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Ecosystem-level significance of acid forest soils

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Abstract

The distribution of plant species is generally thought to be determined by an interaction of soil factors functioning within the constraints of climatic factors. The objectives of this paper are to focus on the significance of soil factors, particularly extreme soil acidity, on ecosystem processes of a southeastern U.S. pine forest, and to address the hypothesis that these acid soils represent the primary component of the ecosystem, controlling such processes as nutrient cycling and plant species dynamics. Soils at this Coastal Plain forest site were derived from acidic, clayey marine-deposited sediments, creating the potential for low-nutrient, acidic soil conditions. Field data support this observation. Mean pH for the top 5-cm of soil throughout the watershed was 4.3. Extractable Na, K, Ca, and Mg were 0.48, 0.50, 5.07, and 3.21 meq kg^{-1}, respectively, suggesting that base saturation could be <10%. 'Available' N (extractable $NH_4^+ + NO_3^-$) was 0.51 meq kg^{-1}. Such conditions are well-suited for the loblolly and longleaf pines that dominate this system. These pines produce acid, nutrient-poor litter, which accumulates from resultant slow decomposition. Fire thus has become important in this ecosystem, selecting for plant communities which are both fire-adapted and acid-tolerant. Coastal Plain pine flatwoods soils appear to be sensitive to further acidification and other related changes in soil and soil solution chemistry from long-term acid deposition.

Introduction

The distribution of plant species classically has been thought to be determined by an interaction of soil factors functioning within the constraints of climatic factors. Cain (1944) discussed several principles, or factors, controlling plant distribution, stating that climatic control is of primary importance, whereas edaphic control is of secondary importance. This relationship, however, is complicated by the reciprocating interaction of climate and vegetation effects on soil development (see Jenny, 1980). Applying these biotic and abiotic influences to the ecosystem concept (for example, a forest), it becomes apparent that a forest ecosystem represents an integration of a whole complex of controlling factors, a notion described by Cain (1944) as 'holocoenotic'.

Indeed, Jenny (1980) discussed the many 'state factors' of which total ecosystem properties, vegetation properties, and soil factors are a function. These factors include climate, parent materials, biotic factors, topography, time, and other variables. It seems clear that, for soils of much of the Coastal Plain of the southeastern United States, parent material is of principal importance. Though there is some variability throughout the Coastal Plain region, these soils are derived from weathered secondary sediments of both alluvial and marine origin. Further weathering during soil development is thus generally limited and the resultant soils are almost invariably infertile and very acidic.

Forest soils in many regions are typically acidic, and several factors contribute to forest soil acidification. These include precipitation amounts (high in forested regions), soil age (usually old in forested regions), and substantial nutrient uptake by tree roots (Binkley and Richter, 1987; Black, 1968). In many conifer forests, inputs of acid litter to the forest floor also contribute to soil acidity. It is suggested here, however, that acidic soils represent pre-existing conditions in Coastal Plain pine flatwoods, such that these soils directed, rather than responded to, ecosystem development.

The objective of this discussion is to focus on the significance of extreme soil acidity on ecosystem processes, such as nutrient cycling and plant species dynamics, using a Coastal Plain pine flatwoods ecosystem as an example. This will address the hypothesis that acid soils represent the primary component of the system controlling these processes, ultimately resulting in conditions favorable for fire and the establishment of a 'fire-type' ecosystem. Finally, practical aspects of ecosystem acidification will be considered, with emphasis placed on the static versus dynamic nature of acidification and on the potential effects of acid deposition.

Materials and methods

Study site

Research for this study was done at one of the gauged watersheds (WS77) at the Santee Experimental Forest, which is located in the lower Coastal Plain of South Carolina, approximately 30 km from the coast (33°N, 80°W). This watershed has extremely low topograph relief, typical of other pine flatwoods of the region.

The region experiences a humid mesothermal climate, characterized by mild winters and warm, moist summers (Trewartha, 1954). Precipitation averages approximately 135 cm annually, whereas evapotranspiration averages around 100 cm annually. The two distinct seasonal peaks in precipitation (Fig. 1) results from shifts in storm system dominance, from frontal storms in early spring to convectional storms in mid-summer. Precipitation typically exceeds evapotranspiration throughout the year (Fig. 1).

