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NITRIFICATION POTENTIALS IN PRIMARY AND SECONDARY SUCCESSION[1]

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Abstract. Potential nitrogen mineralization and nitrification were measured in soils from a primary successional sequence developed on sand dunes and from a secondary successional sequence on old fields. Potential nitrogen mineralization in soils from the primary sere increased through the first five stages and then leveled off. Nitrogen mineralization was relatively constant in soils from the secondary sere, except that the highest rates were observed in the oldest site. Nitrification was very closely correlated with nitrogen mineralization in soils from both the primary and secondary seres. Only one site had both substantial nitrogen mineralization and low nitrification.

The results of this study do not support the hypothesis that nitrification is progressively inhibited in the course of ecological succession.

Key words: dunes; Indiana; mineralization; New Jersey; nitrogen; nutrient cycling.

INTRODUCTION

Rice and Pancholy (1972) proposed that nitrification, the microbial oxidation of ammonium to nitrite and nitrate, progressively decreases in the course of ecological succession. They suggested that the mechanism causing the decrease is allelochemical inhibition of nitrification, and that the decrease is selectively advantageous to mature ecosystems because it conserves both nitrogen and energy. Nitrogen could be conserved by the inhibition of nitrification because ammonium, a cation, is retained within the soils by cation exchange, whereas nitrate, an anion, is excluded from cation exchange sites and easily leached from most soils. They suggested that energy could be conserved because the inhibition of nitrification increases ammonium and decreases nitrate concentrations in soil, thus favoring use of ammonium as a plant nitrogen source. Plants can incorporate ammonium directly into amino acids whereas the assimilation of nitrate involves two reduction steps that can be energetically costly.

Several lines of evidence have been used in support of this hypothesis. Warren (1965) reported that soil nitrate concentrations and numbers of nitrifying bacteria decreased along a South African grassland sere, and concluded that nitrification rates changed similarly. Rice and Pancholy (1972, 1973) took a similar but more comprehensive approach by studying three different three-point seres, one grassland and two forest, in southern Oklahoma. They too found that soil nitrate concentrations and numbers of nitrifying bacteria tended to decrease with succession in each sere, and that soil ammonium concentrations increased. Lodhi (1979) reported similar results in a mine spoil succession in North Dakota. Todd et al. (1975) studied numbers of nitrifiers and nitrate losses from several southern Appalachian watersheds and also concluded that nitrification decreased through succession. Vogt and Edmonds (1977) suggested that allelochemic inhibition of nitrification caused low nitrate and high ammonium concentrations in old low-site-quality Douglas-fir stands in western Washington. Monro (1966) and Rice and Pancholy (1973, 1974) found that various organic compounds in soils and plant extracts were highly toxic to soil or solution cultures of nitrifiers and were found in generally increasing amounts in soils from progressively later stages of succession, although Neal (1969) found the opposite trend in a Canadian prairie sere. Rice (1974, 1979) has thoroughly reviewed much of this research.

Haines (1977), after examining the relative uptake of applied ammonium and nitrate in a Georgia old-field to forest sere, concluded that plants from the younger stages preferentially utilized nitrate while those from the older stages used ammonium. Franz and Haines (1977) examined levels of nitrate reductase in foliage in the same sere and reached the same conclusion.

We question both the evolutionary basis of this hypothesis and the evidence that has been used to support it. As stated, the evolutionary rationale (Rice and Pancholy 1972, Haines 1977) relies mainly on the ecosystem as a unit of selection. While the evolutionary argument could be reformulated in terms of more realistic models of selection, we are more concerned with the evidence that has been used to examine changes in nitrification through succession. Relying on nitrate or ammonium pool size and numbers of nitrifiers to indicate relative rates of nitrification implicitly assumes that (1) nutrient pool size reflects the rate of nutrient utilization, and (2) reported population sizes of nitrifying bacteria accurately reflect nitrifier activi-

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ty. We believe that neither of the assumptions is warranted. First, nutrient concentration alone cannot indicate the relative importance of a nutrient. For example, a consistently small proportion of inorganic nitrogen in the nitrate pool at a site does not necessarily imply a low rate of nitrification. Such a site could have a very high rate of nitrification if plant nitrate uptake, leaching, and/or denitrification were rapidly removing nitrate from the soil. Measures of both nutrient pool size and rate of turnover are necessary to assess adequately the importance of any nutrient.

Although it seems reasonable to assume that nitrification is positively correlated with numbers of nitrifiers, there are at least two difficulties with such an assumption. First, the most-probable-number (MPN) technique counts only those nitrifiers adapted for growth under the specific conditions of the incubation procedure; nitrifiers adapted for growth under different conditions may be overlooked. Consequently, diversity and total population size can be significantly underestimated (Johnson and Sieburth 1976, Focht and Verstraete 1977, Belser and Schmidt 1978). Second, the MPN technique neither differentiates between dormant and active cells nor accounts for differential activity among those cells that *are* active. Yet senescent or resting cells can be more than half of a natural population (Boylen 1973, McLaren 1973); cells in different stages of growth apparently nitrify at different rates (Ardakani et al. 1974, Fliermans and Schmidt 1975); and some nitrifiers may be exposed to inhibitors that slow metabolism rather than stop it (Rice and Pancholy 1973). Witkamp (1974) discussed some of the problems associated with relating serial plate counts of microbes to their productivity. After comparing indirect colony counts of decomposers to direct measurements of productivity and finding very poor correlation, he concluded that it is "difficult if not impossible" to use indirect microbial counts to indicate productivity. Jensen (1936) had reached a similar conclusion after comparing indirect counts of bacteria to CO_2 production in incubated soils. Schmidt (1973) suggested that the "common assumption that microbial numbers reflect activity is probably true under some conditions but it is dangerously fallacious in perhaps most situations."

