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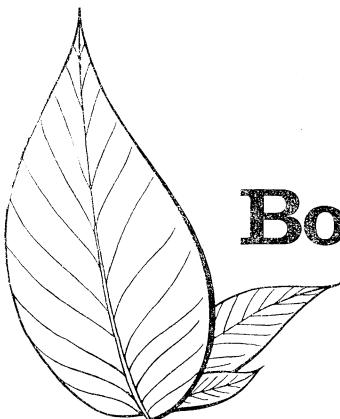
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RATES OF SUCCESSION AND SOIL CHANGES ON SOUTHERN LAKE MICHIGAN SAND DUNES¹

JERRY S. OLSON

Introduction

HENRY CHANDLER COWLES pointed to the Lake Michigan sand dunes as a classic case history of successional change in the landscape. Some of the dunes' "strategic advantages" for ecological research now help us gain deeper understanding of succession. New data on dune ages open new possibilities for estimating long-term rates of succession and soil development. The present study follows the changing soil-plant relations during dune development, from the barren, shifting sand to a complex physical-biological system—the old dune forest. These relations bear on some specific questions which COWLES had to leave unanswered and on some general issues of succession and climax which have been controversial ever since his pioneering dune studies helped to found dynamic ecology.

Some grasp of the succession idea probably dates back to the dawn of agriculture. Since 1685 at least (11), there have been many writings on plant colonization and soil formation on bogs, rocks, dunes, and other bared scars in the earth's vegetation mantle. But it was not until the 1890's that the dune studies of WARMING and COWLES catalyzed the emergence of a new ecological tradition.

The age sequence of dunes, with progressively more developed vegetation on ridges farther from the shore, made the *fact* of successional change seem especially vivid in dunes like those of Denmark (56).

¹ Much of this paper is based on portions of a Ph.D. dissertation (41), research for which was supported in part by Dr. CHARLES E. OLMFSTED's grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago and by Robert Ridgway and Charles L. and Frances K. Hutchinson (Wychwood) Fellowships in the Department of Botany.

and Lake Michigan (13). Dune studies soon vitalized ecology in many other regions (3, 22, 31, 42, 47, 48, 53, 55, 61, and many studies cited in this brief sample of references).

Probably the spark that made the *idea* of succession catch fire so rapidly was its extension of the concept of orderly development of natural systems. Not only the life-cycle of the individual and the evolution of the species but the transformation of the biological community (57) and its habitat—what TANSLEY (51) later called the ecosystem—at last seemed to fall within the domain of natural law. COWLES (13, 14) cited many earlier papers dealing separately with dune floras or dune geography, but he wove the physical and biological threads together into a fabric showing orderly design:

Very little previous work has been done on the geographic phase of the subject from the standpoint of the historical development and the order of genetic succession of the various dune types [or] the modifying influence of vegetation on topography. These latter phases of the subject have given a color to the work which has resulted in this paper [13:386].

The ecologist must endeavor to discover the laws which govern the panoramic changes. . . . Plant formations should be found which are rapidly passing into other types by reason of changing environment. These requirements are met *par excellence* in a region of sand dunes. . . . [They] furnish a favorable region for the pursuit of ecological investigations because of the comparative absence of the perplexing problems arising from previous vegetation. . . . By burying the past, the dune offers to plant life a world for conquest, subject almost entirely to existing physical conditions. The primary motive, then, which prompted this present study was the feeling that nowhere else could many of the living problems of ecology be solved more clearly; that nowhere else could ecological principles be subjected to a more rigid test [13:95-96].

COWLES's enthusiastic teaching, using the dunes as his outdoor laboratory, has indeed colored ecological thought ever since. His explorations charted the field of ecology as "a world for conquest" but left problems in many of its provinces to be surveyed and settled by others. SHELFORD (50) and many other zoölogists (cited in 1: 567) showed how the animal populations correlated with plant communities and contributed to the general concept of the biotic community (7). PARK (43) and others also expanded the microclimatic studies of FULLER (18) in hopes of finding a physiological basis for succession. However, except for KURZ's study of soil pH (29) and passing attention in soil-survey bulletins (8, 9, 54), our knowledge of dune soils represented a major gap in the over-all picture of the sand-dune ecosystem.

SALISBURY (47, 48) took advantage of willow growth rings and old maps of English dunes several centuries old to date the rates of succession and soil formation. Similar methods and direct photographic evidence of rapid early changes in dune development were supplemented in the present study by radiocarbon dating of the ancient Great Lakes shore lines and dunes, some of them at least 12,000 years old.

We shall see that most of the improvement in soil organic matter and nutrients appears to have been accomplished within the first thousand years or so after the dune surface becomes stabilized by vegetation. Leaching of nutrients by soil acids continues slowly over a longer period of time. Quantitative estimates of the rates of change of these opposing processes of improvement and deterioration suggest that soil improvement will not continue indefinitely and that some conditions may eventually get worse instead of better as far as most plants are concerned.

COWLES clearly pointed out that rich mesophytic forests in Indiana, developing through succession of basswood → red oak → sugar maple (*Tilia americana*—*Quercus rubra*—*Acer saccharum*), were restricted to steep lee slopes and protected pockets of relatively young dunes. He knew that the succession of pine → black oak (*Pinus banksiana* or *P. strobus*—*Quercus velutina*) prevailed on the majority of Indiana dune surfaces, including all the oldest. But he wondered if there was a possibility that the oldest black oak dunes might also eventually develop into a mesophytic forest as a result of further soil improvement. Present results make this seem less plausible to us than it seemed to COWLES, and especially to others who accepted his very tentative speculation without the cautious reservations he expressed in his own writings. The implications of these results tend to lengthen the shadow of doubt that is being cast on the rigid theory of convergence of ecological succession to a uniform climatic climax. But the analysis of rates of change helps us to understand ecosystems

—whether they are stable or not and whether they are approaching the same limiting condition or very different conditions under different circumstances.

Dune origin

Only a few essential points of background on the formation and the age of dunes will be reviewed here because the physical aspects of the over-all problem of dune development are to be covered in a series of papers in the *Journal of Geology*, the first appearing in March, 1958.

FORMATION OF THE DUNES

LAKE MICHIGAN AND FORMER SHORE LINES.—During and after the retreat of the glaciers from the Great Lakes region, the changing shore lines of the Lake Michigan Basin left several distinct beach and dune systems about 25, 40, and 55 or 60 feet above the present mean lake level of 580 feet above sea level (fig. 1). The last 15 or 20 feet of lowering was more gradual and left a nearly continuous sequence of beaches spread over several miles in western Gary, Indiana (figs. 1A, 2), but compressed into a narrower belt farther east (figs. 1B, 3, 4). Superimposed on this over-all lowering of lake level have been episodes of a few years, decades, or perhaps centuries of unusually low or high lake level. These seem to account, respectively, for the alternate widening of beaches and dunes and the narrowing by wave cliffing and blowout activity.

SAND HISTORY.—During most of the lake's history, sand which was eroded from wave-cut cliffs in glacial deposits along some portions of the shore line was washed along the beach to the main dune regions, especially in Indiana and many areas in Michigan. Selective transport of the sand by water and then by wind eliminated the coarser and finer particles and left an unusually well-sorted sediment when the material was finally deposited in the dune.

DUNE WINDS.—Strong winds sweeping from the open lake across the barren beach soon become saturated with all the sand they can carry and are forced to drop most of their load as soon as they encounter the dune-building vegetation. Anemometer measurements account for this vegetation influence in terms of a thirty-fold increase in the depth of the film of relatively calm air hugging the sand surface or the effective aerodynamic surface roughness of the dune.

LAND FORMS.—The orientation of vegetation along the beach or subsequent straightening of dunes by wave cliffing results in linear beach margin ridges or *foredunes*, parallel with the shore line (fig. 5). In exposed situations either foredunes or wave-cut cliffs that undermined the vegetation cover of large old dunes may undergo wind erosion on the lakeward

side and migration of the resulting sand to the leeward side. The resulting *blowout* dunes smother other vegetation as they advance (figs. 4, 6, 7) and may pile up on older dunes until they reach heights of about 60 meters in Indiana and about twice that height in Michigan. Large active, or recently active, dunes occur (or occurred prior to natural or artificial stabilization) from the south tip of the lake (fig. 2) eastward. Typical blowouts protruding over older stabilized dunes are shown in black in figure 3 and in white on the left of figure 4. The latter air photo shows typical dune forms stereoscopically. The sever-

(30) and the writer (41 and a forthcoming publication) describe how marram grass (*Ammophila breviligulata*) and other dune-builders adapt to burial by sending up long internodes in early spring through sand deposited each preceding winter, followed by shorter internodes in summer when the growing point approaches the new dune surface. The resulting morphological cycles faithfully record plant- and dune-growth rates; they show how long the most recently active foredune ridge (labeled "F1" in tables 2 and 3) had been growing upward from the rhizomes that first invaded the beach from the next older

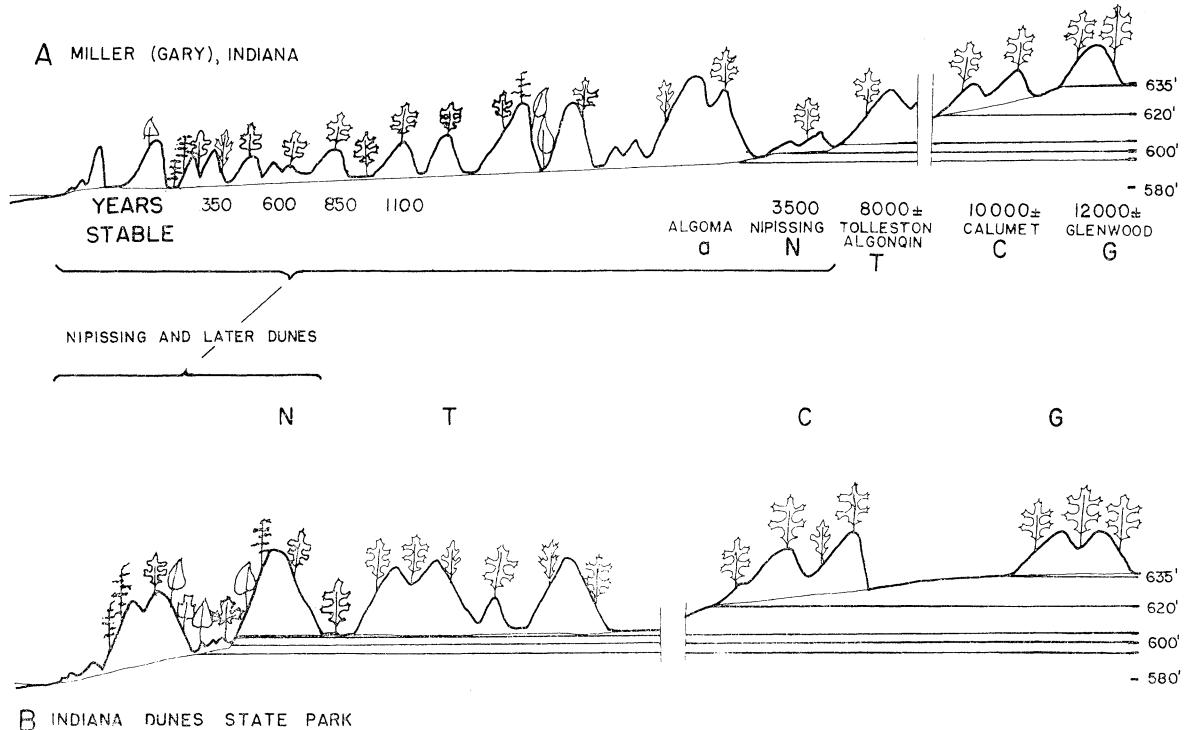


FIG. 1.—Diagrammatic profiles across Indiana sand dunes. Successively older dune systems originated along earlier and higher beaches. Later dunes are compressed into a narrower

band eastward from Gary, profile A (see fig. 2), to the Indiana Dunes State Park area, profile B (see figs. 3 and 4).

al belts of older stabilized dunes shown diagrammatically on figure 1 were mapped on figures 2–4 on the basis of topographic peculiarities as well as by elevations of the shore lines with which they were associated.

DUNE-BUILDING VEGETATION.—COWLES (13) vividly described how plants and dunes grow up together. FULLER (17) traced how the cottonwood (*Populus deltoides*)² association develops from minute seedlings on the margin of a beach or blowout pond, thrives under sand burial, and, finally, may dominate the summit of an otherwise barren blowout dune. LAING

foredune ridge (F2) and show when this new dune intercepted sand that otherwise would have been destined for the dune behind it, thereby leading to the latter's stabilization.

DUNE AGES

The above inference provides the first step in our soil chronology. While the fresh sand of the actively depositing foredune had been in place for only a few months, the ridge behind it had evidently been stable for 4–8 years prior to 1950—mostly about 6 years in the area sampled in the eastern end of the Indiana Dunes State Park.

Behind these two young foredunes was a third

² Nomenclature generally follows FERNALD (15). Local floras are provided by PEATTIE (45) and by PEPOON (46).

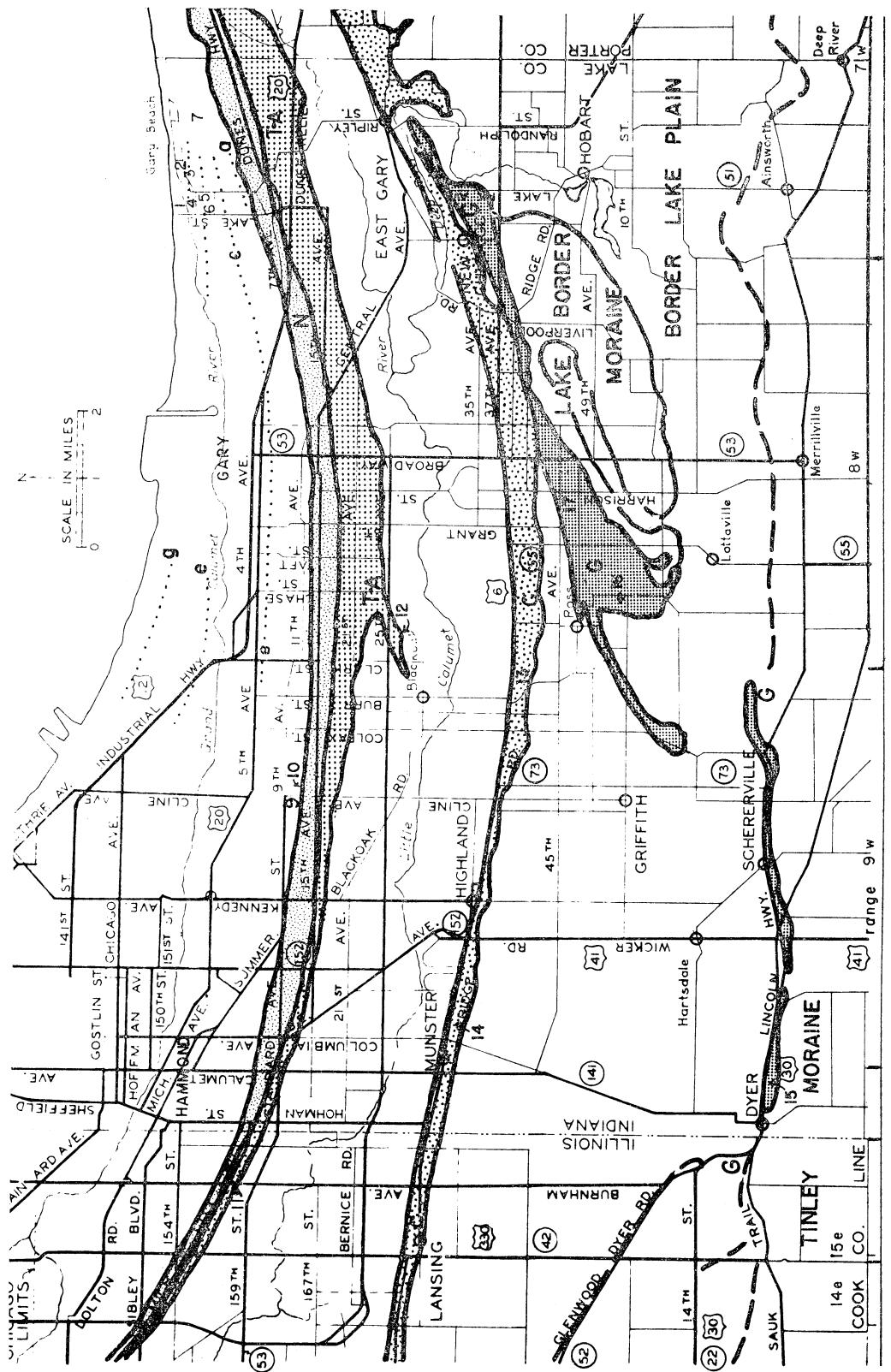


FIG. 2.—Dunes of northern Lake County, Indiana, and vicinity. Successively younger beaches (G = Glenwood, C = Calumet, T-A = Tolleston-Algonquin, N = Nipissing) bordered the northern edges of these dune belts as lake dropped to lower level following each stage. Post-Nipissing beaches have no dunes in west, low dunes in central Gary (especially along beaches labeled a, e, e, g), and rapidly increasing dunes from Lake Street eastward.

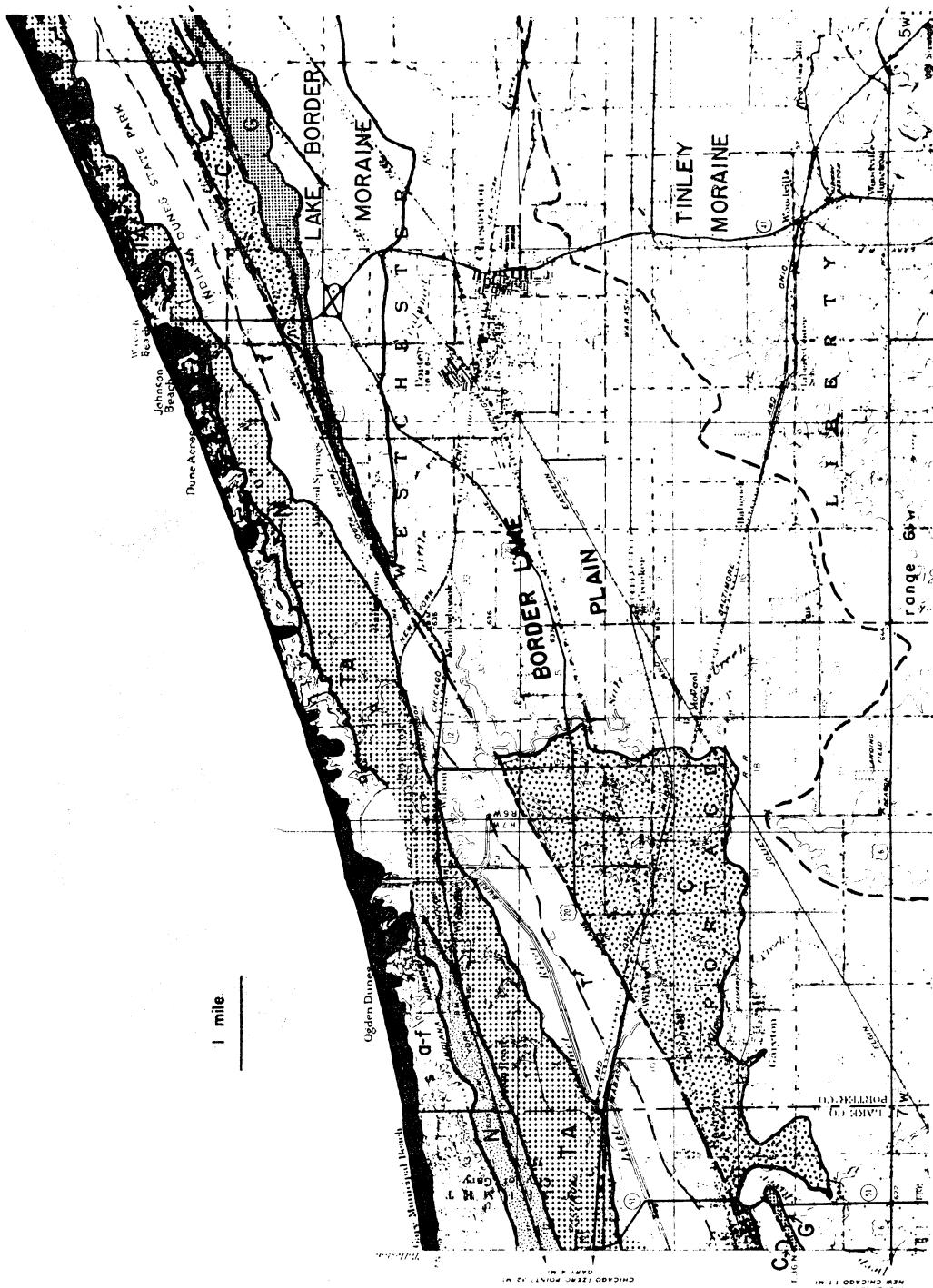


Fig. 3.—Dunes of northern Porter County, Indiana. Glenwood (G) and Calumet (C) dunes are banked along north edge of Lake Border moraine (which was cliffed near Baileytown). Tolleston-Algonquin (TA) dunes developed along an offshore bar north of what is now wet interdune lowland (small T was minor beach south of the former lagoon). Nipissing correlations proposed here are tentative. Post-Nipissing dune belt narrows eastward as bottom slope steepens and exposure to more westerly winds increased intermittently wave-cliffing and blowout migration. Black areas of active or recently stabilized dunes show them parallel to beaches in west, more frequently perpendicular to east where blowouts protrude over older dunes (see figs. 4 and 6).