Historically, the entire Coastal Plain region is one which has experienced alternating periods of inundation and exposure during inter-glacial and glacial times. The current land area has been exposed for at least 35,000 yr (Walker and Coleman, 1987). Geologically, the lower southeastern Atlantic Coastal Plain is dominated by Quaternary sediments and sedimentary rocks. Much of the Atlantic Coastal Plain was formed from sediment transported by rivers draining the Appalachian Mountains, although these alluvial systems were influenced greatly by changes in sea level (Walker and Coleman, 1987).

The soils of WS77 are Udults and Aquults derived from these old, highly-weathered secondary sediments, as well as from montmorillonitic marine deposits. As a result, such soils can be extremely acidic and infertile. Descrip-

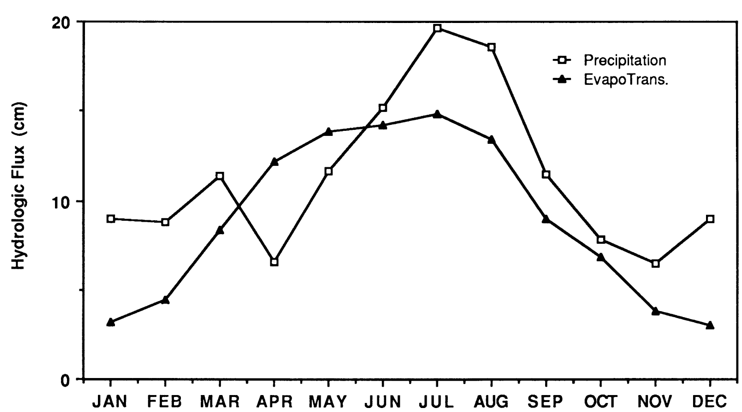

Fig. 1. Mean monthly precipitation and evapotranspiration (pan evaporation) from 1965 to 1979 at the Santee Experimental Forest, South Carolina.

Table 1. Descriptions of prominent soil series at WS77. From Gilliam (1983)

Series	Description	
Bayboro	soil type:	Bayboro clay loam
	classification:	Umbric Paleaquults – clayey, mixed, thermic
	drainage:	very poorly drained
	relief:	nearly level to slightly depressional, saucerlike areas or drainageways
	soil reaction:	very strongly acid (to 158 cm)
Bethera	soil type:	Bethera clay loam
	classification:	Typic Paleaquults – clayey, mixed, thermic
	drainage:	poorly drained
	relief:	level to nearly level flats or slightly depressional areas
	soil reaction:	very strongly acid (to 132 cm)
Craven	soil type:	Craven loam
	classification:	Aquic Hapludults – clayey, mixed, thermic
	drainage:	moderately well-drained
	relief:	nearly level to gently sloping ridgetops or breaks
	soil reaction:	very strongly acid (to 198 cm)
Wahee	soil type:	Wahee loam
	classification:	Aeric Ochraquults – clayey, mixed, thermic
	drainage:	somewhat poorly drained
	relief:	level to nearly level, low marine terraces and terraces along large streams
	soil reaction:	very strongly acid (to 185 cm)

tions of the predominant soil series of WS77 are given in Table 1.

The watershed was dominated by vegetation characteristic of the Coastal Plain pine flatwoods type. Pine species represented approximately 91% of the overstory basal area. Important overstory species and their absolute and relative basal area are presented in Table 2.

Sampling and analysis

WS77, approximately 165 ha in area, was divided into 20 compartments of 8 ha each as part of a larger project which examined the effects of fire on several components of nutrient dynamics of the ecosystem. Results of many of these efforts have been summarized in several publications (Gilliam and Christensen, 1986; Gilliam, 1988; Richter *et al.*, 1982; 1984). This paper will combined some of these data with unpublished results to focus on the overall significance of the extreme acidic nature of the soils in directing ecosystem processes.

Forest floor and mineral soil samples were taken from 10 10-m by 10-m sample plots located in each compartment using a stratified-random procedure. Composites were made throughout the watershed for each sample type. Data presented here, unless otherwise specified, are means for the entire watershed.