Most of these difficulties can be avoided by nitrification potential measurements. This approach was used by Coile (1940), who measured nitrification potentials in incubated soil samples from a five-point sere in the North Carolina Piedmont. He did not find measurable nitrate production in any stages but the first (old-field) and the fourth (70-yr pine) stages. Montes and Christensen (1979) used a similar approach to examine the control of nitrification along a three-point sere in the same area. They too found no clear trend with succession. A difficulty with the interpretation of these incubation studies, however, is that soil texture varies among the sites within these seres. Odum (1960) clearly documented Coile's (1940) observation that differences in soil texture can strongly affect vegetation and rates of succession, and presumably nutrient cycling properties.

The present study was designed further to investigate successional changes in nitrification potential in two well-defined seres and thus to test the hypothesis that nitrification progressively decreases through succession.

Study Sites

Primary sere

The Indiana Dunes study area on the southern edge of Lake Michigan (41°42′N, 87°1′W) has been described at length by Olson (1958*a*). It is within a series of beach and dune systems which stretch inland several kilometres parallel to the current lakeshore. These systems have taken form as the lake has lowered since the most recent glaciation some 12 000 yr ago and newly exposed sand has been selectively transported inland by wind (Olson 1958*b*). The net result is a sequence of dunes in close proximity having soils in successively older stages of development. While the horizontal array of sites in the Indiana Dunes complex may not accurately represent the expected vegetation succession at any one point (cf. McIntosh 1980), vegetation structure and soil development (including texture and organic matter and nutrient contents) do progressively increase inland from the lake (Olson 1958*a*). Thus it can be used as a primary sere for our purposes.

The area receives about 90 cm of precipitation annually, two-thirds of it in the winter months. Mean annual temperature is 10.1°C; the coldest monthly mean is −3° and the highest mean is 23° (Visher 1944).

Plant succession in the Dunes has been extensively studied by Cowles (1899, 1901) and Olson (1958*a*). Six sites within this sere were included in this study. Five of the sites are along the first 500 m of a 4-km north–south transect beginning at the lake about 500 m west of the eastern edge of the Indiana Dunes State Park boundary. These sites are within a part of the park set aside as an ecological preserve. The sixth site is about 3.5 km south of the others on a dune that has been stabilized for about 12 000 yr (Olson 1958*a*). The large diameters of the trees at this site and the presence of many tip-up mounds suggest an old-growth status. The site appears relatively undisturbed except for the absence of fallen boles, which may have been removed by nearby landowners.

The six sites sampled were:

1) *Sand*—bare sand and scattered pebbles midway between the lake and the first foredune; intermittently flooded during periods of high water;
2) *Grass*—on the upper lakeward edge of the first

foredune and stretching several meters inland; dominants include marram grass (*Ammophila breviligulata*) (nomenclature follows Gleason and Cronquist 1963), little bluestem (*Andropogon scoparius*), sand-reed grass (*Calamovilfa longifolia*) and horsetail (*Equisetum hyemale*);

3) *Grass + Shrub*—begins immediately behind the above site and stretches 20–30 m inland to the base of the next dune; dominated by little bluestem, sand-reed grass, sand-cherry (*Prunus pumila*), and goldenrod (*Solidago* spp.), and includes an occasional jack pine (*Pinus banksiana*);
4) *Pine*—begins at the base of the dune following the foredune and continues to just over the top; dominated by jack pine, red cedar (*Juniperus virginica*), creeping juniper (*J. communis*), witch-hazel (*Hamamelis virginiana*), choke cherry (*Prunus virginiana*), and dune grape (*Vitis riparia*), with white pine (*Pinus strobus*) sometimes present;
5) *Oak(1)*—stretches from where the pine site ends for over a kilometre inland; red oak (*Quercus rubra*), basswood (*Tilia americana*), and sassafras (*Sassafras albidum*) dominate the overstory; undercover is sparse but includes witch-hazel, sassafras, false Solomon's-seal (*Smilacina racemosa*), and poison ivy (*Rhus radicans*);
6) *Oak(2)*—an old-growth community; dominants include red oak, white oak (*Quercus alba*), and shagbark hickory (*Carya ovata*) plus other scattered hardwoods; the understory includes red maple (*Acer rubrum*), flowering dogwood (*Cornus florida*), witch-hazel, sassafras, maple-leaved viburnum (*Viburnum acerifolium*), false Solomon's-seal, and Solomon's-seal (*Polygonatum biflorum*).

Secondary sere

The secondary sere is at the William L. Hutcheson Memorial Forest on the New Jersey Piedmont (40°30′N, 74°34′W). The forest and surrounding fields are maintained as an ecological preserve by Rutgers University. The forest itself is a 26-ha old-growth mixed-oak stand believed relatively undisturbed since 1702 (Buell et al. 1954, Buell 1957), and the tract includes a number of adjoining 1-ha known-age abandoned fields. The fields have not been fertilized at least since the site was acquired in 1957. A substantial number of studies have investigated many aspects of the site's ecology (Small 1973) including the successional vegetation (Bard 1952, Monk 1961, Small et al. 1971, Monte 1973, Frye 1978). Forman and Elfstrom (1975) concluded that the forest is broadly representative of other old-growth forests on the New Jersey Piedmont. The climate of the area includes mild winters with humid subtropical summers and about 100 cm of precipitation spread evenly throughout the year (Biel 1958). Average annual temperature is 11.7° with monthly means ranging from 0° to 24° (Biel 1958, United States Weather Bureau 1959).