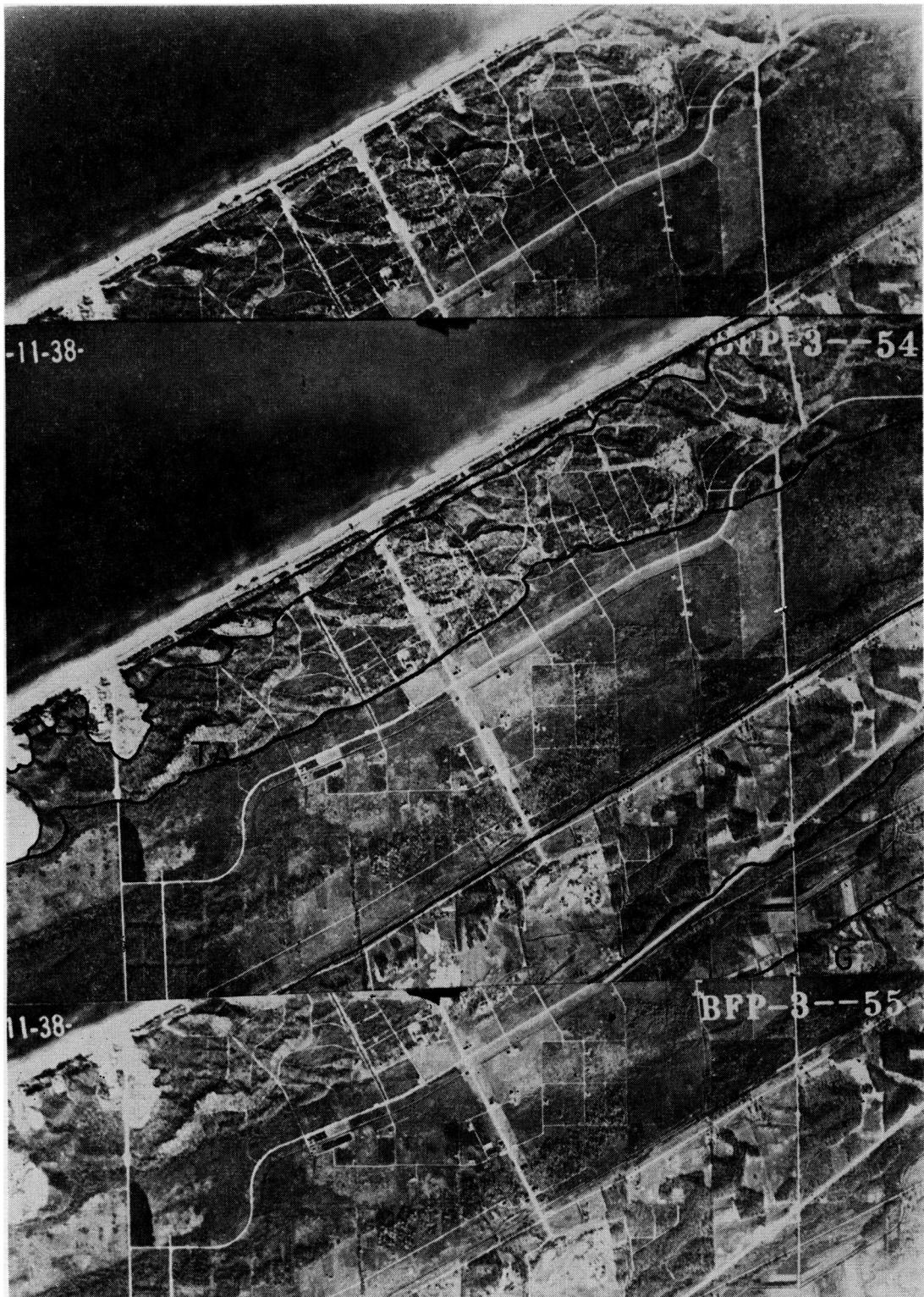


FIG. 4.—Stereoscopic air photo of Beverly Shores, north-eastern Porter County, Indiana. (For three-dimensional image, view upper panel with right eye and upper part of center panel with left eye, using cardboard to separate images; lower panel corresponds with lower half of center panel.) From north to south, note submerged sand bars, white beach and foredune, steep forested cliff dunes parallel with lake, from which high Nipissing(?) dunes migrated eastward. Tolleston-Algonquin (TA) dunes may have remained partly active during post-glacial hot and/or dry climate when southwest winds were

more effective. "TA," "C," and "G" are located near Beverly Shores sample plots. Beech sprout on latter dune is near large beech tree on north-facing Glenwood wave-cut cliff. Note how recent blowouts in Indiana Dunes State Park on west edge of photograph show north winds more effective than do most of fixed dunes. Big Blowout and Link's Blowout (north of it) are shown in figures 7 and 6, respectively. Numbered State Park blowout plots lie along west side of blowout bisected by road (see fig. 10C).

foredune ridge (F3 in tables 2–4). Ages of invading jack pines (*Pinus banksiana*) provided a minimum age estimate of about 18 years for this surface, while firsthand accounts (personal communication from Dr. G. K. K. Link) and reconstruction of physiographic history indicated that the area sampled for soil had been active only 20 years before. Hence an age of 20 years was assigned for these samples, although some of the vegetation just at the foot of the wave-cut cliff lying behind these foredunes (column H in table 2) may belong to a still older surface.

Burial of cottonwood branches within the previous 11 years provides an upper limit on the duration of surface stability of a young blowout at Ogden Dunes (B2OD in table 3). Similarly, slight burial of the fence at the east boundary of the Indiana Dunes State Park, presumably erected in 1925, when the park was established and mapped, provides an upper age limit for a similar dune surface here (B2SP in tables 3 and 4). On the other hand, lack of burial of the same fence on a nearby blowout pocket (B3SP) showed that sample portions of it had been stable for at least 25 years, even though some sand movement along the exposed upper margins has continued more recently (fig. 10C).

On many other blowout surfaces at the State Park and Ogden Dunes (B4SP, B5SP, B4OD, and B5OD in tables 3 and 4), ages of the oldest pines provide minimum estimates of surface age. Prompt pine invasion on foredune 3, where abundant seed was available, suggests that the surface itself may not have been too much older.

Dates for the long series of Nipissing (N), Algoma, and later ridges (figs. 1–3) are contingent upon the validity of tentative radiocarbon dates of slightly over 3500 and 2500 years for the two named stages, the correlation of these stages with the last 600-foot and 595-foot shore lines in our area (see 24), and the assumption of a fairly uniform rate of shore-widening for the younger ridges in the area of western Gary, Indiana, where this series is most complete. By tracing peculiar ridges, the inferred dates were extended farther east, where widening was slower and less regular (fig. 2, dotted lines).

Dates for the highest (Glenwood, Calumet, and Tolleston-Algonquin) shore lines are inferred from a number of self-consistent radiocarbon dates as being somewhat over 12,000, 10,000, and 8000 years, respectively (16).

The round numbers given in the preceding two paragraphs are a few hundred years younger than the current radiocarbon estimates for the shore lines in question, in order to allow roughly for an episode of activity prior to the stabilization of these dunes; clearly, this cannot be guessed exactly. Of course, the radiocarbon dates are subject to statistical errors

of several centuries—more for the older dates than the younger ones. Finally, there is room for alternative correlations and interpretations which may change the basis for some age computations.

Age estimates for young dunes are subject to less absolute error in years but to about the same percentage uncertainty as in old dunes. Although errors cannot be specified exactly, we might guess that a 10 or 20% deviation from the estimates given here might include most of the true values, while few values would fall outside 30 or 40% of the estimated value.

Computations of rates given below are thus not very precise, but their main conclusions would hold even if considerable age readjustments had to be made. Certainly, our present Great Lakes chronology is far superior to any available only a decade ago and covers a much longer period than most previous quantitative studies of succession.

Methods

Because of their unusual possibilities just outlined for estimating approximate rates of change, the dunes take on an added element of interest for ecological methodology. We are still left with the second problem of avoiding or at least recognizing areas which differ so greatly from one another in respects other than age that they cannot be properly considered as parts of a single successional or soil-age sequence. It is desirable to be more explicit about this difficulty before turning to the routine methods of analyzing vegetation and soil properties on chosen areas, because it has led to considerable confusion about this classic dune succession in the literature and recent textbooks.

For brevity the symbol E_d is used for the dependent variables of a local ecosystem: organisms, soil, microclimate, moisture status, and microrelief—all interdependent on one another and dependent on certain other “independent variables” which influence the development of the whole system. The symbol E_i is used for these independent variables, which are listed in table 1 and discussed below.

This dune study was originally conceived as a test case, designed to determine whether JENNY's (25, 26) approach to the factors of soil formation could advantageously be extended to the rest of an ecosystem (41). MAJOR (37) independently discussed this extension at length. He and JENNY considered in detail the special sense in which the “factors of soil formation” or factors conditioning vegetation or a whole community ecosystem had to be defined in order to avoid being confused with the “factors” conditioning individual plants, namely, the micro-environment factors, which are dependent variables as far as the whole ecosystem is concerned.

INDEPENDENT VARIABLES

The classic concept of *developmental* succession or soil formation on a barren surface like a dune—the “autogenic” succession of TANSLEY (51)—tacitly assumes a course of change of an ecosystem E_d that could proceed as a function of time, t , even if all other independent variables E_i remained constant. This last condition is implied by the subscript in equation (1a) which abbreviates the whole course of successional change.

$$E_d = f(t)_{E_i}. \quad (1a)$$

In special cases we can trace these changes at a single place by observations or photographic records (e.g.,

a general equation for ecological succession emerges:

$$E_d = f(t)_{E_i} + \sum \frac{\partial E_d}{\partial E_i} \Delta E_i + \epsilon. \quad (1b)$$

Specific methods of successional study (33, 51) are concerned with the evaluation of the three terms in this equation: estimating dune age (as outlined earlier), “standardizing” the other independent variables or separating them and relating them to the time factor, and the sampling of dependent variables such as vegetation and soil properties surveyed below.

The variables of table 1 are *physically* independent of the local ecosystem in that they are either predetermined at the time of surface stabilization (like initial substrate or parent material, surrounding

TABLE 1
FACTORS CONDITIONING DEVELOPMENT OF SAND DUNE ECOSYSTEMS
AFTER STABILIZATION

Independent variables	Range of variability admitted within main plots
Time (age since stabilization)	0–12,000+ years, ± 10 or 20% uncertainty
Initial substrate	Well-sorted dune sand parent material
Topographic relief	Level ($<10\%$ slope), moderately exposed by surroundings
Hydrographic factors	Moderate elevation (mostly 3–10 m.) above ground-water table or surrounding lowlands
Regional climate	Presently about 10° C. annual mean temperature (-4° to 23° monthly means). Near humid-subhumid boundary (85 cm. precipitation, N.S. quotient 400, THORNTHWAITE [52] P.E. Index 64+)
Biotic factors	
Available flora and fauna	Oak-hickory and beech-maple region species plus relics from northern hardwood-conifer and prairie regions available if other factors are suitable
Human influence	Probably accounts for widespread fire in presettlement and later times; main plots exclude burns of recent decades and cutting which was extensive and recent, as well as more drastically disturbed areas

fig. 7A, B). More commonly we must fall back on the old method of comparing a series of areas which differ in age.

Rarely if ever can sample areas be found that are exactly comparable in all independent variables except age, but areas may be sought where differences due to the variable of time are much greater than those due to other factors.³ We try to average over the inevitable field heterogeneity and minimize sampling or analytical errors, all of which add up to a chance element of random variability, denoted here by ϵ . By putting together the time effect, the effects of other independent variables, and random effects,

³ Specifically, differences or increments in other factors, ΔE_i , should be small enough so their effects on E_d , namely, the products of the partial derivatives $\frac{\partial E_d}{\partial E_i}$ multiplied by ΔE_i , are much smaller than the function which is here of primary interest, namely, $f(t)_{E_i}$. This follows if either the derivatives or the increments can be made sufficiently small (26, 37).

topographic relief, and hydrographic setting) or determined on such a large scale that the vicissitudes of the local system should generally have little effect on them (regional climate and biota). They may be *mathematically* independent of one another in that one does not completely determine another, even though their values may not be statistically uncorrelated. One can be evaluated by “holding” the others constant or nearly so, as was done for dune age in this study by restricting the range of conditions in the right-hand column of table 1.

Some plots which differed markedly from the “standardized” range of conditions were also added for purposes of contrast. These areas differed in topographic exposure and moisture conditions and in exposure to or protection from fire history. They were considered not as different “stages” in the same successional series but as parts of different successions, which could not all be sampled completely. Even within the “main” series used here a more

refined breakdown could no doubt be made if more data were available. JENNY's "factor-function" approach turned out to be a very valuable guide, even though there never is more than a tentative approximation to his ideal single-factor or multiple-factor combination model for the state of an ecosystem.

The dunes' "strategic advantages" for testing this approach include not only the new opportunities for estimating the time variable but also the possibilities for finding interesting combinations of the other factors. A wide range of climatic and biotic conditions is spanned between the prairie peninsula of Illinois and the spruce-fir forests of northern Michigan, but it was more instructive for immediate purposes to restrict attention to a small portion of this gradient in Indiana. As far as parent material is concerned, the dune sand is relatively uniform compared with most other sediments or weathering residues; with certain exceptions noted below, the organic and inorganic colloids developed almost completely during the course of succession. COWLES also emphasized the "strategic" advantage of working with dune successions along fresh-water shore lines where salt-spray gradients and saline soils are not confounded with distance from the shore (e.g., 42).

DEPENDENT VARIABLES

VEGETATION.—Small strip plots (ten 1 × 10 or 2 × 20 dm. strips) were useful for marram-grass populations, which were highly contagious in distribution (table 2). Larger plots were used for sand reed and little bluestem grasses. Nominal bunch diameter of the latter (fig. 8) corresponds to that of a circle having the circumference actually measured. Densities of other species of the grass communities (table 3) are based on still larger nested plots.

Species-area curves (fig. 9) based on these nested plots suggest no standard plot size adequate for representing the less abundant species and the local variations in density of the more abundant ones. Hence nested plots were used through the rest of the succession, with the larger plots sometimes serving to readjust estimates from the smaller ones when the latter were of the wrong order of magnitude.

Table 4 shows the drastic changes in order of magnitude in terms of a logarithmic scale of abundance. It shows *proportional* changes in density (one unit equals tenfold difference) and can be conveniently expressed like pH value:

$$\begin{aligned} \text{"proportional density"} &= pD \\ &= \log_{10} (\text{stems/hectare}) \\ &= 4 + \log_{10} (\text{stems/meter}) . \end{aligned}$$

In many cases a rapid inspection of a large temporary plot seemed more reliable than detailed counts on

small plots, especially for the less common and the more contagiously distributed species. Forest stand tables are here reduced to basal areas (table 5).

For convenience of reference and graphing (fig. 13) the tree, shrub, and herb species have been arranged in several groups designated by lower-case letters. A layer or group society or sociation often may be dominated by only one or two such groups. Diverse combinations of layer societies or synusiae can be found and usually can be related to significant ecological differences (32). Many of these probably correspond generally in scale with the "association" in the sense of GLEASON (22) and GATES (21) or BRAUN-BLANQUET (4) or the *Komplex* of northern European botanists. (Comparison of different phytosociological approaches in the same area of Netherlands dunes is provided by WESTHOFF [61] and VAN DIEREN [55].) Probably the still grosser unit, *Hauptkomplex*, corresponds in scale with the "society" of COWLES (13, 14) and the "association" in the broad sense of FULLER (19) and most other American ecologists. No attempt is made here to impose any of these community classifications on the dune vegetation or to document particular types in monographic style. Units of any rank are mentioned as convenient to characterize whatever vegetation happened to appear on datable plots having specified site and historical background. Some of the more important variations in vegetation still have to be outlined by general description until more intensive analyses can be made.

SOILS.—Profiles were observed extensively before and during sampling. Some individual profile collections involved the careful separation of L, F, and perhaps H layers of the forest floor in a sharp-edged metal frame 2-dm. square or an area of about 10^{-5} acres, and as many soil layers as could be separated. Usually changes were so gradual that arbitrary separations at 4, 8, 12, and 20 dm. were made, and one or more channel samples were taken between these limits so that the whole vertical profile was represented. To average over the obvious heterogeneity of surface soils, most plots also had composite samples of ten cores cut with a brass tube to a depth of 1 dm. below the bottom of the F layer. Data given in figures 15, 17, and 19 apply to this type of composite surface sample.

Weights of samples of known volume showed great differences in apparent density (fig. 18C). Slightly coherent aggregates bound by rootlets and fungi were gently crushed, and sticks, roots, and rare coarse mineral grains then were separated on nested 2-mm. and 1-mm. round-hole sieves. Careful quartering was necessary to provide individual samples for analysis without distorting the proportions of coarse organic debris and fine sand, silt, and organic dust.

In field and laboratory descriptions, colors of damp soil were standardized according to Munsell color sheet 10YR. Depth of carbonate leaching was determined with hydrochloric acid. Field estimates of pH value, to the nearest 0.2 unit with LaMotte color indicators, had the advantage of showing gradients with many small samples measured directly as they were picked from an exposed soil. They generally agreed with laboratory pH measurements made with a glass electrode on collected samples. Accuracy of the latter was limited by drift in the very poorly buffered sands and by fundamental difficulties in applying the concept of simple solution pH to colloidal suspensions.

Estimates of *organic carbon* were made for a few contrasting profiles (fig. 16) by ignition and adsorption of carbon dioxide on ascarite, correcting for CO₂ derived from carbonate. Percentage of organic carbon to total ignition loss of unicorporated organic matter averaged 39% for these profiles. Kjeldahl *nitrogen* analyses (including nitrates) were made for many samples.

Exchangeable hydrogen was displaced from the cation exchange complex with neutral N/2 barium acetate (BaAc) by an hour soaking, filtering, and further rinsing up to a total volume of 250 ml. The displaced acid was then titrated with N/10 sodium hydroxide. Repeated leaching of the same soil with 300 ml. of N/20 hydrochloric acid was then used to displace barium by hydrogen ions. After rinsing the soil with water until free of chloride, another BaAc leaching and titration were used to estimate its total *cation exchange capacity* to the same end point. Exchangeable bases are taken as the difference. Barium acetate was used because of the possible effect of the more commonly used ammonium acetate in destroying part of the exchange complex provided by humus—which accounts for virtually all of it in dune soils. This method is an adaptation of that of CHANDLER (10), using a single sample instead of separate samples for exchange capacity and exchangeable hydrogen, as suggested by LUNT (35).

The small amounts of silt and clay were estimated by the pipette method with sodium hexametaphosphate (Calgon water softener) as a dispersing agent, after destruction of almost all organic matter by hydrogen peroxide. Moisture equivalent was estimated by the usual centrifuge method. Carbonate was estimated by WILLIAMS's manometric method (64), subject to limitations pointed out by MARTIN and REEVE (38).

Vegetation development

Glancing forward to the summary diagram of figure 12, it is apparent that the landward margin of the beach and damp beach depressions, where

foredune development normally starts, are not the only areas bared for plant invasion. Blowout dunes, developed by wind erosion of earlier foredunes or dunes cliffed by waves, provide other initial conditions: damp blowout depressions scoured down to the water table by wind, eroding windward slopes, blowout summits that may or may not be undergoing deposition, and steep lee slopes that are migrating forward as new layers of sand are blown over the crest and slide down at the 32° angle of repose (fig. 6).

Among the several types of pioneer vegetation, the most widespread are the marram, sand reed, and little bluestem grasses (*Ammophila breviligulata*, *Calamovilfa longifolia*, *Andropogon scoparius septentrionalis*). These may occur in mixtures or may segregate in nearly pure stands, according to recent deposition rates and previous dune history, as noted below. Also depending on seedbed history, cottonwood (*Populus deltoides*) and dune-building shrubs such as sand cherry (*Prunus pumila*) may or may not be able to start dunes of their own or be present in mixtures with the grasses.

Any combination of these species may first build up and then stabilize the dune. Stabilization prepares the way for additional shrubs and typically for jack or white pine (*Pinus banksiana*, *P. strobus*), which seem capable of almost immediate invasion if seed is available. Under normal conditions at the present time, black oak (*Quercus velutina*) quickly replaces pine, at least as a dominant. Further changes in the associated trees, shrubs, and herbs of the black oak community take place, but much more slowly.

The other lines of succession outlined on figure 12 belong to contrasting site and climatic conditions to be mentioned briefly later.

PIONEER DUNE GRASSES

AMMOPHILA BREVILIGULATA.—Marram grass occasionally becomes established by seed but normally propagates by rhizome migration onto the beach (fig. 5A) or blowout dunes (fig. 7B). Table 2, column A, illustrates the rapid population build-up in about 6 years along a transect from newly invaded beach (foreground, fig. 5A) to the crest of the active foredune (F1). Table 2, columns B and C, provide additional random samples along this dune crest, while column D shows further increase in population density of stems on the next older foredune (F2) which had been stable about 6 years, long enough for some of the bare sand gaps to be filled in by the criss-crossing of horizontal rhizomes. Populations rarely exceed the density of about 150 stems per square meter, shown in columns E and F.

