

Conversion of deciduous forest to silvopasture produces soil properties indicative of rapid transition to improved pasture

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Abstract Differences in soil properties between forests and pastures have been well documented in the literature, especially under coniferous forests. However, since nearly all of these reports have been time-point comparisons, utilizing long-term paired-sites, properties of transitional states and time of their appearance can only be inferred at present. In this study, a deciduous forest ecosystem was converted to a silvopasture ecosystem by tree thinning, fertilization, and sheep incorporation of seed and forest litter. After 2 years, topsoil (0–15 cm) physico-chemical properties, particularly P fractions, and phosphatases were monitored over the growing season in these ecosystems, and a nearby pasture ecosystem. Initially, before spring vegetative growth, differences were found for pH, exchangeable cations and soil moisture, most of which could be explained by management history. Compared to forest, organic-C (C_o) and organic-N (N_o) concentrations were reduced in silvopasture by 17 and 9%, respectively, indicative of substantial litter decomposition. Most values for all these physico-chemical properties for silvopasture were intermediate between forest and pasture, and generally remained so throughout the growing season. Initial total P (TP_i), organic-P (TP_o) and

inorganic-P (TP_i) concentrations were generally as anticipated for the forest and pasture. Silvopasture, however, had 36 and 23% greater TP_o than forest and pasture, respectively, presumably due to fertilizer-P immobilization induced by incorporation of forest litter. Total P components remained essentially constant over the growing season in all ecosystems, with the exception of pasture, likely due to high forage TP_i uptake. Bray I-extractable-organic-P (BrP_o) and bicarbonate-extractable-organic-P (BiP_o) concentrations, although consistently highest in the forest and silvopasture soils, were not reflective of the increase in TP_o under silvopasture. Acid phosphatase (PMEac) activities were highest in spring in all the ecosystems, then gradually declined to typically 25–50% initial activities. Alkaline phosphatase (PMEal) activities showed a broadly-similar pattern, with exception of forest and silvopasture soils, which exhibited low activities throughout the season. For the entire data set, PMEac and PMEal activities were poorly correlated with TP_i , BrP_i , and BiP_i . These results demonstrate that conversion of forest to silvopasture results in soil changes indicative of its rapid transition to pasture and that an increased P_o reservoir results that should be taken into account in fertilizer-P recommendations for temperate silvopastures.

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Introduction

Differences in temperate soil chemical properties, especially total organic-C (C_o), total organic-N (N_o) and total organic-P (P_o), and biological fertility (microbial biomass, soil respiration, soil enzyme activity, etc.), upon conversion of pastures to coniferous forests, have been well documented, particularly in New Zealand and Australia. However, there is little such literature relevant to reverse conversions, especially from deciduous forests. What exists is invariably of paired-site (side-by-side) comparisons, providing often contradictory results.

For example, Jug et al. (1999) in Germany and Sparling et al. (1994) in New Zealand reported lower C_o and N_o concentrations under deciduous forest than under grasslands. However, Martens et al. (2003) and Conant et al. (2004) in the USA reported just the opposite results, as did Ellert and Gregorich (1996) in Canada and Noble et al. (1999) in Australia. For P_o , higher concentrations have typically been reported under pasture than under forest in Denmark (Magid 1993), Germany (Guggenberger et al. 1996) and Australia (Ellert and Gregorich 1996). These contradictory results for C_o and N_o , and presumably for P_o (and biological fertility), likely have a methodological explanation. Perusal of the soil sampling methods used by these authors indicate that significantly different regimes were often used, viz., from little to complete removal of forest litter (O_i , O_e , and O_a horizons).

More particular to the present work, no literature exists concerning the changes in these major soil organic components (C_o , N_o , P_o) upon conversion of deciduous forest to silvopasture, even from paired-site comparisons, to the best of our knowledge.

In addition to our interest in determining soil C_o , N_o and P_o concentrations relatively soon after conversion of forest to silvopasture, and their relationship to those in pasture, we were also interested in determining if they, and other properties, changed over the growing season. Because of the well-known slow rate of accumulation or disappearance of soil C_o and N_o in the absence of dramatic land-use alterations, we anticipated little seasonal change in these properties. However, because of the more labile nature of certain P_o fractions and microbial biomass (Chen et al. 2003; Perrot et al. 1992; Tate et al. 1991), and of course, P_i (plant-available-P or PO_4 ions), we anticipated that seasonal

effects would be found for them, and for soil enzymes involved in P_o cycling (Harrison and Pearce 1979; Rastin et al. 1988; Ross et al. 1995; Turner et al. 2002).

The overall objective of this work was to obtain baseline data, using a paired-site design, on the changes in soil properties, especially P cycle components, wrought by conversion of a temperate forest ecosystem to a silvopasture ecosystem. More specifically, our objectives were to determine if, after 2 years of conversion and before vegetative growth commenced, differences existed in topsoil C_o , N_o and various P_o fractions, as well as phosphatase activities, between these two ecosystems. Using an additional, adjacent site for comparison, we also sought to determine if the silvopasture ecosystem represented a continuum toward an improved pasture ecosystem. Further, we endeavored to determine if changes in these major organic and enzyme components, and other soil physico-chemical properties, occurred over the growing season. Finally, we sought correlations between soil phosphatases and plant-available-P.