The forest floor was sampled with a 14.7-cm diamater litter cutter. Five samples were taken in each plot and composited to yield one sample

Table 2. Dominant overstory species and absolute and relative basal area. Nomenclature follows Radford et al. (1968)

Species	Basal area $m^2\ ha^{-1}$	Relative basal area (%)
Pinus taeda	23.80	72
P. palustris	5.50	17
P. echinata	0.52	2
Liquidambar styraciflua	1.30	4
Nyssa sylvatica	0.81	2
Quercus stellata	0.40	1
Q. nigra	0.33	1
Acer rubrum	0.30	1

per plot (10 samples per compartment). Forest floor samples were then separated into O1 and O2 horizons. A paired plot design (adjacent burned and unburned plots), as described in Gilliam (1988), was used to more specifically test for effects of fire on the forest floor.

Mineral soil was sampled with a 2.0-cm soil corer. Each core was separated into three depth classes (0–5 cm, 5–10 cm, and 10–20 cm) after organic horizons had been removed. Sample compositing followed that for forest floor.

Forest floor samples were oven-dried at 70°C to a constant weight and then ground in a Wiley mill. Water-extractable and KCl-exchangeable pH was determined on samples in the paired-plot study using a glass electrode. Samples were also digested chemically and analyzed for K, Ca, Mg, N, and P using standard analytical procedures.

Mineral soil samples were air-dried and ground in a hammer mill. Soil pH (H_2O and KCl) was determined with a glass electrode. Dried, ground samples were extracted with a dilute double-acid solution according to Mehlich (1953), a technique well suited for acid clay soils (Gilliam and Richter, 1988). Samples were also wet-oxidized (for organic C) and digested (for total N and P). Extractable ions, organic C, and total N and P were determined using standard procedures.

Results

Not surprisingly from the soil descriptions in Table 1, WS77 soils were extremely acidic. Water-extractable soil pH ranged from 4.3 to 4.6 in the top 20-cm soil depths, whereas KCl-extractable pH ranged from 3.4 to 3.6 (Table 3). Water-extractable pH was lowest at 0–5 cm and increased significantly with depth.

Watershed soils were also low in extractable base cations. These were in the order $Ca^{++} > Mg^{++} > K^{+} > Na^{+}$ and showed no appreciable pattern with soil depth (Table 3). The average sum of base cations for the top 20-cm soil depths was around 9 meq kg^{-1}. Using an estimated cation exchange capacity (not measured in this study) of 70–100 meq kg^{-1} (Richter, 1980; Binkley *et al.* 1989), this indicates that base saturation for soils of WS77 was <10%. The dominant extractable cation was Al^{+++}, which, at around 40 meq kg^{-1}, was greater than four times the sum of base cations (Table 3).

Available (extractable) N and P were also quite low (Table 3), less than 1% and between 2 and 3% of total N and P in mineral soil, respectively (Table 4). Organic C and total N were highest at the 0–5 cm depth and decreased significantly with depth. In contrast, total P did not vary significantly in the top 20 cm of soil (Table 4).

Forest floor litter material was also extremely acidic, with mean litter pH consistently <4.0 (Table 5). Furthermore, the O2 horizon was more acidic than the O1 horizon, showing lower values for both H_2O-extractable and KCl-exchangeable pH. Nutrient concentrations in forest litter were in the order N > Ca > Mg > K > P. There was a consistent pattern of higher nutrient concentrations in the O2 horizon compared to the O1 horizon, especially for K and N, which were 50% higher in the O2 horizon.

Fire decreased forest floor acidity. Figure 2 shows forest floor data from the paired plot study. Each point on the figure represents a single pair of adjacent plots, one burned and the other unburned. The straight line is a 1:1 relationship indicating no fire-caused change in litter pH; thus, points above the line represent increases and points below the line represent decreases in litter pH due to fire. All but three points are above this 1:1 reference line (Fig. 2).