In fact, flowering and general vigor are already decreasing on the second foredune as compared with the first or active one, and much further decline is

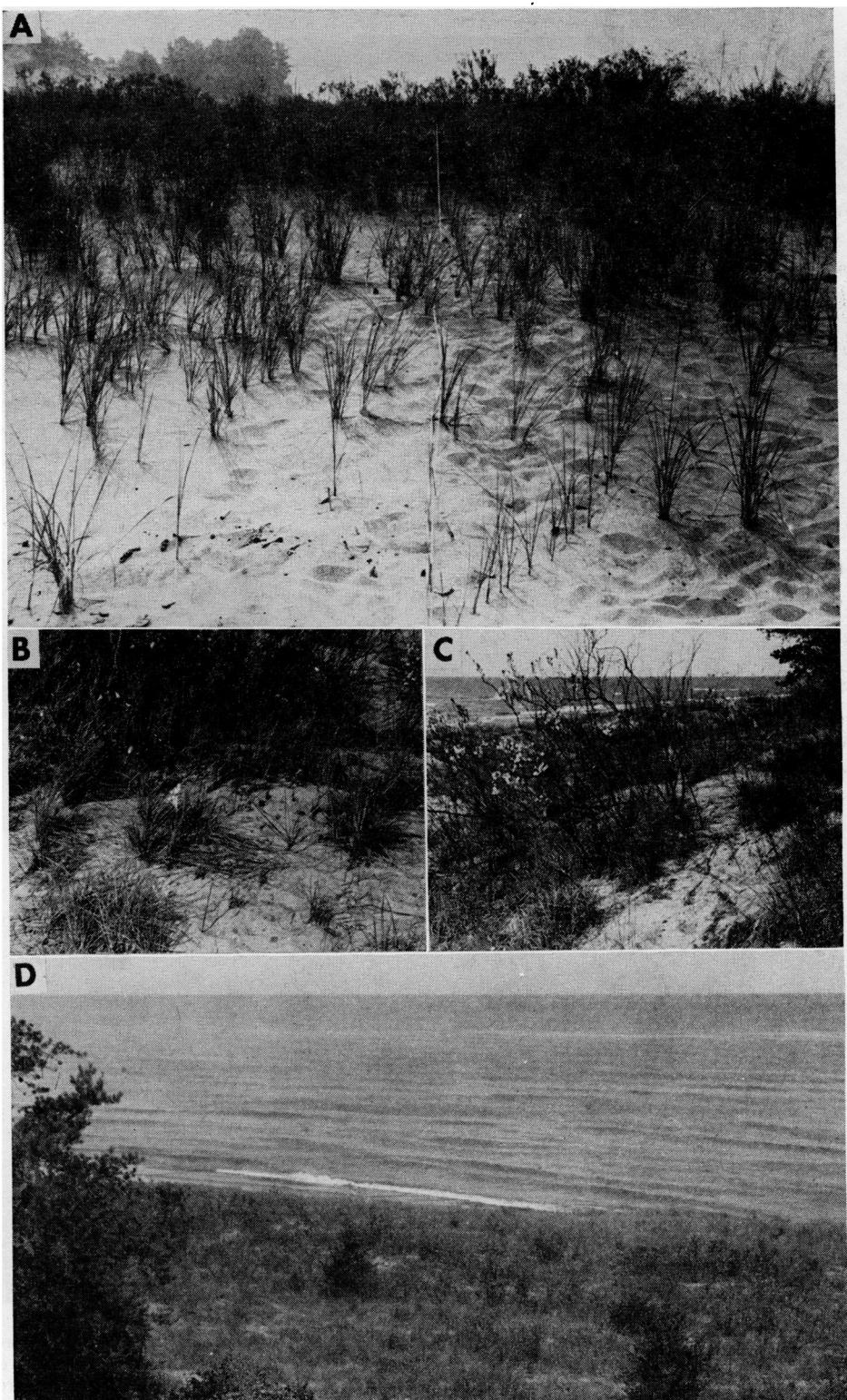


FIG. 5.—Foredune succession, Indiana Dunes State Park. *A*, *Ammophila breviligulata* invading beach in tufts arising along lines of rhizomes spreading out from actively depositing ridge, foredune 1 (F1), north of Big Blowout (1949); this and part of stable dune behind it (foredune 2) were eroded away by waves when lake was high in early 1950's, but new foredunes were again expanding in manner shown here and by seed germination in summer of 1957. *B*, Dense non-flowering *Ammophila*

bunches of low vigor; among sand-cherries and cottonwood sprouts on dune (foredune 3) that has been practically stabilized for 20 years. *C*, *Andropogon scoparius* var. *septentrionalis*, the sand-dune strain of little bluestem-bunchgrass, along with sand-cherry (*Prunus pumila*) on oldest portion of foredune 3 at base of cliffted dune. *D*, Scattered jack pine (*Pinus banksiana*) invading grass and cherry on foredune 3; younger ridges in background.

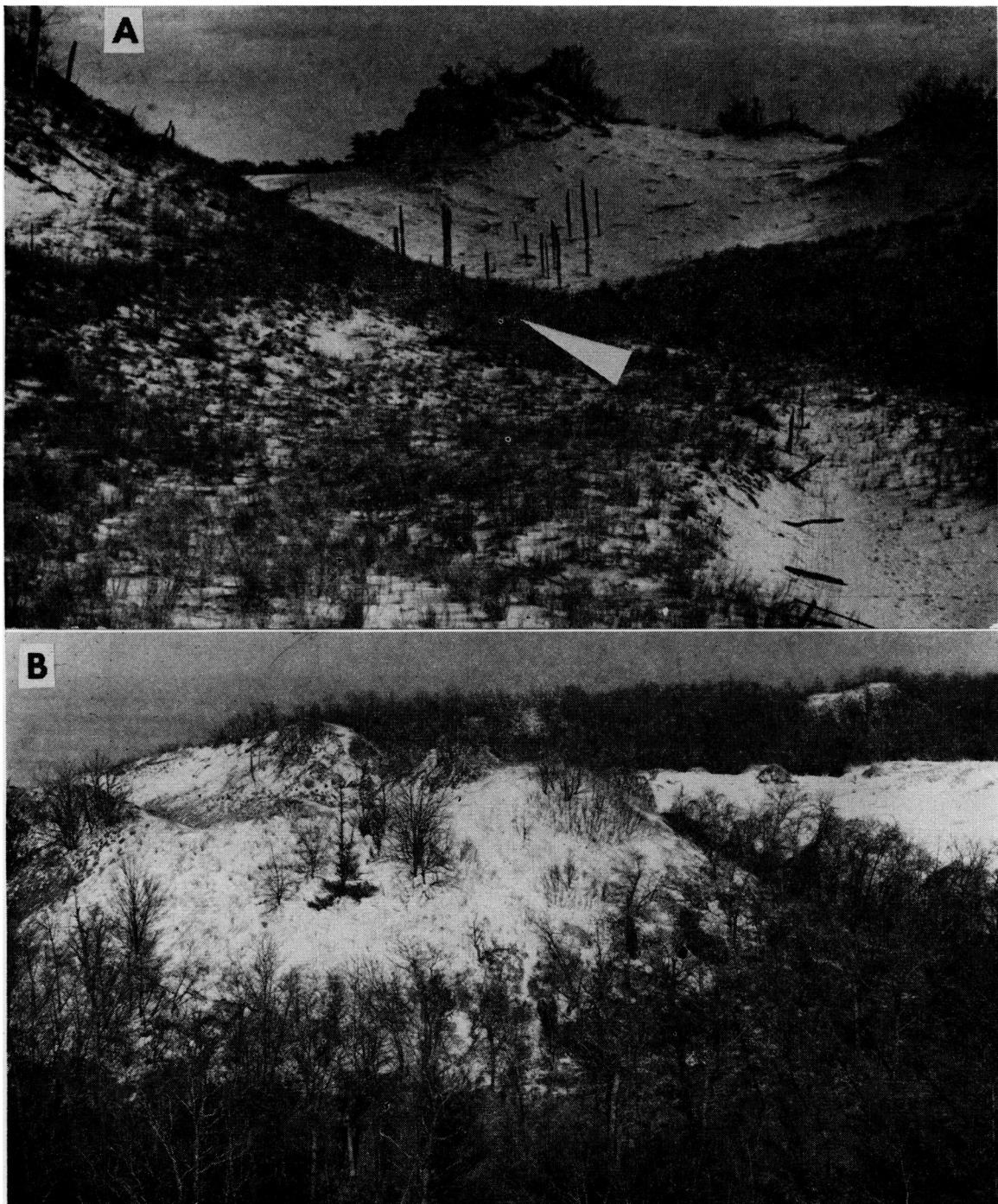


FIG. 6.—Link's Blowout, north of Big Blowout, Indiana Dunes State Park (see fig. 4). *A*, Wind-erosion channel through old dunes has uncovered dead pines since 1939; they were still under highest portion of dune in 1925! *Ammophila* planting by Dr. G. K. K. Link in 1939 stabilized most of formerly bare foreground area. Dark stripe of grass (*in line with white arrow*) shows striking response of growth to nitrogen fertilizer. *B*, right windsweep of *A* built steep parabolic blowout dune form, with aid of basswood (*Tilia americana*) treetops which grow

vigorously as thickets when buried by sand. Sand reed grass (*Calamovilfa longifolia*) and marram grass thrive on more actively depositing lee slopes, while *Andropogon* grows mostly in areas of less deposition or none. White pine and oaks are soon killed by burial. Left windsweep of *A* is shown in background, with horseshoe blowout form having broad summit capped by *Calamovilfa* hummock dunes. Winter aspect of black oak-white oak-blueberry forest in lower right.

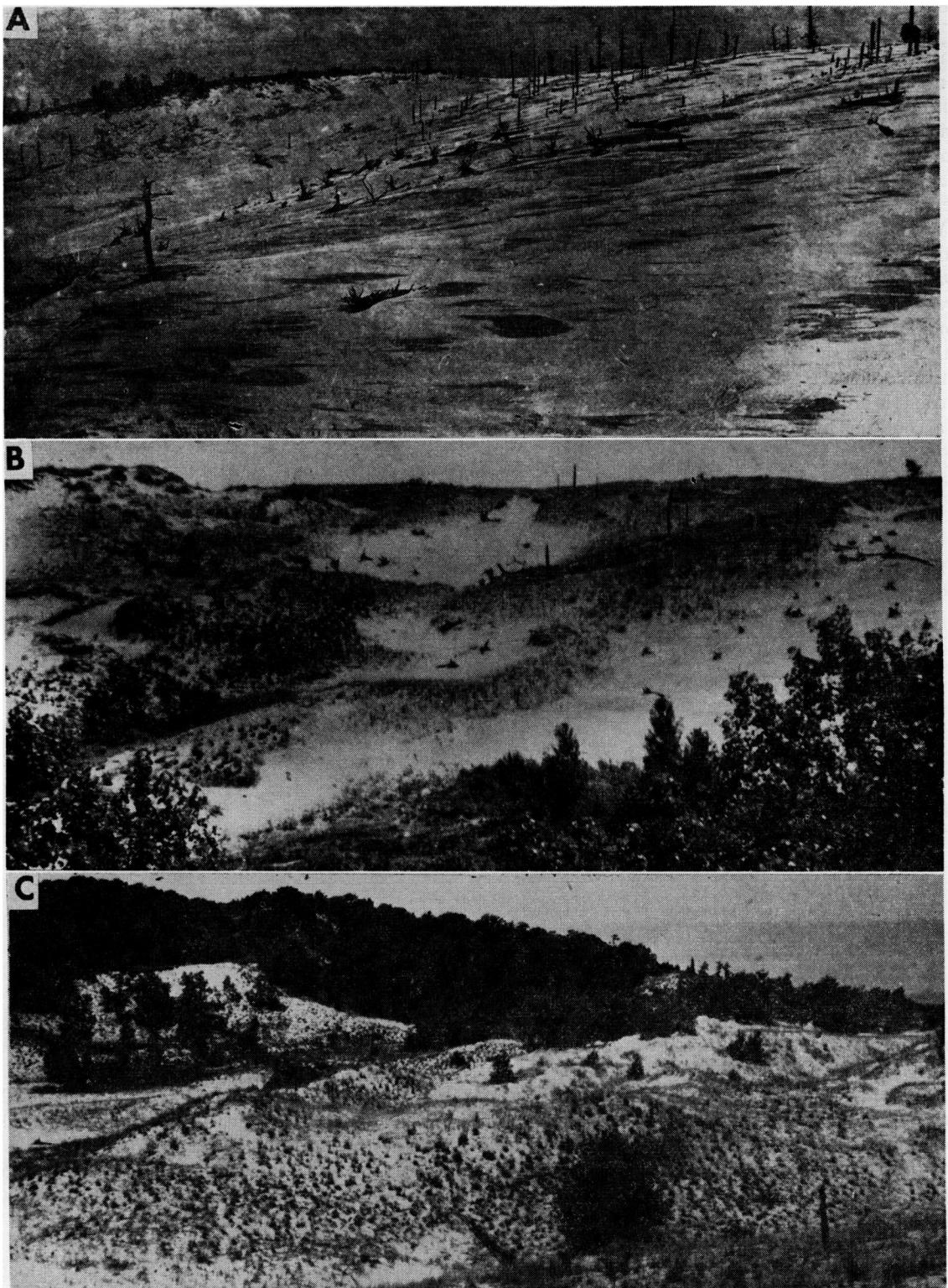


FIG. 7.—Big Blowout, Indiana Dunes State Park. *A*, Bare windward slope showing vast expansion of same type of erosion shown in miniature in figure 6*A*. Large white pine forest grew on stabilized dunes (some with weathered soils) that had been buried by migration like that shown in figure 6*B*, as Big Blowout expanded. (Photo ca. 1900 by I. B. MYERS.) *B*, Similar view, 1952, showing widespread invasion by marram grass and prompt invasion of it by little bluestem bunchgrass as soon as

deposition rate is slowed down. *C*, View opposite from *B*, toward west, showing how medium-scale blowout migrated in from lake to block off some of wind's strength and hasten stabilization shown in *B*. Typical cottonwood life-cycle shown by germination in moist *panne* in background (*foreground of B*), followed by burial and formation of tree-top thicket (*right*). Well-developed white pine stand in background.

conspicuous on the third foredune (F3). Table 2, column G, shows a decline because some old crowded bunches of shoots are dying out after perhaps 20 years of surface stability (fig. 5B), while column H shows that little marram persists among the bunches of *Andropogon* on a still older but undated strip at the back of this dune (fig. 5C).

WESTGATE (60), VAN DIEREN (55), WESTOFF (61), and others have noticed this kind of decline in *Ammophila arenaria*, the European species, or *A. breviligulata*. One interpretation is that fresh nutrient from sea salts or organic matter is blown up along with the fresh sand and accounts for vigorous growth until the surface is stabilized; then the available nutrient is either used up or leached away, supposedly accounting for loss in vigor. This probably does

ments on effects of date and density of planting and fertilization on its growth (6).

Probably this extreme morphological and physiological adaptation of this grass for tolerating sand burial helps explain why it is usually absent from areas where there is only very slow deposition or where there is even some erosion, as on large portions of many blowouts where conditions are suitable for the other dune grasses.

Specifically, it is not known whether the traces of *Ammophila* on some of the recently stabilized blowouts (B2OD, B2SP, B3SP in table 3) represent relics of denser populations at an earlier time, or whether sand reed grass instead of marram grass was the only important pioneer species on these particular dunes.

TABLE 2

TRANSECTS OF AMMOPHILA BREVILIGULATA ON BEACH-MARGIN DUNES (FOREDUNES F1, F2, AND F3),
EAST END OF INDIANA DUNES STATE PARK (1949-1950)^a

PLOT NO.	F1: ACTIVELY DEPOSITING				F2: 6 YEARS			F3: 20 YEARS, AND OLDER?						
	N ^b	A b	N/b	B N	C N	D N	E N	F N	N	G b	N/b	H b	N/b	
1....	5	2	2.5	11	13	15	20	18	43	8	5.4	16	1	16
2....	4	2	2	15	46	5	11	20	41	8	5.1	0	0	...
3....	0	0	...	4	1	14	16	10	39	7	5.6	0	0	...
4....	8	2	4	6	59	19	27	19	25	12	2.1	10	5	2.0
5....	6	3	2	12	5	7	7	15	54	16	3.4	0	0	...
6....	2	2	1	13	16	15	9	15	47	12	3.9
7....	10	5	2	7	55	4	8	10	33	13	2.5
8....	24	6	4	11	8	8	20	18	22	9	2.4
9....	12	2	6	12	25	3	13	15	21	7	3
10....	10	4	2.5	0	37	18	14	15	14	5	2.8
Σ	81	28	...	82	65.5	108	145	154	68.8	39	...	10.4
m^2														

^a Transects A, G, and H are at right angles to the trend of the dune, with increasing number of plot corresponding to increasing age of the grass population. On these transects "b" refers to number per plot of bunches of practically adjacent shoots, usually having a common parent shoot 1 or 2 years previously. E and F were selected to represent typical high population densities. B, C, and D were sampled at random intervals along the respective dune crests and more nearly approximate average conditions.

^b Individual numbers under N represent stems on 0.1 sq. m., except for C, which has 10^{-4} acre (ca. 0.4 sq. m.) plots, and G and H, which have 0.25 sq. m. plots.

not provide an explanation for the phenomenon along the cleaner beaches of fresh-water Lake Michigan.

Another suggestion (41) is that the inherent tendency of this dune-building grass favoring internodal elongation is not overcome completely, even when sand burial stops. The stem growing point rises slightly more each year into the dry surface sand, which provides an unfavorable environment for adventitious root growth and for further propagation of vigorous new erect branch shoots. This and many other aspects of the *Ammophila* population have been elaborated by LAING's intensive studies of its morphology, longevity, and reproduction rates, as well as by field and greenhouse experimentation (30). Large-scale plantings of this species for control of wind erosion provided opportunities for statistical experi-

CALAMOVILEA LONGIFOLIA.—The taller sand reed grass (outlined against the sky, fig. 5A, right) occurs mostly as a minor associate of marram grass on surfaces that are (or were) depositing rapidly (table 3). But it is the dominant dune-builder in other places where lesser wind or sand supply account for less rapid deposition rates (fig. 10A, B) or occurs where there may even be a slow erosion, as on many blowout windward slopes (fig. 12). Regardless of whether deposition or erosion formerly prevailed, this species apparently persists for many decades longer than *Ammophila* (table 3) and even reappears on dunes that are thousands of years old if the sand is slightly disturbed and exposed to the sun. The tolerance of sand reed to slow erosion and its persistence on stable surfaces are probably explained by the normal mode of vegetative propagation by

short rhizomes, initially pointed downward at a slight angle in late summer and later extending horizontally and upward to give rise to a new flowering stalk at whatever location the new surface happens to lie—either higher or lower than, or at, the previous year's surface on dunes that are slowly depositing, eroding, or stabilized, respectively.

ANDROPOGON SCOPARIUS VAR. SEPTENTRIONALIS.—The local sand-dune ecotype of the widespread little bluestem bunchgrass (which generally appears to belong to the variety *septentrionalis* according to herbarium studies by Mr. FLOYD SWINK) also has considerable capacity for internodal elongation of

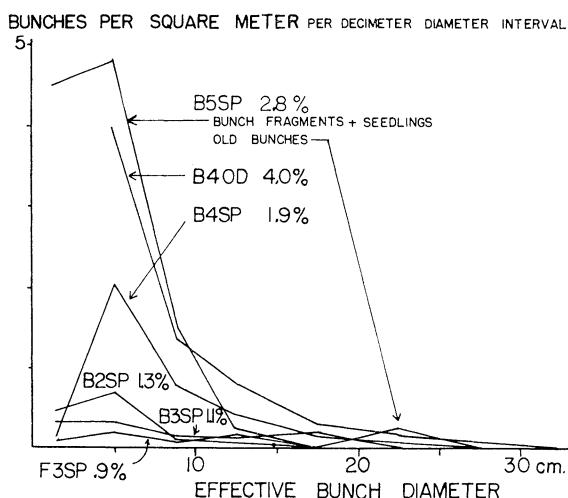


FIG. 8.—Increase in number and size of bunches of little bluestem bunchgrass (*Andropogon scoparius* var. *septentrionalis*). Foredune 3 (F3) and blowouts 2, 3, 4, and 5 from Indiana Dunes State Park (SP) and blowout 4 from Ogden Dunes (OD). See fig. 10C, D, and table 3. "Effective diameter" = circumference/ π . Percentages refer to bunch area as proportion of total plot area.

small seedlings and, more especially, of clumps which have already been vigorously established on a stable surface and subsequently been buried by renewed deposition of sand. But it lacks the rhizomes of the marram and sand reed grasses and is prevented from invading a new dune area until there is at least a temporary lag in deposition to permit the slow-growing seedlings to get established. Thus this grass was absent on foredune 1 at the Indiana Dunes State Park. On foredune 2 it was represented by a very few large clumps which had persisted through the last episode of deposition and by many new seedlings which had just started invading immediately following stabilization. On foredune 3, bunches of many sizes were represented on the plots (fig. 8), and some lying outside the plots were several decimeters across. On successively older blowouts there is further increase in the number of large bunches and small ones

(fig. 10C, D). Some of the latter represent younger generations of seedlings, while others represent fragments of older bunches which first died out in the middle, leaving a "fairy ring" (21, 40) and then lost continuity among different parts of the ring (fig. 8).