Materials and methods

Site selection and soil description

Sites were selected at the USDA-ARS-AFSRC farm, near Bragg, West Virginia, USA (37°47'45" N latitude, 80°58'19" W longitude; altitude, 884 m) on the basis of optimally representing different ecosystems, i.e., forest, silvopasture and pasture, while retaining similarities in soil type and topography (slope, aspect, and altitude), as well as proximity. Because all these conditions could not be met, we chose vegetative type and history as the primary criteria for selection, while minimally compromising on soil type and topography. As a result, sites on gentle slopes were chosen, with minimal distance (<75 m) and altitude differences between any pair. Aspects for the forest, silvopasture and pasture were N6°W, N30°W and S58°W, respectively. The silvopasture was located on a Buchanan (fine-loamy, mixed, mesic, Aquic Fragiudult)-Ernest (fine-loamy, mixed, semiactive, mesic Aquic Fragiudult) soil, whereas the forest and pasture were located on a Gilpin (fine-loamy, mixed, semiactive, mesic Typic Hapludult)-Lily (fine-loamy, siliceous, mesic Typic Hapludult) soil.

Ecosystem management history

The forest (mixed hardwood) resulted from natural succession of cut-over timberland or abandoned pasture for ~60 years, during which time it received no amendments, as far as we are aware. It consisted of a 3rd-growth stand of mature, mixed hardwoods, dominated by white oak (*Quercus alba* L.), with minor amounts of sugar maple (*Acer saccharum* L.) and tulip poplar (*Liriodendron tulipifera* L.). Understory plants were completely absent. The silvopasture (mixed hardwood/grass/legume) was derived from the forest ecosystem, described above, in the spring of 2001. Trees were thinned to allow ~50% full sunlight, followed by sheep trampling to reduce the forest litter and prepare a seedbed. Lime (6.5 mg ha⁻¹ as dolomite) and P (90 kg ha⁻¹ as 0-46-0) were then surface-applied, followed by seeding with Benchmark orchardgrass (*Dactylis glomerata* L.), BG34 perennial ryegrass (*Lolium perenne* L.) and Huia white clover (*Trifolium repens* L.). Sheep were briefly re-introduced to incorporate seeds, then used for 2–3 grazings during the 2001 growing season, and each growing season thereafter. Starter amounts of fertilizer were also surface-applied on 25 May 2002 (34 kg ha⁻¹ as 19-19-19) and 10 July 2003 (34 kg ha⁻¹ as 34-0-0). Vegetation consisted of approximately 90% perennial ryegrass, 5% orchardgrass and 5% white clover. The pasture (improved pasture) was located on an existing pasture of predominantly orchardgrass and native white clover that had been well-managed for ~40 years, receiving NPK (56 kg ha⁻¹ as 10-20-20), annually, and lime (6.7 mg ha⁻¹) every 6–7 years. In the spring of 2000, it was herbicided with Roundup (2.35 l ha⁻¹) and fallowed. The following spring, the site was renovated by overseeding with Benchmark orchardgrass and Huia white clover, followed by surface application of starter fertilizer on 6 August 2001 (34 kg NPK ha⁻¹ as 19-19-19), 14 May 2002 (34 kg NPK ha⁻¹ as 19-19-19) and 13 Jun 2003 (34 kg N ha⁻¹ as 34-0-0). Forage removal consisted solely of sheep grazing during the growing seasons, with seed heads mowed once each growing season. Vegetation consisted of approximately 95% orchardgrass and 5% white clover.

Soil collection, processing and storage

Topsoil (0–15 cm layer) samples were collected from each ecosystem, initially, before vegetative

growth in the spring (8 April 2003/DOY 98) and at 6 week intervals (140, 182, 224, 266 DOY) over the growing season (last sampling on 23 September 2003/DOY 266). All litter horizons were retained before samples were taken from the forest, and the other sites, using an Oakfield soil corer (~2-cm diam.). Soil samples (10–12 cores/sampling) were randomly taken within mini-plots (2 × 2 m) at each site, pooled by site, placed on ice and immediately returned to the laboratory. They were then sieved through stainless steel 4 mm, then 2 mm, screens. All remaining visible woody debris, roots, stones, and invertebrates were removed during sieving. Sub-samples of processed, fresh (never air-dried; held 5°C, <2 d) soil were weighed and oven-dried at 105°C, overnight, to determine soil moisture. Approximately 50 g (oven-dried basis, odb) of the remaining fresh soil was air-dried for later chemical analyses.

