). These changes increase nitrogen input; for example, *P. glandulosa* may contribute 100 kg N/ha yr under its canopy through the fixation of atmospheric nitrogen (Abrams et al. 1990). Nitrogen fixed by N_2-fixing species may become available to other plants and microorganisms, altering ecosystem-level properties. These changes in nutrient input consequently alters primary productivity, decomposition, plant water-use efficiency, and succession in ecosystems (Belsky et al. 1989; Vitousek & Walker 1989). The biogeochemical consequences of grassland invasion by N_2-fixing woody plants may include increased belowground caron storage and increased N_2O emissions from the soils, both of which may have the potential to influence atmospheric chemistry and climate. Despite its potential local, regional, and global importance, little is known about the ecological significance and resource management implications of increased abundance of N_2-fixing woody plants in savanna ecosystems.

A savanna is an ecosystem in which a continuous, well-developed grassland matrix is interspersed with an open discontinuous layer of shrubs or trees (Knoop & Walker 1985; Belsky 1994). Woody landscape elements within savanna ecosystems often have significantly higher concentrations of organic carbon and total nitrogen in soils compared with the surrounding grassland matrix (Jackson et al. 1980; Mordlelet et al. 1993; Frost & Edinger

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1991), presumably due to higher above and below ground productivity and/or accumulation of coarse woody debris with slow decomposition rates. In cases where one or more of the woody species are symbiotic N_2-fixers, nitrogen accumulation in below canopy soils is even more pronounced (Virginia 1986; Mazzarino et al. 1991). Invasion by exotic species into this ecosystem can alter composition and community structure. This can also alter properties of the whole ecosystem, such as productivity, nutrient cycling, and hydrology. Because these invading species differ from native species in resource acquisition and resource use efficiency, they can alter trophic structure, and disturbance frequency and intensity (Vitousek 1990).

The historic *Prosopis-Acacia-Andropogon-Setaria* savannas of the Rio Grande Plains of southern Texas (Kuchler 1964) have been largely replaced by a subtropical thorn woodland in recent history (Archer 1994; Boutton et al. 1994). Intensification of livestock grazing and changes in fire and climatic regimes are believed to account for the vegetational shift (Hastings & Turner 1965; Grover & Musick 1990). In heavily grazed ecosystems, reductions in soil fertility and alterations in physical and chemical properties may occurr with loss of vegetative ground cover and erosion (Thurow 1991; Walker & Steffen 1993). This reduction in soil fertility would potentially favor N_2-fixing woody plants (van Auken & Bush 1989; Vitousek & Howarth 1991) and growthforms tolerant of low nutrient conditions (Goldberg 1982). Recent studies have indicated that the dominant woody plant species which have increased in abundance in the Rio Grande Plains of southern Texas are capable of symbiotic nitrogen fixation (Zitzer et al. 1991; Boutton et al. 1992).

Since woody plant encroachment into grasslands has been occurring over large areas worldwide, ecosystem level changes in nutrient pool sizes and fluxes could potentially influence regional and global biogeochemistry and climate (Whitford 1992; Walker & Steffen 1993). The replacement of grassland and savanna ecosystems by woodlands must be considered as a local problem with economic impacts on livestock production, and also in the context of regional changes in biogeochemistry and climate that will influence landscape evolution and future land use options in arid and semiarid ecosystems worldwide.

Despite many investigations on the carbon cycle, approximately 2 Pg of carbon remain unaccounted for. Various researchers have suggested that land vegetation acts as a sink for carbon dioxide (Schlesinger 1993). The increase in abundance of woody plants in subtropical, ecosystems worldwide may temporarily sequester the buildup of atmospheric carbon dioxide (Alban & Perala 1992; Sombroek et al. 1993).

The purpose of this study was to document some of the biogeochemical changes resulting from increased woody plant abundance in the Rio Grande Plains of southern Texas. Specifically, I will utilize a previously documented (Archer 1994) successional chronosequence from open grassland to closed canopy woodland to quantify changes in carbon and nitrogen storage in belowground biomass and soils.

OBJECTIVE AND HYPOTHESES

Objective: Quantify the magnitude and rate of change in belowground N and C pool sizes along a successional chronosequence from remnant grassland to woodland.

Hypothesis 1: As a consequence of both greater above- and belowground productivity and the presence of N_2-fixing woody plants, N and C pools in belowground biomass and soils will increase with time habitation by woody plants and will be significantly greater in areas that are now woodland relative to remnant grasslands.

Hypothesis 2: C/N ratios of biomass and soil organic matter will be lower in acreas dominated by N_2-fixing woody plants relative to grasslands.

PROCEDURES

Study Area: The research was conducted at the 1093 ha Texas Agriculture Experiment Station LaCopita Research Area, 65 km west of Corpus Christi, Texas, in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. Mean annual rainfall is 680 mm, and mean annual temperature is 22.4°C. Elevations range from 75-60 m. Soils range from fine sandy loams to sandy clay loams, from slightly acid to alkaline and include Ustolls and Ustalfs on uplands, and Aqualfs in lower landscape positions.

Upland vegetation consists of discrete multi-species woody plant clusters embedded within a continuous matrix of herbaceous vegetation (grassland) dominated by tropical and subtropical C4 grasses (Archer et al. 1988). In the uplands, successional processes from grassland to woodland are initiated by the establishment of *Prosopis glandulosa*, a nitrogen-fixing legume (Archer et al. 1988). Once established, *Prosopis* appears to facilitate the colonization of other woody plant species beneath its canopy. Thus, *Prosopis* is always the oldest plant in any particular stand of woody plants. Upland wooded areas that consist of single *Prosopis* plant and up to 15 other woody plant species are referred to as clusters. Soils beneath clusters always have an argillic horizon (Bt) present. Upland wooded areas that consist of multiple *Prosopis* plants and up to 15 other woody plant species are referred to as groves. Soils beneath groves always lack an argillic horizon. Low-lying landscape positions (drainages) consist of closed-canopy subtropical thorn woodland,dominated by *Prosopis*, but with the same understory woody species as occur in the upland woodlands., This site has been grazed since the mid 1800s.

Soil Sampling and Tree Age Determination: For each landscape position, 40 sites were identified that provided a range of *Prosopis* tree sizes/ages. At each site, three soil cores (2.5 cm wide x 20 cm deep) were taken directly beneath the largest (oldest) *Prosopis* tree in the stand in April 1994. All three cores were divided into 0-10 cm and 10-20 cm depth increments, and the three samples from each depth interval were pooled. Samples were dried at 60°C for 5 days, and ground to pass a 2 mm screen. Large roots and organic matter fragments were removed during this step. A subsample of this soil was used for determination of texture. Another subsample was pulverized (particle size < 5µm) with an Angstrom ring grinder, and utilized for all other analyses.

At the same time the soil cores were taken, the largest *Prosopis* tree in the stand was cut down at ground level with a chain-saw, and a cross-section of the trunk was removed. The age of each tree was determined by counting annual rings in the cross-sections prepared using methods described previously (Flinn et al. 1994). Regressions were developed to determine relationships between tree diameter and tree age for each landscape position.

Soil samples for bulk density determination were sampled in December 1994. Samples were taken from 12 sites within each landscape position. At each site, one clod was taken from the 0-10 cm depth, and another from the 10-20 cm depth. Clods were wrapped in hair nets, dipped in liquid saran, and transported back to the lab for further processing.

Soil Characterization: Soil texture was determined on all samples using the pipette method (Gee and Bauder 1986). All fractions were corrected for moisture content. Soil pH was determined on a 2:1 (water:soil) mixture using a pH meter (McLean 1982). Bulk density was determined on both oven dry soil, and soil at 0.03 Mpa using the clod method (Blake and Hartge 1986). Differences in percent sand, percent silt, percent clay, pH, and bulk density due to landscape position, soil depth, and their interaction were determined by analysis of variance. Specific differences between landscape units were revealed by Tukey's pairwise comparison test.

Nutrient Concentrations and Accumulation Rates: Organic carbon and total nitrogen concentrations were determined on finely pulverized (<5μm) soil samples by combustion/gas-chromatrography using a Carlo Erba NA-1500 elemental analyzer (Verardo et al. 1990). Mass per unit area (g/m2) of organic carbon and total nitrogen was determined for each site by multiplying the nutrient concentration by the appropriate bulk density. Differences in carbon and nitrogen concentrations and mass/area due to landscape position, soil depth, and their interaction were determined by analysis of variance. Specific differences between landscape units were revealed by Tukey's pairwise comparison test. Rates of changes in nutrient concentrations and nutrient mass/area were determined by regression against tree age. In these regressions, I assumed that nutrient concentrations and mass at time 0 in the wooded areas (clusters, groves, drainages) were equivalent to mean values for these parameters from areas that are presently grassland. Therefore, all regression lines were forced through the nutrient concentrations or masses for grasslands at time 0.

RESULTS

Analysis of soil texture revealed that soils in grasslands, clusters, and groves were loamy sands while drainages were sandy clay loams (Fig. 1). The relative proportions of sand, silt, and clay were significantly different between landscape units (Table 1). This difference was due to the fact that drainages had more clay and silt and less sand than all of the other landscapes (Table 2). Sand and silt did not differ between soil depths, but clay was significantly greater at the 10-20 cm depth interval (Table 1). There were no significant landscape unit x soil depth interactions for any of the particle size classes.

Values for soil pH did not differ significantly between landscape units or soil depths (Fig. 2; Table 1). Mean values for soil pH ranged from approximately 6.7 to 7.4 (Fig. 2). Similarly, bulk density did not differ significantly between landscape units or soil depth (Fig. 3; Table 1). Mean values for bulk density ranged from 1.37 to 1.41 g/cm^3 (Fig. 3).

Concentrations of soil organic carbon varied significantly between landscape units and soil depths (Fig 4; Table 1). At 0-10 cm, values for organic carbon ranged from 6.9 g kg^{-1} in the grasslands to 24.1 g kg^{-1} in the drainage woodlands. All pairwise comparisons between landscape units were significantly different, except for the cluster-grove comparison (Table 2). Concentrations of soil total nitrogen also varied significantly between landscape units and soil depths (Fig. 4; Table 1). At 0-10 cm, values for total nitrogen ranged from 0.72 g kg^{-1} in the grasslands to 2.2 g kg^{-1} in the drainage woodlands (Fig. 4). The drainage woodlands were significantly different from all of the upland landscape units (Table 2). The upland landscape units did not differ significantly (Table 2).

The carbon/nitrogen ratio varied significantly between landscape units, soil depths, and the interaction between landscape units and soil depths (Table 1.) All pairwise comparisons differed significantly except the cluster-grove and drainage-grassland comparisons (Table 2). Values in the 0-10 cm depth range from 10.6 in the groves to 12.6 in the drainages (Fig. 4).

Mass per unit area of organic carbon differed significantly between landscape units and between soil depths (Fig. 5; Table 1). There was no significant interaction between landscape units and soil depth (Table 1). Values in the 0-10 cm depth increment range from 944 g/m^2 in the grassland to 3297 g/m^2 in the drainage woodland (Fig. 5). All pairwise comparisons were significantly different except the cluster-grove comparison (Table 2). Mass per unit area of nitrogen was also significantly different between landscape units and soil depth (Fig. 5; Table 1). There was not a significant interaction between landscape unit and soil depth (Table 1). Values in the 0-10 cm depth range from 98 g/m^2 in the grassland to 304 g/m^2 in the drainage. All pairwise comparisons were significantly different except the cluster-grove and grove-grassland comparisons (Table 2).

Regression analyses predicting *Prosopis* tree age from tree basal diameter were all highly significant (Fig. 6). Values for r^2 ranged from 0.76 for clusters to 0.83 for groves and drainages. Paired t-tests showed that all three regression lines were significantly different from each other ($p<0.001$).

Soil organic carbon concentrations at 0-10 cm and 10-20 cm increased significantly with tree age, as revealed by linear regression (Fig. 7). All regressions were statistically significant, except for clusters at the 10-20 cm depth. At 0-10 cm, rates of increase in organic carbon concentrations ranged from 0.09 g C kg^{-1} yr^{-1} (groves) to 0.28 g C kg^{-1} yr^{-1} (drainages) (Fig. 7). At 10-20 cm, rates of increase in organic carbon concentration ranged from 0.05 g C kg^{-1} yr^{-1} (groves to 0.23 g C kg^{-1} yr^{-1} (drainages) (Fig. 7). Similarly, soil total nitrogen concentrations at 0-10 cm and 10-20 cm increased significantly with tree age, as revealed by linear regression (Fig. 8). All regressions were statistically significant, except for clusters at the 10-20 cm depth increment. At 0-10 cm, rates of increase in total nitrogen concentrations ranged from 0.01 g N kg^{-1} yr^{-1} (clusters and groves) to 0.03 g N kg^{-1} yr^{-1} (drainages) (Fig. 8). At 10-20 cm, rates of increase in total nitrogen concentrations ranged from 0.003 g N kg^{-1} yr^{-1} (clusters) to 0.02 g N kg^{-1} yr^{-1} (drainages) (Fig. 8).

Carbon/nitrogen ratios at 0-10 cm and 10-20 cm decreased significantly with tree age, as revealed by linear regression (Fig. 9). All regressions were statistically significant, except for clusters at the 0-10 cm depth and drainages at the 10-20 cm depth. At 0-10 cm, rates decreased from 0.02 yr^{-1} (clusters and drainages) to 0.03 yr^{-1} (groves) (Fig. 9). At 10-20 cm, rates decreased from 0.01 yr^{-1} (drainages) to 0.05 yr^{-1} (clusters) (Fig. 9).

Mass/unit area of organic carbon at 0-10 cm, 10-20 cm, and combined 0-20 cm depths, increased significantly with tree age, as revealed by linear regression (Fig. 10). All regressions were statistically significant. At the combined 0-20 cm depth, rates of increase in mass/unit area of organic carbon ranged from 9.72 g/m^2 (groves) to 35.84 g/m^2 (drainages) (Fig. 10). At the 0-10 cm depth, rates of increase in mass/unit area of organic carbon ranged from 11.38 g/m^2 (groves) to 38.14 g/m^2 (drainages) (Fig. 10). At the 10-20 cm depth, rates of increase ranged from 8.01 g/m^2 (groves) to 31.59 g/m^2 (drainages) (Fig. 10).

Mass/unit area of total nitrogen at 0-10 cm, 10-20 cm, and combined 0-20 cm depths, increased significantly with tree age, as revealed by linear regression (Fig. 11). All regressions were statistically significant, except for clusters at the 10-20 cm depth. At the combined 0-20 cm depth, rates of increase in mass/unit area of total nitrogen ranged from 0.83 g/m^2 (groves) to 2.96 g/m^2 (drainages) (Fig. 11). At the 0-10 cm depth, rates of increase in mass/unit area of total nitrogen ranged from 0.92 g/m^2 (groves) to 3.50 g/m^2 (drainages) (Fig. 11). At 10-20 cm, rates of increase in mass/unit area of total nitrogen ranged from 0.73 g/m^2 (clusters) to 2.45 g/m^2 (drainages) (Fig. 11).

Figure 1. Soil texture for different landscape units and soil depths at LaCopita Research Area. Texture was measured by the pipette method, and all fractions were corrected for moisture content.