As shade and competition increase, bunchgrass is reduced in abundance and vigor, though some plants may persist in small openings or sparse shade (fig. 10E; table 4). Especially on sunny south slopes and burned "prairie" undercover types of the black oak dunes it may again become an herb of major importance.

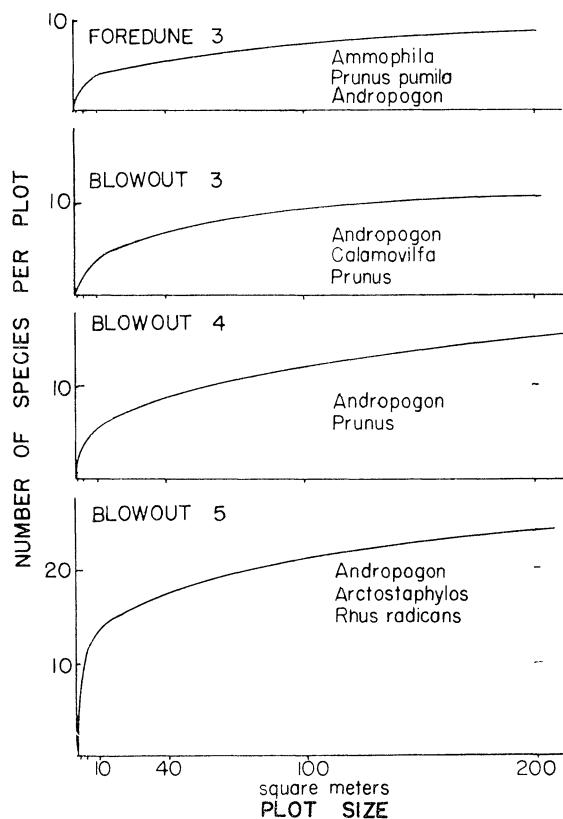


FIG. 9.—Species-area curves and dominants, Indiana Dunes State Park. Foredune 3 and series of blowouts as in figure 8.

HERBS ASSOCIATED WITH DUNE GRASSES.—The species-area curves of figure 9 illustrate the increase in number and abundance of species on several successively older dunes of the Indiana Dunes State Park. Table 3 identifies the prevailing herbs in the areas still dominated by grass, while table 4 shows, in addition, some of the species that are already beginning to invade these areas from surrounding thickets and forests.

The sand annuals (herb group *a* in table 3) may invade beaches and blowouts even before the grasses arrive and may be distributed in the more open

patches of sand afterward—more abundantly in wet years than in dry ones. Among the early biennials or perennials (herb group *b* in table 3), wormwood (*Artemisia caudata* var. *calvens*) is most abundant and may occur sporadically even on older sandy soils (table 4). *Lithospermum croceum*, *Solidago racemosa* var. *gilmanii*, *Monarda punctata* var. *villicaulis*, and some other species of group *d* (tables 3, 4) are almost always present on surfaces that have been stabilized for several years or decades but vary great-

ly in abundance owing to chance circumstances of establishment and local secondary dispersal. Some of these and other intolerant herbs (group *e*, table 4) are normally becoming suppressed by shade just about the time that soil has become favorable enough for really vigorous growth, but they find excellent conditions on older soils where fire or other disturbance or exposed topographic location spares them from dense shade.

Anywhere in the foregoing herbaceous vegetation

TABLE 3
DENSITY AND PRESENCE OF SPECIES TYPICAL OF GRASS COMMUNITIES^a

	FOREDUNES 1-3			BLOWOUT DUNES ^b					
	Indiana Dunes State Park			Ogden Dunes	Indiana Dunes State Park		Ogden Dunes	Indiana Dunes State Park	
	F1	F2	F3	B2OD	B2SP	B3SP	B4OD	B4SP	B5SP
Years since stabilization ^c									
	<1	6	20	10	20	40	60	90	120
Shrubs									
<i>Cornus stolonifera</i> var. <i>baileyi</i>	0.02	0.01	10.0	—	—	—	—	—	—
<i>Prunus pumila</i>					0.1	0.76	—	2.75	—
Herbs									
a) Sand annuals:									
<i>Cakile edentula</i>	—	—	—						
<i>Corispermum hyssopifolium</i>	—	—	—			—			
<i>Cycloloma atriplicifolia</i>	—	—	—						
<i>Euphorbia polygonifolia</i>	—	—	—						
b) Early perennials or biennials:									
<i>Artemisia caudata</i> var. <i>calvens</i>	—	0.1	0.8	0.01	1.95	+	1.75	—
<i>Cirsium pitcheri</i>	—	—		—	—			
c) Dune-building grasses:									
<i>Ammophila breviligulata</i> ^d	68.8	108.0	67.8	—	—	—			
<i>Calamovilfa longifolia</i>	1.0	1.0	0.75	+	4.75	4.35	2.35	0.7	1.75
d) Bunchgrass associates:									
<i>Andropogon scoparius</i> >10 cm.....	0.01	0.35	0.5	+	0.4	1.35	0.65	0.5
var. <i>septentrionalis</i> <10 cm.....	0.02	0.30	6.8	+	0.55	4.7	2.6	7.8
<i>Asclepias syriaca</i>	—	—		0.1	—			
<i>A. tuberosa</i>	—	—		—				
<i>Cyperus schweinitzii</i>	—	—		0.01	0.28		0.10	—
<i>Equisetum hyemale</i> var. <i>intermedium</i>	0.05	2.0						
<i>Lithospermum croceum</i>	—	0.8	—	1.0	0.38	0.06	0.72	2.5
<i>Monarda punctata</i> var. <i>villicaulis</i>	—	—	—	—	4.7	—	1.88	5.0
<i>Oenothera rhombipetala</i>	—	—		0.01	—		0.33	—
<i>Panicum villosissimum</i> var. <i>pseudopubescens</i>	—	—			0.25		3.10	2.5
<i>Solidago racemosa</i> var. <i>gilmanii</i>	—	0.35	9.5	1.0	0.23	0.06	1.55	0.12

^a Density in stems/square meter (or bunches of specified diameter in the case of *Andropogon*) on measured plots. Presence nearby indicated by + if locally abundant, — if not.

^b This list includes only species typical of grassy portions of the blowouts indicated. See table 4 for other species present to a minor extent in these plots and to a greater extent in other undercover societies dominated by *Arctostaphylos*, *Rhus*, *Smilacina*, and others.

^c Ages refer to 1950 when most plot work was done. Since then foredune 1 and parts of 2 and 3 have suffered severe wave erosion or fresh deposition of sand near the new wave-cut cliff.

^d *Ammophila* data taken from table 2, columns B and C, D, and G.

one may find woody plants, either relics of the dune-builders or progenitors of the future forest, as noted in the next three subsections.

CHANGES IN SHRUB STRATUM

The foliage, shade, decaying wood, and humus conditions around shrubs and pioneer trees are important in the differentiation of niches or small-scale ecosystems within the larger community ecosystems. They have special populations of small animals (50) and serve as outposts for larger ones who normally dwell in older communities but temporarily range out into the more open dunes and beach. Thus woody pioneers provide a link which ties together communities of many different ages into a larger ecosystem.

Some shrubs may precede tree invasion, but the largest number of species and, probably, individuals occurs after the invasion of pines and early oaks but before their canopies are dense enough to prevent direct sun from reaching most parts of the ground surface for several hours per day (fig. 13, second graph from top). As in the case of herbs, gradual shifts in populations on the plots, and elsewhere, can be described conveniently in terms of somewhat arbitrary species groups, referred to by lower-case letters in table 4 and the following discussion.

DUNE-BUILDING SHRUBS (group *a*).—Sand-cherry may be established prior to dune-building and contribute to it, so that a population may already be thriving when the surface becomes stabilized. Many additional seedlings evidently germinated on the new surface within a year or two after it was stabilized in the case of foredune 2. Such seedling invaders and holdovers from vegetative propagation during dune growth both contributed to the large sand-cherry population on foredune 3 (fig. 5C, D). Tables 3 and 4 show how it is sporadically abundant elsewhere (as fig. 10A-C).

WATERMAN (59) traced sand-cherry seedling growth and showed how its roots tend to exploit the organic layers left in the soil through burial of dune-builders like *Ammophila*. (He noted that *A. breviligulata* roots grow mostly through fresh sand, although SALISBURY [48] indicated that *A. arenaria* roots tend to follow organic layers.)

Red osier dogwood (*Cornus stolonifera* var. *baileyi*) was a minor shrub on plot areas but may dominate extensive thickets on some active lee slopes. Choke-cherry (*Prunus virginiana*) will not reach greatest abundance until forest cover is well developed (group *d*, table 4), but it should be noted here that it achieves unusual vigor where sand is deposited over previously established shrubs, which then form thickets many meters across.

Salix syrticola is the most important dune willow, although *S. glaucocephaloides* var. *glaucocephala* and *S.*

interior may also develop extensive thickets accumulating sand. As in the case of cottonwood, germination of their small, short-lived seeds probably required the damp sand of a former beach or blowout pond margin.

OTHER INTOLERANT SHRUBS OF OPEN DUNES (group *b*, table 4).—Evergreen shrubs, loosely termed "heath" by COWLES (13) and GATES (21), include three distinct strata which may be represented by scattered invaders, in various mixtures or as nearly pure thickets (fig. 10). Experiments as well as field observations by the writer show that the bearberry (*Arctostaphylos uva-ursi coactilis*) may thrive under slow burial by sand that does not cover most of the foliage at one time (fig. 10A). It is even more common as an invader of the bunchgrass, creeping steadily around the bunches and apparently restricting herbaceous reproduction in favor of pines and other woody species in the interstices of its branches.

Thicker and even more exclusive mats of *Juniperus horizontalis* provide a distinctive stage in many northern Michigan areas and southward along the west side of the lake to Waukegan (fig. 10B) and a locality near Lake Bluff, Illinois. The specified 1.5-m. height for the variety *Juniperus communis* var. *depressa* (fig. 10C) is frequently exceeded by this vigorous shrub in older thickets (as on B5, where it is gradually being shaded out by invading pines and oaks after over a century of stabilization). Contrasting with these three horizontally oriented shrubs are the spires of the northern red cedar (*Juniperus virginiana* var. *crebra*), which rarely become more than small trees in the dunes (fig. 10E, right).

The prickly-pear cactus (*Opuntia humifusa*) attracts attention as soon as it invades the bunchgrass on young dunes, but it actually reaches its most spectacular development in the sedge-prairie undercover type of certain old black oak dunes, with *Amorpha canescens*. *Potentilla fruticosa* and *Hypericum kalmianum* are other shrubby species abundant on Illinois and Wisconsin beaches (27) and "pine bottoms" northward. *Hudsonia tomentosa* var. *intermedia* provides low ground cover on dry as well as damp sands in the north and locally on open oak dunes and sand pits in Indiana.

POISON IVY AND OTHER DECIDUOUS CREEPERS (group *c*, table 4).—Along with the junipers comes an even larger number of more or less recumbent or climbing deciduous shrubs or vines. Many remain longer than the preceding in the shady forest and even reach their maximum development in the crowns of sparse stands of pine, oak, or basswood. *Rhus radicans* var. *rydbergii* ranks with the most abundant herbs, such as *Smilacina stellata*, in the ground cover of such stands as well as occurring in the tree tops. Abundantly fruiting bittersweet (*Celastrus scandens*)

TABLE 4
SPECIES ABUNDANCE^a

TREES	COTTONWOOD			—			PINE			BLACK OAK																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																										
	Sand-cherry-bunchgrass	Poison ivy	Choke-cherry <i>Smilacina stellata</i>	(Blueberry)	Rose-prairie grass, <i>Smilacina racemosa</i>	Sedge	Sassafras-witch hazel Blueberry	(see numbers on fig. 2)																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																												
LOCATION ^a	1 M	2 S ^b	3 S ^b	4 S ^b	5 S ^b	6 OD	7 SP	8 OD	9 SP	10 SP	11 SP	12 SP	13 SP	14 SP	15 SP	16 SP	17 SP	18 SP	19 SP	20 SP	21 SP	22 SP	23 SP	24 SP	25 SP	26 SP	27 SP	28 SP	29 SP	30 SP	31 SP	32 SP	33 SP	34 SP	35 SP	36 SP	37 SP	38 SP	39 SP	40 SP	41 SP	42 SP	43 SP	44 SP	45 SP	46 SP	47 SP	48 SP	49 SP	50 SP	51 SP	52 SP	53 SP	54 SP	55 SP	56 SP	57 SP	58 SP	59 SP	60 SP	61 SP	62 SP	63 SP	64 SP	65 SP	66 SP	67 SP	68 SP	69 SP	70 SP	71 SP	72 SP	73 SP	74 SP	75 SP	76 SP	77 SP	78 SP	79 SP	80 SP	81 SP	82 SP	83 SP	84 SP	85 SP	86 SP	87 SP	88 SP	89 SP	90 SP	91 SP	92 SP	93 SP	94 SP	95 SP	96 SP	97 SP	98 SP	99 SP	100 SP	101 SP	102 SP	103 SP	104 SP	105 SP	106 SP	107 SP	108 SP	109 SP	110 SP	111 SP	112 SP	113 SP	114 SP	115 SP	116 SP	117 SP	118 SP	119 SP	120 SP	121 SP	122 SP	123 SP	124 SP	125 SP	126 SP	127 SP	128 SP	129 SP	130 SP	131 SP	132 SP	133 SP	134 SP	135 SP	136 SP	137 SP	138 SP	139 SP	140 SP	141 SP	142 SP	143 SP	144 SP	145 SP	146 SP	147 SP	148 SP	149 SP	150 SP	151 SP	152 SP	153 SP	154 SP	155 SP	156 SP	157 SP	158 SP	159 SP	160 SP	161 SP	162 SP	163 SP	164 SP	165 SP	166 SP	167 SP	168 SP	169 SP	170 SP	171 SP	172 SP	173 SP	174 SP	175 SP	176 SP	177 SP	178 SP	179 SP	180 SP	181 SP	182 SP	183 SP	184 SP	185 SP	186 SP	187 SP	188 SP	189 SP	190 SP	191 SP	192 SP	193 SP	194 SP	195 SP	196 SP	197 SP	198 SP	199 SP	200 SP	201 SP	202 SP	203 SP	204 SP	205 SP	206 SP	207 SP	208 SP	209 SP	210 SP	211 SP	212 SP	213 SP	214 SP	215 SP	216 SP	217 SP	218 SP	219 SP	220 SP	221 SP	222 SP	223 SP	224 SP	225 SP	226 SP	227 SP	228 SP	229 SP	230 SP	231 SP	232 SP	233 SP	234 SP	235 SP	236 SP	237 SP	238 SP	239 SP	240 SP	241 SP	242 SP	243 SP	244 SP	245 SP	246 SP	247 SP	248 SP	249 SP	250 SP	251 SP	252 SP	253 SP	254 SP	255 SP	256 SP	257 SP	258 SP	259 SP	260 SP	261 SP	262 SP	263 SP	264 SP	265 SP	266 SP	267 SP	268 SP	269 SP	270 SP	271 SP	272 SP	273 SP	274 SP	275 SP	276 SP	277 SP	278 SP	279 SP	280 SP	281 SP	282 SP	283 SP	284 SP	285 SP	286 SP	287 SP	288 SP	289 SP	290 SP	291 SP	292 SP	293 SP	294 SP	295 SP	296 SP	297 SP	298 SP	299 SP	300 SP	301 SP	302 SP	303 SP	304 SP	305 SP	306 SP	307 SP	308 SP	309 SP	310 SP	311 SP	312 SP	313 SP	314 SP	315 SP	316 SP	317 SP	318 SP	319 SP	320 SP	321 SP	322 SP	323 SP	324 SP	325 SP	326 SP	327 SP	328 SP	329 SP	330 SP	331 SP	332 SP	333 SP	334 SP	335 SP	336 SP	337 SP	338 SP	339 SP	340 SP	341 SP	342 SP	343 SP	344 SP	345 SP	346 SP	347 SP	348 SP	349 SP	350 SP	351 SP	352 SP	353 SP	354 SP	355 SP	356 SP	357 SP	358 SP	359 SP	360 SP	361 SP	362 SP	363 SP	364 SP	365 SP	366 SP	367 SP	368 SP	369 SP	370 SP	371 SP	372 SP	373 SP	374 SP	375 SP	376 SP	377 SP	378 SP	379 SP	380 SP	381 SP	382 SP	383 SP	384 SP	385 SP	386 SP	387 SP	388 SP	389 SP	390 SP	391 SP	392 SP	393 SP	394 SP	395 SP	396 SP	397 SP	398 SP	399 SP	400 SP	401 SP	402 SP	403 SP	404 SP	405 SP	406 SP	407 SP	408 SP	409 SP	410 SP	411 SP	412 SP	413 SP	414 SP	415 SP	416 SP	417 SP	418 SP	419 SP	420 SP	421 SP	422 SP	423 SP	424 SP	425 SP	426 SP	427 SP	428 SP	429 SP	430 SP	431 SP	432 SP	433 SP	434 SP	435 SP	436 SP	437 SP	438 SP	439 SP	440 SP	441 SP	442 SP	443 SP	444 SP	445 SP	446 SP	447 SP	448 SP	449 SP	450 SP	451 SP	452 SP	453 SP	454 SP	455 SP	456 SP	457 SP	458 SP	459 SP	460 SP	461 SP	462 SP	463 SP	464 SP	465 SP	466 SP	467 SP	468 SP	469 SP	470 SP	471 SP	472 SP	473 SP	474 SP	475 SP	476 SP	477 SP	478 SP	479 SP	480 SP	481 SP	482 SP	483 SP	484 SP	485 SP	486 SP	487 SP	488 SP	489 SP	490 SP	491 SP	492 SP	493 SP	494 SP	495 SP	496 SP	497 SP	498 SP	499 SP	500 SP

^a Abundance scale approximates log of the number of stems per hectare, or 4 plus log of the number of stems per square meter. Species seen at or near plots but missed in the series of nested samples are denoted by + or —, if they are locally abundant or very minor, respectively.

^b Abbreviations for locations: M, Miller (eastern Gary) samples and others west of Gary are located by map (fig. 2); OD, Ogden Dunes; SP (State Park) sites located just west of the road forming the eastern boundary of the Indiana Dunes State Park, except for 2500-year-old State Park location which lies southwest of Mount Holden. n = north slope; s = south slope; others (including ridge 3a) horizontal.

^c Includes species that are normally small and others which are smaller than usual when they occur on normal dune sites.

TABLE 4—Continued

Miner Trees—Continued

TABLE 4—Continued

b) Early perennials and biennials:

Artemisia candata var.
calvensis...

c) Dune-building grasses;

Ammophila brevilineata
Calamovilfa longifolia
D) *Prunichrysa annulata*

a) Buntgrass associates:
Andropogon scoparius
var. *septentrionalis*

Anemone cylindrica...
Asclepias syriaca...