Soil physical and chemical analyses

Bulk density was determined from pooled soil core volumes and oven-dry masses. Air-dried soil was used in the determination of soil pH_w (1:1; m/v, soil to water, 30 min equilibration), ammonium acetate exchangeable cations, and potassium chloride exchangeable acidity and aluminum, by standard chemical procedures.

Soil total organic-C (C_o) and total organic-N, essentially TC and TN in these acidic and low fertility soils, was analyzed after combustion to CO₂ and N₂, using a Model PDZ Europa ANCA unit in line with their 20-20 Isotope Ratio Spectrometer (Sercon, Ltd., Crewe, Cheshire, UK).

Whole soil total P (TP_t) and total inorganic-P (TP_i) were determined by use of combusted (550° for 1 h) and non-combusted soils, respectively (Kuo 1996). Samples (1.0 g, odb) were weighed into 50-ml tubes and 25 ml H₂SO₄ (0.5 M) added, followed by mixing at 200 rpm for 16 h at room temperature. Tubes were centrifuged, followed by recovery of extracts after filtration through Whatman #42 paper. Extracts were analyzed for TP_t and TP_i by spectrophotometry at 610 nm using a Model Cary 100 Bio UV-Visible Spectrometer (Varian, Walnut Creek, California, USA) by the malachite green method (Irving and McLaughlin 1990). Total organic-P (TP_o) was determined by difference.

Bicarbonate-extractable-P was determined by use of 1.5 g (odb) soil, weighed into 50-ml tubes (Kuo 1996). Into each tube, 30 ml of 0.5 M NaHCO_3 (adjusted to pH 8.5) was added, followed by mixing at 200 rpm for 30 min at room temperature and recovery of extracts after filtration through Whatman #42 paper. Sub-samples (5 ml) of extracts were neutralized with HCl (5 M) until cessation of bubbling and brought to 30-ml volume. Extracts were analyzed for total bicarbonate-extractable-P (BiP_t) by emission spectroscopy using a Model JY 46P Inductively Coupled Plasma Emission Spectrometer (Instruments S.A., Jobin Yvon Emission Division, Edison, New Jersey, USA), while they were analyzed for bicarbonate-extractable-inorganic-P (BiP_i) by spectrophotometry, using the malachite green method described above for TP_i . Bicarbonate-extractable-organic-P (BiP_o) was determined by difference.

Bray I-extractable-P was determined by use of 2.0 g (odb) soil, weighed into 125-ml flasks (Kuo 1996). Into each flask, 20 ml of Bray I solution (pH 2.6) was added, followed by mixing at 200 rpm for 5 min at room temperature and recovery of extracts after filtration through Whatman #42 paper. Extracts were analyzed for total Bray I-extractable-P (BrP_t) by emission spectroscopy as described above for BiP_t , while they were analyzed for Bray I-extractable-inorganic-P (BrP_i) by spectrophotometry, using the malachite green method as described above for TP_i . Bray I-extractable-organic-P (BrP_o) was determined by difference.

Soil phosphatase analyses

Acid phosphomonoesterase (PMEac ; EC 3.1.3.2) and alkaline phosphomonoesterase (PMEal ; EC 3.1.3.1) were determined by use of fresh soils as slurries (Tabatabai 1994). Into 50-ml flasks, 1.0 g (odb) fresh soils were weighed, followed by 4.0 ml of modified universal buffer (adjusted to pH 6.5 for PMEac or pH 11.0 for PMEal), 1.0 ml *p*-nitrophenyl phosphate (also, appropriately pH adjusted), and 0.2 ml toluene. Flasks were stoppered, well-mixed by hand and statically incubated at 37°C for 1 h. Enzymatic reactions were stopped by addition of 1.0 ml of 0.5 M CaCl_2 and 4.0 ml of 0.5 M NaOH to each flask. Slurries were filtered through Whatman #42 paper and filtrates analyzed for yellow color intensity by spectrophotometry at 420 nm, using a Model DU 640 Spectrophotometer (Beckman Instruments, Inc., Fullerton, California, USA).

Statistical analyses

Mean separation, correlations and regression analyses were done by General Linear Model (GLM) procedures in SAS System for Windows, 2001, Release 8.02 (SAS Institute, Inc., Cary, North Carolina, USA). Unless otherwise stated, significant differences are at 5% ($P \leq 0.05$) level.

Results

Ecosystem site comparability

Because of the difficulties that comparative ecosystem-level studies present to designing statistically robust experiments, simply matching soils as closely as possible is often the only alternative. Although statistically limited, this strategy, coupled with repeated sampling from the same square area, was employed in the present study.

Despite a concerted effort to match soils to the series level, with the requisite vegetation, we were unable to do so. We were, however, successful in locating soils that were identical to the suborder level, with all of them being classified as Udic Ultisols. Although the forest and pasture were on a Lily-Gilpin soil, whereas the silvopasture was on a Buchanan-Ernest soil, both of these soils have the same parental material and differ only in layers beyond our sampling depth of 0–15 cm. Elevations varied by less than 1%, while slopes ranged from only 13–18%.