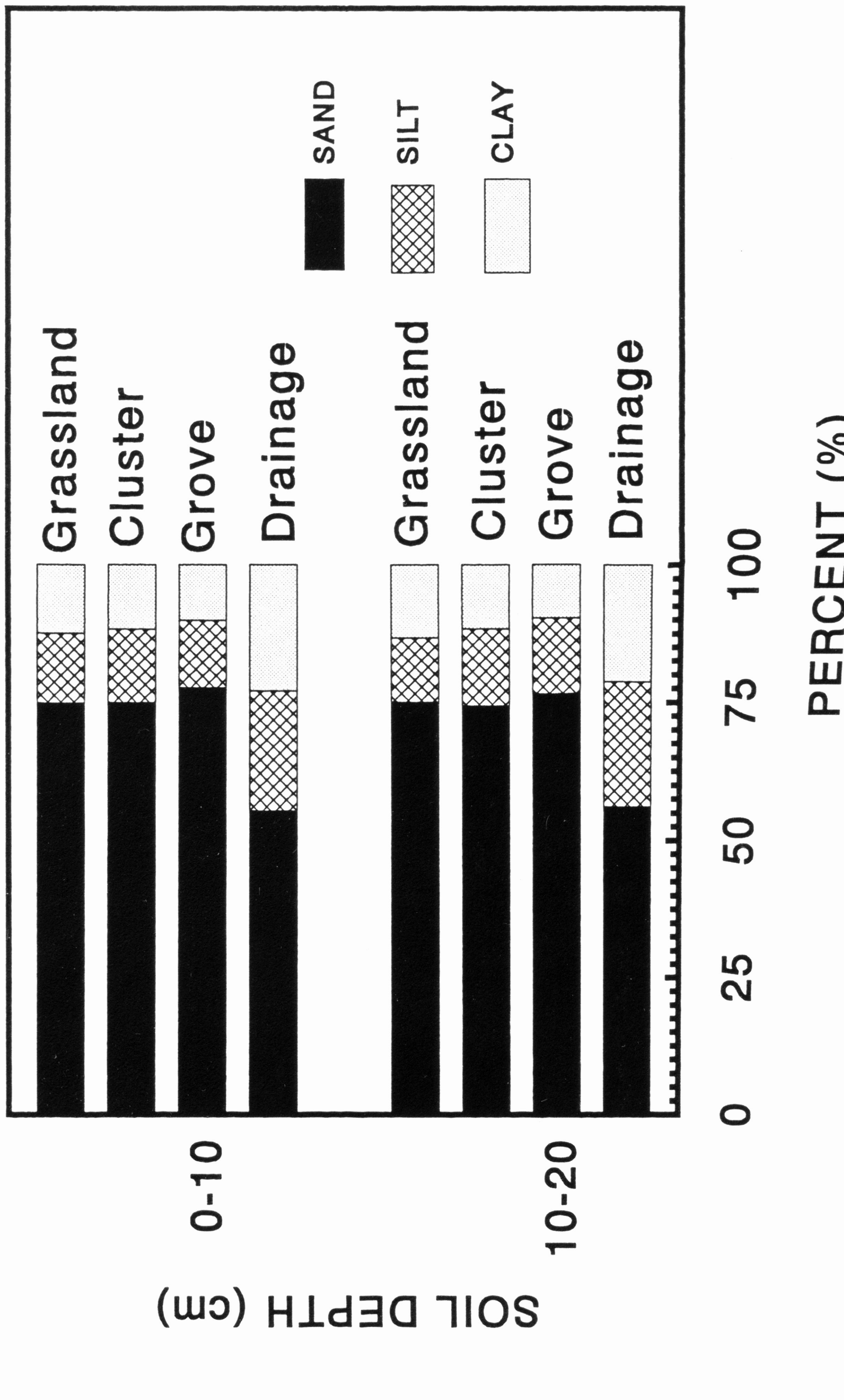

SAND
SILT
CLAY
Grassland
Cluster
Grove
Drainage
Grassland
Cluster
Grove
Drainage
0
25
50
75
100
PERCENT (%)
0-10
10-20
SOIL DEPTH (cm)

Table 1. Results of analysis of variance to test for effects of landscape unit, soil depth, and their interaction on different soil characteristics.

		Texture			Bulk		C/N	Organic Carbon		Total Nitrogen	
	DF	Sand	Silt	Clay	Density	pH	Ratio	g/kg	g/m^2	g/kg	g/m^2
Landscape unit	3, 304	***	***	***	NS	NS	***	***	***	***	***
Soil Depth	1, 304	NS	NS	**	NS	NS	**	***	***	***	*
Interaction	3,304	NS	NS	NS	NS	NS	*	NS	NS	NS	NS

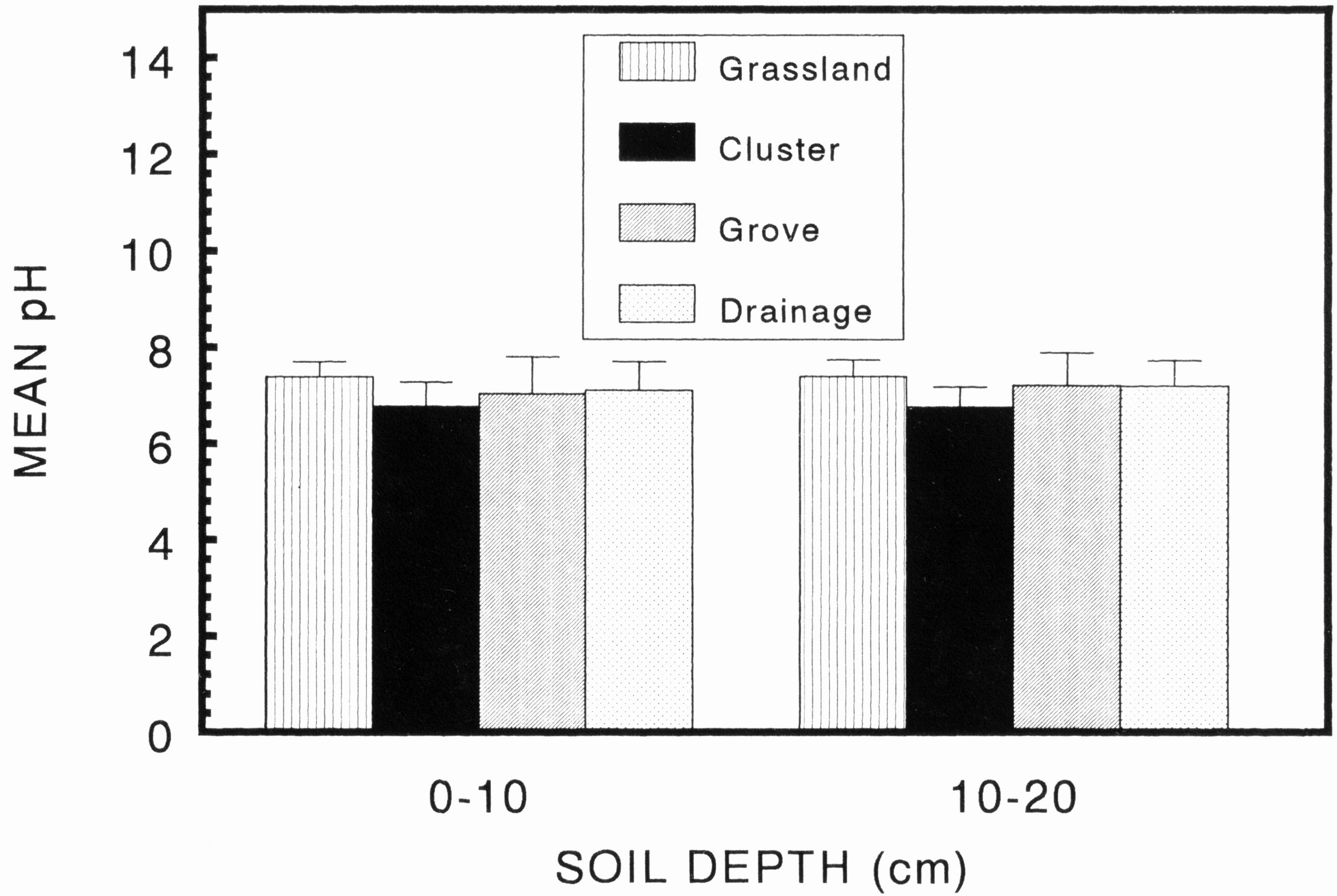
* = P<0.05
** = P<0.01
*** = P<0.001

Table 2. Results of Tukey's pairwise comparisons to determine specific differences between landscape units with respect to soil physical and chemical characteristics.

Pairwise	Texture			Bulk		C/N	Organic Carbon		Total Nitrogen	
Comparison	Sand	Silt	Clay	Density	pH	Ratio	g/kg	g/m^2	g/kg	g/m^2
cluster-grove	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
cluster-drainage	*	*	*	NS	NS	*	*	*	*	*
cluster-grassland	NS	NS	NS	NS	NS	*	*	*	NS	*
grove-drainage	*	*	*	NS	NS	*	*	*	*	*
grove-grassland	NS	NS	NS	NS	NS	*	*	*	NS	NS
drainage-grassland	*	*	*	NS	NS	NS	*	*	*	*

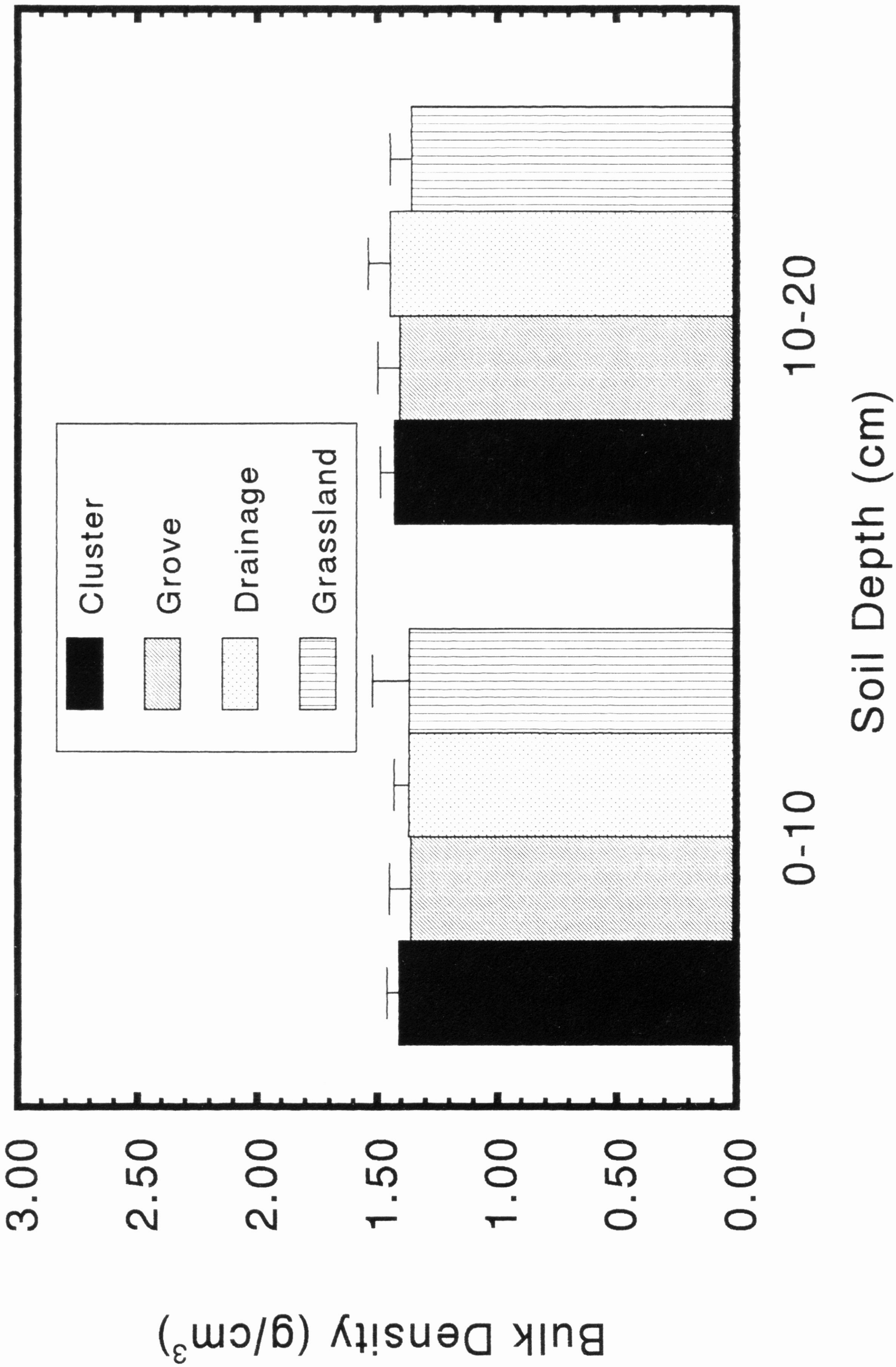
* = $P<0.05$
** = $P<0.01$
*** = $P<0.001$

Figure 2. Soil pH for different landscape units and soil depths at LaCopita Research Area. pH was measured on a 2:1 (water:soil) mixture. Error bars represent one standard deviation.



Grassland
Cluster
Grove
Drainage
MEAN pH
14
12
10
8
6
4
2
0
0-10
10-20
SOIL DEPTH (cm)

Figure 3. Bulk density (oven-dry) for different landscape units and soil depths at LaCopita Research Area. Bulk density was determined by the clod method. Error bars represent one standard deviation.



Bulk Density (g/cm³)
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Cluster
Grove
Drainage
Grassland
0-10
10-20
Soil Depth (cm)

Figure 4. Organic carbon and total nitrogen concentrations, and carbon/nitrogen ratios, for different landscape units and soil depths at LaCopita Research Area. Organic carbon and total nitrogen concentrations were determined by combustion/gas-chromatography. Error bars represent one standard deviation.