Four sites in this tract were studied, corresponding to the annual, perennial herb, shrub, and old-growth forest stages of succession. An early-forest site was also studied but subsequent analysis showed significantly different soil texture from the other sites. All of the sites are within several hundred meters of each other and each of the three young sites was plowed in early spring prior to abandonment (Frye 1978). The sites studied were:

1) *Annual*—in the 1st yr of abandonment; principal dominant is ragweed (*Ambrosia artemisiifolia*), though wild radish (*Raphanus raphanistrum*), and lamb's-quarters (*Chenopodium album*) are also important;
2) *Perennial Herb*—in the 4th yr of abandonment; dominants include quack grass (*Agropyron repens*), orchard grass (*Dactylis glomerata*), and Queen Anne's lace (*Daucus carota*);
3) *Shrub*—in the 19th yr of abandonment; dominants include *Hieracium* sp., strawberry (*Fragaria virginiana*), and Kentucky bluegrass (*Poa pratensis*);
4) *Old-growth Forest*—over 250 yr since the last systematic disturbance; the almost-continuous 30-m canopy is composed principally of white oak, black oak (*Quercus velutina*), and red oak; flowering dogwood dominates a 10-m subcanopy and maple-leaved viburnum dominates the shrub layer. Local successional annuals may revegetate openings due to wind-throws (Monk 1961), which are apparently the most frequent cause of tree mortality (Reiners and Reiners 1965).

METHODS

Sampling

In both study areas, five subsites were sampled within each site in May 1978, August 1978, and December 1978 or January 1979. The old-growth site at the Indiana Dunes was not sampled in May, and the sand and grass sites were frozen and inaccessible in December–January. On each sample date the five subsites were randomly located along a 100-m transect which was perpendicular to the principal north–south transect at the Indiana Dunes and which bisected each of the abandoned fields at the Hutcheson Forest. The transect direction was arbitrary in the old-growth New Jersey site.

On each sample date at least three cylindrical soil cores 15 cm deep by 6 cm diameter were removed from within a 1-m^2 area at each subsite. Both forest floor (if any) and mineral soil were included in the cores. The three cores were composited (combined and mixed) in polyethylene bags and were then refrigerated at 0–3°C for transport back to the laboratory. Processing the collected samples took place as

soon as possible after collection; except as indicated below this was within 10 h of collection for the Indiana Dunes sites and within 30 h for the New Jersey sites.

Soil analyses

Soils for all analyses were passed through a 4-mm sieve. Exchangeable cations were measured by extracting soils at a 1:10 (wet mass:volume) extraction ratio in 2 mol/L NaCl adjusted to pH 2.5 (Jackson 1958) and containing 0.5 mg/L phenylmercuric acetate to retard microbial growth in the extracts. Three 10-g replicates were extracted from each subsite composite collected in May and five replicates from each collected in August and December–January. Acid-extractable phosphorus was estimated separately on site-composite samples from the August collections; five replicates from each of these composites were extracted in $NH_4F \cdot HCl$ (Olsen and Dean 1965). All extractions were shaken for 1 min and allowed to equilibrate for 18–30 h before centrifuging. Percent water was determined for each subsite composite by drying three 30-g replicates for at least 48 h in an 80° forced-air oven.

Soil extracts were analyzed for nitrate, nitrite, ammonium and phosphate colorimetrically with a Technicon Autoanalyzer II system (Technicon Instruments Corporation 1973*a*, 1973*b*, 1977). Concentrations of calcium, potassium and magnesium were determined with a Jarrell-Ash Model 800 atomic absorption spectrophotometer. Lanthanum chloride to 0.2% was added to the latter samples.

Bulk soil pH was determined for each of two or three replicates from each subsite composite. Ten grams of soil were mixed with 20 mL of distilled water and the pH of the mixture determined after at least 30 min of equilibration.

Total nitrogen was determined for two replicates of three subsite composites within each site. Dried samples stored at <0° were thawed and digested in a Technicon block digestor. Samples were then analyzed for NH_4-N as described above.

Percent carbon analysis followed the Walkley-Black procedure for oxidizable matter using a correction factor of 1.33 (Allison 1965). Two dried and frozen samples from three subsite composites within each site were analyzed.

Bulk densities were estimated for each of three subsites per site by weighing known-volume soil core composites with a calibrated field scale and then correcting for water content. Water-holding capacity was estimated for three subsites at each site using a modification of the technique reported by Peters (1965). Sieved soil (300 g) was placed in a Buchner funnel fitted with fast filter paper and saturated with water, covered with a loose-fitting Petri plate and allowed to drain. After 24 h three known-mass subsamples were removed from each funnel, dried at 80° for at least 48 h and reweighed. Soil textural analysis was carried out on two replicates from three subsite composites within each site using the Bouyoucos (1926) hydrometer method as described by Day (1965).

Numbers of ammonia-oxidizing bacteria were estimated by the most-probable-number technique (Halvorson and Ziegler 1933, Alexander 1965) for three subsites in each site for soils collected in August. Ten-fold dilutions from 10^{-2} to 10^{-9} with 10 tubes per dilution were used and qualitative nitrite + nitrate production determined colorimetrically (Alexander and Clark 1965).

Incubations

Soils from each of the five subsites per site were sieved as above and incubated for 15 and 30 d. Each of three 50-g replicates from the May collection and five 15-g replicates from the August and December–January collections was placed in a 150-mL polyethylene cup, brought to about 60% field capacity with distilled water, and capped with a snap-on lid that had a 5-mm hole punched near its center. The cups were incubated in the dark in a controlled-environment cabinet under high-humidity conditions at 21° (±0.5°). Water loss from a subset of the cups was monitored gravimetrically and original water content in all cups was restored weekly. At the end of each incubation period the soils were extracted in NaCl as described earlier.