Table 3. Mineral soil pH and extractable ions at different sampling depths for WS77

Depth (cm)	pH (H_2O)	pH (KCl)	Na^+ (meq kg^{-1})	K^+	Ca^{++}	Mg^{++}	Al^{+++}	NH_4^+	NO_3^-	PO_4^{3-}
0–5	4.26c*	3.40b	0.63a	0.92a	7.74a	3.64a	45.95a	0.88a	0.03a	0.20a
5–10	4.43b	3.62a	0.39a	0.41b	4.47a	2.74a	30.93a	0.44b	0.03a	0.10b
10–20	4.55c	3.62a	0.45a	0.33b	4.03a	3.22a	N.D.	0.31c	0.02a	0.05c

* Mean differences between soil depths by Duncan's Multiple Range Test ($P < 0.05$) indicated by lower case letters.

Table 4. Organic C, total N, and total P at different sampling depths for WS77 soils

Depth (cm)	Organic C (%)	Total N mg cm^{-3}	Total P mg cm^{-3}
0–5	3.46a*	1302.8a	131.1a
5–10	1.95b	815.8b	128.9a
10–20	1.19c	615.8c	120.3a

* Mean differences between soil depths by Duncan's Multiple Range Test ($P < 0.05$) indicated by lower case letters.

Table 5. Forest floor pH and nutrient concentrations for WS77

Horizon	pH (H_2O)	pH (KCl)	K (mg kg^{-1})	Ca	Mg	N	P
O1	3.88	3.23	6	52	9	109	3.7
O2	3.81	3.15	9	62	13	165	4.8

Discussion

The results presented here, along with those published from other studies, will be discussed within the context of a relatively simple and wholly conceptual model, ultimately relating patterns of soil development in Coastal Plain pine flatwoods to the existence of high fire frequencies and to the dependence of these ecosystems on fire. The time scale for this sequence begins 35,000 yr BP, the duration of continuous exposure for the current land mass of the Atlantic Coastal Plain (Walker and Coleman, 1987).

Parent materials, forest soil acidity, and low soil fertility

The predominant parent materials from which pine flatwoods soils of this region developed are largely Quaternary sediments. Much of the sediment is secondary, weathered alluvium being brought to the Coastal Plain by rivers from the Appalachian Mountains and from the former peneplain of the Piedmont region to the west of the Coastal Plain (Mills *et al.*, 1987). Other sediments were montmorillonites of a marine origin, being deposited during the previous interglacial period when sea level was higher than it is presently (Walker and Coleman, 1987).

Soils of WS77 illustrate the consequences of soil development from such parent materials. These soils are described as very strongly acidic to depths greatly exceeding 1 m (Table 1) and data in Table 3 support this observation. Water-extractable pH was at or below 4.5 in the top 20-cm of soil. The large difference between H_2O-extractable and KCl-exchangeable pH is suggestive of another characteristic of extremely acidic forest soils, that is, the dominance of Al^{+++} on the cation exchange complex. Indeed, extractable Al in WS77 soils was greater than four times the sum of base cations, resulting in a base saturation which is probably <10%. Another factor which has historically contributed to low base saturation is a climatic regime wherein precipitation exceeds evaporation throughout

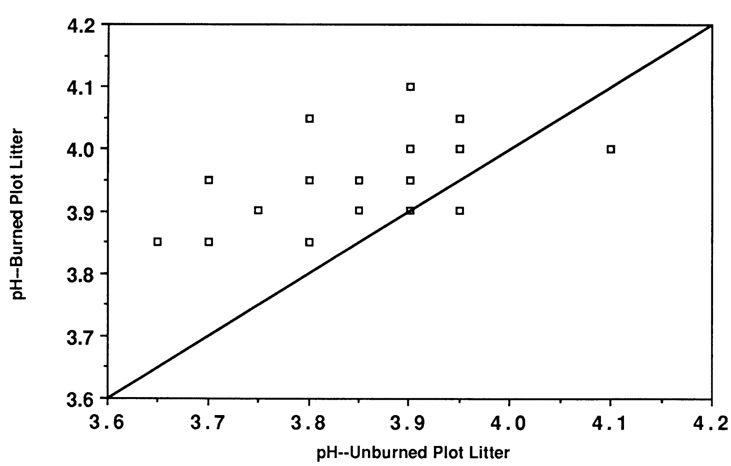

Fig. 2. Forest litter pH in paired burned and unburned plots. Each point represents a single pair of plots.

the year, resulting in extensive leaching of weathered and exchangeable ions.