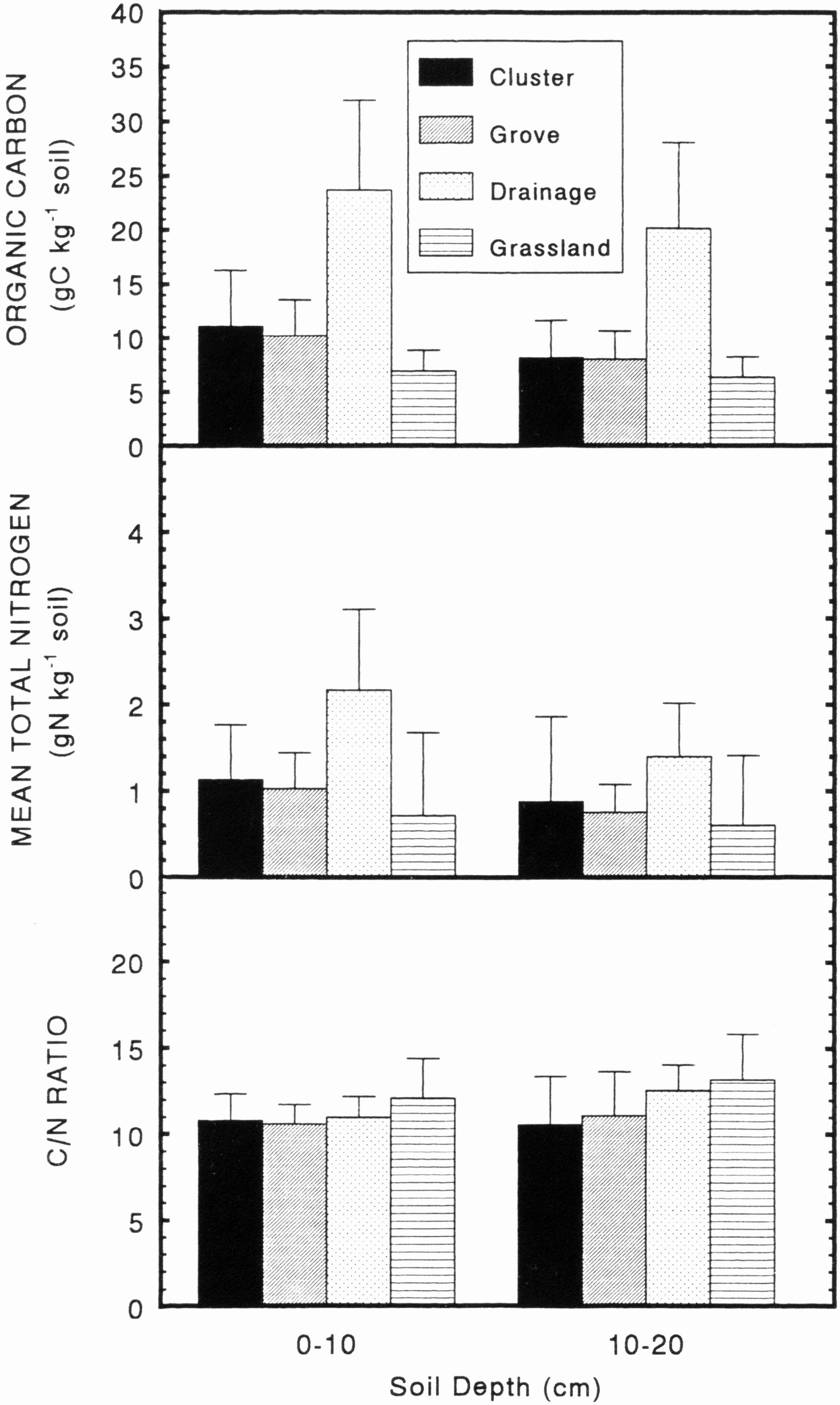
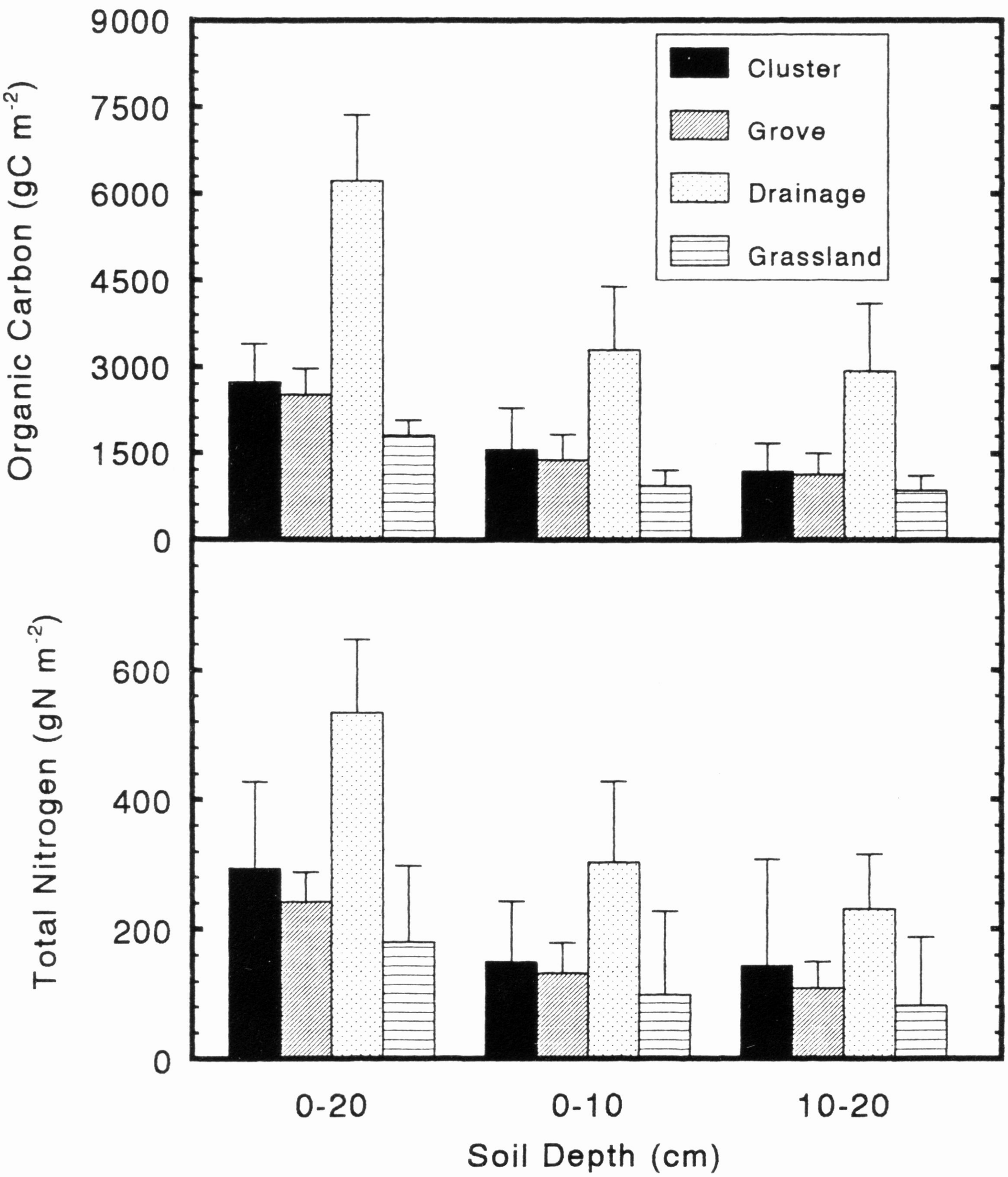
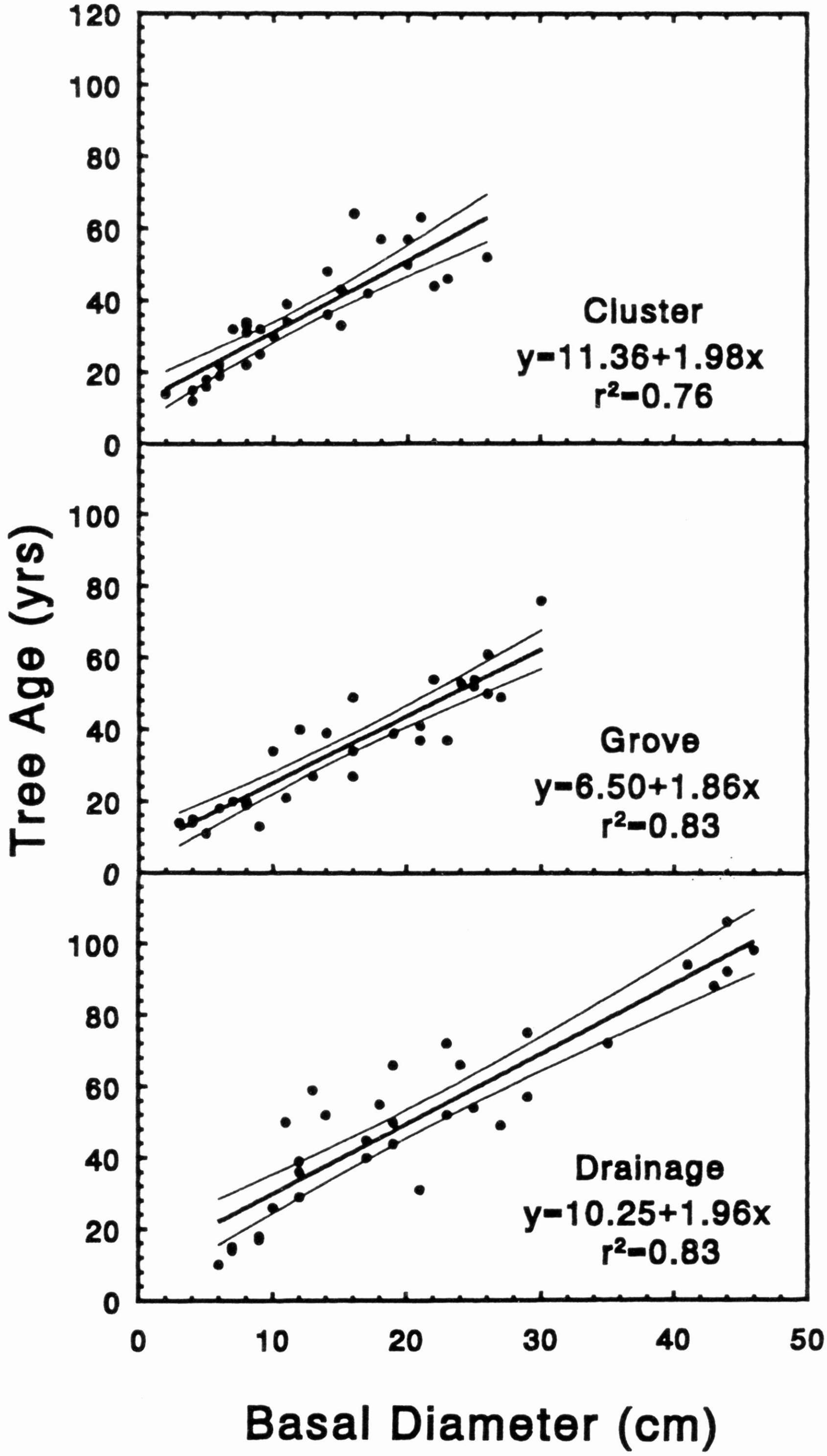

ORGANIC CARBON
(gC kg-1 soil)
Cluster
Grove
Drainage
Grassland
MEAN TOTAL NITROGEN
(gN kg-1 soil)
C/N RATIO
0-10
10-20
Soil Depth (cm)

Figure 5. Mass of organic carbon and total nitrogen for different landscape units and soil depths at LaCopita Research Area. Nutrient mass was determined as the product of nutrient concentration and bulk density. Error bars represent one standard deviation.



9000
7500
6000
4500
3000
1500
0
Organic Carbon (gC m-2)
Cluster
Grove
Drainage
Grassland
600
400
200
0
Total Nitrogen (gN m-2)
0-20
0-10
10-20
Soil Depth (cm)

Figure 6. Relationships between basal diameter and age of mesquite trees in different landscape positions at LaCopita Research Area. Tree age was determined by counting annual rings. Regression lines are shown as dark, heavy lines, and 95% confidence intervals are shown as lighter, thinner lines. Analysis of variance revealed that all regressions were significant at $p<0.001$.



120
100
80
60
40
20
0
Cluster
y=11.36+1.98x
r²=0.76
Tree Age (yrs)
Grove
y=6.50+1.86x
r²=0.83
Drainage
y=10.25+1.96x
r²=0.83
0
10
20
30
40
50
Basal Diameter (cm)

Figure 7. Change in soil organic carbon concentrations with increasing age of mesquite trees in different landscape units at LaCopita Research Area. The three graphs on the left are for the 0-10 cm soil depth, while the three on the right are for the 10-20 cm soil depth. Analysis of variance revealed that all regressions were statistically significant ($p<0.05$), except for clusters (10-20 cm).