Statistical analysis

Data from site characterizations and incubations were subjected to analysis of variance, with all data transformed to $\log_n (X + 1)$ to homogenize the variance inherent in measuring chemical parameters. Analysis of the incubation data was performed on production values (final N concentration minus the mean N concentration for the initial subsite composite) and each production period (15 or 30 d) was analyzed separately. This effectively removed the bias due to heterogeneous variances among incubation periods and the nonstationarity of the $\log_n$ transformation. Between-site contrasts were based on Tukey's honest-significant-difference measure (Winer 1971). Analysis of variance was performed with the MANOVA subprogram of SPSS (Statistical Package for the Social Sciences) version 7.0 (Cohen and Burns 1977) except for contrasts which were done separately.

Results

Site characterizations

Primary sere.—Physical analyses of soils from the Indiana Dunes sites revealed marked trends in bulk density, water-holding capacity, and soil texture along the successional gradient (Table 1A). Bulk density dropped from 1.7 g/cm^3 in the first three sites to around 1.1 g/cm^3 in the pine and oak sites. Water-holding capacity increased from 20% water by mass at field ca-

TABLE 1. Physical characteristics of soils from different stages of a primary sere at the Indiana Dunes and a secondary sere on the New Jersey Piedmont. Values are the unweighted means (± standard error) of three subsites with two replicates per subsite.

Site	Bulk density (g/cm^3)	Water-holding capacity (% H_2O)	Texture		
			% sand	% silt	% clay
A. Primary sere					
Sand	1.66 (0.03)	20.3 (0.2)	97.6 (0.5)	1.3 (0.6)	1.1 (0.2)
Grass	1.69 (0.01)	21.3 (0.7)	98.5 (1.0)	1.1 (0.6)	0.4 (0.4)
Grass + shrub	1.71 (0.03)	23.1 (1.7)	96.4 (0.7)	3.2 (0.7)	0.4 (0.1)
Pine	1.15 (0.08)	27.6 (0.6)	93.0 (1.3)	5.2 (1.8)	1.8 (1.4)
Oak(1)	1.04 (0.08)	28.6 (0.5)	89.4 (1.5)	6.7 (0.8)	3.9 (1.8)
Oak(2)	1.07 (0.04)	33.7 (1.0)	76.1 (2.1)	18.8 (4.6)	5.1 (2.5)
B. Secondary sere					
Annual	1.32 (0.01)	36.1 (0.9)	21.7 (1.7)	68.8 (2.0)	9.5 (1.0)
Perennial	1.33 (0.02)	35.0 (0.8)	18.0 (2.5)	70.7 (1.2)	11.4 (1.9)
Shrub	1.22 (0.04)	28.4 (2.6)	21.9 (1.9)	68.7 (2.8)	9.4 (1.0)
Old-growth forest	1.01 (0.05)	39.9 (1.1)	23.1 (0.9)	66.3 (2.5)	10.6 (1.8)

pacity in the sand stage to 34% in the old-growth oak site. Percent sand decreased from 98% near the beach to about 76% for the oldest soil, while percent silt and clay correspondingly increased along the transect.

Soil chemistry changed markedly as well (Table 2A). Exchangeable NH_4-N increased through the vegetated sites from 0.6 kg/ha in the grass stage to around 4.0 kg/ha in the oak stages. Acid-soluble phosphorus followed a similar trend except that the older oak site had significantly less than the younger oak. Calcium and magnesium also increased only through the first oak stage; levels of both nutrients were strikingly low in the older oak stage relative to all other stages. Trends in NO_3-N and potassium concentrations were not apparent, although the highest concentrations of NO_3-N (0.1 kg/ha) were found in the older oak site.

The pH of the sites differed considerably, dropping monotonically from around 7.9 in the first three sites to 4.2 in the older oak site. Organic carbon and total nitrogen both increased with soil age. The highest carbon concentrations (around 2.0%) were found in the older oak site; the three earliest stages contained <0.2%. Likewise, total nitrogen varied from <0.01% to ≈0.11%. Since percent nitrogen rose more sharply from the sand site inland than did the organic carbon, the C:N ratio decreased through the succession, ranging from a high of 31.8 in sand stage soils to 11.8 in the older oak stand.

Olson (1958*a*) reported similar trends for comparable measurements (bulk density, texture, pH, Ca, organic C, total N and C:N ratios). He has also suggested (Olson 1958*a*) that part of the silt content of the oldest dune may be due to a "trace" of loess received shortly after the last two glacial retreats.

Analysis of variance for soil chemical properties showed that most of the within-site variation was due to differences among subsites within the sites rather than to analytical variation.

TABLE 2. Extractable ions, pH, % organic C, total N and C:N ratios for soils from different stages of primary sucession on the Indiana Dunes and different stages of secondary succession on the New Jersey Piedmont. Each value is the unweighted mean (± standard error) of five subsites per site with five replicates per subsite, except for PO_4-P which is a site-composite with five replicates per site. Within each column different superscript letters indicate significantly different sites ($P < .05$) based on analysis of variance. Samples were collected in August 1978.