Given these similarities, we suggest that it is unlikely that the relatively minor mineralogical and topographical differences in the sites were of much consequence. Thus, it seems reasonable to expect that management strategy, and its resultant effect on plant productivity and species diversity, was the primary factor responsible for any changes in soil biogeochemical processes among our ecosystems, rather than different soil and/or topographic factors.

Soil physico-chemical properties (initial differences)

Selected soil physico-chemical properties for our initial sampling of the ecosystems in the spring (8 April 2003; DOY 98) are presented in Table 1.

Table 1 Selected physico-chemical properties of topsoils at initial sampling (8 April 2003) from various ecosystems^A

Ecosystem	Soil pH	Exchangeable cations					Base sat. ^B (%)	Soil moisture (g 100 g ⁻¹)	Bulk density (g cm ⁻³)	C _o (g kg ⁻¹)	N _o (g kg ⁻¹)	C _o /N _o (g kg ⁻¹)
		Ca (cmol kg ⁻¹)	Mg (cmol kg ⁻¹)	K (cmol kg ⁻¹)	Al (cmol kg ⁻¹)	H (cmol kg ⁻¹)						
Forest	4.7	0.33 c ^C	0.081 c	0.201 c	1.71 a	0.60 a	21.0 c	30.9 b	0.86	42.7 a	2.61 a	16.3 a
Silvopasture	5.5	1.73 b	1.10 a	0.621 a	0.33 b	0.19 b	86.8 b	36.3 a	0.82	35.5 b	2.37 b	15.0 ab
Pasture	6.8	3.18 a	1.05 ab	0.501 b	0.02 c	0.06 c	98.3 a	27.3 c	1.01	27.1 c	2.06 c	13.2 b

^A Soil samples taken from 0- to 15-cm soil layer; all values given on an oven-dry (105°C) basis^B CEC = (Ca + Mg + K + Na + Al + H); % base saturation = [(Ca + Mg + K + Na)/CEC] × 100; all Na concentrations ≤0.01 cmol kg⁻¹^C Within ecosystem, means followed by the same letter are not significantly different ($P > 0.05$) as determined by the Student–Newman–Keuls test

The forest was the most acidic (lowest pH and highest exchangeable Al and H), having never received any lime amendments. The decreased acidity of the silvopasture (pH 5.5), compared to the forest from which it was derived, obviously reflected its first and only liming. The further decreased acidity (pH 6.8) of the pasture reflected its accumulative (every 6–7 years) liming over ~40 years, possibly combined with a lack of plant residue inputs due to forage removal by grazing.

The exchangeable cation concentrations likewise reflected the particular ecosystem management history. The concentration of Ca was lower in the forest than in the silvopasture and pasture, with the silvopasture being of intermediate concentration. This lime rate effect was also generally evident by the Mg concentrations and base saturation percentages, and with the consistently and inversely related Al and H concentrations. The CEC was significantly different in all ecosystems, consistently increasing from forest to silvopasture to pasture, likely explained by the pH increase.

Soil moisture was essentially the same in the forest and pasture at this initial sampling, but substantially increased in the silvopasture. Bulk density (D_b) was essentially the same for the forest and silvopasture. The increased D_b of the pasture was expected, since it had been intensely managed for grazing for ~40 years, whereas the other sites had received little or no management.

The forest had the highest C_o concentration (42.7 g kg⁻¹). The silvopasture, despite incorporation of all the forest litter horizons, showed a C_o reduction of 17%. At a concentration of 35.5 g C_o kg⁻¹, it still exceeded that for pasture (27.1 g C_o kg⁻¹) by 31%. The N_o concentrations, with a 9% decrease from forest to silvopasture, showed the same ecosystem order of reduction, but to a lesser extent, resulting in a slight N enrichment (lower C_o – N_o ratio) from forest and silvopasture to pasture.

Soil physico-chemical properties (growing season changes)

Considering the non-phosphorus chemical and physical properties, few agronomically-important changes were found over the growing season, when the data were analyzed using linear regression statistics.

From the initial sampling, soil pH, bulk density, exchangeable H, and base saturation remained constant in all ecosystems over the growing season (data not shown). Although reductions in Ca concentrations were found in the silvopasture and pasture, none exceeded 18% (Fig. 1a). No changes in Mg concentrations were found, except under pasture, where it decreased by 13% (Fig. 1b). Similarly, no changes in K concentrations were found, except under pasture, where its decrease was

most evident in the spring (Fig. 1c). The Al concentrations, persistently highest in the forest soil, showed no temporal effects in any of the ecosystems (Fig. 1d).

Soil moisture temporarily declined during mid-summer (July) in all ecosystems, with the highest values being consistently found under silvopasture (Fig. 2a). As anticipated, no changes in concentrations of C_o and N_o , nor their ratio (Fig. 2b–d), were found over the growing season.