The acidic nature of watershed soils undoubtedly contributes to the low values for extractable N and P in Table 3, especially N (Gilliam and Richter, 1988). Exceedingly acidic conditions are unfavorable for microbial populations which mineralize soil organic matter and oxidize residues of N and P to forms available to plants (Alexander, 1977).

Thus, the weathered, secondary parent material sediments have resulted in soils which are 1) highly acidic, 2) high in exchangeable Al, and 3) very infertile. It is reasonable to assume that there has been selection through time for plant species which are tolerant of these extreme conditions (Monk, 1966). Dominant tree species for WS77 (Table 2) appears to reflect this.

Acid, infertile soil and pine species

Pine dominance in this region extends back to >20,000 yr BP (Frey, 1953). Changes on overstory dominance before that time are consistent with changes in global climate and sea level fluctuations. Although acidic soil conditions selected for pine species, the long-term presence of these speices is also responsible for the maintenance of acidic, nutrient-poor conditions, since an important adaptation of plants to low-nutrient soils is continued growth at low tissue nutrient concentrations (Chapin *et al.*, 1986; Gilliam, 1988). That pine species, especially loblolly (*Pinus tadea*) and longleaf pine (*P. palustris*), comprise approximately 90% of the overstory basal area of WS77 (Table 2) indicates that the forest floor is predominantly pine litter. This is consistent with data in Table 5, which shows that litter material is not only quite acidic, but is much more so at the interface between the forest floor and mineral soil.

This charaterization of the forest floor is of great significance here because of the importance of the forest floor in providing nutrients (especially N) to the mineral soil. This notion is supported by patterns of soil organic C and total (largely organic) N concentrations. These were both highest in the 0–5 cm soil depth and attenuated significantly downward (Table 4).

Pine species, litter, and fire cycles

Two major variables influencing forest floor development are litter production and decomposition; thus, net build up of the forest floor will occur when inputs (litterfall) exceed outputs (decomposition). Another contributing influence can be fire, although the occurence of fire is, in turn, influenced by the amount of litter available for fuel.

Several factors are responsible for relatively rapid build up of litter material through time at WS77. These include low litter quality (*i.e.*, nutrient content), high C/N ratios, and high lignin content (Meentemeyer, 1978; Waring and Schlesinger, 1985). Indeed, breakdown of litter is typically low in conifer forests compared to deciduous forests. Cole and Rapp (1981) found that mean residence time for organic matter in temperate conifer forests was 17 yr, compared to 4 yr for temperate deciduous forests.

The direct consequence of excessive build up of the forest floor in areas with climates that include high frequencies of thunderstorms, such as the southeastern Coastal Plain, is fire. Available evidence, for example, charcoal fragments in pollen and peat profiles (Frey, 1983), suggests that fire has been an important component of many Coastal Plain ecosystems throughout the Quaternary (Christensen, 1981). Fire cycles of the region can be between five and seven years, depending on local conditions and prevailing weather patterns. Thus, through long periods of time in much of the Coastal Plain, there has also been selection for plant species which are both fire-tolerant and dependent on fire for successful growth and/or regeneration (Mutch, 1970).

A well documented example of a fire-tolerant, fire-dependent species is longleaf pine. One of the more recent studies of the relationship between the population dynamics of this species and fire was by Platt *et al.* (1988). Within the natural range of longleaf pine, which extends throughout most of the Coastal Plain, development of longleaf pine forests and their associated communities is limited largely to areas which experience chronic fires. At WS77, Gilliam (1983) demonstrated sharp declines in longleaf pine regeneration following 40 yr of fire exclusion.