Site	kg/ha									
	NO_3-N	NH_4-N	PO_4-P	Ca	K	Mg	pH	% organic C	% total N	C:N
A. Primary sere										
Sand	0.01 (0)^a	1.12 (0.08)^a	2.85^a	287 (4)^a	45.4 (12.1)^a	67.1 (0.5)^a	8.1 (0.1)^a	0.06 (0.006)^a	0.002 (0.0005)^a	31.8 (10.5)
Grass	0.01 (0)^a	0.57 (0.08)^b	3.10^a	323 (10)^{ab}	64.1 (11.3)^b	69.1 (1.5)^a	7.8 (0.1)^a	0.13 (0.01)^b	0.008 (0.0006)^b	29.4 (6.7)
Grass + shrub	0.07 (0.04)^b	0.97 (0.17)^a	2.52^a	403 (16)^{bc}	34.0 (6.6)^a	71.6 (5.3)^a	7.7 (0.2)^a	0.17 (0.006)^c	0.005 (0.002)^b	21.0 (1.3)
Pine	0.01 (0)^a	2.09 (0.35)^c	2.76^a	571 (80)^c	77.4 (12.1)^{bc}	95.4 (3.3)^b	6.5 (0.1)^b	0.77 (0.15)^d	0.041 (0.001)^c	18.6 (3.8)
Oak(1)	0.04 (0.03)^{ab}	4.78 (1.43)^d	31.5^b	629 (126)^c	88.4 (21.1)^c	124.0 (5.7)^c	5.9 (0.4)^c	1.55 (0.15)^e	0.112 (0.023)^d	14.8 (2.5)
Oak(2)	0.11 (0.04)^c	3.26 (0.34)^d	14.0^c	208 (10)^d	94.6 (5.5)^c	31.5 (1.0)^d	4.2 (0.1)^d	2.03 (0.19)^f	0.110 (0.023)^d	11.8 (5.1)
B. Secondary sere										
Annual	2.24 (0.17)^a	2.61 (0.53)^a	95.0^a	966 (26)^a	225 (15)^a	126.4 (2.4)^a	5.0 (0.02)^a	1.28 (0.08)^a	0.118 (0.005)^a	11.0 (1.1)
Perennial	0.87 (0.15)^b	2.37 (0.28)^a	61.4^b	934 (40)^a	165 (12)^b	134.9 (7.3)^a	4.9 (0.07)^a	1.36 (0.02)^a	0.128 (0.010)^{ab}	10.7 (0.8)
Shrub	1.63 (0.04)^c	2.75 (0.17)^a	106.0^a	754 (66)^b	239 (3)^a	97.2 (11.2)^b	4.9 (0.02)^a	1.66 (0.19)^a	0.137 (0.005)^b	12.1 (1.4)
Forest	2.33 (0.27)^a	3.56 (0.18)^b	35.7^c	325 (40)^c	154 (9)^b	29.2 (3.0)^c	4.4 (0.06)^b	3.22 (0.91)^b	0.164 (0.005)^c	19.7 (5.7)

TABLE 3. Most-probable-numbers (MPN) of ammonia-oxidizing bacteria (cells/g dry soil) along a primary sere at the Indiana Dunes and a secondary sere on the New Jersey Piedmont. Values are unweighted means of three subsites; 95% confidence limits appear in parentheses. Different superscript letters within a column indicate significantly different ($P < .05$) sites based on these confidence limits.

Site	MPN
A. Primary sere	
Sand	370* (0–1110)[a]
Grass	2400 (1840–2960)[b]
Grass + shrub	500 (0–1650)[a]
Pine	530 (0–1450)[a]
Oak(1)	2400 (1620–3180)[b]
Oak(2)	240* (0–710)[a]
B. Secondary sere	
Annual	100 000 (38 000–162 000)[a]
Perennial	167 000 (0–396 000)[ab]
Shrub	113 000 (29 000–196 000)[a]
Forest	25 000 (0–51 000)[b]

* Two of the three subsites in these sites had <90 cells/g; these were treated as zeros.

Significant differences in the numbers of ammonia-oxidizing bacteria among sites in this sere during August were few, despite a relatively large number of replicate tubes per dilution, and no successional trend was apparent (Table 3A). The grass and the younger oak sites apparently had higher populations of nitrifiers than the others.

Secondary sere.—Bulk density along the secondary sere (Table 1B) was somewhat higher earlier in the succession; the measured density of the forest soil (1.0 g/cm^3) is in close agreement with values reported by Ugolini (1964) and Lang and Forman (1978). Water-holding capacity was apparently greatest in the old-growth forest soils, about 40% by mass at field capacity. No significant differences in soil texture among these sites were apparent. Overall values of 21% sand and 69% silt are in general agreement with Ugolini's (1964) values for the old-growth forest.

Calcium, Mg, pH, organic C, total N, and the C:N ratio all appeared to change significantly with succession (Table 2B). Ca, Mg, and pH were all higher earlier in succession, though the differences in pH among sites were not great. Organic carbon was lowest in soils from the three early stages (about 1.4% vs. 3.2% in the forest) as was total nitrogen (0.12% vs. 0.16%). The C:N ratio of the upper 15 cm of soil increased with succession from 10.8 in the first two sites to 19.7 in the old-growth forest, with substantial subsite variation in the forest. The C:N ratio in particular soil horizons may be quite different; Lang and Forman (1978), for example, reported a C:N ratio of 6.0 in the humus layer of the old-growth forest. While differences among sites exist for concentrations of NO_3-N, NH_4-N, K and acid-soluble PO_4-P, no consistent trends could be identified (Table 2B). As with the results from the primary sere, most of the within-site variation was due to variation among subsites within the sites rather than to analytical variation.

The number of ammonia-oxidizing bacteria in the forest soil (25 000 cells/g) was significantly less than the number in the earlier stages (about 130 000 cells/g; Table 3B).