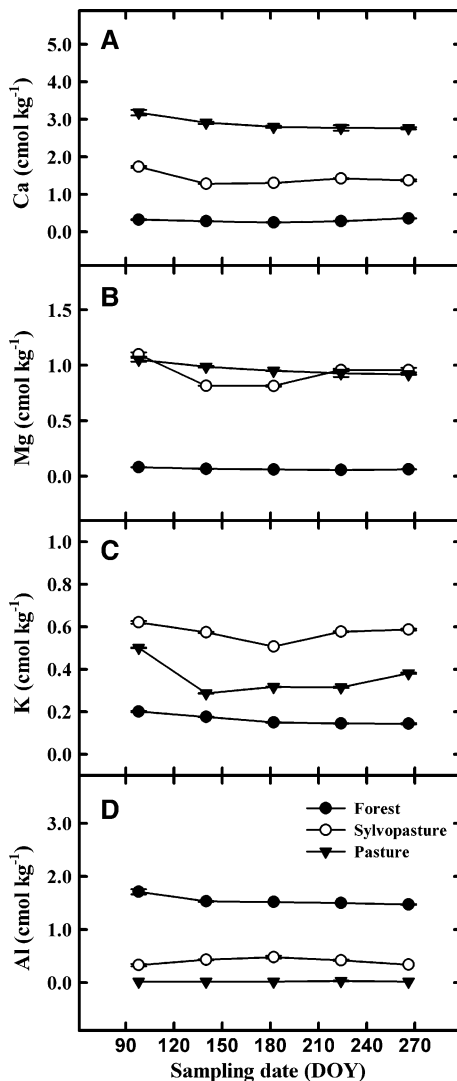


Fig. 1 Changes in ecosystem topsoil exchangeable Ca, Mg, K and Al over the growing season. Vertical bars represent ± 1 SE of mean ($n = 3$); bars not visible are concealed by symbols

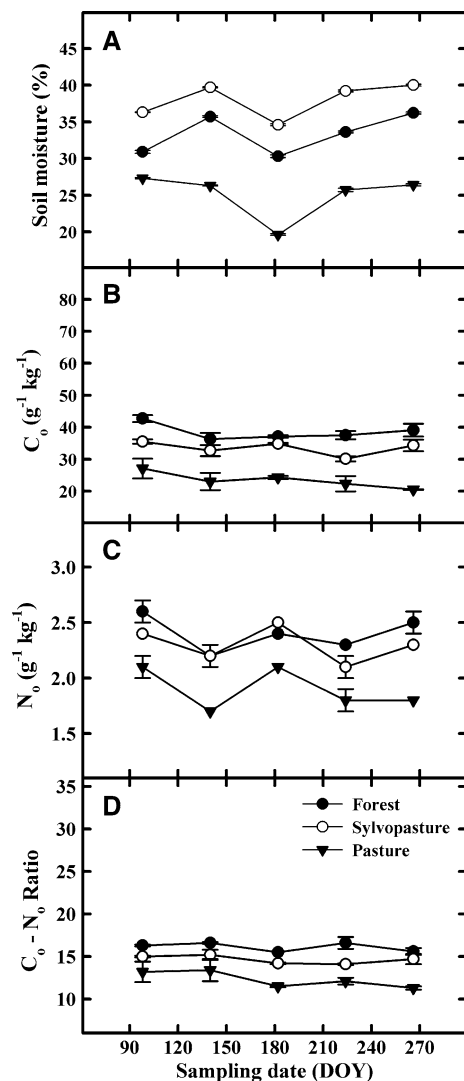


Fig. 2 Changes in ecosystem topsoil soil moisture, total organic-C (C_o), total organic-N (N_o) and $C_o - N_o$ ratio over the growing season. Vertical bars represent ± 1 SE of mean ($n = 3$); bars not visible are concealed by symbols

Soil phosphorus fractions

For our initial sampling, whole soil P concentrations also generally reflected the particular management history of the ecosystems (Table 2). The forest, having never received fertilizer-P, had the lowest concentrations of total inorganic-P (TP_i) and total organic-P (TP_o), and hence, total P (TP_t). However, it had the highest percentage of TP_o (85%) of all the ecosystems. The pasture had a TP_t concentration 28% greater than the forest. The silvopasture had the highest concentration of TP_t , as a consequence of higher concentrations of both TP_i and TP_o . The TP_o concentration in the silvopasture was increased by 36% over that for the forest, and exceeded that for the pasture by 23%. In summary, the concentrations of all whole soil TP fractions at this initial sampling were increased (although there was no significant difference in TP_o between the forest and pasture) in the order: forest < pasture < silvopasture.

Over the course of the experiment, TP_i and TP_o concentrations remained essentially constant in all the ecosystems (Fig. 3a). Although there appeared to be a small decrease in TP_i in the silvopasture and pasture, as would be expected, regression analyses revealed a significant difference only for the pasture. No changes for TP_o , nor TP_t , were found for any of the ecosystems.