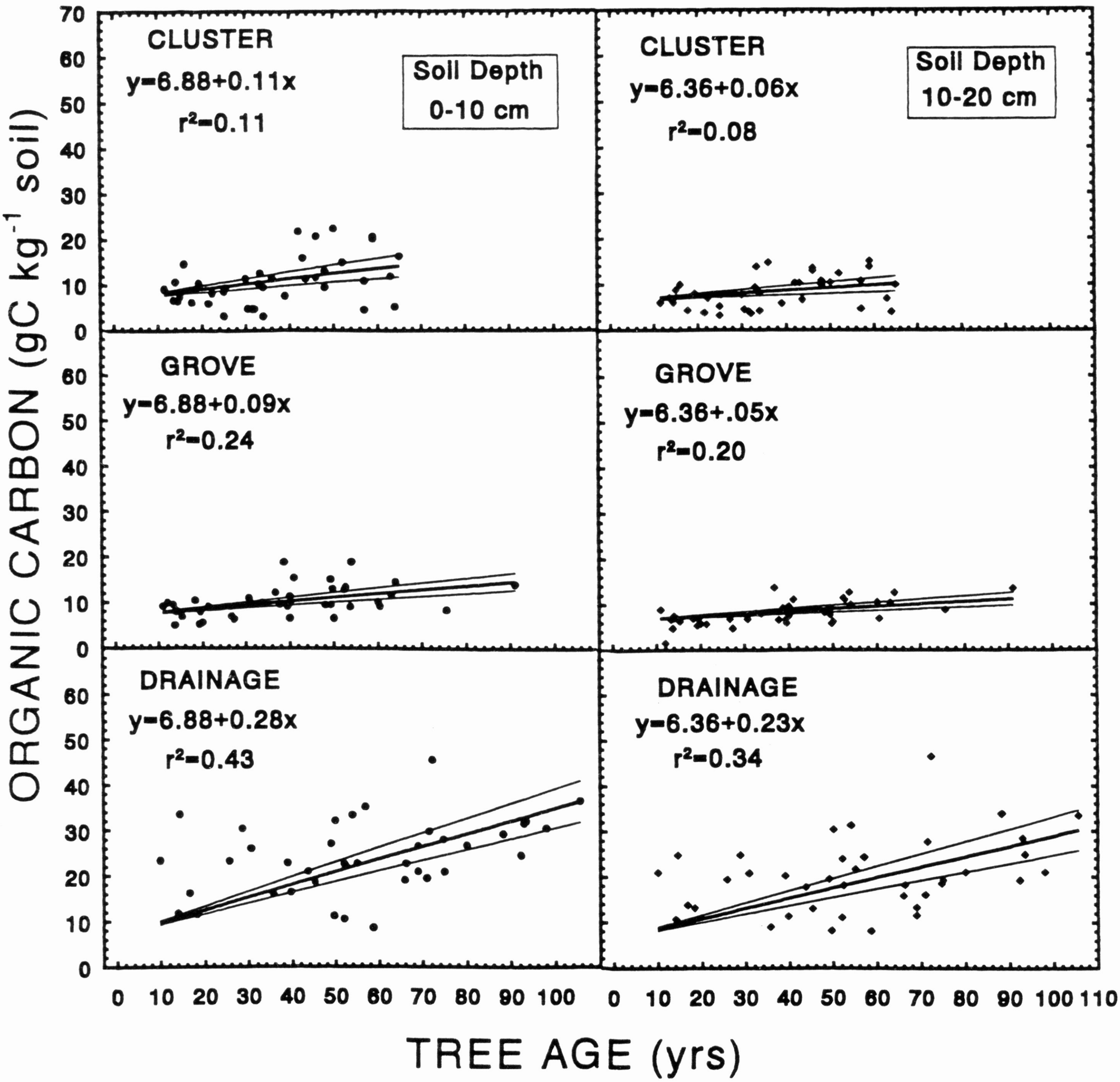
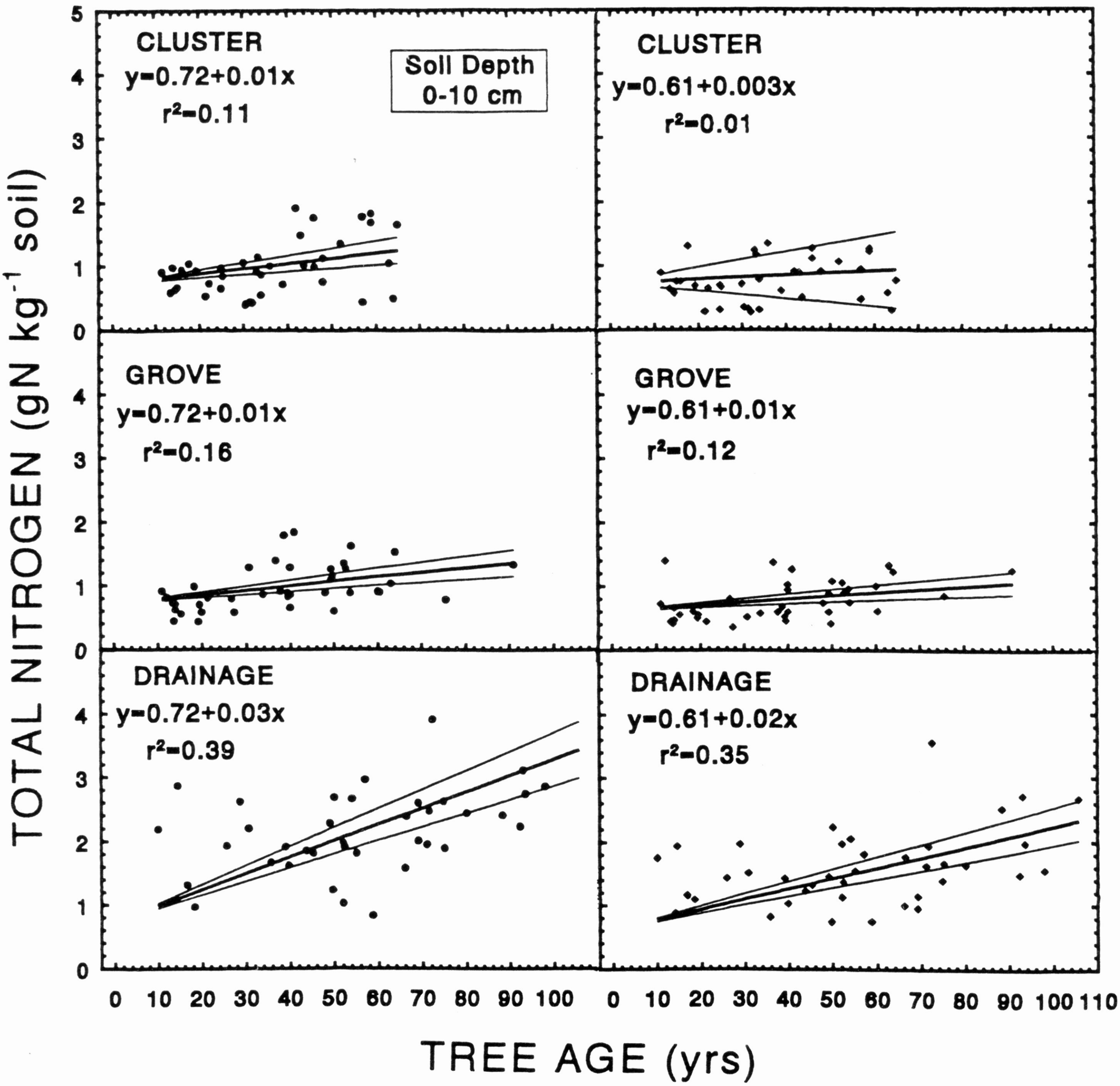

CLUSTER
y=6.88+0.11x
r²=0.11
Soil Depth
0-10 cm
CLUSTER
y=6.36+0.06x
r²=0.08
Soil Depth
10-20 cm
GROVE
y=6.88+0.09x
r²=0.24
GROVE
y=6.36+.05x
r²=0.20
DRAINAGE
y=6.88+0.28x
r²=0.43
DRAINAGE
y=6.36+0.23x
r²=0.34
ORGANIC CARBON (gC kg⁻¹ soil)
TREE AGE (yrs)

Figure 8. Change in soil total nitrogen concentrations with increasing age of mesquite trees in different landscape units at LaCopita Research Area. The three graphs on the left are for the 0-10 cm soil depth, while the three on the right are for the 10-20 cm soil depth. Analysis of variance revealed that all regressions were statistically significant ($p<0.05$), except for clusters (10-20 cm).



CLUSTER
y=0.72+0.01x
r²=0.11
Soil Depth
0-10 cm
CLUSTER
y=0.61+0.003x
r²=0.01
GROVE
y=0.72+0.01x
r²=0.16
GROVE
y=0.61+0.01x
r²=0.12
DRAINAGE
y=0.72+0.03x
r²=0.39
DRAINAGE
y=0.61+0.02x
r²=0.35
TOTAL NITROGEN (gN kg⁻¹ soil)
TREE AGE (yrs)
0 10 20 30 40 50 60 70 80 90 100
0 10 20 30 40 50 60 70 80 90 100 110
0 1 2 3 4 5

Figure 9. Change in soil carbon/nitrogen ratio with increasing age of mesquite trees in different landscape units at LaCopita Research Area. The three graphs on the left are for the 0-10 cm soil depth, while the three on the right are for the 10-20 cm soil depth. Analysis of variance revealed that all regressions were statistically significant ($p<0.05$), except for clusters (0-10 cm) and drainage (10-20 cm).

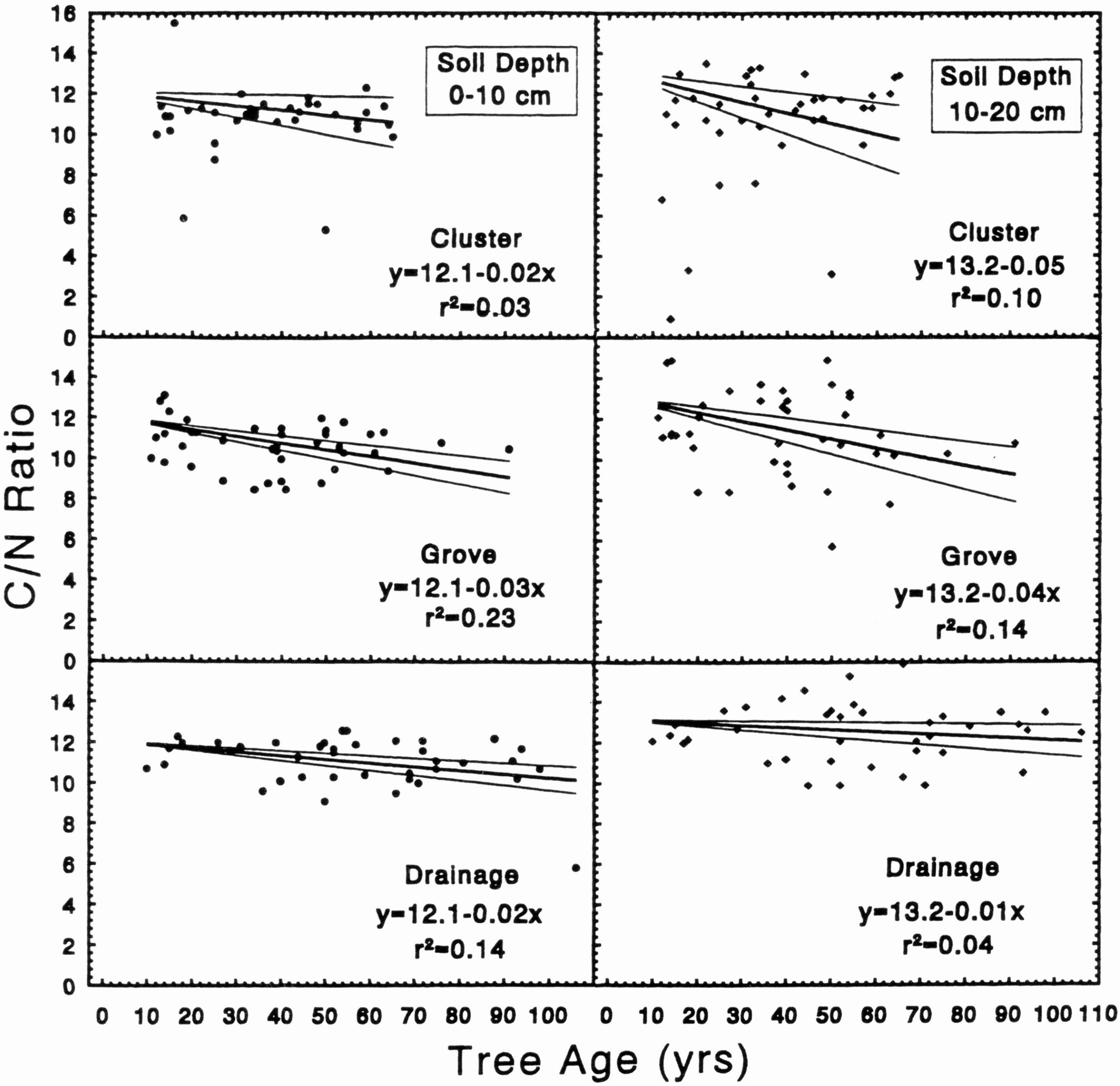

Soil Depth
0-10 cm
Soil Depth
10-20 cm
Cluster
y=12.1-0.02x
r²=0.03
Cluster
y=13.2-0.05
r²=0.10
Grove
y=12.1-0.03x
r²=0.23
Grove
y=13.2-0.04x
r²=0.14
Drainage
y=12.1-0.02x
r²=0.14
Drainage
y=13.2-0.01x
r²=0.04
C/N Ratio
Tree Age (yrs)
0 2 4 6 8 10 12 14 16
0 10 20 30 40 50 60 70 80 90 100 110

Figure 10. Change in mass of soil organic carbon with increasing age of mesquite trees in different landscape units at LaCopita Research Area. The three graphs on the left are for the 0-20 cm soil depth, the three graphs in the middle are for the 0-10 cm soil depth, and the three graphs on the right are for the 10-20 cm soil depth. Analysis of variance revealed that all regressions were statistically significant ($p<0.05$).

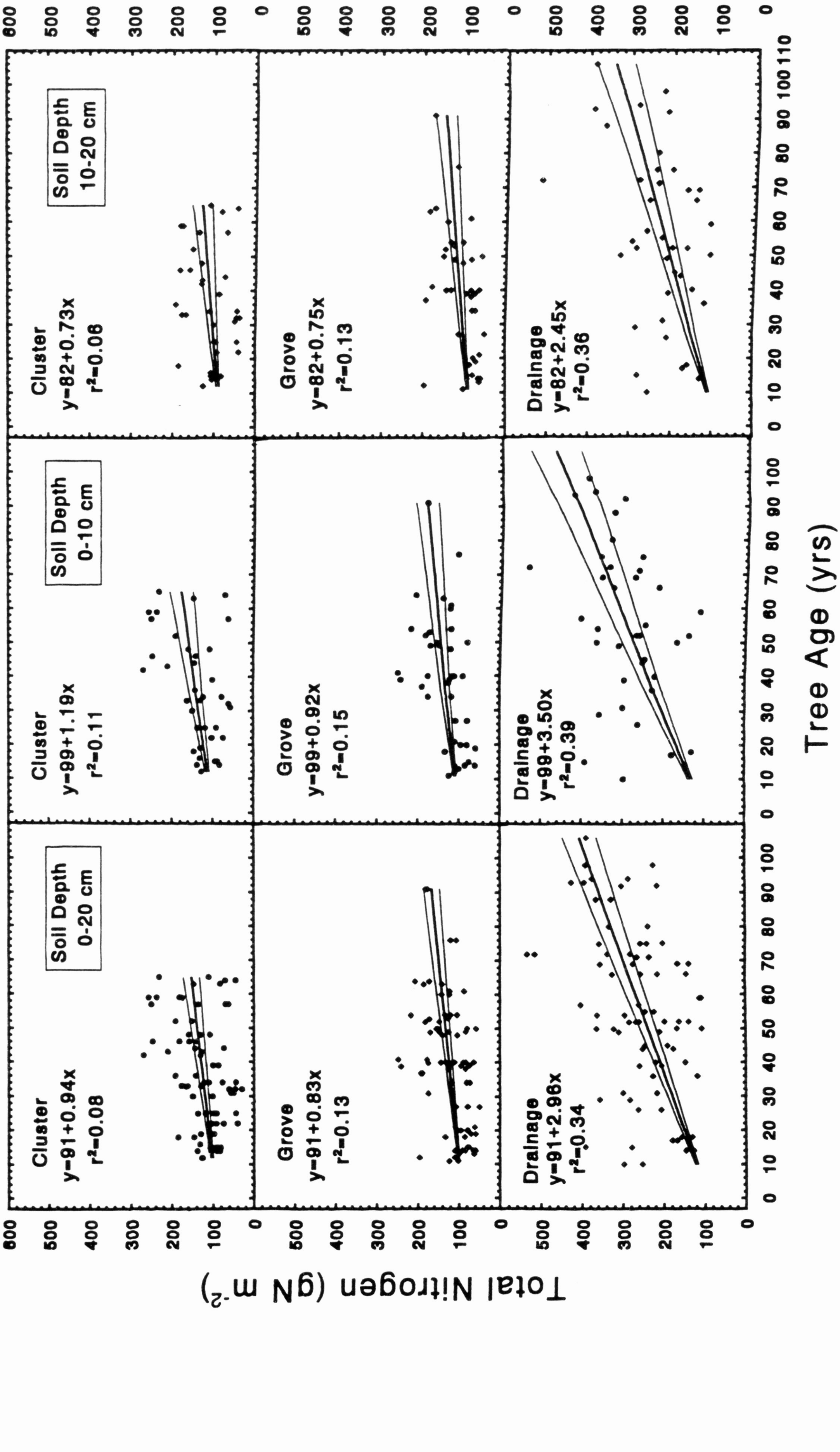
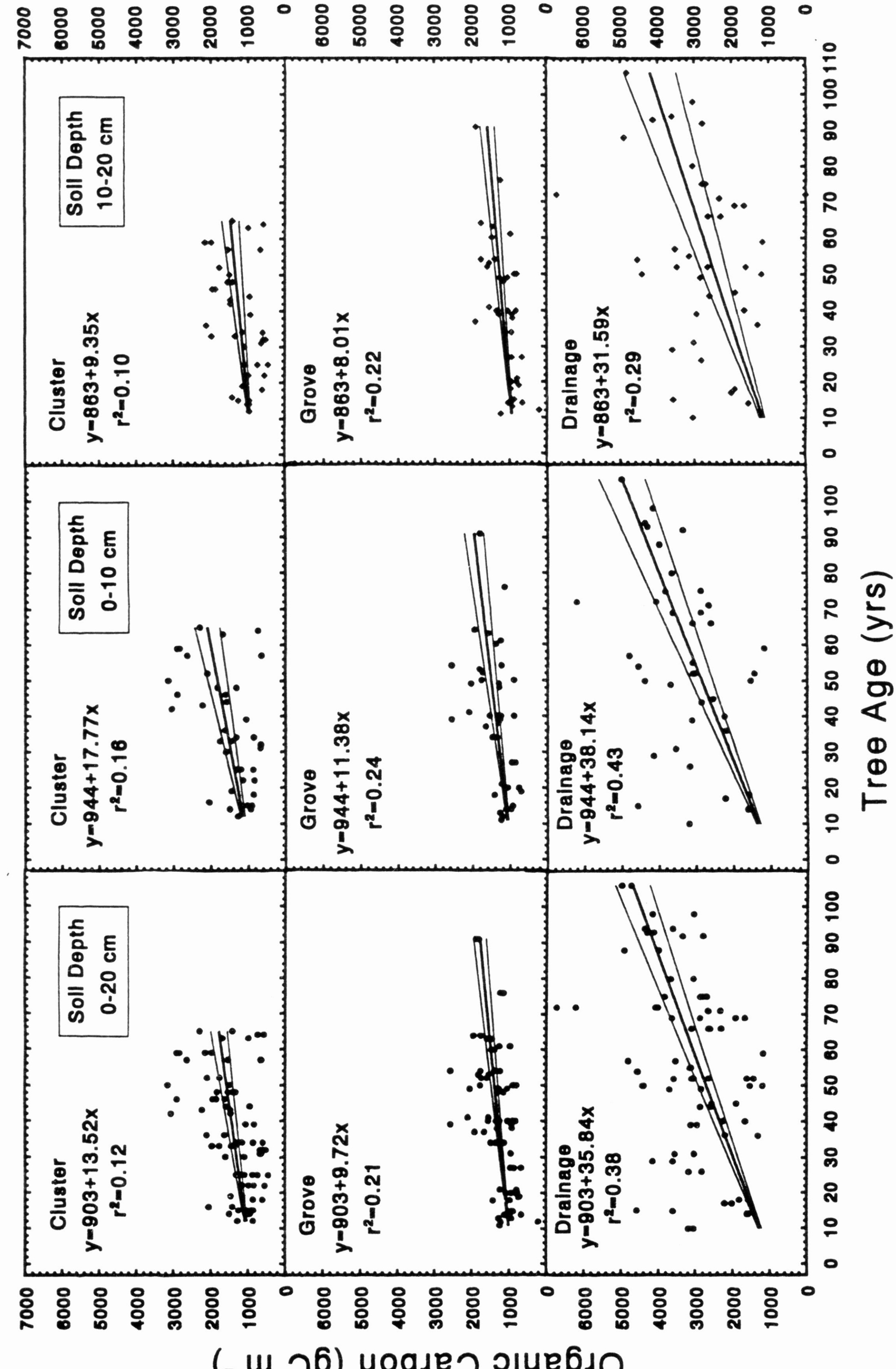