Incubations

Primary sere.—Both net nitrogen mineralization and nitrate production increased consistently through the first five sites of the primary sere (Table 4, Fig. 1). The largest increase in both mineralization and nitrate production occurred between the grass + shrub site and the pine site.

Mineralization and nitrification rates of soils collected in May, August, and January varied significantly, with the August values generally below those from the other times. The relative rates of nitrogen mineralization and nitrate production among the sites remained the same, however. Nitrate production closely reflected nitrogen mineralization except in the old-growth oak site and perhaps the sand site in May (Fig. 1).

Secondary sere.—The only consistent difference among sites in the secondary sere was that the old-growth forest had significantly higher net nitrogen mineralization and nitrate production than the three younger sites (Table 5, Fig. 2). The results from May, August, and December incubations did not vary consistently in all sites, but both net nitrogen mineralization and nitrate production were low in the perennial herb and shrub sites in December.

Nitrate production was closely correlated with nitrogen mineralization in all of the sites at all times, except that nitrate production was rather low relative to mineralization in the shrub stage in May (at 15 d only) and in August and December (at 30 d only) (Fig. 2).

DISCUSSION

If the hypothesis that nitrification is progressively inhibited in the course of ecological succession (Rice and Pancholy 1972) is correct, we would expect our incubations to yield two results. First, the amount of nitrate produced in the incubations (in the absence of nitrate uptake, leaching, and substantial denitrification) should decrease in the older sites. Such a decrease in nitrate production could result from either a lower rate of nitrogen mineralization or from a lower rate of conversion of mineralized nitrogen to nitrate; the hypothesis is concerned with the latter transformation only. Consequently, we would further expect that nitrate would represent a progressively smaller proportion of the net nitrogen mineralized in each sere.

The results of this study do not yield the pattern

TABLE 4. Net nitrate and total mineral nitrogen (ammonium plus nitrate) production (μg N per g dry soil per incubation period) in incubated soils collected along a primary sere at the Indiana Dunes in May, August and January. Values reported are 15-d and 30-d N contents minus initial N contents. Each value is the unweighted mean (±SE) of five subsites with three replicates per subsite in May and five replicates per subsite in August and January. Mineral-N production can be less than NO_3-N production because the NH_4-N pool size can decrease during incubation. Common superscript letters in a column indicate no significant difference ($P < .05$) between sites as determined by analysis of variance. . . . indicates no data.

		NO_3-N production		Mineral-N production	
Month	Site	15-d	30-d	15-d	30-d
May	Sand	1.68 (0.22)[a]	2.14 (0.11)[a]	1.75 (0.29)[a]	5.51 (1.88)[a]
	Grass	1.88 (0.62)[a]	3.39 (0.66)[a]	1.91 (0.42)[a]	3.84 (0.55)[a]
	Grass + shrub	2.63 (0.38)[a]	3.87 (0.63)[a]	2.38 (0.39)[a]	4.74 (0.56)[a]
	Pine	4.68 (0.69)[b]	13.4 (4.5)[b]	6.65 (1.93)[b]	16.6 (5.5)[b]
	Oak(1)	10.3 (1.8)[c]	21.3 (4.6)[c]	8.92 (1.04)[b]	21.5 (3.1)[c]
	Oak(2)	. . .	. . .	. . .	. . .
August	Sand	0.53 (0.04)[ab]	0.38 (0.06)[a]	0.36 (0.04)[a]	−0.06 (0.04)[a]
	Grass	0.53 (0.25)[ab]	0.94 (0.43)[ab]	0.38 (0.22)[a]	1.37 (0.53)[b]
	Grass + shrub	1.39 (0.15)[b]	2.44 (0.49)[b]	1.15 (0.15)[b]	2.16 (0.43)[b]
	Pine	3.64 (0.70)[c]	7.99 (1.33)[c]	5.09 (0.69)[c]	10.8 (1.3)[c]
	Oak(1)	4.13 (1.46)[c]	12.1 (3.0)[d]	6.08 (0.63)[d]	13.6 (2.8)[c]
	Oak(2)	0.43 (0.11)[a]	1.16 (0.66)[ab]	6.18 (0.81)[d]	13.1 (1.0)[c]
January	Sand	. . .	. . .	. . .	. . .
	Grass	. . .	. . .	. . .	. . .
	Grass + shrub	1.32 (0.10)[a]	2.56 (0.12)[a]	0.90 (0.09)[a]	1.91 (0.19)[a]
	Pine	4.53 (1.50)[b]	12.0 (4.0)[b]	3.71 (1.79)[ac]	10.7 (3.9)[b]
	Oak(1)	8.23 (3.95)[b]	27.8 (14.9)[c]	9.77 (5.35)[b]	26.7 (13.9)[c]
	Oak(2)	0.05 (0.02)[a]	0.21 (0.08)[a]	4.69 (1.36)[bc]	11.1 (1.7)[b]

predicted by the hypothesis. Overall nitrate production increased with successional age until the last stage of the primary sere, while nitrate production in the secondary sere showed no consistent pattern except that soils from the oldest stage produced the most nitrate. Moreover, most of the nitrogen mineralized was transformed to nitrate in most of the sites. Only in the older oak site in the primary sere was there clear, consistent evidence that nitrogen was mineralized but not converted to nitrate. Similar though less striking results were observed at times in the shrub site in the secondary sere. In any case, these results show no clear evidence for a successional trend in the inhibition of nitrification. In this they conform with all of the previous studies in which nitrification potentials have been measured (Coile 1940, Lamb 1979, Montes and Christensen 1979).