A. tuberosa.....
A. viridiflora.....

Equisetum hyemale var.
intermedium

TABLE 4—Continued

Herbs—Continued									
	1	2	3	4	5	6	7	8	9
<i>Kuhnia eupatorioides</i> ...	—	—	—	—	—	—	—	—	—
<i>Lithospermum croceum</i> ...	3	+	3	3	2	2	2	2	2
<i>Monarda punctata</i> var. villaeus...	3	5	4	4	4	2	1	1
<i>Oenothera rhombipetala</i> ...	3	2	4	1	1	4
<i>Panicum effusissimum</i>	2	2	2	2
var. <i>pseudophaceloides</i> ...	2	3	3	3	2	2	2	2	2
<i>P. virginicum</i> ...	3	2	2	2	2	2	2	2
<i>Solidago racemosa</i> var. <i>gibmania</i> ...	5	5	4	3	4	+	3	2	2
e) Other intolerant herbs:									
<i>Apocynum androsaemifoliu</i> m...	2	2	2	1	5	3	3	1	2
<i>Arabis lyallii</i> ...	2	3	2	2	3	3	1	4
<i>Asparagus officinalis</i> ...	3	3	3	2	2	3	3	1	2
<i>Aster azureus</i> ...	2	2	2	3	2	3	5	2	3
<i>A. linariifolius</i> ...	2	2	2	3	2	2	2	3	2
<i>Campanula rotundifolia</i> ...	2	2	2	2	2	2	2	3	2
<i>Coreopsis palmata</i>	5	5	5	5
<i>C. tripteris</i>	2	3	3	2
<i>Fragaria pectinacea</i>	2	2	5	2
<i>Fragaria virginica</i>	4	4	4	3
<i>Helianthemum canadense</i> ...	3	2	4	2	2	2	2	4	5
<i>Lithospermum divaricatum</i> ...	3	2	4	3	2	2	2	4	5
<i>H. grosseserratum</i> ...	3	2	4	4	3	2	2	5	4
<i>H. occidentalis</i> ...	2	3	4	3	2	2	2	5	4
<i>Koeleria cristata</i> ...	2	2	2	2	2	2	2	5	4
<i>Lespedeza capitata</i> ...	2	2	2	2	2	2	2	5	4
<i>Lithospermum canescens</i> ...	1	3	3	2	2	2	2	3	2
<i>Liatris aspera</i> ...	1	3	3	2	2	2	2	4	4
<i>Lupinus perennis</i> var. occidentalis...	4	4	3	4	3	3	2	1	2
<i>Monarda fistulosa</i> ...	4	5	2	2	3	2	2	2	3
<i>Pilosella pilosa</i> ...	1	4	3	4	3	3	2	4	5
<i>Poa compressa</i> ...	1	3	3	2	2	2	2	4	5
<i>P. pratensis</i> ...	3	2	2	2	2	2	2	1	1
<i>Pteridium aquilinum</i> var. <i>latiusculum</i> ...	4	2	2	2	2	2	2	5	4
<i>Rudbeckia hirta</i> ...	2	2	2	2	2	2	2	1	2
<i>Solidago</i> spp...	4	2	3	4	3	4	3	4	4
<i>Sorghastrum nutans</i> ...	2	2	2	2	2	2	2	5	3
<i>Stipa spartea</i> ...	2	3	1	4	3	3	3	3	3
<i>Tephrosia virginica</i> ...	3	3	1	4	3	3	3	5	2
<i>Tradescantia ohioensis</i> ...	2	3	3	1	4	4	4	2	2
f) Early forest herbs:									
<i>Aquilegia canadensis</i> ...	3	4	3	3	2	2	2	3	2
<i>Arilia nudicaulis</i> ...	3	4	3	4	4	4	4	4	1
<i>Aster macrophyllus</i> ...	4	3	3	3	3	3	3	3	2

TABLE 4—Continued

TABLE 4—Continued

	Herbs—Continued		
	2	3	2
<i>Panicum depauperatum</i>	3	5	2
<i>P. praeocciosum</i>	+	4	4
<i>Pedicularis canadensis</i>	3	4	3
<i>Phlox diffida</i>	1	2	3
<i>Physalis virginiana</i>			3
<i>Potentilla simplex</i>			2
<i>Scrophularia marilandica</i>			3
<i>Veronicastrum virginicum</i>	1	2	4
<i>Viola pedata lineariloba</i>		4	3
<i>Zizina aurea</i>		3	

and grape (*Vitis* spp.) are almost as impressive. Impenetrable tangles of woody and herbaceous *Smilax* (*S. rotundifolia*, *S. tamnoides* var. *hispida*; *S. ecirrhata*, *S. lasioneura*) occur here too but are even more characteristic of secondary openings in old dunes than they are of the initial forest. *Rosa* spp. (mostly *R. blanda*, apparently) are widespread in all these places and also with prairie grasses and thickets of the old black oak dunes around the southwestern corner of the lake.

CHOKE-CHERRY AND FOREST SHRUBS (group *d*, table 4).—Although *Prunus virginiana* may already be present and extremely vigorous on active or rejuvenated dunes, greatest size (exceeding 1 decimeter d.b.h.) is attained in young forests. Choke-cherry persists for many centuries as the most characteristic thicket shrub of the black oak woodlands. *Rhus aromatica*, *R. copallina* var. *latifolia*, and several others in group *d* also invade early and persist in canopy openings but not so well in the shade. *Viburnum acerifolium* increases in the black oak forests after several centuries.

BLUEBERRY-HUCKLEBERRY COMMUNITY (group *e*, table 4).—Lowbush blueberries (*Vaccinium vacillans* and *V. angustifolium*) and huckleberry (*Gaultheria procumbens*) dominate a very characteristic shrub stratum on the older black oak and pine dunes. Unlike the preceding groups, these do not begin to invade until after 6–10 centuries in the black oak dunes south of Marquette Park in eastern Gary (table 4; fig. 13). The blueberry-huckleberry grouping remains—in fact, is most prevalent—on the oldest Indiana dune systems, about 8000–12,000 years old. Associated minor evergreen ground cover includes *Gaultheria procumbens*, *Mitchella repens*, and, sporadically, *Epigaea repens*, and species of *Pyrola* and *Chimaphila*.

MESOPHYTIC SHRUBS (group *f*, table 4).—Another group of species, including relatively large ones like spice bush (*Lindera benzoin*) and low ground cover like creeping euonymus (*E. obovatus*), rarely if ever enters the succession on normally exposed Indiana dunes but does occur in special topographic and microclimatic conditions in Indiana and, to a greater extent, in Michigan.

PIONEER PINE COMMUNITIES

In spite of the over-all simplicity in the successional pattern of young dunes near the lake and older dunes inland, certain complications led COWLES to declare:

No order of succession in this entire [Chicago] region is so hard to decipher as is that of the established dunes. There are at least three types of these dunes and it is not yet possible to figure out their relationships. . . . Probably the oaks follow the pines, but the evidence on which this is based is not voluminous. The pines certainly have a

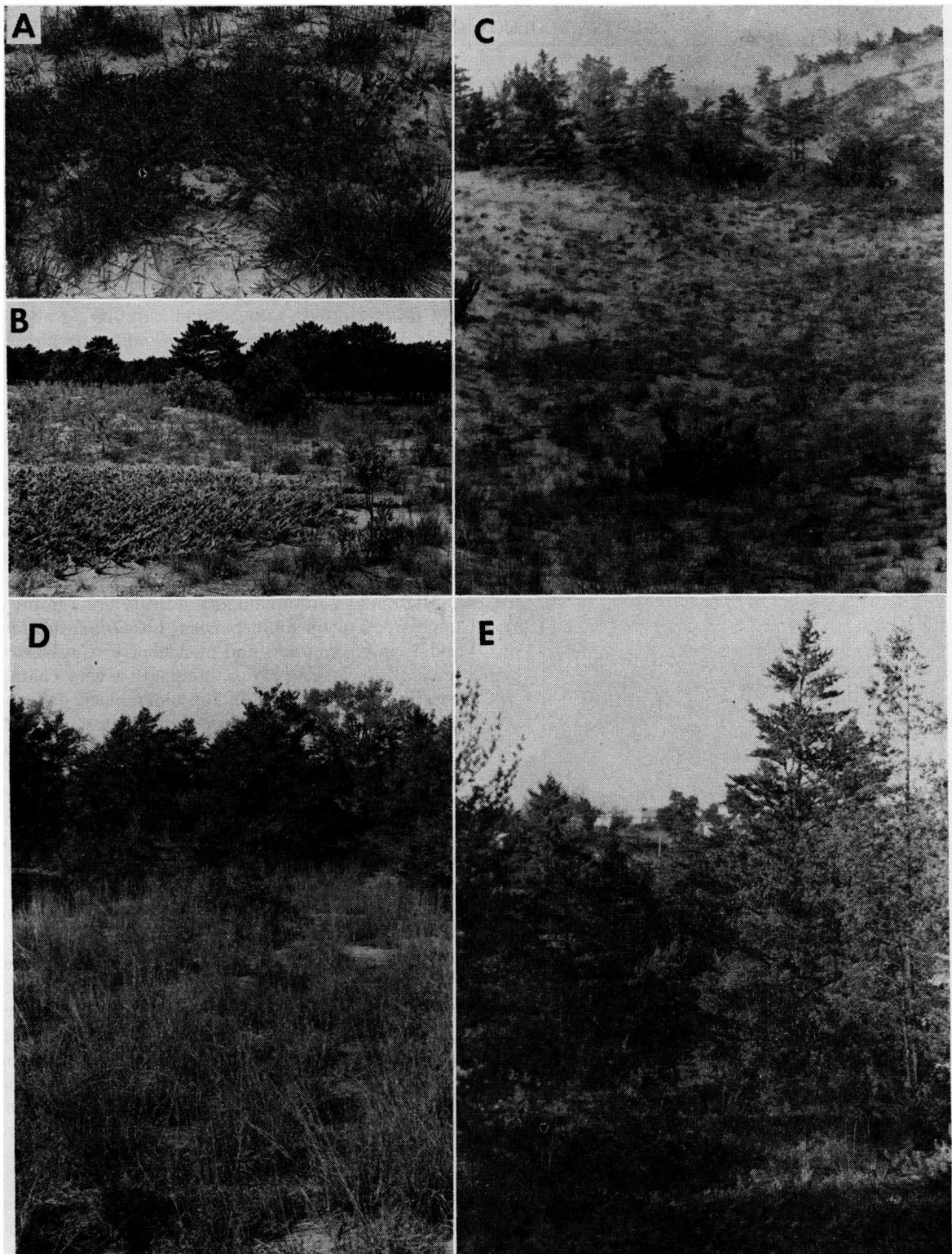


FIG. 10.—Evergreen shrubs and trees invading bunchgrass. *A*, burial plot of bearberry (*Arctostaphylos uva-ursi coactilis*), showing little change with 1–2 cm. of deposition, death of most stems with 4- or 10-cm. burial accompanied by rejuvenation of a few unburied stems, and death of all stems with 20-cm. burial except for growth around edge. *Andropogon* decreased, but *Calamovilfa* was not changed by 20-cm. burial. *B*, dense mat of creeping juniper (*Juniperus horizontalis*) expanding on low *Andropogon*-*Calamovilfa*-*Prunus pumila* dunes that are typical of Illinois Beach State Park. Artificially sown Austrian and Scotch pine (*Pinus nigra* and *P. sylvestris*) are regenerating nat-

urally where white pine had been eliminated by cutting and fire. *C*, common juniper (*Juniperus communis* var. *depressa*) invading blowout 3, Indiana Dunes State Park. White (and jack) pine established on blowout 4 in right background, next to road (see fig. 4 for orientation, NNE). *D*, jack pine (*Pinus banksiana*) expanding into unusually dense bunchgrass, blowout 4, Ogden Dunes. *E*, second-generation jack pine closing open stand on blowout 5, Ogden Dunes. Red cedar (*Juniperus virginiana* var. *crebra*) on right; white pine on left. *Calamovilfa* and *Andropogon* mostly crowded out by *Arctostaphylos* and *Rhus radicans*.

wider range of habitat than the oaks, occurring in wetter and in drier soil and also in more exposed situations. The mutual relations of the pines and the oaks are certainly interesting and deserve some very careful study [14:173-176].

One of the confusing elements is the great difference between (a) first-generation pine stands on young dune sands which are *rapidly replaced* by oaks and (b) certain pine stands and pine-hardwood admixtures on very much older dune soils, the latter often associated with the blueberry-huckleberry undercover that is common to the old black oak dunes. The former develop commonly, though by no means universally, in the primary succession on many sites, while many of the latter are restricted to special topographic niches or may be products of secondary succession following blowdown in wet spots and certain types of fire history on the dry dunes.

JACK PINE.—The occurrence of *Pinus banksiana* at the south end of Lake Michigan is 100 km. south of the rest of its natural range, which extends southward from Muskegon to dunes south of Grand Haven and just north of Saugatuck, Michigan. Everywhere its densest stocking and quickest invasion is in moist "pine bottoms" (13:374) of blowout depressions.

Rapid but sparser invasion was noted almost immediately upon stabilization of the foredune sequence (fig. 5A) and the adjacent older clifftop dunes. Figures 10D and E illustrate its rapid invasion of *Andropogon* and the unusually favorable second-generation reproduction on two Ogden Dunes blowouts (B4OD, B5OD). Adjacent to similar jack pine stands in a nearby blowout in Ogden Dunes can be seen the still commoner situation of the older pines (probably still first generation) dying or dead, already replaced by hardwoods—in this case not only the usual black oak but also some red oak and basswood on this relatively favorable site (B6OD on table 4).

The second-growth jack pine on the youngest ridge south of the former mouth of the Grand Calumet River, eastern Marquette Park, Gary, may be on a 200-year-old dune surface (fig. 1; a in fig. 2) whose south slope has already succeeded to black oak. Both white and jack pine are subordinate on all but a few north-slope surfaces and exposed summits (fig. 12) on the progressively older ridges south of here.

WHITE PINE.—*Pinus strobus* occurs to a limited extent in all the habitats mentioned for *P. banksiana* and is even more common than is jack pine on most of the steeper blowout or wave-cut slopes. On many level dunes invasion has been very slow in recent decades—for example, in the foreground of figure 10C (B3SP)—although there evidently was very abundant reproduction on slightly older blowout surfaces in the nineteenth century, shown on blow-

outs in the background of the same figure. On blowout 5 in the State Park the oldest pines (about 105 years old) have already died, and black oak is already reproducing more vigorously than pine over most of the area (fig. 11A).

Canopy, undercover, and humus distribution are much less uniform in all these dune pine stands than in well-stocked old-field pine stands that are so popular in succession studies (2). Patches of bare sand with herb groups a-d and shrub groups a and b may persist for a century or longer (fig. 13). Herb groups e and f and shrub groups c and d range into the shadier as well as sunny spots.

The rapid accumulation of fresh and partly decomposed litter (L and F layers of forest floor, fig. 13) is vividly demonstrated around shaded pine trunks where there happens to have been secondary deposition of sand from adjacent active dunes only 30 or 40 years ago. The roots and rhizomes of the ubiquitous *Rhus radicans* and *Smilacina stellata* seem primarily responsible for binding these into a coherent mat. This transformation of the dune surface completely changes the conditions for establishment of subsequent generations of tree and undercover species.

BLACK OAK ASSOCIATIONS

The extreme heterogeneity within the black oak "major community" (1:436) is manifest even from Cowles's brief discussion (13:379-382) and the following somewhat arbitrary outline of the diverse combinations of shrub and herb layer and group societies.

PRUNUS-SMILACINA UNDERCOVER.—The squirrels' efficient dispersal of acorn caches, even several hundred meters from the nearest seed tree, may introduce *Quercus velutina* into the earliest grass or *Prunus pumila* stages of vegetation. Here it may become the first tree cover without benefit of either cottonwood or pine generations to prepare its way, in case seed source or germination conditions happened not to be favorable for these species.

Meanwhile, undercover strata of *Prunus virginiana*, *Rhus* spp., and *Smilacina stellata* develop essentially as described already for the pines, and they persist with somewhat diminished vigor as the oak canopy slowly gets denser over the centuries. Dominance tends to shift slowly to *Prunus serotina*, *Parthenocissus*, and more *Vitis*, and *Smilacina racemosa* or other more shade-tolerant herbs of groups f and g on the dunes which have become several thousand years old. This latter type of an undercover, with many similarities to that on morainic substrates, continues to dominate some of the shadier woodlots on old dunes in Illinois and in Lake County, Indiana. Even more commonly, however, the undercover on

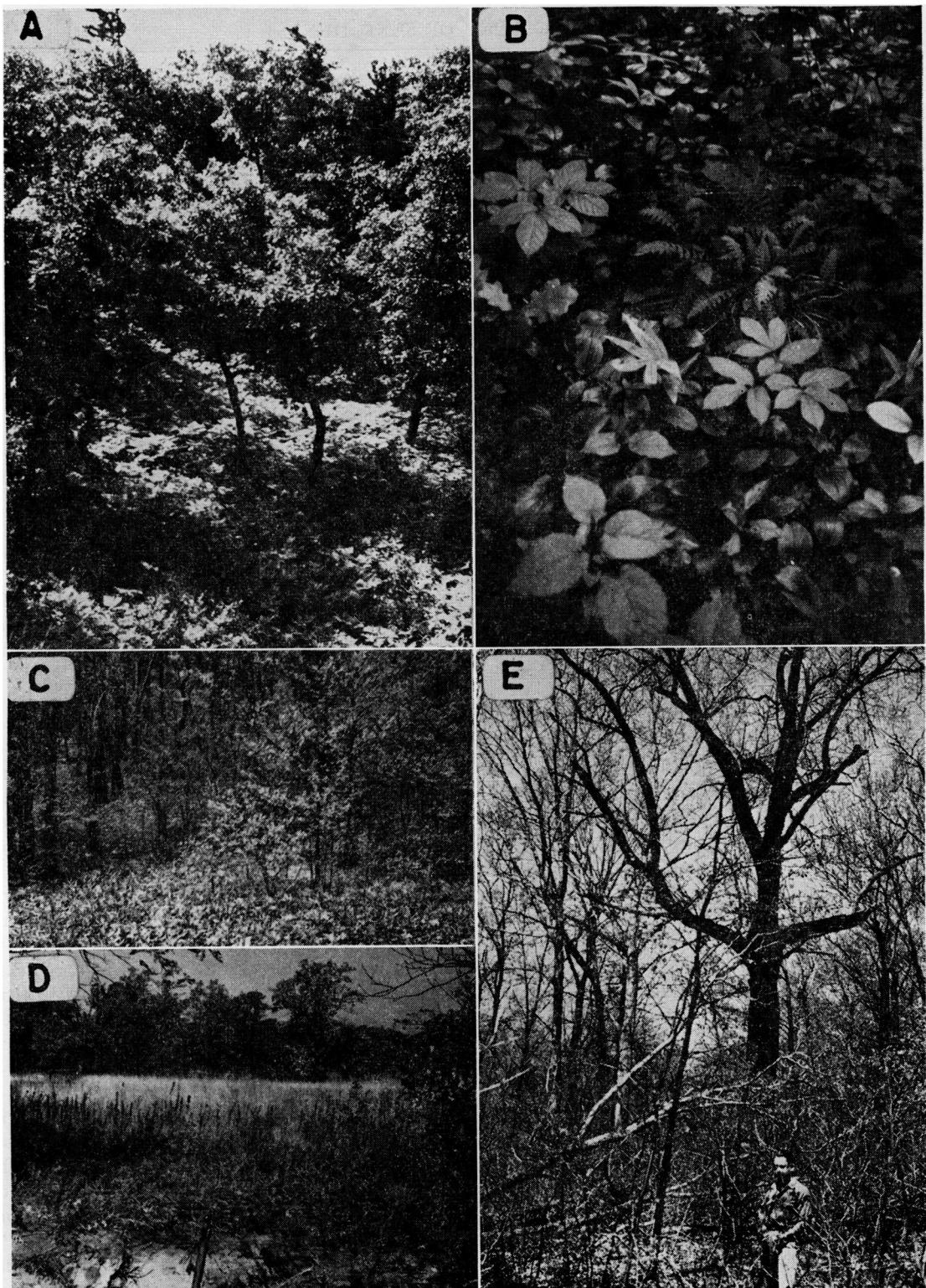


FIG. 11.—Contrasting types of undercover in black oak woodlands. *A*, scrubby black oaks replacing white pine, accompanied by open-dune herbs, *Smilacina stellata*, *Pteridium*, and woodland herbs, vines, and shrubs (blowout 5, State Park). *B*, mesophytic undercover in first-generation black oak forest that may soon develop into mesophytic forest instead of typical older black oak undercover types shown in *C-E* (Young dunes west of Lake Street, Miller, Indiana). *C*, mosaic of *Smilacina stellata* and *Carex pensylvanica* (*left*) and thickets of *Prunus virginiana* and early *Vaccinium* thickets (Wirt School Preserve,

Miller). *D*, deeper-than-usual organic matter in soil under "prairie" undercover of *Andropogon scoparius* and *Lespedeza capitata*, typical of open black oak savanna (Tolleston dunes along Michigan City Road, Calumet City, Ill.). *E*, old black oak-white oak forest with many age classes and natural replacement in openings resulting from blowdown and occasional fire. Many strata, represented by *Amelanchier*, *Hamamelis*, *Gaylussacia* and *Vaccinium*, and forest herbs, are characteristic (Calumet dune, Beverly Shores).

older dunes has developed into one of the next two complexes.

“PRAIRIE”-GRASS UNDERCOVER.—The early grassy *Andropogon* association can be eliminated almost entirely within a century or two where a pine or oak canopy closes over fairly completely. However, canopy openings commonly remain even on level dunes and more especially on south slopes on which the sun shines more directly (fig. 10D). As long as herbs of groups *d* and *e* persist in or near the woodland, they are ready to increase in abundance and vigor wherever the canopy reopens as a result of the death of individual trees from old age, disease, lightning, or fires due to natural or human causes.

The thick insulating bark of black oak protects it from death due to the usual ground fires, but burning commonly results in fire scars around part of the trunk, fungal attacks, and death or thinning of part of the crown. Prolific sprouting may replace the top if it does die, but several decades could elapse before the sprouts from widely spaced stumps would close their canopy again. Where combinations of climatic, biotic, and topographic factors favor a high probability of burning every few years, fire directly favors the growth of prairie species (table 4) in competition with the ever invading woody ones. As a result, a bunchgrass type of undercover developed on some dunes, just as it did where fire frequently burned through the bur oak openings on the moraine and lake-plain substrates.

Of course, many gradations can be found with black or choke-cherry and blueberry undercover which has been increasingly disturbed but not yet eliminated by fire. Also there are now many places where woodland undercover has invaded former prairie following increased protection from fire on woodlots and forest preserves in recent decades.