The total bicarbonate-extractable-P (BiP_t) and total Bray I-extractable-P (BrP_t) concentrations at our initial sampling ranged from 1 to 5% and 3 to 8%, respectively, of TP_t (Table 2), which are within the ranges typically reported. As anticipated, concentrations of BrP_t and BrP_i were consistently higher than for BiP_t and BiP_i by about 2-times, likely because the Bray-I extractant solubilizes Fe and Al phosphates to some extent. The forest had much lower BrP_i and BiP_i concentrations than either the silvopasture or pasture. The highest BrP_o and BiP_o concentrations were consistently found in the forest and silvopasture, and both differed from the pasture in the case of the Bray-I results.

The concentrations of BrP_i and BiP_i were dramatically decreased between the first two samplings under pasture, and gradually decreased over the growing season under silvopasture (Fig. 3b and c). The BrP_o and BiP_o concentrations in each ecosystem showed broadly-similar patterns over the growing season (Fig. 3b and c). Regression analyses revealed

Table 2 Phosphorus fractions in topsoils at initial sampling (8 April 2003) from various ecosystems^A

Ecosystem	Phosphorus fraction					
	Whole soil ^B			Bicarbonate extractable ^B		
	TP_t (mg kg ⁻¹)	TP_i (mg kg ⁻¹)	TP_o (mg kg ⁻¹)	BiP_t (mg kg ⁻¹)	BiP_i (mg kg ⁻¹)	BiP_o (mg kg ⁻¹)
Forest	368 c ^C	55 c	313 b (85.0) ^D	13.7 b	4.3 c	9.4 a (68.4) ^D
Silvopasture	596 a	171 a	425 a (71.3)	28.1 a	18.4 a	9.7 a (34.4)
Pasture	470 b	125 b	345 b (73.4)	16.8 b	13.9 b	3.0 a (17.6)
				BrP_t (mg kg ⁻¹)	BrP_i (mg kg ⁻¹)	BrP_o (mg kg ⁻¹)
Forest				22.3 c	6.1 c	16.2 a (72.7) ^D
Silvopasture				34.2 b	27.7 b	6.5 b (19.1)
Pasture				38.2 a	35.8 a	2.5 c (6.4)

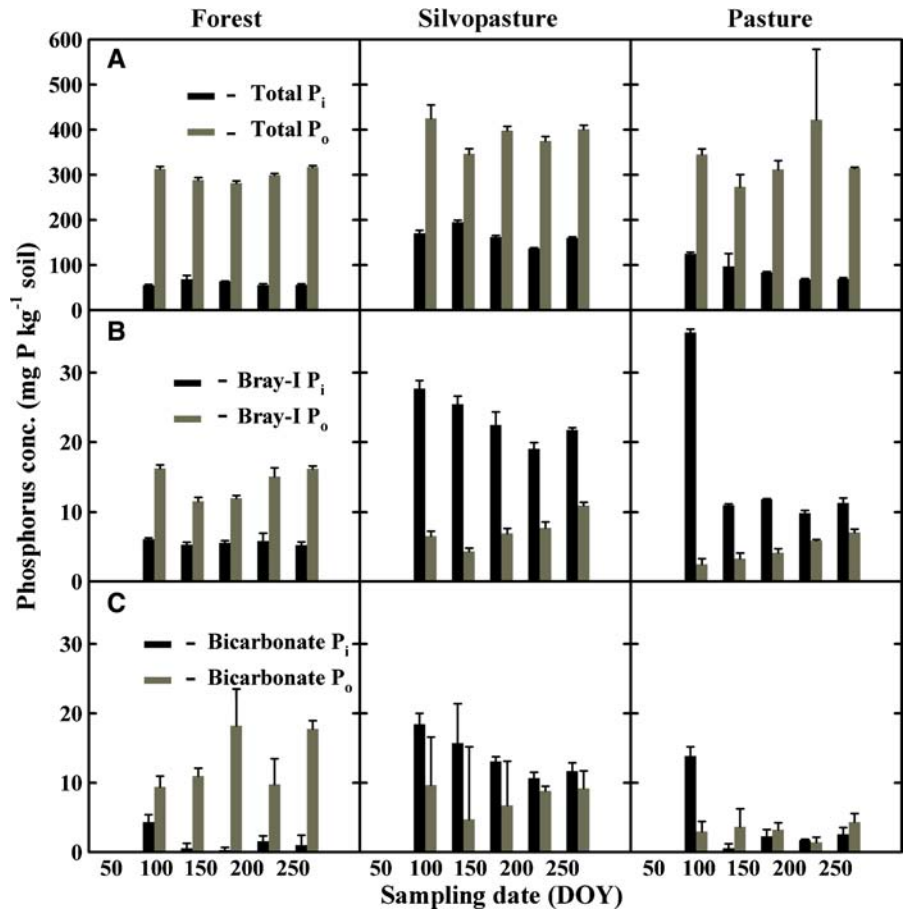
^A Soil samples taken from 0- to 15-cm soil layer; all values given on an oven-dry (105°C) basis