Soil Depth 0-20 cm
Soil Depth 0-10 cm
Soil Depth 10-20 cm
Cluster
y=91+0.94x
r²=0.08
Grove
y=91+0.83x
r²=0.13
Drainage
y=91+2.96x
r²=0.34
Cluster
y=99+1.19x
r²=0.11
Grove
y=99+0.92x
r²=0.15
Drainage
y=99+3.50x
r²=0.39
Cluster
y=82+0.73x
r²=0.08
Grove
y=82+0.75x
r²=0.13
Drainage
y=82+2.45x
r²=0.36
Tree Age (yrs)
Total Nitrogen (gN m⁻²)

Figure 11. Change in mass of soil total nitrogen with increasing age of mesquite trees in different landscape units at LaCopita Research Area. The three graphs on the left are for the 0-20 cm soil depth, the three graphs in the middle are for the 0-10 cm soil depth, and the three graphs on the right are for the 10-20 cm soil depth. Analysis of variance revealed that all regressions were statistically significant ($p<0.05$), except for clusters (10-20 cm).


Organic Carbon (gC m-2)
Tree Age (yrs)
Soil Depth 0-20 cm
Cluster
y=903+13.52x
r²=0.12
Grove
y=903+9.72x
r²=0.21
Drainage
y=903+35.84x
r²=0.38
Soil Depth 0-10 cm
Cluster
y=944+17.77x
r²=0.16
Grove
y=944+11.38x
r²=0.24
Drainage
y=944+38.14x
r²=0.43
Soil Depth 10-20 cm
Cluster
y=863+9.35x
r²=0.10
Grove
y=863+8.01x
r²=0.22
Drainage
y=863+31.59x
r²=0.29

DISCUSSION

The study site was previously a savanna ecosystem with an open grassland matrix interspersed with woody plants. Recently, it has been encroached by woody plants and is predominantly a subtropical thorn woodland (Archer 1994; Boutton et al. 1992). For the purpose of this research, the grassland landscape unit was considered as the original vegetation element. The drainages, closed canopy woodlands, were considered as the oldest landscape element, with the clusters and groves as intermediate in age. The grasslands reflected lower quantities of organic carbon concentrations, total nitrogen concentrations, and organic carbon and total nitrogen masses than any of the wooded landscape positions (Fig. 4 and 5). In all of the regressions for organic carbon and total nitrogen, I am assuming that the mean grassland value represents the original vegetation condition (time 0).

All regressions show an increase in nutrient accumulation (both concentrations and masses) through time. This is consistent with previous literature on savannas--there are greater quantities of nutrients under tree canopies than in the grassland matrix (Belsky et al. 1989; Bernard-Reverstat 1982; Mazzarino 1991). Some explanations for the change in nutrients under tree canopies are as follows: the trees have larger roots that can search for nutrients at further distances (resource allocation), trees possess greater above ground biomass, which means they produce more litter and input more soil organic matter than herbaceous zones, a greater microbial biomass is found beneath tree canopies to make nutrients available, and also from dung deposits from birds that utilize the branches and shade of the tree. Rundel et al. (1982) noted only 45 g N/m^2 under grassland vegetation and 1020 g

N/m^2 under the canopy of *Prosopis glandulosa*. I found that the grassland landscape unit contained an average of 91 g N/m^2 and 903 g C/m^2 whereas the drainage woodland contained an average of 268 g N/m^2 and 3112 g C/m^2 under the canopy of *Prosopis glandulosa*.

The drainage consisted of the highest total and greatest rate of increase (for both organic carbon and total nitrogen concentrations and masses) (Fig. 4 through 11). This can be explained because of the particle size distribution. Fine textured soils were found to be more abundant in the drainage woodlands (Fig. 1). Clay soils have a higher cation exchange capacity and retain nutrients in greater amounts and for longer amounts of time. Virginia and Jarrell (1983) also found that total soil nitrogen was greatest on soil with the highest clay content and lowest in aeolian sand dunes. Clusters and groves, both upland woody landscape units increase in nutrients at a similar rate that is not as dramatic as the drainages. This is due to the coarser texture of the uplands. Sandier textures do not accumulate as much carbon and nitrogen because the nutrients are lost, for example, by leaching, decomposition, erosion, volitalization, or denitrification.

The carbon/nitrogen ratios decreased with time (age of mesquite trees) (Fig. 9). This is because more litter is accumulating from nitrogen-fixing woody plants. *Prosopis* is known to form symbiotic associations with Rhizobium and fix atmospheric nitrogen (Boutton et al. 1992) which it contributes to the soil through litter. Nornberg et al. (1993) found that carbon/nitrogen ratios also decreased under the canopy of oak trees. The carbon/nitrogen ratio is greatest in the grasslands (Fig. 4) because there are no woody species present to input greater amounts of nitrogen relative to carbon.

Each woody landscape unit has a different relationship between tree age and basal diameter (Fig. 6). Woody plants in each landscape unit grows at different rates due to different environmental conditions. The drainage woodlands have the fastest growth rate. They are present in the lowland areas of the landscape, and therefore obtain more runoff which contributes more water and nutrients. This landscape also contains finer textured soils (clay), which retains nutrients more effectively than coarser textured soils.

Nutrients stored in the upper soil horizons represents the most active nutrient pool and the pool most sensetive to change as a result of agricultural land uses (Moraes et al. 1995). The 0-10 cm depth accumulated greater quantities of nutrients than the 10-20 cm depth for all analyses. In all of the regressions (nutrients vs. tree age), the top soil depth showed a greater rate of nutrient increase with time than the 10-20 cm depth. The 10-20 cm depth did show a slower increase in nutrient accumulation. This is because there are more litter/soil organic matter inputs to the top of the soil. There is also a greater microbial biomass in the top portion of the soil to assist with mineralization of nutrients.

The low r^2 of all regressions are due to the variability of this ecosystem. Different plant species produce varying amounts of nitrogen and carbon and their decomposition rates differ due to the chemical composition of each species. At the LaCopita Research Area, there are many species of woody plants, forbs, and grasses, each contributing to the variability of the landscape.

CONCLUSIONS

Although the ages of trees sampled ranged over a relatively short period of time, less than 106 years, a significant increase in both organic carbon and total nitrogen from grasslands to all woody landscapes was apparent. This is especially evident in the fine textured drainage woodlands. Because the carbon/nitrogen ratios decreased in the woody landscapes, nitrogen seems to be accumulating at a greater rate than carbon due to the fact that nitrogen-fixing mesquite trees are adding a significant amount of nitrogen from the atmosphere to the soil. In the drainage woodland, total nitrogen is increasing at a rate of 2.96 $g/m^2/yr$ and organic carbon is increasing at a rate of 35.84 $g/m^2/yr$ in the top 20 cm of the soil.

The increase in abundance of woody plants is influencing carbon and nitrogen dynamics of this subtropical savanna ecosystem in the Rio Grande Plains of southern Texas. The increase of nutrients beneath *Prosopis* canopies suggests that the soils are temporarily sequestering a significant amount of carbon and nitrogen from the atmosphere. This could potentially change the regional biogeochemistry and climate. If woody plants continue to increase in abundance worldwide at the rates observed at this site, the increased storage of carbon and nitrogen could affect global biogeochemical cycles.

Further studies could evaluate what is happening to the carbon and nitrogen in the soils by measuring soil respiration rate and other mechanisms.

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APPENDIX 1. Results of soil characterization. The first number in the sample code identifies the sample number, the second number in the sample code identifies the landscape unit (1=cluster, 2=grove, 3-drainage, and 4=grassland.) The last number in the sample code identifies the soil depth (1=0-10 cm depth, 2=10-20 cm depth.)

APPENDIX 1. Results of soil characterization.

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
1-1-1	24.3	65	70.6	15.1	14.3	6.98	1.41	1.37
2-1-1	20.0	57	68.1	15.8	16.0	6.96	1.41	1.37
3-1-1	12.2	44	72.8	13.4	13.8	6.75	1.41	1.37
4-1-1	7.9	33	71.1	10.7	18.2	6.85	1.41	1.37
5-1-1	5.1	16	74.1	11.3	14.6	7.59	1.41	1.37
6-1-1	8.0	34	78.4	8.1	13.5	7.04	1.41	1.37
7-1-1	9.1	25	80.5	10.8	8.6	6.16	1.41	1.37
8-1-1	6.7	25	75.9	10.0	14.1	7.60	1.41	1.37
9-1-1	5.2	18	79.2	9.8	11.0	7.01	1.41	1.37
10-1-1	20.2	50	76.4	12.6	11.1	5.62	1.41	1.37
11-1-1	16.8	42	79.2	11.3	9.5	6.41	1.41	1.37
12-1-1	21.8	59	73.0	13.5	13.5	6.28	1.41	1.37
13-1-1	26.3	52	73.6	14.2	12.2	6.20	1.41	1.37
14-1-1	1.6	14	72.6	13.9	13.5	6.69	1.41	1.37
15-1-1	17.0	48	73.5	14.8	11.8	6.26	1.41	1.37
16-1-1	14.5	33	72.5	15.6	11.9	6.62	1.41	1.37
17-1-1	2.5	15	71.1	12.6	16.3	6.99	1.41	1.37
18-1-1	10.1	30	77.1	12.0	11.0	7.21	1.41	1.37
19-1-1	2.1	14	71.1	14.2	14.8	7.02	1.41	1.37
20-1-1	6.1	22	70.6	13.9	15.5	7.12	1.41	1.37
21-1-1	3.5	15	72.9	12.8	14.3	7.05	1.41	1.37
22-1-1	10.5	39	76.8	11.9	11.3	6.98	1.41	1.37
23-1-1	3.8	12	73	14.9	12.2	7.37	1.41	1.37
24-1-1	17.5	57	82.6	8.2	9.2	6.16	1.41	1.37
25-1-1	15.4	43	69.4	16.5	14.1	7.15	1.41	1.37
26-1-1	22.5	46	67.6	17.3	15.1	6.77	1.41	1.37

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
27-1-1	8.0	31	74.2	14.1	11.7	6.36	1.41	1.37
28-1-1	21.8	59	73.3	13.1	13.6	5.84	1.41	1.37
29-1-1	14.0	36	7.35	13.1	13.4	6.82	1.41	1.37
30-1-1	14.2	48	74.4	12.4	13.2	6.02	1.41	1.37
31-1-1	5.7	18	73.5	11.5	14.9	6.83	1.41	1.37
32-1-1	9.3	25	75.7	12.6	11.8	6.55	1.41	1.37
33-1-1	16.0	46	72.2	11.7	16.1	7.12	1.41	1.37
34-1-1	11.4	34	74.8	12.8	12.3	6.11	1.41	1.37
35-1-1	16.0	64	82.4	9.0	8.6	6.04	1.41	1.37
36-1-1	8.5	32	80.5	9.5	9.9	7.36	1.41	1.37
37-1-1	7.5	22	81.6	6.8	11.6	6.76	1.41	1.37
38-1-1	7.3	32	81.7	7.2	11.1	6.62	141	1.37
39-1-1	20.5	63	78.1	9.3	12.6	6.38	1.41	1.37
1-1-2	24.3	65	66.9	13.1	19.9	6.72	1.43	1.37
2-1-2	20.0	57	67.9	11.8	20.3	6.72	1.43	1.37
3-1-2	12.2	44	70.4	10.8	18.9	6.30	1.43	1.37
4-1-2	7.9	33	70.3	12.2	17.5	7.15	1.43	1.37
5-1-2	5.1	16	71.3	14.0	14.8	7.23	1.43	1.37
6-1-2	8.0	34	77.1	8.2	14.7	7.01	1.43	1.37
7-1-2	9.1	25	80.8	10.1	9.1	6.11	1.43	1.37
8-1-2	6.7	25	78.5	12.1	9.4	7.05	1.43	1.37
9-1-2	5.2	18	78.8	12.2	9.1	6.71	1.43	1.37
10-1-2	20.2	50	78.5	11.3	10.2	6.41	1.43	1.37
11-1-2	16.8	42	79.5	10.5	10.0	6.78	1.43	1.37