VACCINIUM-CAREX PENNSYLVANICA UNDERCOVER.—Existing thickets of choke-cherry and other shrubs tend to trap blowing oak leaves. After many centuries, the blueberry-huckleberry low-shrub-layer community may begin developing in the resulting humus. It is then able to expand its own thickets and traps leaves even more efficiently because of its stoloniferous growth habit. Whether blueberry comes in as a result of gradually increasing acidity, or whether its presence tends to increase acidity, or both, there is a distinct correlation of this undercover vegetation with the presence of a relatively acid A₂ horizon (see fig. 13 and later discussion).

In the less dense portions of these thickets or on more open ground between them are herbs of group *e* and, especially, group *f* (table 4). *Smilacina stellata* remains dominant for more than a thousand years but is eventually replaced entirely by *S. racemosa* on the oldest dunes. The commonest species accom-

panying either of them were *Maianthemum canadense* and *Solidago caesia*.

Carex pensylvanica gradually increases in abundance. It commonly dominates patchy sedge “greens” interspersed with blueberry or other thickets, where litter blows away and does not smother the tufts. The most extensive sedge “lawns” occur on recently burned dunes whose forest floor has been more or less removed by fire (see sedge-*Smilacina racemosa* columns on table 4). A miscellaneous group of herbs that occur most abundantly here or on other old dunes are labeled *g* in table 4.

In older forests, less recently burned or cut and less exposed to sun and wind, the canopy and litter become more uniform, and local differentiation into shrub and herb group societies may be less sharp than in the cases just mentioned. The whole community becomes more differentiated into layer societies where there has been time for the development of low tree strata, including *Sassafras*, *Amelanchier*, and especially *Hamamelis* (fig. 11E) as well as the tall and low shrubs and the sedge and other herb strata (figs. 11C, 13).

“MESOPHYTIC FOREST” UNDERCOVER.—*Smilacina*, *Polygonatum*, *Maianthemum*, *Aralia nudicaulis*, *Aquilegia canadensis*, and *Solidago caesia* (group *f*, table 4) are frequent in mixtures of all the preceding undercover types of oak and pine. In addition, they reach their own best development in certain mesophytic dune pockets, lee slopes, and north-facing dunes, or moist lowlands (fig. 11B). On these special sites there may be many additional mesophytic herbs (group *h*, table 4), including *Arisaema*, *Trillium*, and *Polystichum*, and shrubs such as *Lindera* and *Euonymus* (group *f*). All gradations can be found toward the more widespread undercover types mentioned before. Black oak dominates some of these mesophytic forests, but there is more likely to be mixture with red oak and basswood and some reason to suspect a succession toward these latter species *here* than there is on the great majority of black oak dunes.

VEGETATION DISCUSSION

SUMMARY OF “NORMAL” SUCCESSIONS.—In the central portion of the oversimplified succession diagram of figure 12 are indicated the most widespread communities of the Indiana dunes, which develop on normally exposed foredune ridges and the windward slopes, summits, and depressions that are not strongly influenced by water table and protection from surrounding high dunes.

Pioneer grasses, with or without accompanying cottonwoods or dune-building shrubs, eventually lead to various types of black-oak communities, often with an intervening stage of jack or white pine.

Figure 13 and tables 3 and 4 show the sharp decrease in pioneer herbs, groups *a*, *b*, and *c*, the rise and fall of herbs in groups *d* and *e*, and the slightly delayed arrival of woodland herbs in groups *f* and *g*. Pioneer shrubs, groups *a* and *b*, give way to the more versatile and persistent creeping and erect woodland shrubs, groups *c* and *d*, respectively; finally, the blueberry-huckleberry group, *e*, invades after many centuries of surface stability and soil leaching and comes to dominate most of the oldest dunes.

The transformed time scale of figure 13 clearly shows how basal area increases very rapidly in the

Of course, comparison of a series of dunes of different ages does not exactly represent the past or future course of succession on any single dune. But it is probably safe to say that data of tables 4 and 5, and other observations throughout the dunes between 1942 and 1952, at least provide no positive evidence of succession of normal old dunes toward a mesophytic forest.

Except on certain sites like north slopes and lowlands, red oak occurs only sporadically on either young or old dunes. Rare occurrences of small individuals of three hickories (*Carya cordiformis*, *C.*

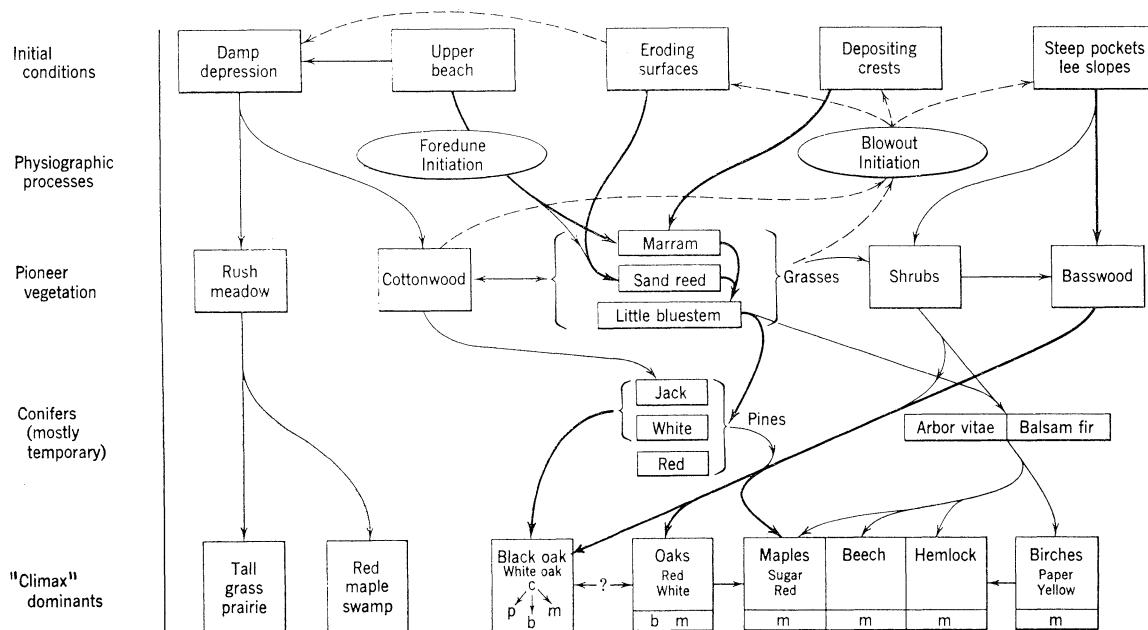


FIG. 12.—Alternative dune successions. Beaches, foredunes, and blowout dunes provide diverse sites which undergo different successions. Center of diagram gives oversimplified outline of "normal" succession, from dune-builders to jack or white pine to black oak-white oak with several undercover types: choke-cherry-poison ivy (c), "prairie" (p), blueberry-huckleberry (b), or mesophytic herbs (m), depending on topography, water table, and biotic and fire history. Wet depressions (*left*) and protected lee slopes and pockets (*right*) may lead to richer

forests including basswood, red oak, and many mesophytic trees and herbs. Beech and hemlock are added in mesophytic pockets of Michigan and become more widespread northward; in northern Michigan red oak-white oak-blueberry (b) may take place of black oak on some dry dunes; pines, including red pine, are more widespread, and fir joins arbor vitae, basswood, and birches near lake. (Diagram published in *Elements of Ecology*, by G. L. CLARKE, from data of present writer. Reproduced here by permission of John Wiley & Sons, New York.)

first few hundred years, and little if any after a thousand years or so, compared with sampling variability. The six oldest plots listed in table 5, on areas ranging from about 850 to about 12,000 years old, average 19.3 square meters per hectare, or about 84 square feet per acre.

As in many old-field successions, pine is reduced to a minor species after the first generation or two (except perhaps for certain north-slope and lowland situations not included here). Black oak remains dominant, even on the oldest dunes. White oak may or may not be abundant.

ovata, *C. tomentosa*) are noted on table 4. The basal area contribution of *Liriodendron tulipifera* in the last column of table 5 represents a single tree 17 inches in diameter.

The only beech found on "standard" topographic conditions was a double sapling that probably had resprouted after dying down on the Glenwood dune at Beverly Shores (near *G* on fig. 4); even this minor exception to the general absence of beech on the dunes might be explainable by seepage over compact till underlying the dune and giving rise to a red maple-paper birch swamp forest nearby. Large beech trees

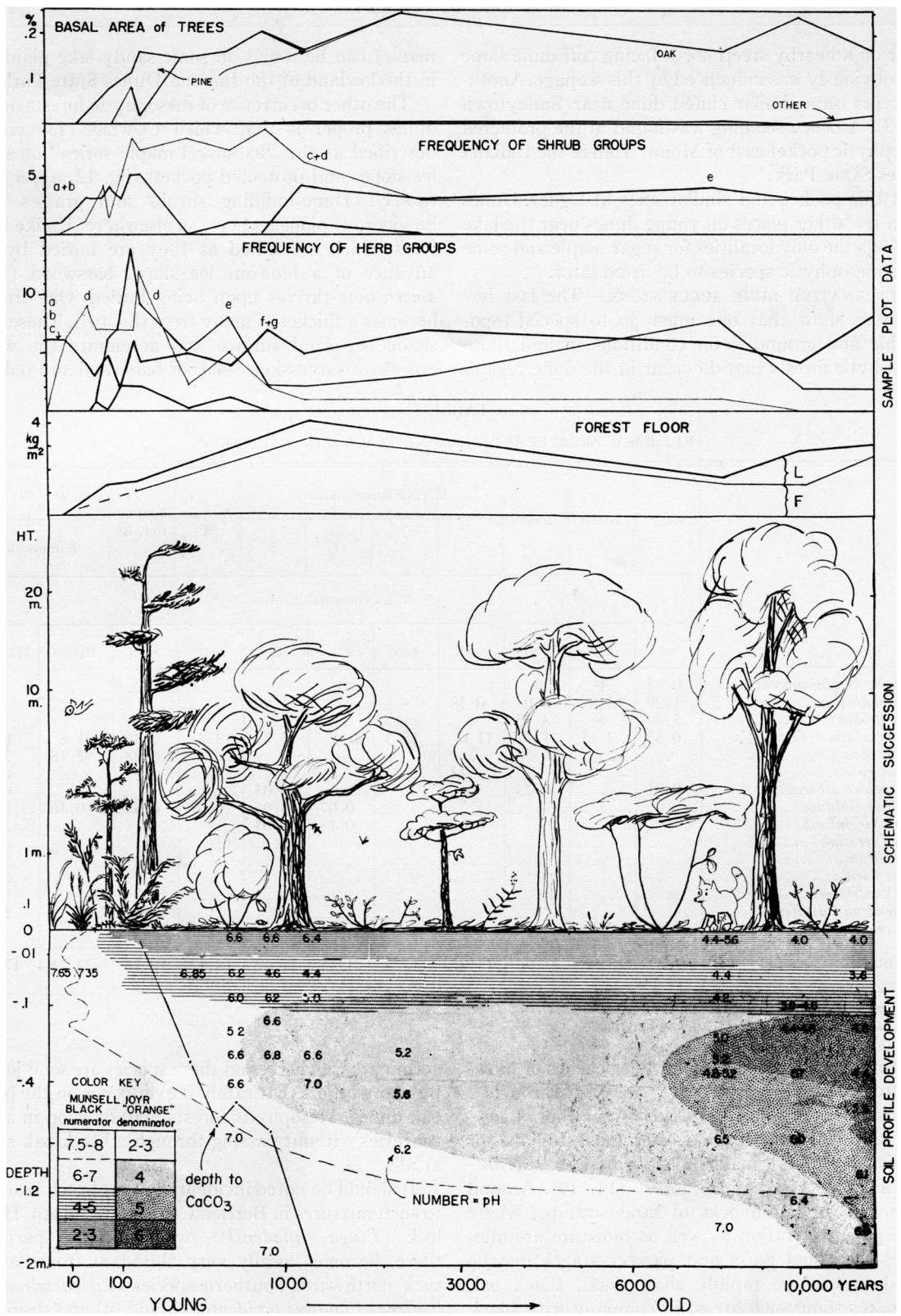


FIG. 13.—Succession and soil development as function of dune age (note transformed scales). Changes of species groups (tables 3 and 4), basal area (table 5), litter layers, and gross soil-profile characteristics. A horizon darkens rapidly with humus. B horizon slowly turns orange as small fraction of

unstable minerals in dune sand oxidize. Faintly bleached A₂ horizon develops acid pH (4.5) after about 1000 years when carbonates have been leached from soil. Further deepening of low pH value occurs as exchange acidity increases (fig. 19).

occur on a nearby steep north-facing cliff dune slope that obviously was influenced by this seepage. Another occurs on a similar cliffted dune near Baileytown (fig. 3). A beech seedling was found in the protected mesophytic pocket east of Mount Tom in the Indiana Dunes State Park.

In this pocket and similar ones at Ogden Dunes and a few other places on young dunes near the lake one finds the only localities for sugar maple and some other mesophytic species to be listed later.

ALTERNATIVE DUNE SUCCESSIONS.—The last few examples show that one must go to special topographic and ground-water conditions to find those mesophytic forests that do occur in the dune region.

(maple) can be found on some sandy lake plains, as in the lowland of the Indiana Dunes State Park.

The other occurrence of mesophytic forests on the dunes proper is that which COWLES (13) vividly described as the "basswood-maple series" on steep lee slopes and protected pockets (fig. 12, *upper right corner*). Dune-building shrubs and grasses may be vigorous pioneers here, as elsewhere. Unlike most trees which are killed as they are buried by the advance of a blowout lee slope, basswood (*Tilia americana*) thrives upon being buried. One treetop becomes a thicket of many trees (fig. 6B). These help shade the sand surface and accelerate the whole process of succession. Seeds of basswood and red oak

TABLE 5
TREE BASAL AREA^a OF INDIANA PINE-BLACK OAK SUCCESSION^b

	B4SP	B5OD	B5SP	MILLER RIDGES (GARY)				ALGOMA, SP	TOLLES- TON, BS	CALUMET	GLENWOOD				
				2	3	4	5								
Years since stabilization															
				90	150	120	350	600	850	1100	2500	8000			
												10,000			
												12,000			
<i>Juniperus virginiana</i> var. <i>crebra</i>	0.45	+	+												
<i>Pinus banksiana</i>	1.20	13.8	0.03	0.48	+	+		1.99							
<i>Pinus strobus</i>	5.49	+	3.45	+											
<i>Quercus velutina</i>	0.35	2.15	7.97	11.0	15.3	21.2	15.3	18.8	7.42	21.8	8.66				
<i>Quercus alba</i>			0.38						8.38	2.78	5.63				
<i>Quercus rubra</i>				3.42							0.77				
<i>Amelanchier arborea</i>	0.31	0.13				0.05		+		0.07			
<i>Sassafras albidum</i>												0.81			
<i>Prunus virginiana</i>	+		0.05			0.07	0.04	0.07	0.38	0.16			
<i>Prunus serotina</i>								0.13	0.04						
<i>Acer rubrum</i>											+	0.11			
<i>Cornus florida</i>											+	0.11			
<i>Carya cordiformis</i>											+	0.06			
<i>Liriodendron tulipifera</i>												0.04			
<i>Tilia americana</i>	0.07										1.58			
Total.....		7.87	15.95	11.96	13.95	15.3	21.4	17.42	18.87	16.18	24.74	17.83			

^a Sq m/hectare = 100 × % total area = 0.2296 × sq ft/acre.

^b Locations and ages explained on table 4 or in the text.

Damp depressions left by former beaches or blowout erosion (fig. 12, *upper left*) may go through a *Juncus-Carex* meadow stage toward either a lowland tall-grass prairie (in westernmost Indiana or Illinois) or a red maple–pin oak (*Acer rubrum*–*Quercus palustris*) swamp forest (14, 19). Around margins or on hummocks of sand swamps, where drainage and aeration as well as moisture are adequate, the usual grass and pioneer stages may be passed even more rapidly than usual. Black oak dominates some such areas, in company with black gum (*Nyssa sylvatica*) and white pine, but various gradations to red oak–white oak–basswood mesophytic forests (including some beech and sugar

germinate well here, and these species are soon joined by many others that rarely if ever occur on the black oak dunes. Mesophytic forests may develop in a few centuries without passing through a black oak stage at all.

It should be noted incidentally that beech is added to such mixtures in Berrien County, Michigan. Hemlock (*Tsuga canadensis*), which occurs sparingly there, becomes locally very abundant from Saugatuck northward. Southern species (*Liriodendron tulipifera*, *Platanus occidentalis*, and others) drop out as the typical "northern hardwoods–hemlock" region is reached. Here also black oak becomes rare, but a red oak–white oak–blueberry woodland still oc-

cupies many of the less protected sites. Pines, including *P. resinosa*, may lead the way to either beech-maple-hemlock or oak vegetation and show more tendency to persist in the latter type than they do farther south. *Arbor vitae* (*Thuja occidentalis*) occasionally is found on north slopes near the lake as far south as Warren's Dunes State Park. It and balsam fir (*Abies balsamifera*) and a few white spruce (*Picea glauca*) occur in a narrow strip along the lake north of Frankfort, especially on lee slopes and in pockets with basswood and yellow and paper birch. The last species is common in secondary successions in the north.

DISTURBANCE HISTORY.—Most oak dunes have been influenced by some cutting and fire, usually both. Clear-cutting for cordwood has left open or dense even-age stands of multiple sprouts. Thinning of farm woodlots maintained a many-age structure but temporarily reduced basal area and crown cover, increasing growth on small trees and shrubs and readmitting less tolerant herbs. In some areas like the Indiana Dunes State Park there has been considerable time for recovery, since lumbering and homestead clearing after the Civil War (5, 12), while in other areas disturbance has increased in recent years.

Fire has no doubt favored species which are less damaged by burning or better able to revive after fire than is the case for most species of the mesophytic forests. Hence there are probably some areas where the latter have been kept out by fire but where they would be capable of reinvading if these areas are protected from future disturbance and if the species are available in the vicinity. But such areas would probably be those favored by ground-water, topographic, or climatic conditions more favorable than those outlined in table 1. Under these latter conditions, there is still no evidence of future marked improvement toward mesophytic forest. The inference that such improvement should eventually take place here, too, has been based on rather speculative considerations which must be reviewed next.

"SYNTHETIC SUCCESSION."—Values of single variables, like evaporation (17) or soil properties considered later, can be arranged on a linear scale whether they belong to communities of a single linear succession or not. Whole communities or ecosystems can sometimes be ordered in a line, even though those at one end are not likely to be transformed into those at the other end. Such a linear arrangement has provided a convenient pedagogical device for outlining the main communities of the dunes (1, 7, 19, 50): one could find a continuum grading from pioneer grasses or cottonwoods through pine and black oak to red oak-basswood (to sugar maple-beech-hemlock if Michigan dunes are included).

But just because transitions could be found in different conditions between any one member of this sequence and the next, this does not mean that any one place was likely to pass through the *whole* sequence of stages. COWLES clearly stated how the basswood-maple succession did not usually go through pine or black oak stages, while the pine-black oak succession had not developed to a mesophytic forest; these conclusions are emphasized by the present study. The single, somewhat fictional "synthetic" succession, as one might call it, was patched together as best it could be from all the natural successions of the region.

By this device, truly successional differences were confounded with effects of factors other than dune age (E_i of table 1) whose influence was judged merely according to whether it was "toward or away from the mesophytic, i.e., progressive or retrogressive. . . . In this way all possible conditions are accounted for" (14:81). This particular kind of synthesis helped to make ecology seem simple and therefore popular (11). It tended to hide the unanswered questions about the relative importance of various factors that might lead to diversity of biotic communities, instead of calling attention to the need for answering them.

FUTURE OF DUNE SUCCESSIONS AND SOILS.—Perhaps the preceding historical note helps explain why COWLES and others cherished the hope that the old black oak dunes might *eventually* succeed to typical mesophytic forest even though they had not done so in all of postglacial time—that it was merely a question of too slow a rate and too little time. COWLES frankly admitted that "the future of the vegetation of the established dunes and beaches is somewhat problematical" (14:177). Yet he speculated immediately: "From analogy with other plant societies in this region and from established dunes in Michigan, we should expect a mesophytic forest probably of the white oak-red oak-hickory type at first and then followed by a beech-maple forest" (italics mine). As "evidences that some such changes are now taking place" he cited the presence of mesophytic herbs and sugar maple, but such cases probably refer to the special topographic or water-table situations distinct from those of table 1.

Precisely because the evidence for successional improvement was so sparse or dubious, COWLES blamed "the slowness of humus accumulation . . . , perhaps more than all else." He evidently did not consider the possibility that soil improvement might have long since proceeded as far as it was going to or that some soil conditions might be getting *less* favorable for the mesophytic species instead of more favorable.

OLMSTED raised this latter alternative: that "the podsolization inherent in the maturation of the sandy

soil profile . . . will accentuate rather than diminish many of the edaphic factors inimical to [mesophytic climax] forests" on certain sand plains (40). He has repeatedly suggested to classes that this might apply to the black oak-blueberry dunes as well.

Clearly, COWLES was right in declaring that rates of soil changes and their relations to plants needed "much further investigation" before ecology could judge the future of his own classic dune succession—or of successional theory in general.

Dune soil formation

The quartz sand of the dune essentially provides an inert skeleton, but in its interstices take place many changes of vital importance for the biological future of the dune. These changes depend on organisms, just as the organisms depend on the soil.