Fire and nutrient dynamics

Fire increases availability of nutrients in many ecosystems (Boerner, 1982), although this can be particularly pronounced in those that are oligotrophic (nutrient-poor) (Christensen, 1987). Many pine flatwoods ecosystems are deficient in N, P, and K (Shoulders and Tiarks, 1990) and fire has been shown to increase the availability of each of these nutrients in such systems (Christensen, 1987; Gilliam, 1988).

Based on nutrient budgets and plant/soil nutrient correlations, WS77 appears to be especially limited by P and K deficiencies. Gilliam (1983, 1988) showed that fire serves a significant function of decreasing soil acidity and increasing availability of these nutrients. Much of this effect can be explained by increases in litter pH following fire (Fig. 2). In addition to representing additions of essential base cations in the form of ash, higher litter pH should cause a flush of microbial activity (Alexander, 1977), increasing the availability of N, as well as K and P. It is hypothesized that nutrient availability declines sharply during periods of long-term fire exclusion (Christensen, 1987; Gilliam and Christensen, 1986).

Acid deposition effects

One of the currently serious environmental problems is that of anthropogenically-increased acidity of the atmosphere and of atmospheric deposition. It was a commonly held opinion that strongly acidic soils such as those of the lower Coastal Plain would not be sensitive to effects of acid deposition, since soil acidity was actually greater than the acidity of atmospheric deposition. It has been demonstrated using model simulations, however, that several soil types in the southeastern United States are quite sensitive further acidification (Binkley *et al.*, 1989). In fact, the criteria for acid sensitivity established in that study, which are 1) cation exchange capacity <100 meq kg^{-1}, 2) base saturation <10%, and 3) soil solution pH <5.00, all apply to soils of WS77.

Results of simulations for two watershed soil series, taken in part from Binkley *et al.* (1989), are presented in Table 6. Both soils show similar patterns. Long term (140 yr) changes in soil pH are actually quite small, especially in relation to the other parameters. Base saturation, already quite low, decreases further. Acid neutralizing capacity, a measure of the buffering capacity of the soil, drops to large negative numbers, indicating that the system becomes acidifying. Aluminium mobility increases sharply, suggesting future problems for aluminium toxicity. Decreases in Ca/Al ratios in soil solution are consistent with decreases in base saturation and increases in soil solution Al.

Conclusions

It is certainly a valid view that acid forest soils are the consequence of the several pedogenic processes, including climate and vegetation, which bring about soil formation (Jenny, 1980). It is also valid, however, in the case of this lower Coastal Plain pine flatwoods, to view acidic soils as 'pre-existing conditions' which were to a large degree responsible for directing ecosystem de-

Table 6. Simulated present (1984) and future (2124) concentrations in soils and soil solutions for two WS77 soil series. Data are summarized from Binkley et al. (1989) and Gilliam (unpublished data)

Series	Time	pH	Base saturation (%)	ANC[a] (μeqL^{-1})	Al	Ca/Al[b]
Bayboro	1984	4.9	6.1	24.7	17.4	6.1
	2124	4.6	1.7	−78.4	86.9	0.8
Wahee	1984	4.9	5.5	13.0	22.3	6.1
	2124	4.6	1.7	−103.0	109.5	0.8

[a] Acid neutralizing capacity in soil solution
[b] Ratio of Ca to Al in soil solution.

velopment. From the data presented here, a logical sequence can be constructed that essentially views fire as an unavoidable consequence of acid soils which derived from weathered parent materials.

The validity of this generalization would be in its predictive power (or applicability) in other analogous ecosystems. Although it is not the intent of this study to achieve this, one example is worthy of mention. The Eucalyptus forests of Australia show a high degree of fire-dependence, one which was discussed previously by Mutch (1970). Many of these ecosystems are characterized as having extremely acidic soils with high exchangeable Al, having been derived from weathered sedimentary parent materials (Khanna and Raison, 1986).

Although pedogenic processes are often regarded as relatively slow and requiring long periods of time, it has been shown both empirically and through modeling that some processes of acidification and other related soil chemical changes can occur over shorter time periods. Thus, another consequence of acid soil development in pine flatwoods ecosystems may be increased sensitivity toward detrimental effects of acid deposition. This possibility represents a distinct threat to both natural, as well as managed, pine flatwoods of the Coastal Plain region.

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