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
12-1-2	21.8	59	72.5	13.0	14.5	5.93	1.43	1.37
13-1-2	26.3	52	73.7	16.8	9.5	6.50	1.43	1.37
14-1-2	1.6	14	74.3	11.6	14.1	6.92	1.43	1.37
15-1-2	17.0	48	74.5	13.0	12.5	6.31	1.43	1.37
16-1-2	14.5	33	76.8	11.4	11.8	6.49	1.43	1.37
17-1-2	2.5	15	70.7	13.2	16.1	7.10	1.43	1.37
18-1-2	10.1	30	71.8	13.5	14.7	7.32	1.43	1.37
19-1-2	2.1	14	70.0	13.4	16.6	6.86	1.43	1.37
20-1-2	6.1	22	70.0	12.8	17.2	6.95	1.43	1.37
21-1-2	3.5	15	67.0	15.6	17.4	7.10	1.43	1.37
22-1-2	10.5	39	73.1	11.5	15.4	7.11	1.43	1.37
23-1-2	3.8	12	73.6	13.7	12.7	7.06	1.43	1.37
24-1-2	17.5	57	74.7	14.9	10.4	6.70	1.43	1.37
25-1-2	15.4	43	69.3	15.3	15.4	7.16	1.43	1.37
26-1-2	22.5	46	67.7	15.7	16.6	6.71	1.43	1.37
27-1-2	8.0	31	75.1	12.9	12.1	6.32	1.43	1.37
28-1-2	21.8	59	71.1	13.6	15.3	6.15	1.43	1.37
29-1-2	14.0	36	74.8	10.5	14.7	6.65	1.43	1.37
30-1-2	14.2	48	74.6	15.9	9.5	5.87	1.43	1.37
31-1-2	5.7	19	68.6	5.1	16.3	7.00	1.43	1.37
32-1-2	9.3	25	74.6	11.7	13.8	6.90	1.43	1.37
33-1-2	16.0	46	70.1	12.5	17.4	7.03	1.43	1.37
34-1-2	11.4	34	73.0	11.1	15.9	6.30	1.43	1.37
35-1-2	16.0	64	80.1	9.9	10.0	6.28	1.43	1.37
36-1-2	8.5	32	81.3	8.7	10.0	6.41	1.43	1.37

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
37-1-2	7.5	22	82.9	6.2	10.9	6.35	1.43	1.37
38-1-2	7.3	32	82.5	7.0	10.5	6.33	1.43	1.37
39-1-2	20.5	63	80.1	8.4	11.5	6.56	1.43	1.37
1-2-1	15.6	34	75.9	6.7	17.5	6.54	1.36	1.34
2-2-1	8.5	13	75.7	13.1	11.2	6.81	1.36	1.34
3-2-1	24.7	54	70.7	17.4	11.8	7.80	1.36	1.34
4-2-1	27.1	49	72.5	14.8	12.7	7.01	1.36	1.34
5-2-1	14.0	39	74.3	12.7	13.0	6.45	1.36	1.34
6-2-1	11.1	21	81.7	2.8	15.4	6.93	1.36	1.34
7-2-1	2.25	12	78.2	10.6	11.3	8.12	1.36	1.34
8-2-1	23.5	53	80.2	7.2	12.5	5.75	1.36	1.34
9-2-1	13.2	27	85.0	4.5	10.5	6.54	1.36	1.34
10-2-1	25.9	50	62.3	25.1	12.7	5397	1.36	1.34
11-2-1	11.9	40	77.8	8.4	13.8	6.12	1.36	1.34
12-2-1	18.9	39	74.5	9.7	15.8	8.00	1.36	1.34
13-2-1	9.5	34	78.0	6.7	15.3	7.54	1.36	1.34
14-2-1	21.6	48	69.2	10.7	20.1	8.18	1.36	1.34
15-2-1	11.5	40	76.3	14.4	9.3	7.04	1.36	1.34
16-2-1	3.9	14	77.2	10.2	12.6	7.92	1.36	1.34
17-2-1	15.5	91	75.5	13.9	10.5	7.99	1.36	1.34
18-2-1	22	54	68.4	21.2	10.5	7.65	1.36	1.34
19-2-1	28.5	60	81.2	9.1	9.7	6.81	1.36	1.34
20-2-1	4.0	14	74.4	14.0	11.6	7.32	1.36	1.34
21-2-1	4.2	15	78.8	11.0	10.2	8.08	1.36	1.34
22-2-1	8.3	19	79.2	12.2	8.5	7.32	1.36	1.34

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
23-2-1	7.2	20	81.1	9.8	9.0	7.10	1.36	1.34
24-2-1	28.8	76	70.3	14.4	15.3	8.12	1.36	1.34
25-2-1	5.3	11	79.5	9.5	11.0	7.61	1.36	1.34
26-2-1	30.2	63	79.1	11.0	9.9	6.79	1.36	1.34
27-2-1	15.5	49	74.1	12.6	13.3	7.79	1.36	1.34
28-2-1	26.2	61	80.3	9.9	9.8	7.12	1.36	1.34
29-2-1	23.0	50	81.9	9.6	8.5	7.25	1.36	1.34
30-2-1	6.0	18	79.7	5.9	14.3	7.15	1.36	1.34
31-2-1	3.1	14	82.8	4.0	13.2	7.71	1.36	1.34
32-2-1	17.5	40	82.7	3.0	14.2	7.60	1.36	1.34
33-2-1	20.8	37	77.2	9.5	13.4	6.61	1.36	1.34
34-2-1	30.5	64	76.7	8.2	15.0	4.98	1.36	1.34
35-2-1	25.3	52	76.5	10.1	13.4	5.60	1.36	1.34
36-2-1	17.5	40	78.8	7.1	14.2	6.35	1.36	1.34
37-2-1	21.2	41	78.3	11.1	10.7	7.49	1.36	1.34
38-2-1	15.5	27	81.1	5.3	13.6	6.11	1.36	1.34
39-2-1	7.6	20	83.9	8.0	8.1	6.99	1.36	1.34
40-2-1	22.5	38	83.1	9.0	7.8	7.36	1.36	1.34
1-2-2	15.6	34	66.8	19.5	13.7	6.43	1.41	1.42
2-2-2	8.5	13	73.3	13.2	13.5	6.75	1.41	1.42
3-2-2	24.7	54	73.4	14.8	11.8	7.02	1.41	1.42
4-2-2	27.1	49	73.3	12.4	14.3	7.11	1.41	1.42
5-2-2	14.0	39	76.6	12.5	10.9	6.99	1.41	1.42
6-2-2	11.1	21	78.4	7.8	13.8	6.86	1.41	1.42
7-2-2	2.3	12	69.9	13.3	16.8	7.52	1.41	1.42

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
8-2-2	23.5	53	80.7	5.5	13.8	6.25	1.41	1.42
9-2-2	13.2	27	80.9	5.2	13.8	6.62	1.41	1.42
10-2-2	25.9	50	74.4	9.8	15.8	7.48	1.41	1.42
11-2-2	11.9	40	77.4	6.9	15.7	6.81	1.41	1.42
12-2-2	18.9	39	75.6	9.1	15.3	8.12	1.41	1.42
13-2-2	9.5	31	78.9	7.7	13.3	7.91	1.41	1.42
14-2-2	21.6	48	72.6	10.2	17.2	8.16	1.41	1.42
15-2-2	11.5	40	72.2	13.9	13.9	7.04	1.41	1.42
16-2-2	3.9	14	74.0	11.9	14.1	8.03	1.41	1.42
17-2-2	15.5	91	76.5	11.5	12.0	7.91	1.41	1.42
18-2-2	22	54	75.5	12.0	12.5	7.62	1.41	1.42
19-2-2	28.5	60	77.2	11.4	11.5	7.75	1.41	1.42
20-2-2	4.0	14	74.0	11.4	14.6	7.32	1.41	1.42
21-2-2	4.2	15	77.7	10.6	11.7	7.99	1.41	1.42
22-2-2	8.3	19	80.6	10.2	9.2	7.45	1.41	1.42
23-2-2	7.2	20	78.5	8.9	12.6	7.51	1.41	1.42
24-2-2	28.8	76	74.0	13.0	13.0	8.11	1.41	1.42
25-2-2	5.3	11	74.9	11.3	13.8	7.92	1.41	1.42
26-2-2	30.2	63	72.8	13.9	13.3	7.03	1.41	1.42
27-2-2	15.5	49	70.2	13.2	16.6	8.09	1.41	1.42
28-2-2	26.2	61	79.7	9.0	11.3	7.24	1.41	1.42
29-2-2	23.0	50	80.6	9.7	9.8	7.39	1.41	1.42
30-2-2	6.0	18	67.2	16.8	16.8	7.22	1.41	1.42
31-2-2	3.1	14	81.3	4.8	13.9	7.90	1.41	1.42
32-2-2	14.5	40	76.5	8.3	15.2	7.68	1.41	1.42

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
33-2-2	20.8	37	74.0	9.8	16.2	6.30	1.41	1.42
34-2-2	30.5	64	78.6	5.0	16.3	5.23	1.41	1.42
35-2-2	25.3	52	76.7	7.7	15.6	5.91	1.41	1.42
36-2-2	17.5	40	76.9	11.3	11.8	6.20	1.41	1.42
37-2-2	21.5	41	76.3	16.3	7.4	7.51	1.41	1.42
38-2-2	15.5	27	78.1	5.1	16.8	6.06	1.41	1.42
39-2-2	7.6	20	77.1	9.4	13.5	6.68	1.41	1.42
40-2-2	22.5	38	81.0	7.9	11.2	7.22	1.41	1.42
1-3-1	19.0	50	59.5	20.4	20.1	8.11	1.37	1.27
2-3-1	16.6	40	68.2	17.2	14.5	7.65	1.37	1.27
3-3-1	28.5	69	60.6	20.8	18.6	7.22	1.37	1.27
4-3-1	28.6	69	60.5	20.7	18.9	7.49	1.37	1.27
5-3-1	19.1	66	49.8	26.3	23.9	6.15	1.37	1.27
6-3-1	43.9	82	56.0	25.4	18.7	6.35	1.37	1.27
7-3-1	11.5	36	70.4	15.6	14.0	7.10	1.37	1.27
8-3-1	19.2	44	47.4	27.9	24.7	6.78	1.37	1.27
9-3-1	46	98	42.4	30.7	26.9	6.65	1.37	1.27
10-3-1	29.1	75	48.1	29.9	21.9	6.01	1.37	1.27
11-3-1	6.8	14	62.9	16.5	20.5	7.72	1.37	1.27
12-3-1	20.5	52	48.5	25.2	26.3	8.13	1.37	1.27
13-3-1	13.1	59	51.6	22.8	25.6	8.17	1.37	1.27
14-3-1	31.0	75	62.2	19.1	18.7	6.70	1.37	1.27
15-3-1	29.1	71	65.8	18.2	16.0	7.91	1.37	1.27
16-3-1	16.8	45	63.3	18.7	18.0	8.15	1.37	1.27
17-3-1	24.1	66	46.4	39.6	13.9	7.99	1.37	1.27

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
18-3-1	12.4	29	53.8	24.0	22.2	7.41	1.37	1.27
19-3-1	6.7	15	53.3	23.9	22.7	7.12	1.37	1.27
20-3-1	12.0	39	56.2	22.8	21.0	7.41	1.37	1.27
21-3-1	28.5	57	51.4	26.3	22.3	7.48	1.37	1.27
22-3-1	40.5	94	53.2	25.0	20.8	7.16	1.37	1.27
23-3-1	13.8	53	58.7	20.4	20.9	7.35	1.37	1.27
24-3-1	33.5	80	56.9	22.6	20.5	7.30	1.37	1.27
25-3-1	21.0	31	53.0	22.4	24.6	7.07	1.37	1.27
26-3-1	26.8	49	58.7	22.2	19.1	7.14	1.37	1.27
27-3-1	10.0	266	54.5	21.3	24.2	7.11	1.37	1.27
28-3-1	44.0	106	42.1	29.3	28.6	7.30	1.37	1.27
29-3-1	23.2	72	49.3	25.7	25.0	6.41	1.37	1.27
30-3-1	18.2	55	50.1	23.8	26.0	6.93	1.37	1.27
31-3-1	25.2	54	43.1	30.4	26.6	6.90	1.37	1.27
32-3-1	10.5	50	39.3	28.9	31.7	7.01	1.37	1.27
33-3-1	42.5	88	41.3	28.5	30.3	6.62	1.37	1.27
34-3-1	35.3	72	42.5	30.0	27.5	6.84	1.37	1.27
35-3-1	22.8	52	52.7	20.8	26.6	7.29	1.37	1.27
36-3-1	6.1	10	52.7	21.0	26.3	7.72	1.37	1.27
37-3-1	39.5	93	49.7	24.6	25.7	7.22	1.37	1.27
38-3-1	9.0	17	72.2	13.0	14.8	7.03	1.37	1.27
39-3-1	8.8	18	72.8	11.9	15.4	7.92	1.37	1.27
1-3-2	19.0	50	66.1	15.0	18.9	8.06	1.45	1.36
2-3-2	16.6	40	66.4	15.5	18.1	7.78	1.45	1.36
3-3-2	28.5	69	62.3	18.8	18.9	7.45	1.45	1.36

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Texture (%) Silt	Texture (%) Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
4-3-2	28.6	69	66.9	14.7	18.4	6.90	1.45	1.36
5-3-2	19.1	66	48.6	27.0	24.4	6.59	1.45	1.36
6-3-2	43.9	92	56.8	24.4	18.8	6.68	1.45	1.36
7-3-2	11.5	36	70.7	12.0	17.3	6.07	1.45	1.36
8-3-2	19.2	44	46.9	28.4	24.7	6.43	1.45	1.36
9-3-2	46.0	98	69.7	35.4	24.9	5.82	1.45	1.36
10-3-2	29.1	75	45.6	28.8	25.6	6.74	1.45	1.36
11-3-2	6.8	14	65.0	11.9	23.1	7.60	1.45	1.36
12-3-2	20.5	52	54.2	22.2	23.5	8.19	1.45	1.36
13-3-2	13.1	59	50.6	20.7	28.7	8.12	1.45	1.36
14-3-2	31.0	75	60.5	18.4	21.0	6.84	1.45	1.36
15-3-2	29.1	71	65.9	17.4	16.7	7.91	1.45	1.36
16-3-2	16.8	45	65.7	17.1	17.1	8.09	1.45	1.36
17-3-2	24.1	66	66.4	17.9	15.7	7.94	1.45	1.36
18-3-2	12.4	29	54.9	21.3	23.8	7.31	1.45	1.36
19-3-2	6.7	15	55.4	21.8	22.8	7.13	1.45	1.36
20--2	12.0	39	54.1	21.2	24.7	7.25	1.45	1.36
21-3-2	28.5	57	52.2	22.8	25.0	7.29	1.45	1.36
22-3-2	40.5	94	56.5	22.1	21.4	7.12	1.45	1.36
23-3-2	13.8	52	57.8	19.7	22.6	7.53	1.45	1.36
24-3-2	33.5	80	54.9	21.4	23.7	7.21	1.45	1.36
25-3-2	21.0	31	53.5	21.9	24.6	7.45	1.45	1.36
26-3-2	26.8	49	59.2	18.0	22.8	6.89	1.45	1.36
27-3-2	10.0	26	55.0	20.0	24.9	7.12	1.45	1.36
28-3-2	44.0	106	42.0	28.5	29.5	7.41	1.45	1.36