^B P_o , organic-P; P_i , inorganic-P; P_t , total P

^C Within ecosystem, means followed by the same letter are not significantly different ($P > 0.05$) as determined by the Student–Newman–Keuls test

^D Percent organic-P (P_o)

Fig. 3 Changes in ecosystem topsoil phosphorus fractions [total inorganic- and organic-P (TP_i and TP_o), Bray I-extractable-inorganic- and organic-P (BrP_i and BrP_o), bicarbonate-extractable-inorganic- and organic-P (BrP_i and BrP_o)] over the growing season. Vertical bars represent ± 1 SE of mean ($n = 3$); bars not visible are concealed by symbols



significant increases in BrP_o by at least 2-times in the silvopasture and pasture, but not the forest. No such increases were found for BiP_o . Averaging over all samplings, both the BrP_o and BiP_o concentrations decreased in the order: forest > silvopasture > pasture, again demonstrating the intermediate position of the silvopasture ecosystem. Percentages of P_o of the total extractable-P ($\%P_o$), either for the bicarbonate or Bray-I extracts, changed little over the growing season from the initial values, except as noted above for the pasture during the spring (Table 2; Fig. 3b and c).

Soil phosphatase activity and plant-available-P

The activities of acid phosphatase (PMEac) and alkaline phosphatase (PMEal) were oppositely related to the soil source from which the initial sampling was done (Fig. 4, DOY 98).

The highest PMEac activity was found in the forest, whereas the lowest activity was found in the

pasture soil. PMEac activity for the silvopasture soil was thus intermediate between the forest (15% lower) and pasture (138% greater). PMEac activity was highly correlated with C_o ($R^2 = 0.81$, $P \leq 0.001$) and BrP_i ($R^2 = -0.69$, $P \leq 0.01$). However, it should be noted that PMEac and TP_i or BiP_i were poorly correlated ($R^2 < -0.15$, $P > 0.05$) at this time. The highest PMEal activity was found in the pasture, whereas the lowest activities were found in the forest and silvopasture (~ 10 - to 20 -times difference). PMEal activity in all the ecosystems was also highly correlated with C_o ($R^2 = -0.67$, $P \leq 0.01$) and BrP_i ($R^2 = 0.56$, $P \leq 0.05$) at this initial sampling. As for PMEac, PMEal was poorly correlated ($R^2 < 0.07$, $P > 0.05$) with TP_i or BiP_i at this sampling time.

Over the course of the experiment, the activity of PMEac was highest in the spring for all ecosystems, then gradually declined to ~ 25 – 50% of the initial activities (Fig. 4a). PMEal activity showed a broadly-similar

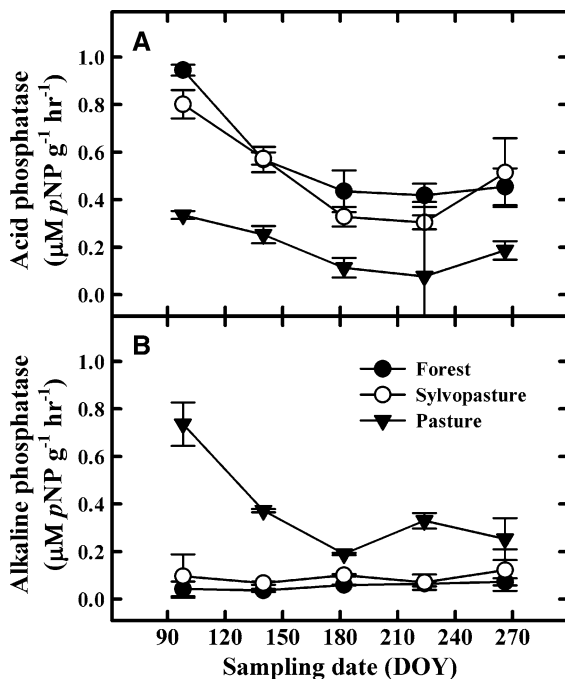


Fig. 4 Changes in ecosystem topsoil acid and alkaline phosphomonoesterase (PME) activity over the growing season. Vertical bars represent ± 1 SE of mean ($n = 3$); bars not visible are concealed by symbols

pattern for the pasture, while activities for the forest and silvopasture were consistently low over the entire growing season (Fig. 4b). Again demonstrating the intermediate position of the silvopasture, the activities were, in general, in the order: forest > silvopasture > pasture for PMEac and pasture > silvopasture = forest for PMEal. For the entire growing season, the correlation coefficient (R^2) for PMEac and C_o decreased to 0.41 ($P \leq 0.01$), while that for PMEal and C_o decreased to -0.42 ($P \leq 0.01$), from the initial sampling correlation coefficients. For the soil total, bicarbonate-extractable, and Bray I-extractable P_i fractions, correlations with PMEac and PMEal activities never exceeded $R^2 = 0.08$ ($P > 0.05$).