We believe that the evidence presented here is more appropriate for studying the changes in nitrification in succession than are examinations of the instantaneous pool sizes of ammonium and nitrate or of the population sizes of nitrifying bacteria. In fact, for reasons discussed earlier, both pool size and population measurements alone would have yielded misleading conclusions. For example, the older oak site in the primary sere had the highest soil nitrate pool size that we observed in August 1978 (Table 2A), yet it was the one site where nitrification was clearly prevented or delayed (Fig. 1). Similarly, the old-growth forest site in the secondary sere had the lowest populations of *Nitrosomonas* in that sere (Table 3B), but the highest rate of nitrate production (Table 5).

On the other hand, our measurements reflect potential nitrification under controlled conditions, and not actual rates of nitrification in the field. If our incubations systematically underestimated nitrification in early successional sites or overestimated it in late successional sites, the Rice and Pancholy (1972) hypothesis could be correct for our seres. The one way that this might occur is if nitrification is suppressed by highly labile inhibitors later in succession. Such compounds would have to be continuously added to the soil by throughfall or root exudation (Moleski 1976), and they would have to be rapidly inactivated since no evidence for their importance can be found after 15 d of incubation in samples from most sites. Most compounds which have been suggested as inhibitors are highly recalcitrant (Rice 1965, Rice and Pancholy 1973, 1974), and their influence would not disappear in a brief incubation. Nonetheless, this mechanism is possible (and testable), although we know of no reason why only late successional species would produce such inhibitors.

In general, our results suggest that rates of nitrification may be controlled by rates of nitrogen mineralization in these seres. Rates of both nitrogen mineralization and nitrification were higher later in our seres, but we believe that this explanation can be extended to situations in which nitrification rates are higher in disturbed or early successional systems. Sites where high rates of nitrification following disturbance have been demonstrated include a northern hardwoods forest shortly after clearcutting (Smith et al. 1968, Likens et al. 1970) and a tulip-poplar forest

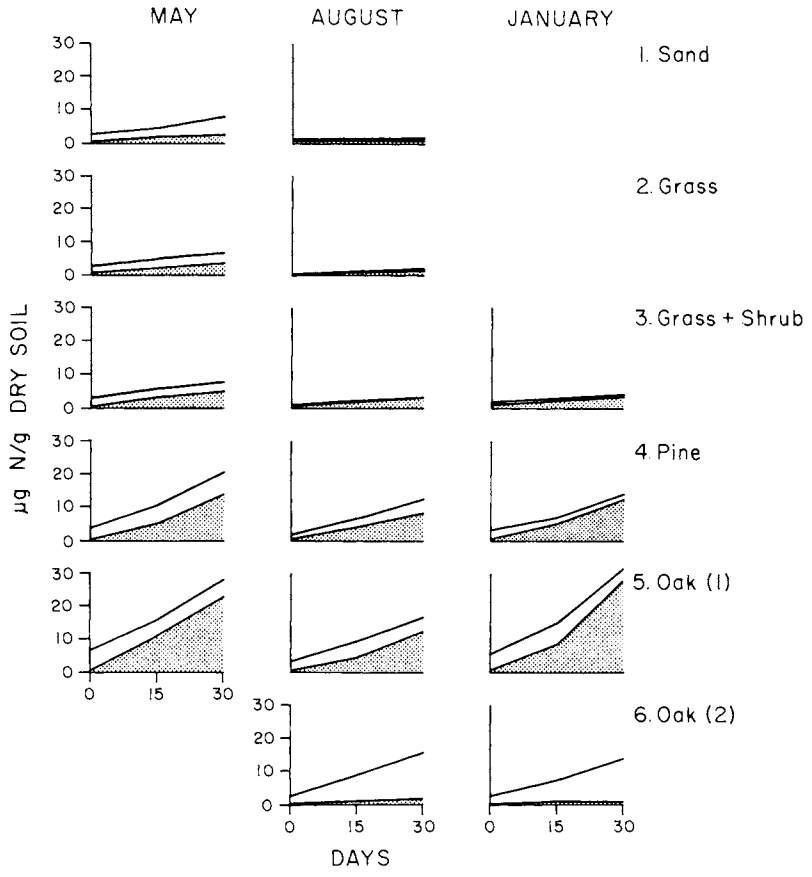

FIG. 1. Net NO_3-N and total mineral nitrogen (NH_4-N plus NO_3-N) accumulation in soil samples collected along a primary sere at the Indiana Dunes in May, August and January 1978–79 and incubated for 0, 15 and 30 d. The upper line in all cases represents total mineral-N accumulation (not net production as in Table 4); the lower line (shaded underneath) represents NO_3-N accumulation.

shortly after stem girdling (Johnson and Edwards 1979). High rates of nitrification may also occur early in succession on recently fertilized agricultural land (Woodwell 1979); the seres studied by Rice and Pancholy (1972, 1973, 1974) and Haines (1977) may fall into this category, although they do not report fertilization history. All of these situations have in common a high availability of mineral nitrogen early in succes-

TABLE 5. Net nitrate and total mineral nitrogen production (μg N per g dry soil per incubation period) in incubated soils collected along a secondary sere on the New Jersey Piedmont in May, August, and December. The results are treated as in Table 4.