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
29-3-2	23.2	72	49.0	23.3	27.8	6.51	1.45	1.36
30-3-2	18.2	55	47.3	33.3	19.4	6.75	1.45	1.36
31-3-2	25.2	54	34.4	31.0	34.6	6.82	1.45	1.36
32-3-2	10.5	50	40.2	27.0	32.8	7.19	1.45	1.36
33-3-2	42.5	88	43.3	25.5	31.2	6.91	1.45	1.36
34-3-2	35.3	72	39.5	32.0	28.5	7.07	1.45	1.36
35-3-2	22.8	52	49.6	22.6	27.8	7.56	1.45	1.36
36-3-2	6.1	10	54.4	19.4	26.2	7.71	1.45	1.36
37-3-2	39.5	93	52.7	27.0	20.3	7.74	1.45	1.36
38-3-2	9.0	17	65.9	15.9	18.3	7.10	1.45	1.36
39-3-2	8.8	18	66.0	13.6	20.4	7.69	1.45	1.36
1-4-1	0	0	64.5	18.3	17.2	7.55	1.37	1.31
2-4-1	0	0	70.1	16.3	13.6	7.81	1.37	1.31
3-4-1	0	0	69.1	17.0	13.9	7.58	1.37	1.31
4-4-1	0	0	75.9	11.4	12.6	8.15	1.37	1.31
5-4-1	0	0	70.7	15.9	13.4	7.40	1.37	1.31
6-4-1	0	0	59.0	27.4	13.7	7.15	1.37	1.31
7-4-1	0	0	70.9	13.3	15.8	7.65	1.37	1.31
8-4-1	0	0	69.9	13.9	16.2	7.74	1.37	1.31
9-4-1	0	0	69.7	12.2	18.1	7.71	1.37	1.31
10-4-1	0	0	73.3	12.5	14.2	7.59	1.37	1.31
11-4-1	0	0	72.5	13.9	13.7	8.01	1.37	1.31
12-4-1	0	0	71.2	13.2	15.6	7.51	1.37	1.31
13-4-1	0	0	65.9	15.2	18.9	7.54	1.37	1.31
14-4-1	0	0	65.1	14.7	20.1	7.67	1.37	1.31

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
15-4-1	0	0	69.1	14.0	16.9	7.35	1.37	1.31
16-4-1	0	0	80.3	15.1	4.6	7.35	1.37	1.31
17-4-1	0	0	80.7	10.4	8.9	7.61	1.37	1.31
18-4-1	0	0	82.0	8.3	9.7	7.56	1.37	1.31
19-4-1	0	0	81.7	7.8	10.5	7.55	1.37	1.31
20-4-1	0	0	82.7	8.3	9.0	7.32	1.37	1.31
21-4-1	0	0	81.2	8.0	10.8	7.31	1.37	1.31
22-4-1	0	0	63.9	21.9	14.2	7.50	1.37	1.31
23-4-1	0	0	70.2	13.9	15.9	7.42	1.37	1.31
24-4-1	0	0	72.5	13.0	14.4	7.31	1.37	1.31
25-4-1	0	0	78.0	11.0	11.0	7.12	1.37	1.31
26-4-1	0	0	78.6	12.1	9.3	7.55	1.37	1.31
27-4-1	0	0	80.5	10.8	8.6	6.92	1.37	1.31
28-4-1	0	0	82.4	9.1	8.5	6.88	1.37	1.31
29-4-1	0	0	79.9	11.1	9.0	6.91	1.37	1.31
30-4-1	0	0	82.4	8.0	9.6	6.76	1.37	1.31
31-4-1	0	0	81.4	10.0	8.6	6.75	1.37	1.31
32-4-1	0	0	81.9	8.9	9.2	6.91	1.37	1.31
33-4-1	0	0	78.7	11.5	9.8	7.15	1.37	1.31
34-4-1	0	0	74.0	14.3	11.8	7.08	1.37	1.31
35-4-1	0	0	80.1	12.1	7.8	7.39	1.37	1.31
36-4-1	0	0	74.6	12.3	13.1	7.20	1.37	1.31
37-4-1	0	0	77.4	11.8	10.8	7.29	1.37	1.31
38-4-1	0	0	75.8	10.6	13.6	7.31	1.37	1.31
39-4-1	0	0	81.1	5.9	13.0	7.35	1.37	1.31

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Silt	Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
1-4-2	0	0	67.2	14.2	18.6	7.37	1.36	1.29
2-4-2	0	0	72.1	12.2	15.7	7.75	1.36	1.29
3-4-2	0	0	69.9	14.4	15.7	7.66	1.36	1.29
4-4-2	0	0	76.4	9.8	13.8	8.22	1.36	1.29
5-4-2	0	0	74.0	10.3	15.7	7.32	1.36	1.29
6-4-2	0	0	70.8	14.1	15.1	7.45	1.36	1.29
7-4-2	0	0	69.4	13.9	17.7	7.66	1.36	1.29
8-4-2	0	0	67.8	14.5	17.7	7.72	1.36	1.29
9-4-2	0	0	69.3	11.4	19.3	7.71	1.36	1.29
10-4-2	0	0	72.5	8.8	18.7	7.81	1.36	1.29
11-4-2	0	0	70.1	13.5	16.4	7.95	1.36	1.29
12-4-2	0	0	69.6	11.5	19.0	7.30	1.36	1.29
13-4-2	0	0	65.3	14.4	20.3	7.45	1.36	1.29
14-4-2	0	0	63.3	15.4	21.3	7.81	1.36	1.29
15-4-2	0	0	63.6	18.2	18.1	7.40	1.36	1.29
16-4-2	0	0	83.0	6.4	10.6	7.24	1.36	1.29
17-4-2	0	0	80.4	10.2	9.3	7.42	1.36	1.29
18-4-2	0	0	81.0	7.9	11.1	7.79	1.36	1.29
19-4-2	0	0	81.1	8.0	10.9	7.55	1.36	1.29
20-4-2	0	0	81.6	8.9	9.5	7.23	1.36	1.29
21-4-2	0	0	83.6	8.0	8.5	7.28	1.36	1.29
22-4-2	0	0	69.9	15.7	14.4	7.57	1.36	1.29
23-4-2	0	0	71.6	11.8	16.6	7.67	1.36	1.29
24-4-2	0	0	70.5	12.0	17.5	7.15	1.36	1.29
25-4-2	0	0	75.6	10.3	14.0	7.02	1.36	1.29

APPENDIX 1. Results of soil characterization. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	Texture (%) Sand	Texture (%) Silt	Texture (%) Clay	pH	Oven Dry Bulk Density g/cm^3	0.03 MPa Bulk Density g/cm^3
26-4-2	0	0	77.7	10.9	11.4	7.71	1.36	1.29
27-4-2	0	0	80.8	10.1	9.1	6.80	1.36	1.29
28-4-2	0	0	80.9	10.0	9.1	7.13	1.36	1.29
29-4-2	0	0	80.4	9.7	9.9	7.01	1.36	1.29
30-4-2	0	0	80.5	9.1	10.4	6.95	1.36	1.29
31-4-2	0	0	80.4	9.9	9.7	6.75	1.36	1.29
32-4-2	0	0	81.0	9.7	9.4	6.80	1.36	1.29
33-4-2	0	0	77.7	12.5	9.8	7.24	1.36	1.29
34-4-2	0	0	76.6	11.1	12.3	7.15	1.36	1.29
35-4-2	0	0	80.6	8.7	10.8	7.32	1.36	1.29
36-4-2	0	0	72.3	13.0	14.7	7.12	1.36	1.29
37-4-2	0	0	76.2	11.7	12.0	7.29	1.36	1.29
38-4-2	0	0	80.2	7.7	12.1	7.41	1.36	1.29
39-4-2	0	0	76.7	11.4	12.0	7.51	1.36	1.29

APPENDIX 2. Soil nutrient concentrations and masses per unit area. The first number in the sample code identifies the sample number, the second number in the sample code identifies the landscape unit (1=cluster, 2=grove, 3-drainage, and 4=grassland.) The last number in the sample code identifies the soil depth (1=0-10 cm depth, 2=10-20 cm depth.)

APPENDIX 2. Soil nutrient concentrations and mass per unit area.

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon $g\ kg^{-1}$	Organic Carbon $g\ m^{-2}$	Total Nitrogen $g\ kg^{-1}$	Total Nitrogen $g\ m^{-2}$
1-1-1	24.3	65	0.7	16.31	2300	1.65	231
2-1-1	20.0	57	0	18.72	2639	1.77	250
3-1-1	12.2	44	0	11.33	1597	1.02	144
4-1-1	7.9	33	0	12.57	1772	1.15	162
5-1-1	5.1	16	0	14.59	2056	0.94	132
6-1-1	8.0	34	0	6.11	860	0.55	77
7-1-1	9.1	25	0	6.22	877	0.65	91
8-1-1	6.7	25	0	8.53	1203	0.97	137
9-1-1	5.2	18	0	6.14	865	1.04	146
10-1-1	20.2	50	0	22.37	3153	4.26	599
11-1-1	16.8	42	0	21.76	3067	1.91	269
12-1-1	21.8	59	0	20.66	2913	1.68	237
13-1-1	26.3	52	0	14.90	2101	1.36	191
14-1-1	1.6	14	0	6.70	943	0.59	83
15-1-1	17.0	48	0	13.02	1835	1.13	159
16-1-1	14.5	33	0	10.29	1450	0.92	129
17-1-1	2.5	15	0	7.33	1033	0.67	94
18-1-1	10.1	30	0	11.39	1605	1.06	149
19-1-1	2.1	14	0	10.66	1503	0.98	138
20-1-1	6.1	22	0	8.18	1153	0.73	102
21-1-1	3.5	15	0.3	6.44	907	0.63	88
22-1-1	10.5	39	0	7.55	1064	0.72	100
23-1-1	3.8	12	0.2	9.10	1283	0.91	127
24-1-1	17.5	57	0	4.55	641	0.44	62
25-1-1	15.4	43	0	15.90	2242	1.49	210
26-1-1	22.5	46	0	20.65	2911	1.76	247

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon g kg^{-1}	Organic Carbon g m^{-2}	Total Nitrogen g kg^{-1}	Total Nitrogen g m^{-2}
27-1-1	8.0	31	0	4.83	680	0.40	56
28-1-1	21.8	59	0	20.18	2844	1.82	257
29-1-1	14.0	36	0	11.59	1634	1.01	142
30-1-1	14.2	48	0	9.42	1328	0.76	107
31-1-1	5.7	18	0	10.38	1463	0.93	130
32-1-1	9.3	25	0.1	9.36	1319	0.84	118
33-1-1	16.0	46	0	11.55	1627	1.001	141
34-1-1	11.4	34	0	9.45	1331	0.87	122
35-1-1	16.0	64	0.1	5.23	737	0.50	70
36-1-1	8.5	32	0.2	4.77	672	0.44	61
37-1-1	7.5	22	0	5.97	841	0.53	74
38-1-1	7.3	32	0	4.72	664	0.43	60
39-1-1	20.5	63	0	11.94	1684	1.05	147
1-1-2	24.3	65	0	9.90	1417	0.77	110
2-1-2	20.0	57	0.7	10.73	1536	0.95	136
3-1-2	12.2	44	0	6.64	951	0.51	73
4-1-2	7.9	33	0	13.79	1974	1.17	167
5-1-2	5.1	16	0	9.93	1422	0.75	107
6-1-2	8.0	34	0	4.18	598	0.31	44
7-1-2	9.1	25	0	3.13	448	0.31	44
8-1-2	6.7	25	0	5.17	740	0.69	99
9-1-2	5.2	18	0	4.27	610	1.30	185
10-1-2	20.2	50	0	10.42	1492	3.36	481
11-1-2	16.8	42	0	10.26	1468	0.91	130

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				$g\ kg^{-1}$	$g\ m^{-2}$	$g\ kg^{-1}$	$g\ m^{-2}$
12-1-2	21.8	59	0	15.03	2125	1.27	181
13-1-2	26.3	52	0	12.32	1763	1.06	151
14-1-2	1.6	14	0	7.08	1013	0.64	91
15-1-2	17.0	48	0	10.78	1543	0.91	130
16-1-2	14.5	33	3.0	9.39	1344	1.24	177
17-1-2	2.5	15	0	8.77	1256	0.75	107
18-1-2	10.1	30	0	7.65	1095	0.71	101
19-1-2	2.1	14	0	6.68	956	0.74	105
20-1-2	6.1	22	0	6.87	983	0.64	92
21-1-2	3.5	15	0.3	6.01	860	0.57	81
22-1-2	10.5	39	0.4	5.81	831	0.61	87
23-1-2	3.8	12	2.4	6.02	861	0.89	126
24-1-2	17.5	57	0.5	4.61	659	0.48	69
25-1-2	15.4	43	0	10.30	1474	0.90	128
26-1-2	22.5	46	0.2	12.95	1854	1.11	158
27-1-2	8.0	31	0	4.47	639	0.35	49
28-1-2	21.8	59	0	13.83	1980	1.22	175
29-1-2	14.0	36	0	14.76	2113	1.35	192
30-1-2	14.2	48	0	9.87	1412	0.91	130
31-1-2	5.7	19	0	7.97	1141	0.68	97
32-1-2	9.3	25	0.1	7.62	1090	0.66	95
33-1-2	16.0	46	0	13.63	1952	1.27	182
34-1-2	11.4	34	0	8.09	1157	0.78	110
35-1-2	16.0	64	0	3.99	571	0.31	44
36-1-2	8.5	32	0	4.11	588	0.33	46

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				g kg^{-1}	g m^{-2}	g kg^{-1}	g m^{-2}
37-1-2	7.5	22	0	3.80	544	0.28	40
38-1-2	7.3	32	0	3.60	515	0.27	38
39-1-2	20.5	63	0.04	6.90	988	0.58	82
1-2-1	15.6	34	0	9.96	1351	0.87	117
2-2-1	8.5	13	0	9.43	1278	0.74	100
3-2-1	24.7	54	0	18.99	2574	1.62	218
4-2-1	27.1	49	0.8	15.15	2054	1.26	170
5-2-1	14.0	39	1.7	18.96	2570	1.79	242
6-2-1	11.1	21	0	9.14	1239	0.81	109
7-2-1	2.25	12	2.0	8.95	1213	0.82	110
8-2-1	23.5	53	1.3	13.49	1828	1.27	172
9-2-1	13.2	27	0.6	6.39	865	0.59	79
10-2-1	25.9	50	0	13.09	1774	1.15	155
11-2-1	11.9	40	0	9.21	1248	0.83	111
12-2-1	18.9	39	2.0	9.40	1274	0.90	122
13-2-1	9.5	34	2.0	10.96	1485	1.28	174
14-2-1	21.6	48	5.6	9.60	1301	0.89	120
15-2-1	11.5	40	0	9.92	1344	0.86	116
16-2-1	3.9	14	1.2	8.00	1084	0.81	110
17-2-1	15.5	91	2.0	14.16	1920	1.34	181
18-2-1	22	54	0.8	9.13	1238	0.89	120
19-2-1	28.5	60	0	10.24	1388	0.91	123
20-2-1	4.0	14	0	8.27	1120	0.63	85
21-2-1	4.2	15	0	6.87	931	0.56	75
22-2-1	8.3	19	0.2	5.25	711	0.44	59