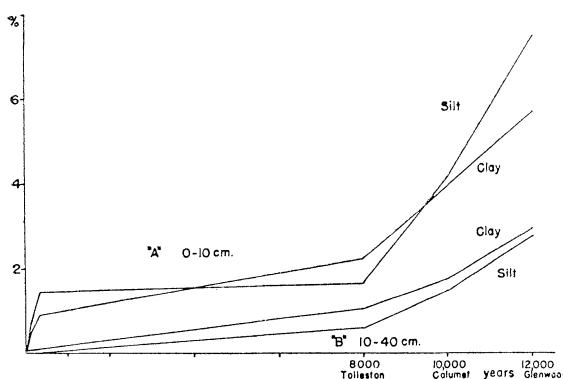


FIG. 14.—Silt and clay percentage of dune soils increases from negligible amounts in dune sand parent material. Silt and part of clay interpreted as dust deposit on dunes soon after stabilization, and more especially on certain old (Glenwood and Calumet) dunes which were contemporaneous with late-glacial loess conditions.

Even a physical soil-forming process, the settling of silt and clay as dust, is aided by the vegetation's stilling effect on the air. Carbon dioxide and organic acids doubtless hasten the rapid leaching of carbonates and the slower weathering of silicates. Accumulation of organic matter not only directly increases the nutrient reserve of nitrogen and other elements but modifies the moisture and aeration characteristics and the base exchange capacity. The exchange complex seems especially significant for the nutritional reserve of metallic elements or bases. But some of the exchangeable bases are displaced by exchange acidity as the soil becomes leached for longer periods of time.

Rates of change and possible equilibria in several of these soil developments involve a rather sensitive balance of opposing processes. These will be analyzed quantitatively in a very preliminary way.

COLOR

The two basic processes of soil development can be traced generally by observations of colors on successively older profiles of dune soil. In the composite cross-section of figure 13 the horizontal ruling (Munsell numerator or "blackness" index, changing from 8 to 2) shows the relatively rapid increase in humus, especially in the black surface soil (A_1). The stippling (denominator or "orange" color, changing from 1 to 8) shows the somewhat slower process of weathering of iron colloids which stain the larger mineral grains, giving character to a "color B" horizon. Between the blackest and most orange horizons on the older soils is a grayish A_2 horizon (unstippled light horizontal ruling).

At the south end of the lake this never reaches the ashy-white condition of true podzols, but it does have a relatively low pH value, commonly around 4.6 and, in rare cases (in dry weather), as low as 3.6. The resulting gray-brown podolic "Plainfield fine sand" profile (8, 9, 54) is classified along with similar soils on outwash, lacustrine, and dune sands in many parts of the Great Lakes region.

SILT AND CLAY

Only a few silt-clay analyses were made, but their results suggested some interesting tentative interpretations (fig. 14). In the surface decimeter of soil, silt rises rapidly at first, then shows little addition for considerably older dunes, and finally shows far greater amounts for the Calumet (4%) and, especially, Glenwood dunes (7%). The first increase can be interpreted as the settling of fine material being winnowed out of active dunes that were not far distant during early centuries after stabilization. The lack of much further increase for older dunes would not be surprising if there were no immediate source. The larger quantities on the two oldest soils can be accounted for by the special explanation that these are contemporaneous in origin with the last two glacial retreats (Valders and Cary) and could have received their own small share of wind-blown sediments swept up from newly uncovered moraine and outwash materials. In other words, these soils may have received a trace of loess which would have gone unnoticed if it were not for the exceedingly small amounts of silt and clay in the parent materials.

The clay curve increases in a roughly similar manner for the surface decimeter, suggesting that some fraction of the dust that settled belonged to this size ($<2\mu$ effective diameter). However, the increase is more gradual, with some clay increase even without much increase in silt in the case of the Tolleston dune. This fraction of the clay which increases out of proportion to the silt may be all

that represents a true weathering residue from the less stable feldspar or ferromagnesian sand grains.

In the 10–40-cm. depth there is no early increase in silt, as might be expected if the silt is being added to the top of the profile. A slow increase later on might likewise be expected from the washing-down of a few particles from the surface layer.

Clay in the lower horizon increased faster than silt, a little over 1% in perhaps 8000 years for the Tolleston soil. On the Glenwood and Calumet dunes both clay and silt are much higher than on the younger dunes in the B horizon, as they were in the A horizon, presumably again because of the excess of particles filtering down from above, beyond those being produced by weathering.

Further analyses of dune soils would offer interesting possibilities for generalizing on rates of dust fall and weathering that could not so readily be determined from soils whose parent materials were higher and more variable in their initial silt and clay contents. Aside from genetic interpretations, the very presence of this fine material in the two oldest dune systems must provide a warning against interpreting them as necessarily representing the future condition for the younger dune soils.

CARBONATES

One early drastic soil change is the leaching of carbonate mineral grains. Figure 15 shows that the rate of loss in the surface decimeter is high at first and diminishes along with the residue of carbonate. Computing all carbonate as calcite, there is a fair fit to the negative exponential function

$$\text{Carbonate} = y = De^{-vt} = 1.48 e^{-0.0046t}, \quad (2a)$$

which implies that the rate of loss is proportional to the carbonate left at any time:

$$\text{Rate of loss} = \frac{dy}{dt} = -vy. \quad (2b)$$

Actually, however, some of the carbonate is dolomite, which should dissolve more slowly. Perhaps this difference in solubility helps explain why the initial rate of loss (mostly calcite) seems higher than that which is fitted by the equation, while later losses may be slower. The accuracy of estimating the small traces of carbonate on old surface soils is not great (38), but it seems clear at least that most of the free carbonate in the surface decimeter is gone within a few hundred years after stabilization (cf. 47, 48).

Even after the carbonate percentage in the surface decimeter drops below the level which can be detected audibly by hydrochloric acid, this method can be used to find the *depth* to which the profile is leached

of detectable carbonate (fig. 13). It takes about a thousand years to deepen the leached zone to 2 meters.

ORGANIC MATTER

Beach debris, buried tree trunks, and buried soils locally provide extra concentrations of organic matter even on the bare dune; these obviously account for some differences in the vigor of pioneer plants. As long as dune-builders are being buried by sand, they leave a network of residues which provide a dilute concentration of humus within the depths of the dune, which may have some ecological importance at this early stage (55). After deposition stops or slows down, dune grass "straw" and other plant and animal residues begin to collect near the surface

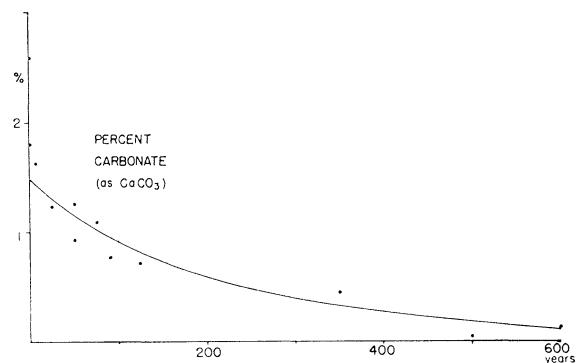


FIG. 15.—Leaching of carbonates from surface decimeter of dune soil, rapid at first and slower as last mineral grains are dissolved after several centuries of stabilization. (Approximate manometric estimates of carbonate, here computed as CaCO_3 .)

and provide the first visible darkening of humus—within only 4–6 years on foredune 2.

ORGANIC CARBON.—Except at the very surface, organic carbon content (fig. 16) of a young (5-year-old) foredune soil averaged less than 0.05% carbon, as did the deeper soil on a cottonwood foredune (vegetation listed under B2SP in tables 3 and 4). Cottonwood litter increased humus in a shallow layer, while grasses associated with it and with the older pine stand (B4SP on tables 3, 4) contributed more humus to greater depths. An old black oak-blueberry dune soil not only had a very large reserve of unincorporated organic matter (see forest floor L and F for 10,000-year soil on fig. 13) but had a high content of humus to a considerable depth. Presumably, this resulted from humus infiltration as well as root growth.

A few preliminary C:N ratios suggested that grassy pioneer vegetation breaks down to humus with a low ratio, near 10, while some of the old forest soils had considerably higher ratios, around 20, as has been observed in many other forest soils (34–36,

63). In addition to the foregoing incorporated organic matter, considerable loose material is caught on the sieves, which had an organic carbon content averaging 39% of ignition loss.

NITROGEN.—The increase in humus can also be traced in terms of per cent nitrogen, N. This element is especially significant for plant nutrition, but most of that present in the soil is unavailable at any one time. Quantitatively, some small fraction, k' , of the

the difference between income and outgo must be zero;

$$k_2 - k'N = \frac{dN}{dt}, \quad (3a)$$

the general equation for the rate of change of nitrogen, must equal zero.

What change would soil nitrogen follow if the hypothetical k_2 and k' remained constant, but if the initial content of N were exceedingly low, as in dune sand? Losses $k'N$, would be low, in proportion to the total; gains would greatly exceed losses at first, and N would rise rapidly. But, as N increased, so would $k'N$; annual loss would gradually overtake annual income. The difference between income and loss—the net increase—would become slower and slower as nitrogen leveled off toward the value N_{lim} .

The general equation describing this situation, the integral of equation (3a), can be expressed in several equivalent forms:

$$N = N_{lim} (1 - Ge^{-kt}), \quad (3b)$$

$$= N_{lim} - GN_{lim} e^{-kt}, \quad (3c)$$

$$= N_{lim} - (GN_{lim}) r^t. \quad (3d)$$

The last computationally convenient form is related to the others by

$$r = e^{-k} = 1 - k'. \quad (3e)$$

Equations (3b)–(3c) represent the modified exponential curve which *increases* toward an asymptotic value instead of decreasing to zero as did equation (2a); here it is the *difference* between the current value and the limiting value which diminishes toward zero with time. The *rate* of approach is proportional to this difference as it was in the case of equation (2a). A similar analysis of forest litter development is provided by JENNY *et al.* (28).

Soil nitrogen data of figure 17A fit this pattern of change in a general way. The most rapid rise occurs in the first few decades and centuries following surface stabilization (fig. 17B). Already the *rate* of increase or slope of the graph is tapering off. There is little net increase between dunes that are 1000 years old and those that are 8000 years old, approximately. One should expect that in nature, too, some kind of balance of income and loss—no doubt, a fluctuating balance—is being approached after the first thousand years or so following stabilization of the dune surface.

However, the two oldest dune systems (Glenwood and Calumet) do not seem to fit this ideal scheme: instead of scattering around the same trend, their levels of nitrogen and other properties related to humus content seem to be higher. These seem like

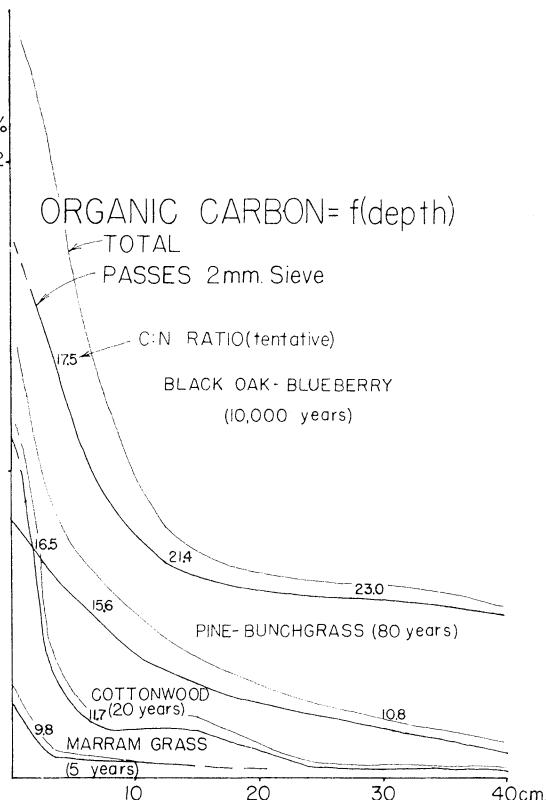


FIG. 16.—Selected profiles of organic carbon from four dunes of contrasting ages. Heavy lines represent material in sieved soil; differences between these and upper "total" lines represent rootlets and other debris. Distribution shows main organic contribution at surface (and also a slightly buried former surface layer in cottonwood profile). Deeper distribution in open pine area due mainly to bunchgrass roots; in old oak-blueberry area it has probably increased greatly by infiltration of humus.

total is being decomposed each year into forms that can be either absorbed by plants or lost from the ecosystem by denitrification or leaching.

In an idealized "climax" forest with a "mature" soil, the total nitrogen, by definition of a steady state, has reached a constant limiting value, N_{lim} . This implies that the loss from the soil, k' multiplied by N_{lim} , must be balanced by a certain average annual income we shall denote by k_2 . In other words,

more than chance sampling deviations. If they represent an upward "hook" in the curve of nitrogen against dune age, will this be reflected in a sudden future rise in nitrogen levels of dune soils that otherwise seemed to have long since approached a limiting value? Or is there perhaps something unusual about these two old dune systems which might explain why they might continue to have humus or nitrogen levels superior to that of the Tolleston dune soils which are only slightly younger?

One may recall the higher silt and clay contents of these soils and might suspect that the resulting textural and moisture difference would help maintain higher nitrogen levels here. These nitrogen values may represent the late stage of different nitrogen-time curves, even though all fall within the same family of modified exponential curves: *light solid* and *dashed* lines as compared with the *heavy solid* line that was fitted to the data for Tolleston and younger dunes. Until more information becomes available, one may at least allow for this possibility and restrict attention to the latter curve as one possible representative in this family of curves.

A rough estimate of the limiting value N_{lim} for the heavy curve is provided by the average content for available Tolleston dune samples, 0.087%. The difference between the initial value of 0.003% and this final value, expressed as a fraction of the final value, gives the constant $G = (0.087 - 0.003)/0.087 = 0.966$ in equations (3b)–(3d). Preliminary estimates for r can be based on the values of three or more sample points (44) or points selected on the tentative curve. These estimates can be improved by successive approximations in the regression of N on r^t (eq. [3d]) to decrease the sample variance. Approximately, $r = 0.997 = e^{-0.003}$, so that $k = 0.003$ by equation (3e). This leads to the interesting conclusion that there should be a loss of only about 0.3% of total soil nitrogen, since $k' = 1 - r = 0.003$. (In general, $k = -\ln[1 - k']$, but this reduces to $k = k'$ for values near or less than 0.003.) This rate is slower than provisional rates computed for tropical and Sierra Nevada soils (27).

If this rate of loss actually applied in a mature surface soil of a "climax" ecosystem which had $N_{lim} = 0.087\%$, then $(0.003)(0.087) = 0.00026\%$ would be the annual loss, and this would have to be compensated by an annual income of the same amount. Actually, this income is about that indicated by the initial slope of the nitrogen-time curve in figure 17B.

For the original dune sand having a density of 1.55 gm. per cubic centimeter (see below), this would correspond roughly to an annual income of slightly over 0.004 gm. of nitrogen per cubic decimeter of surface soil or 4.03 kg. per hectare (3.5 lb. per acre in the surface 4 inches). This estimate and various

refinements of it lie close to previous estimates of nitrogen income from rainfall, ranging from 4.6 to 9.2 kg. per hectare for the nominal 15-cm. plow depth of agricultural soils (39).

Since legumes (*Lathyrus japonicus* var. *glaber*, *Lespedeza capitata*, *Lupinus perennis* var. *occidentalis*) are distributed irregularly in the dunes, symbiotic nitrogen fixation would favor only local areas. The possibility of non-symbiotic nitrogen fixation deserves direct study, along with repeated analyses of specific components of the nitrogen budget.

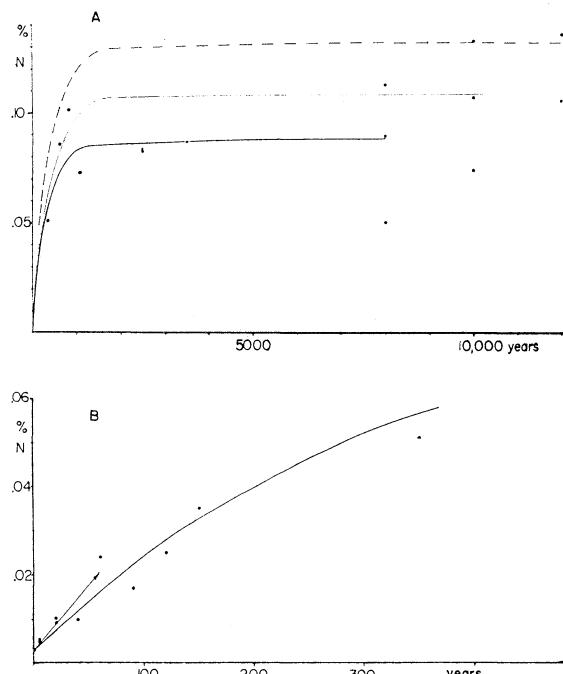


FIG. 17.—Soil nitrogen increase in surface decimeter of soil as function of dune age. A, approximate fit of modified exponential function for black oak dunes up to about 8000 years old (Tolleston) (*heavy solid line*). Unusually high values of old (Calumet and Glenwood) dunes may represent end points of separate curves (*light solid and dashed lines*, respectively) and hence are not fitted with the rest. B, expansion of left portion of A, showing additional nitrogen estimates for young dune soils. Arrow represents initial rate of increase (dN/dt for time zero) which corresponds roughly to annual income of nitrogen. Net gain slows down as annual losses increase in rough proportion to total nitrogen.

Further refinement of the obviously oversimplified theoretical treatment could allow for variation in the parameters for income, k_2 , and rate of loss, k' , for slightly different conditions of site or parent material—along the line mentioned above for the Calumet and Glenwood dunes. Then there would be a problem of relating a given dune to a whole family of curves like the three given on figure 17A. Almost certainly the parameters would change some between the very

early and very late successional stages on the same dune, so that a more perfect formula describing the change through time would be more complicated. Finally, the wide scatter of sample points around the trend may be due to real oscillations in the forest floor and soil conditions of old forests, related to changes in canopy density and occasional interruption of the equilibrium by fire. The latter would cause immediate loss of humus which might take decades or centuries to restore.

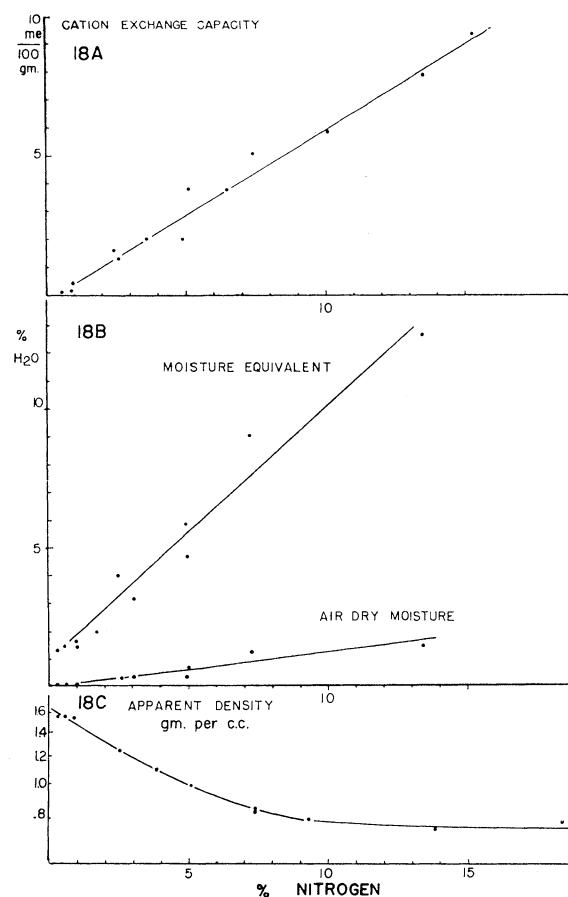


FIG. 18.—Soil properties correlated with total nitrogen (horizontal scale) for 0–1 dm. and 1–4 dm. soils. A, cation exchange capacity. B, moisture equivalent and air dry moisture %. C, apparent density (volume weight), gm/cc.

PHOSPHORUS.—There is evidence in unpublished data from greenhouse nutrient experiments with *Andropogon* by LAING and the writer that phosphorus may be at least as serious a limiting factor as nitrogen on very young alkaline dune soils. Since this element is only gradually released by weathering of apatite and is not replenished from outside the local ecosystem like nitrogen, it is especially in need of further study. Sulfur might be expected to be a limiting factor also, in view of its rarity in the dune sands,

if it were not for the considerable income brought down in the rainfall in recent years following industrialization (39).

PROPERTIES RELATED TO ORGANIC MATTER

APPARENT DENSITY.—As organic accumulation, plant-root growth, and animal activity of diverse sorts continue, the initial density of about 1.55 gm/cc for fresh dune sand gradually decreases to about half that value (fig. 18C) in the top decimeter of mineral soil (cf. 34).

This curve can be used to transform the data given here on a percentage dry-weight basis to a volume basis if desired. For a variable that decreases with time, like carbonates, this adjustment will tend to accentuate the decrease. Variables which increase with time, like percentage nitrogen, will not appear to change quite so much on a volume basis as they seem to do on a weight basis.