Discussion

Most of the physico-chemical differences found between the forest and silvopasture, which essentially persisted over the growing season, could be explained by some aspect of the management history. The substantial increase in soil moisture (Fig. 2a) under silvopasture likely resulted from an increased water

retention capacity due to the incorporated forest litter. Similarly, the differences in pH and exchangeable cations (Fig. 1; Table 1) were undoubtedly due to the lime and fertilizer amendments to the silvopasture. However, the reduction in C_o by 17% (Table 1) cannot be explained by management, per se. We propose that the trampling in of the forest litter has subjected the silvopasture to increased decomposition by soil biota, potentiated by its increased soil moisture.

The rapid transition from forest to pasture, via silvopasture, is suggested by comparing the above-mentioned soil chemical properties to those for the pasture. In nearly all cases, the silvopasture concentrations were intermediate between forest and pasture. In cases where they were not, such as for the plant nutrients, Mg and K, greater uptake by orchardgrass in the pasture and lesser uptake by ryegrass in the silvopasture, probably accounts for the discrepancies (acknowledging, of course, the considerably different management inputs).

Our finding of a 36% increase in whole soil TP_o (Table 2) upon conversion of the forest to the silvopasture (and a 23% increase over the pasture), which also effectively persisted over the growing season (Fig. 3), was unexpected. We propose that the incorporation of the forest litter of a high C–P ratio, in combination with the application of fertilizer-P over 2 years, induced substantial P_i immobilization in the silvopasture soil. Although we have no direct evidence, we speculate that a substantial proportion of this TP_o is in the form of microbial biomass, particularly fungal biomass (Plante 2007).

As for most of the chemical property differences among the ecosystems, the extractable-P fraction results could generally be explained by particular management inputs. The high silvopasture and pasture concentrations of BrP_i and BiP_i at the initial sampling (Table 2) obviously reflected the fertilizer-P inputs, as their marked decline over the growing season reflected their utilization by the forages, being greater in the pasture and lesser in the silvopasture. Interestingly, the BrP_o and BiP_o results only vaguely mimicked the high concentrations of TP_o in the silvopasture and pasture, when compared to those for the forest (Fig. 3). We suggest that this increase in non-extractable TP_o in the silvopasture is further presumptive evidence of its being microbial biomass.

The relationship between phosphatases and P_i has received much attention. In both plant root and

microfloral solution culture, they have been shown to be inversely related because phosphatase synthesis is regulated by external P_i (i.e., feedback). In soils, however, this principal is frequently not demonstrable. For example, in USA soils under forest (Zou et al. 1995), in a New Zealand soil under pasture (Ross et al. 1995), and in a Scottish soil under forest (Carreira et al. 2000), phosphatase activity was not found to be correlated with BiP_i . In another USA study under forest, Compton and Cole (2001) reported that fertilizer-P amendment had no effect on phosphatase activity. Also, in a New Zealand study under forest or pasture, Chen et al. (2000), reported higher phosphatase activity under forest, than under pasture, although the former had higher concentrations of BiP_i . Even investigations using explicitly rhizospheric soils, where regulation of phosphatase by P_i should be most apparent, have failed to definitely establish a causal relationship (Haussling and Marschner 1989; Scott and Condon 2003). Thus, the relationship between these two soil properties is still uncertain, as opined by Speir and Ross (1978) in their review of the mostly arable soil literature.

Indeed, our results (Fig. 4) essentially confirmed the uncertain relationship between soil phosphatases and various forms of P_i (TP_i , BrT_i , and BiT_i). Our finding that $PMEac$ activity in the forest, silvopasture and pasture soils at the initial sampling was negatively correlated with BrP_i ($R^2 = -0.69$, $P \leq 0.01$) suggested that the feedback was operative in our ecosystems. However, the positive correlation of $PMEal$ ($R^2 = 0.56$, $P \leq 0.05$) suggested that it was not operative. Additionally, considering the individual ecosystem data for the entire growing season, all P_i fractions were poorly correlated ($R^2 = 0.083$, $R > 0.05$) with both $PMEac$ and $PMEal$. More vividly, considering only the silvopasture, in which high concentrations of BrP_i were found (Fig. 3b), in combination with a high $PMEac$ activity (Fig. 4), it is obvious that this ecosystem does not reflect this principle.

Conclusions

Differences in soil properties, upon conversion of a forest ecosystem to a silvopasture ecosystem were mostly explained by their previous management history and resultant vegetative growth. The

substantial decrease in C_o under the silvopasture was likely due to the incorporation of forest litter, resulting in enhanced decomposition, potentiated by increased soil moisture. Comparing these properties to those for a pasture ecosystem, indicated that the silvopasture represented a continuum between the forest and pasture. However, the silvopasture was unique in accumulating a sizable TP_o reservoir above that for the forest and pasture. These results demonstrate that conversion of temperate climate forests to silvopastures results in a rapid and significant change in the soil C and P cycles that should be taken into account when future management options are considered.

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