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon $g\ kg^{-1}$	Organic Carbon $g\ m^{-2}$	Total Nitrogen $g\ kg^{-1}$	Total Nitrogen $g\ m^{-2}$
23-2-1	7.2	20	0	7.94	1077	0.71	95
24-2-1	28.8	76	4.8	8.52	1155	0.79	106
25-2-1	5.3	11	0	9.18	1244	0.92	124
26-2-1	30.2	63	0	11.76	1594	1.04	141
27-2-1	15.5	49	1.7	9.68	1312	1.10	148
28-2-1	26.2	61	0	9.30	1260	0.90	122
29-2-1	23.0	50	0	6.64	900	0.60	80
30-2-1	6.0	18	0	10.51	1425	0.99	133
31-2-1	3.1	14	0	5.05	684	0.45	60
32-2-1	17.5	40	1.5	11.47	1555	1.29	175
33-2-1	20.8	37	2.2	12.23	1657	1.40	189
34-2-1	30.5	64	1.1	14.47	1961	1.53	207
35-2-1	25.3	52	1.1	12.85	1742	1.35	182
36-2-1	17.5	40	0	6.63	899	0.66	90
37-2-1	21.2	41	1.0	15.55	2107	1.84	248
38-2-1	15.5	27	0.5	7.06	957	0.80	107
39-2-1	7.6	20	0.3	5.67	768	0.59	80
40-2-1	22.5	38	0	9.72	1317	0.92	125
1-2-2	15.6	34	0	7.86	1119	0.58	81
2-2-2	8.5	13	0	6.68	939	0.45	63
3-2-2	24.7	54	0	9.93	1395	0.75	104
4-2-2	27.1	49	0	9.01	1266	0.60	84
5-2-2	14.0	39	0	9.16	1288	0.68	95
6-2-2	11.1	21	0	5.67	797	0.45	62
7-2-2	2.3	12	12.1	1.55	217	1.40	196

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				$g\ kg^{-1}$	$g\ m^{-2}$	$g\ kg^{-1}$	$g\ m^{-2}$
8-2-2	23.5	53	0.23	10.99	1544	0.90	126
9-2-2	13.2	27	0	4.76	669	0.36	50
10-2-2	25.9	50	0.1	5.72	804	0.42	58
11-2-2	11.9	40	0	5.87	824	0.46	64
12-2-2	18.9	39	0	6.63	931	0.53	74
13-2-2	9.5	31	0	6.75	949	0.52	73
14-2-2	21.6	48	1.9	8.19	1150	0.74	104
15-2-2	11.5	40	0	7.40	1040	0.60	84
16-2-2	3.9	14	0.7	7.48	1051	0.66	92
17-2-2	15.5	91	1.1	13.52	1901	1.26	176
18-2-2	22	54	0	12.56	1765	0.96	134
19-2-2	28.5	60	2.4	10.45	1469	1.01	142
20-2-2	4.0	14	0	6.96	978	0.47	65
21-2-2	4.2	15	0.3	6.31	886	0.56	79
22-2-2	8.3	19	0.4	5.35	751	0.51	71
23-2-2	7.2	20	0	6.74	947	0.56	78
24-2-2	28.8	76	4.2	8.77	1233	0.86	120
25-2-2	5.3	11	0	8.85	1243	0.73	102
26-2-2	30.2	63	4.0	10.35	1454	1.33	186
27-2-2	15.5	49	5.7	7.50	1053	0.89	125
28-2-2	26.2	61	0.4	6.92	972	0.62	87
29-2-2	23.0	50	4.5	6.18	869	1.08	151
30-2-2	6.0	18	0	6.83	973	0.61	96
31-2-2	3.1	14	0	4.76	669	0.42	59
32-2-2	14.5	40	1.1	9.58	1346	1.03	144

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				$g\ kg^{-1}$	$g\ m^{-2}$	$g\ kg^{-1}$	$g\ m^{-2}$
33-2-2	20.8	37	0	13.63	1916	1.38	193
34-2-2	30.5	64	0.7	12.53	1761	1.23	172
35-2-2	25.3	52	0	11.35	1595	1.06	148
36-2-2	17.5	40	0	9.34	1312	0.95	133
37-2-2	21.5	41	0.7	11.03	1550	1.27	178
38-2-2	15.5	27	1.0	6.77	951	0.81	113
39-2-2	7.6	20	0.6	5.77	811	0.69	97
40-2-2	22.5	38	0	6.55	920	0.60	84
1-3-1	19.0	50	6.0	11.22	1533	1.23	168
2-3-1	16.6	40	0	16.42	2242	1.32	221
3-3-1	28.5	69	0	26.63	2627	2.60	355
4-3-1	28.6	69	0	21.03	2872	2.01	274
5-3-1	19.1	66	0	19.07	2605	1.58	215
6-3-1	43.9	82	0	24.61	3361	2.23	303
7-3-1	11.5	36	1.1	16.05	2192	1.67	227
8-3-1	19.2	44	0	20.94	2859	1.85	252
9-3-1	46	98	0.7	30.52	4168	2.86	390
10-3-1	29.1	75	0	28.06	3832	2.63	358
11-3-1	6.8	14	0.9	11.78	1609	1.08	147
12-3-1	20.5	52	13.0	10.52	1436	1.02	138
13-3-1	13.1	59	14.0	8.59	1173	0.83	112
14-3-1	31.0	75	1.2	20.98	2866	1.89	257
15-3-1	29.1	71	2.9	19.56	2658	1.95	265
16-3-1	16.8	45	3.8	18.65	2548	1.81	247
17-3-1	24.1	66	3.2	22.72	3102	2.39	326

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				g kg^{-1}	g m^{-2}	g kg^{-1}	g m^{-2}
18-3-1	12.4	29	0	30.37	4149	2.62	357
19-3-1	6.7	15	0	33.50	4575	2.87	392
20-3-1	12.0	39	0	22.81	3115	1.91	260
21-3-1	28.5	57	0	35.16	4702	2.97	404
22-3-1	40.5	94	0	32.07	4380	2.74	374
23-3-1	13.8	53	0	22.27	3041	1.91	260
24-3-1	33.5	80	0.2	26.82	3663	2.44	333
25-3-1	21.0	31	0	26.03	3555	2.20	300
26-3-1	26.8	49	0	27.05	3695	2.28	311
27-3-1	10.0	266	0	23.23	3173	1.93	263
28-3-1	44.0	106	0	36.56	4994	6.26	854
29-3-1	23.2	72	0	29.84	4075	2.48	337
30-3-1	18.2	55	0	22.74	3106	1.81	246
31-3-1	25.2	54	0	33.37	4558	2.66	363
32-3-1	10.5	50	0	32.12	4387	2.68	365
33-3-1	42.5	88	0	29.26	3997	2.41	328
34-3-1	35.3	72	0	45.53	6218	3.91	534
35-3-1	22.8	52	0	22.65	3094	1.97	268
36-3-1	6.1	10	1.2	23.36	3190	2.18	298
37-3-1	39.5	93	2.0	31.61	4317	3.11	425
38-3-1	9.0	17	0	16.21	2214	1.32	180
39-3-1	8.8	18	0	11.55	1577	0.97	131
1-3-2	19.0	50	3.6	8.25	1194	0.74	107
2-3-2	16.6	40	0	11.43	1656	1.03	148
3-3-2	28.5	69	0	13.29	1925	1.15	165

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				$g\ kg^{-1}$	$g\ m^{-2}$	$g\ kg^{-1}$	$g\ m^{-2}$
4-3-2	28.6	69	0	11.55	1673	0.96	138
5-3-2	19.1	66	0	15.91	2305	1.00	144
6-3-2	43.9	92	0	19.33	2801	1.49	216
7-3-2	11.5	36	0	9.06	1312	0.82	118
8-3-2	19.2	44	0	17.85	2576	1.23	177
9-3-2	46.0	98	0.8	21.07	3053	1.56	225
10-3-2	29.1	75	0	18.60	2694	1.40	202
11-3-2	6.8	14	0.3	10.84	1570	0.88	127
12-3-2	20.5	52	10.8	11.15	1615	1.13	163
13-3-2	13.1	59	13.6	8.09	1172	0.75	108
14-3-2	31.0	75	1.1	19.26	2790	1.67	241
15-3-2	29.1	71	4.2	16.08	2330	1.63	235
16-3-2	16.8	45	3.9	13.11	1898	1.32	191
17-3-2	24.1	66	3.2	18.23	2641	1.77	256
18-3-2	12.4	29	0	24.90	3607	1.96	283
19-3-2	6.7	15	0.5	24.90	3608	1.93	279
20--2	12.0	39	0	20.29	2940	1.43	206
21-3-2	28.5	57	0	24.41	3537	1.81	261
22-3-2	40.5	94	0	25.01	3624	1.98	286
23-3-2	13.8	52	0	18.21	2638	1.37	198
24-3-2	33.5	80	0	21.08	3053	1.64	237
25-3-2	21.0	31	0	20.88	3026	1.51	218
26-3-2	26.8	49	0	19.56	2834	1.46	211
27-3-2	10.0	26	0	18.45	2817	1.43	207
28-3-2	44.0	106	0	33.41	4841	2.68	388

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				g kg^{-1}	g m^{-2}	g kg^{-1}	g m^{-2}
29-3-2	23.2	72	0	27.73	4017	1.94	281
30-3-2	18.2	55	0	21.73	3147	1.55	224
31-3-2	25.2	54	0	31.38	4547	20.5	296
32-3-2	10.5	50	0	30.48	4416	2.23	323
33-3-2	42.5	88	0	33.91	4913	2.52	365
34-3-2	35.3	72	0	46.46	6731	3.56	515
35-3-2	22.8	52	0	24.03	3482	1.97	285
36-3-2	6.1	10	1.1	21.06	3051	1.75	253
37-3-2	39.5	93	2.0	28.54	4135	2.72	393
38-3-2	9.0	17	0	13.93	2017	1.16	168
39-3-2	8.8	18	0	13.25	1920	1.09	157
1-4-1	0	0	0	7.63	1046	0.76	104
2-4-1	0	0	0	8.50	1165	0.80	110
3-4-1	0	0	0	8.85	1213	0.73	100
4-4-1	0	0	0.4	4.63	635	0.42	57
5-4-1	0	0	0	6.23	854	0.57	78
6-4-1	0	0	0	8.93	1224	0.98	135
7-4-1	0	0	0	7.40	1015	0.67	92
8-4-1	0	0	0	7.95	1091	0.71	96
9-4-1	0	0	0	7.47	1024	0.69	94
10-4-1	0	0	0	7.97	1093	0.73	99
11-4-1	0	0	0	7.61	1044	0.69	94
12-4-1	0	0	0	8.29	1136	0.73	100
13-4-1	0	0	0	11.46	1572	0.88	120
14-4-1	0	0	0	11.18	1533	0.88	120

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				$g\ kg^{-1}$	$g\ m^{-2}$	$g\ kg^{-1}$	$g\ m^{-2}$
15-4-1	0	0	0.7	11.55	1585	0.99	135
16-4-1	0	0	0	4.78	655	0.42	58
17-4-1	0	0	0	5.53	758	0.44	60
18-4-1	0	0	0	6.13	840	0.48	66
19-4-1	0	0	0.3	5.99	821	0.52	70
20-4-1	0	0	0	5.74	787	0.45	62
21-4-1	0	0	0	5.49	739	0.49	67
22-4-1	0	0	0.3	7.36	1009	0.70	96
23-4-1	0	0	0	7.17	983	0.59	81
24-4-1	0	0	0	7.45	1022	0.66	90
25-4-1	0	0	0	4.48	614	0.33	45
26-4-1	0	0	0	5.61	769	0.39	53
27-4-1	0	0	0	4.63	635	0.35	48
28-4-1	0	0	0	4.93	675	0.35	47
29-4-1	0	0	0	4.64	636	0.32	44
30-4-1	0	0	0	4.68	641	0.32	44
31-4-1	0	0	0	4.49	615	0.31	41
32-4-1	0	0	0	5.17	695	0.33	44
33-4-1	0	0	0	5.28	723	0.35	48
34-4-1	0	0	0	8.30	1138	6.41	87
35-4-1	0	0	0	5.29	725	0.41	55
36-4-1	0	0	0	7.86	1078	0.64	88
37-4-1	0	0	0	6.02	825	0.43	58
38-4-1	0	0	0	8.65	1186	0.67	91
39-4-1	0	0	0	7.69	1013	0.52	70

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon g kg^{-1}	Organic Carbon g m^{-2}	Total Nitrogen g kg^{-1}	Total Nitrogen g m^{-2}
1-4-2	0	0	0	7.79	1055	0.69	92
2-4-2	0	0	0	8.27	1121	0.68	91
3-4-2	0	0	0	7.20	976	0.66	89
4-4-2	0	0	0	5.29	717	0.43	58
5-4-2	0	0	0	6.19	839	0.51	69
6-4-2	0	0	0	7.43	1007	0.63	85
7-4-2	0	0	0	7.15	970	0.60	81
8-4-2	0	0	0	7.73	1048	0.63	85
9-4-2	0	0	0	7.92	1073	0.67	91
10-4-2	0	0	0	7.57	1012	0.61	83
11-4-2	0	0	0	7.24	981	0.57	77
12-4-2	0	0	0	7.08	960	0.55	74
13-4-2	0	0	0	10.81	1465	0.74	100
14-4-2	0	0	0	10.47	1418	0.87	117
15-4-2	0	0	0	11.28	1529	0.88	119
16-4-2	0	0	0	4.04	547	0.30	40
17-4-2	0	0	0	4.65	630	0.34	46
18-4-2	0	0	0.3	4.51	611	0.34	46
19-4-2	0	0	0	4.74	642	0.34	46
20-4-2	0	0	0	4.69	635	0.39	52
21-4-2	0	0	0	4.14	561	0.34	45
22-4-2	0	0	0	7.10	963	0.62	83
23-4-2	0	0	0	7.01	950	0.58	79
24-4-2	0	0	0	7.12	965	0.58	78
25-4-2	0	0	0	4.70	637	0.33	45

APPENDIX 2. Soil nutrient concentrations and mass per unit area. (continued)

Sample Code	Tree Diameter (cm)	Tree Age (yr)	$CaCO_3$ equivalent	Organic Carbon		Total Nitrogen	
				g kg^{-1}	g m^{-2}	g kg^{-1}	g m^{-2}
26-4-2	0	0	1.0	5.22	707	0.40	54
27-4-2	0	0	0	4.05	549	0.25	33
28-4-2	0	0	0	4.62	626	0.31	42
29-4-2	0	0	0	4.40	597	0.24	32
30-4-2	0	0	0	4.44	602	0.29	39
31-4-2	0	0	0	3.84	521	0.22	29
32-4-2	0	0	0	4.22	572	0.33	44
33-4-2	0	0	0	5.55	751	0.32	43
34-4-2	0	0	0	7.97	1080	5.34	724
35-4-2	0	0	0	5.15	698	0.34	46
36-4-2	0	0	0	7.34	995	0.54	73
37-4-2	0	0	0	5.54	751	0.38	51
38-4-2	0	0	0	6.80	921	0.44	58
39-4-2	0	0	0	6.93	939	0.42	56