Month	Site	NO_3-N production		Mineral-N production	
		15-d	30-d	15-d	30-d
May	Annual	9.05 (1.22)[a]	9.12 (0.88)[a]	8.45 (1.12)[a]	8.27 (0.94)[a]
	Perennial	7.16 (1.25)[a]	16.6 (2.2)[b]	7.10 (1.40)[a]	16.4 (2.1)[b]
	Shrub	4.88 (2.05)[b]	14.0 (2.3)[b]	9.37 (2.28)[a]	14.6 (2.3)[b]
	Forest	18.2 (1.2)[c]	29.7 (1.3)[c]	18.4 (1.1)[b]	25.9 (3.9)[c]
August	Annual	4.64 (1.06)[a]	14.0 (1.4)[a]	4.96 (0.83)[a]	13.6 (1.3)[ab]
	Perennial	3.84 (0.35)[a]	15.8 (0.9)[a]	3.39 (0.43)[b]	15.8 (0.9)[b]
	Shrub	1.68 (0.57)[b]	9.78 (1.33)[b]	2.05 (0.64)[c]	13.3 (2.0)[a]
	Forest	13.3 (0.1)[c]	26.9 (2.1)[c]	12.3 (0.9)[d]	24.9 (2.1)[c]
December	Annual	0.64 (0.19)[ab]	8.42 (0.93)[a]	−0.38 (0.21)[a]	8.05 (0.81)[a]
	Perennial	−0.16 (0.05)[a]	3.87 (1.61)[b]	−0.55 (0.11)[a]	4.47 (1.64)[b]
	Shrub	1.00 (0.50)[b]	4.58 (1.63)[b]	0.28 (0.63)[a]	5.61 (3.25)[b]
	Forest	16.5 (2.5)[c]	28.3 (4.9)[c]	12.3 (3.3)[b]	25.4 (4.5)[c]

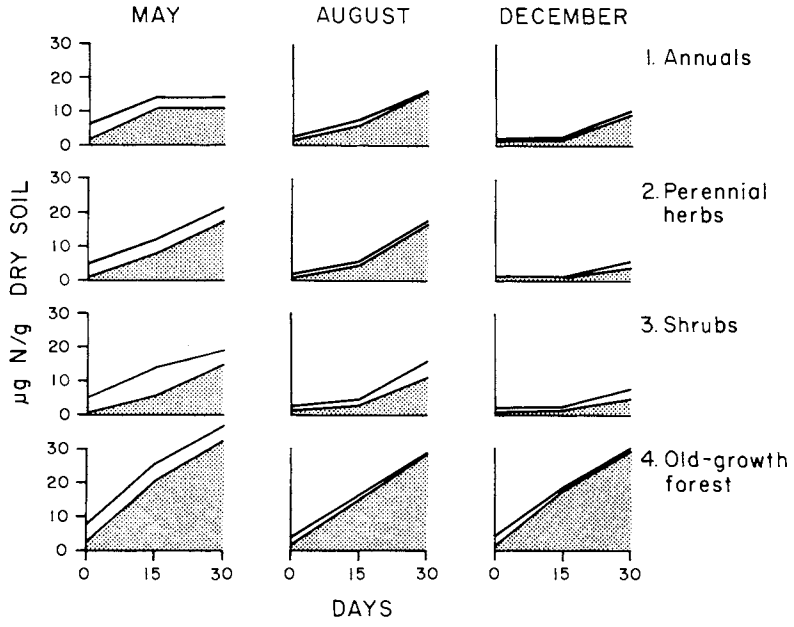

FIG. 2. Net NO_3-N and total mineral nitrogen accumulation in soil samples collected along a secondary sere on the New Jersey Piedmont in May, August and December 1978 and incubated for 0, 15 and 30 d. See Fig. 1 legend for further explanation.

sion. This nitrogen availability is a consequence of accelerated nitrogen mineralization and low plant nitrogen uptake in disturbed forests (Vitousek and Reiners 1975, Vitousek and Melillo 1979, Bormann and Likens 1979) and of nitrogen fertilization in old fields. Thus the apparent pattern of rates of nitrification with succession reported by Rice and Pancholy (1972) and others may be caused not by progressive allelochemical inhibition of nitrification in older sites, but by systematically elevated nitrogen availability early in certain kinds of succession.

If this suggestion is correct, we would expect that the pattern of nitrification in primary succession should be the reverse of that suggested by Rice and Pancholy (1972). Primary seres start with a nitrogen-poor substrate and gradually increase in total-nitrogen pool size (and presumably nitrogen cycling) as a result of nitrogen fixation (Stevens and Walker 1970). Consequently, rates of nitrogen mineralization and nitrification should progressively increase for many years. The results from the Indiana Dunes sere are in accordance with this suggestion (Fig. 1). It is not clear that any consistent pattern should be expected in secondary succession.

While we believe that in general nitrogen mineralization potentials are a good predictor of nitrification potentials, a number of sites have been studied in which this association does not hold. Low rates of nitrate production in the presence of apparently adequate ammonium were found in our older oak site in Indiana and in several other systems (Ellenberg 1977, Melillo 1977, Nakos 1977, Johnson and Edwards 1979, Vitousek et al. 1979). The relatively low rate of nitrification in these sites could be caused by the allelochemic inhibition of nitrification (Rice and Pancholy 1972), or they could be caused by low pH (Weber and Gainey 1962), by competition between nitrifiers and decomposers for some other limiting nutrient (Purchase 1974), or by low initial populations of viable nitrifiers (Sabey et al. 1959). Johnson and Edwards (1979), for example, experimentally demonstrated that low initial population sizes were probably the most important of these factors in a Tennessee tulip-poplar forest. Further research designed to determine which of these mechanisms are important and why they occur in particular kinds of sites would be most useful to our understanding of the control of nitrification.

CONCLUSIONS

1) A progressive decrease in the rate of nitrification with successional time was not observed in either a primary sere on the Indiana Dunes or a secondary sere on the New Jersey Piedmont.
2) Rates of nitrification in 9 of the 10 sites studied were strongly correlated with rates of nitrogen mineralization. Systematic variations in nitrogen availability in the course of succession may control nitrification more strongly than does allelochemic inhibition.

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