MOISTURE CHARACTERISTICS.—Moisture equivalent and air-dry moisture content and presumably other reference points on the moisture-energy curve tend to increase linearly with nitrogen content (fig. 18B). Moisture equivalent is considerably below field capacity in these very sandy soils, but it is clearly suggested that there would be an increase in available moisture on the older dunes following a pattern resembling that of the increase in nitrogen as a function of time. The oldest dunes, with higher silt and clay contents, are especially favorable for both moisture and nitrogen status.

CATION EXCHANGE RELATIONS

The cation exchange capacity of dune soils is another important variable that increases along with humus content. The exchange complex is initially saturated with calcium and other metallic ions that are valuable in plant nutrition, but gradually these basic ions are partially replaced by hydrogen ions (exchangeable acidity) as soil development proceeds under the influence of vegetation.

CATION EXCHANGE CAPACITY.—Exchange capacity of both surface soils and lower horizons increases in proportion to soil nitrogen (fig. 18A). One can estimate exchange capacity from soil nitrogen and vice versa. As in the case of nitrogen, exchange capacity should increase rapidly at first and more slowly later on (fig. 19A), following a modified exponential function with approximately the same exponent, $k = 0.003$. (Compare eq. [4a] following with eq. [3b] preceding.)

The average exchange capacity for Tolleston dune samples, roughly 8000 years old, is around 5.3 milliequivalents per 100 gm. of soil. For the two older dune series it is higher, averaging 6.5 and 8.0. This is expected in view of the higher silt-clay and nitrogen

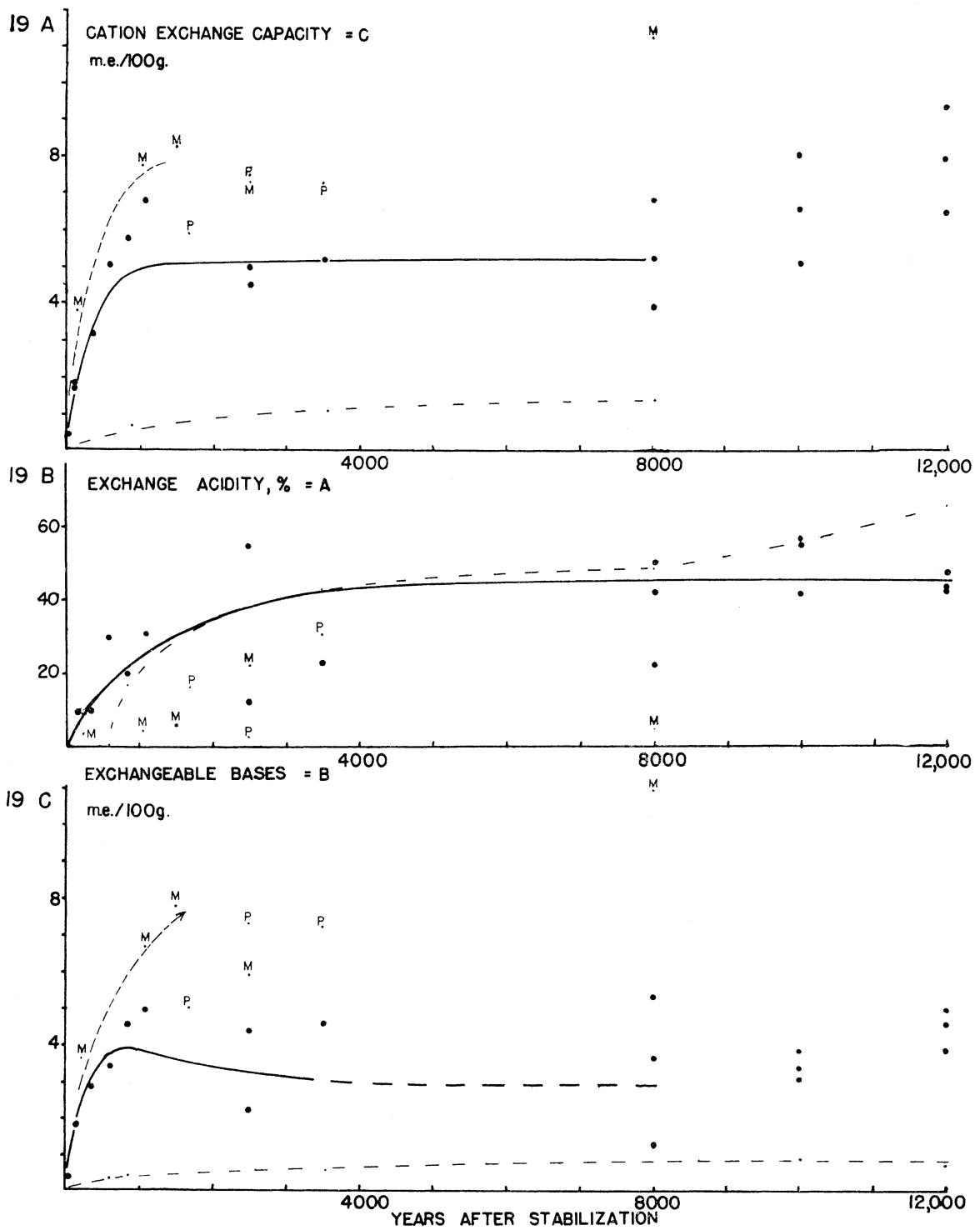


FIG. 19.—Cation exchange relations as function of dune age.
A, cation exchange capacity. *B*, exchange acidity as percentage of total exchange capacity. *C*, exchangeable bases, provisionally estimated as difference between exchange capacity and exchangeable acids.

levels of these soils but does not necessarily show a developmental tendency for reasons given above. Hence the heavy line of figure 19A is not projected to these older dunes. This line provides a fair fit through points (*heavy dots*) representing a variety of black oak dune soils. But certain additional samples that were intentionally selected from special topographic, moisture, and microclimatic situations deviated markedly from the general trend for black oak dunes.

Samples for three areas with more than the usual prairie cover (see table 4) are marked by "P." They came from west of Gary (locations 8, 9, and 10 on fig. 2), where ridges are lower, moisture conditions better, and organic-matter productivity perhaps higher than for the typical black oak woodlands. The dense mat of grass roots, which is so conspicuous when the soil profile is excavated, suggests that a higher proportion of the organic matter may be produced *within* the soil; this may account for the greater humus content, as with the true prairie soils.

Samples from mesophytic pockets or lee slopes are marked by "M." These situations were peculiar in showing some basswood, red oak, or sugar maple which were absent on more "normal" topographic situations. As COWLES noted, these mesophytic forests are mostly on young dunes and represent a distinct succession of their own rather than a stage in the pine-black oak succession. It was necessary to go out of the local climatic region, to a protected pocket in Warren's Dunes State Park, Michigan, to find a mesophytic forest on a Tolleston (or Algonquin) dune. This dune had more than twice as much cation exchange capacity (11.5 me/100 gm) as the average for Indiana black oak-blueberry dunes of the same age. Presumably, if one had been able to sample any of these mesophytic pocket soils repeatedly during their development, it would have been found that their exchange capacity followed a consistently higher curve than the black oak curve on figure 19A, even though the forms of the curves may have belonged to the same family.

EXCHANGE ACIDITY.—Organic-matter contributions have diverse effects on soil acidity. Wastes and decomposition of plants and animals produce carbonic acid and specific organic acids. Also the vital return of nutrients from these materials to living plants involves the exchange of hydrogen ions, displacing metallic ions which would have tended to keep the soil more basic. Yet the eventual return of these bases in forest litter should tend to counteract acidity produced there, as would the initial content of carbonate minerals as long as it lasts.

These processes help explain the changes of exchange acidity, expressed as a percentage of total exchange capacity, which are summarized in figure 19B. The increase is relatively slower than that of

exchange capacity (fig. 19A), but it continues longer before an average upper limit of 45% is approached.

No acids were detectable in the 10-40-cm. horizon in dunes up to several hundred years old, presumably because carbonates had neutralized them already in the surface decimeter of soil. But, as carbonates are leached out through deeper and deeper horizons, exchange acidity increases in these lower horizons as well. In fact, it reaches a higher percentage here than it does in the surface. Perhaps this is because there is less return of bases from organic debris to counteract the acid leaching here in the old soils.

These tendencies help in interpreting some of the representative soil pH measurements given in figure 13. The high initial pH value, around 7.65, is clearly due to the soluble carbonates. Except perhaps in local pockets of acid organic matter, pH values do not drop below 6.0 until carbonate is practically leached from the sand. Even after this the surface soil does not get extremely acid so long as soluble carbonates remain within the first meter or two of the dune surface, presumably because fairly considerable quantities of calcium are constantly being recycled to the surface.

But after about a thousand years, when carbonates can no longer be detected within reach of most tree roots, a thin, faintly bleached A₂ horizon (pH often 4.5) is found below the thicker mats of black oak litter, especially in thickets of blueberries which are becoming widespread at this stage of dune development. Still one need dig only to the 20- or 30-cm. depth to find soil pH values again above 6.5. But the depth of acidification continues to increase regularly on progressively older black oak-blueberry dunes, along with the depth of the orange, hydrous iron colloid stain which begins to coat the soil minerals. The bleached layer from which these colloids have been dispersed gradually becomes more conspicuous, although under black oak at the southern tip of Lake Michigan this never approaches the ashy color of the thick A₂ horizon of true podzols.

Even on those thousand-year-old dunes with incipient acid A₂ horizons, the darker humified surface soil may retain a pH above 6.0, presumably because of bases still being returned to the surface in litter. But these surface soils eventually become extremely acid when developed under black oak-blueberry litter on old dunes which have become acidified to considerable depth.

By contrast with the soils of the black oak-blueberry vegetation, those under the more pronounced "prairie" and "mesophytic" undercover types (P and M on fig. 19B) both have lower exchange acidity. Presumably, the reasons differ somewhat for these very different types of vegetation, and they will be considered further below.

EXCHANGEABLE BASES.—Time did not permit sep-

arate determination of the various metallic ions and ammonium in the exchange complex, or investigation of analytical methods other than that using barium acetate, as outlined above. Therefore, exchangeable bases, B, were tentatively estimated by the difference between the values for exchange capacity, C, and exchange acidity, A.

We saw how C approached a limiting value sooner than did A, where exchange acidity was expressed as a percentage of the estimated total exchange capacity (figs. 19A, B). If so, this implies that B should increase for a time but should later begin to decline after passing a maximum level. This maximum would be passed when the total exchange capacity no longer increased fast enough to balance the loss of bases which continued to be displaced by exchange acidity.

More quantitatively, one can see how this argument would follow if one assumes an idealized model of a modified exponential increase for both exchange capacity and percentage exchange acidity. The argument relating rates of increase and loss and theoretical balance of these rates in an old forest-soil ecosystem would follow lines resembling those covered already for soil nitrogen. For simplicity, it is clearly legitimate to modify the form of equation (3b) by taking G as 1, that is, by assuming negligible exchange capacity in the original barren dune sand (fig. 19A). Because of the practically linear relation between exchange capacity and total nitrogen (fig. 18A), k is still assumed to be about 0.003. Then the equation for exchange capacity becomes

$$C = C_{\text{lim}} (1 - e^{-kt}) = 5.3 (1 - e^{-0.003t}), \quad (4a)$$

where one tentatively assumes an asymptotic limit of 5.3 me/100 gm for all but the Glenwood and Calumet dune soils. The percentage of exchangeable acidity increases more slowly, with an exponent (call it j) estimated as roughly 0.00078, and an upper limit of about 45% averaging over all the old dune soils:

$$A = A_{\text{lim}} (1 - e^{-jt}) = 0.45 (1 - e^{-0.00078t}). \quad (4b)$$

To find the time required for attaining, for example, 95% of the limiting values, one may take natural logarithms of equations (4a) and (4b), as JENNY (27, 28) did for equations for forest floor and soil organic matter. Then $y = -\ln [(100 - 95)/100]/k$, which becomes $t = 3/0.003 = 1000$ years for reaching 95% of the "final" exchange capacity. For exchangeable acidity, $t = 3/j = 3846$ or about 4000 years ago.

Obviously, these estimates are very rough because of the small quantity and large variability of sample data, errors in chronology, and doubts as to the exact applicability of the simple exponential model assuming constant coefficients. Further study of the rates of change of soil organic matter, nitrogen, and the

exchange complex is badly needed for an understanding of both soil formation and primary succession. In the meantime, it may be helpful to discuss the bearing that each of these topics has on the other, in the dunes and elsewhere.

Discussion of soil-vegetation interactions

SOIL AND OTHER LIMITATIONS ON DUNE SUCCESSION

Even after plants have overcome the instability of the dune sand, this infertile medium for growth must be sufficiently poor to exclude all but a few typical sand plants, such as those listed in table 3; and it places severe restrictions on their vigor, as shown in exceptional areas where old organic matter buried in the dune permits an uncommon vigor of these species. In most places they must be admirably adapted to reusing what limited nitrogen supply they have, but they respond dramatically when additional nitrogen is added in the field (see marram grass in fig. 6A) or greenhouse (HICK's study of *Artemesia* [23]; also an unpublished study by LAING and the writer on *Andropogon scoparius*).

Early woody plants are almost always chlorotic, though they may produce bountiful crops of fruit; perhaps a wide carbohydrate-nitrogen balance and contrasting day and night temperatures favor this. All the soil properties associated with soil organic matter increase rapidly when trees begin to shade the surface and litter accumulates. If lack of seed source, poor site conditions, or human or other biotic disturbance delays invasion of trees, lack of shade and of surface litter may delay many of the changes outlined above.

Where the sand spills down lee slopes in the shade of shrubs and trees like the typical basswood (fig. 6B), soil improvement may proceed even more rapidly than usual. Such lee slopes and protected pockets very early develop soils whose nitrogen and base status is much better than is usual in the normal black oak-blueberry succession (fig. 19C). It can hardly be doubted that soil-nutrient relations provide part of the explanation for the occurrence here of many tree and undercover species whose litter is known to be generally higher than usual in calcium (36, 49): *Tilia americana*, *Liriodendron tulipifera*, *Ostrya virginiana*, *Fraxinus* spp., *Carya* spp., *Morus rubra*, *Prunus serotina*, *Celtis occidentalis*, *Platanus occidentalis*, and *Acer saccharum*; *Trillium grandiflorum*, *Thalictrum dioicum*, *Podophyllum peltatum*, *Arisaema triphyllum*, and others. All of these occur in the dune pocket east of Mount Tom, Indiana Dunes State Park, or in the high dunes of Warren's Dunes State Park, Michigan.

The difference between such rich dune pockets and the normal black oak-blueberry dunes is not "caused" by soil. Parent materials were probably

about the same. But a different course of successional development for the vegetation-soil ecosystem occurred in the contrasting habitats. In part this difference must be related to microclimatic and moisture characteristics which ultimately depend on the independent variable of predetermined topographic position. Solar radiation and wind are less effective in drying out the protected pockets, and the possibility should not be overlooked that a reserve of moisture might be carried downward from the higher surrounding dunes by the faint inequalities of the sand bedding on lee slopes. Less protected upper slopes and summits, even of moderate exposure, can depend only on the rainfall that reaches them, and this is rapidly withdrawn by sun and wind. FULLER (18) showed how intense root competition normally removes growth water from the soil sometime almost every summer, and exceptional droughts parch the dunes for weeks every few decades. Then even the hardy black oak may suffer some crown die-back, opening the forest floor to more direct desiccation.

The moisture equivalent and field capacity of old dune soils may be high enough to provide plenty of water for mesophytic seedlings to get started, especially in the moister springs. But this gives no assurance that it can enable them to survive normal summer drying, much less the extreme droughts that are likely to occur several times in a normal life-span. On the Glenwood dunes relatively high silt and clay and nitrogen contents may help explain the occurrence of the few rare hickories and tulip trees (tables 4, 5). Neither these nor the mesophytic "climax" species seems to be on the verge of generally replacing black oak, even here.

Charcoal in soil profiles and scars on trees suggest that fire has been important on most dunes and has tended further to favor sprout species like black oak, especially, and white oak. It is not clear whether the sporadic distribution of red oak (with the other oaks and, locally, white pine or red maple on many north slopes and with the above-listed mesophytic species in rich dune pockets) is due to lesser fire resistance or narrower moisture or temperature requirements.

Of course, the independent variable of abrupt topographic relief tends to isolate the rich dune pockets from spread of fire as well as to make their forest floor moister and less inflammable. We can probably evaluate the fire factor as an independent variable only in special cases where a fire happened to burn out, or be started, on one part of an area but not on another, where site factors seemed otherwise comparable. On some favorable dune sites, fire has probably helped keep black oak well represented, although mixtures of red oak-basswood and other species may persist here in spite of occasional fire;

these and other more shade-tolerant species may replace black oak here if fire is prevented in the future. But cases like this provide no assurance at all that most black oak-blueberry dunes are ready for natural change to some other type of forest, even if their long past history of fire is suddenly brought to an end by human controls, as in the State Park and more valued resort or residential areas.

VEGETATION'S ROLE IN SOIL FORMATION

PINE-BLACK OAK-BLUEBERRY SUCCESSIONS.—Pines, especially *Pinus banksiana*, are well known for their low requirements for many nutrients, especially the bases like calcium. This is presumably one of several reasons why they are so well adapted to many primary and secondary successions on poor soils, as compared with most hardwoods. The foliage of red and white oak is intermediate between that of the pines and of the more exacting species listed earlier for the dune-pocket vegetation for the elements just noted (36). Adequate data for black oak are lacking, but Connecticut studies (20, 35) suggest that scarlet oak-black oak-blueberry mixtures have less calcium in their litter than mixtures of red oak-white oak-hickory and other hardwoods. For undercover species data are also sparse, but *Gaultheria procumbens* and especially *Carex pensylvanica* have extremely low base contents in Connecticut. Although more information is needed on other species and on the influence of available nutrients on foliage content of any given species, present data suggest strongly that the species noted in this paragraph have consistently lower contents of calcium and usually several other bases than do the species of the mesophytic dune forests (36).

Lower base *contents* for these species presumably means lower base *requirements* and help explain why they can invade the dunes at a fairly early stage and persist on the base-poor soils of the old black oak-blueberry dunes. Lower base contents suggest also that less nutrient can be returned to the surface litter than would be possible if some of the more exacting species had been available. If so, the black oak-blueberry community would have inherently lower *efficiency* with respect to maintaining calcium and other bases in the surface layers of the soil and thereby to lessening their leaching out of the soil-plant system through ground water.

The role of occasional fire in helping to maintain the "chemically inefficient" species composition of the black oak-blueberry ecosystem was noted. Occasional fire might conceivably aggravate its nutritional deterioration more directly. As usual, a mat of partially decomposed oak litter begins accumulating after each fire—especially where wind gathers the leaves in the blueberry-huckleberry thickets.

Incidentally, this means that some fraction of the limited nutrient capital of the system is tied up in a form that is even less available than it might otherwise be. When another ground fire sweeps through, it suddenly releases a considerable amount of this meager reserve at once. Some may be quickly reabsorbed; but, if more is released than can be taken up by vegetation or by the limited exchange capacity of the soil, the remainder is presumably flushed away in the ground water.

Such losses could gradually be made up as long as there was a reserve of calcium-magnesium carbonates and perhaps other ready base supplies within reach of the roots. But after a thousand years or so, when the carbonates were gone, the only reserve would be the limited quantity of less soluble silicate minerals in the predominantly quartzose sand. At this point it is difficult to see how such an ecosystem could become progressively more suitable for the exacting species listed for the mesophytic dune forests.

BLACK OAK-PRAIRIE "SAVANNAH."—Lest fire be considered in *only* the preceding context, speculation should include quite different effects that might appear in some of the prairie undercover types of black oak dunes. Here fires may be so frequent (every year or two) that the canopy is opened enough to favor grasses with deep fibrous root systems which contribute more exchange capacity through the body of the profile and which may be more efficient in returning leached bases from the deeper horizons back toward the surface. (On the lower ridges where the tall-grass prairie undercover is best developed, with soils marked by P on figure 19, roots may reach to the ground-water table and extract ions that would otherwise be moving laterally toward the drainage channels of the region.)

Not only is a smaller fraction of organic matter being produced in the form of oak leaves that favor acid metabolism of fungi but part of this is burned into ash which helps neutralize acidity instead of accentuating it. It is thus not especially surprising to find the base status of these prairie undercover communities somewhat better than on black oak-blueberry dunes.

Most dunes have probably undergone considerable vicissitudes during their history of natural, Indian, and white man's fires. This must account for some of their variability. The older dunes with elements of grassy cover (table 4) are not so different from the normal black oak dunes as the younger ones, probably because soil deterioration has had time to get precedence in spite of the tendencies just noted. On the other hand, the lesser abundance of blueberry and less acid pH of some of the oldest black oak-black cherry dunes near the Indiana-Illinois border (not included in the present series of soil samples)

may be partly explainable in terms of a prairie episode in the vegetation history of these dunes.

MESOPHYTIC DUNE POCKETS.—Another contrasting type of soil development follows the basswood-red oak-sugar maple succession on protected dunes. For basswood the content, and presumably the requirements, of potassium and phosphorus are not particularly high (36), and this may help explain its success as a pioneer on bare sand of lee slopes. It has high calcium and magnesium contents, but its requirements for these elements would probably be provided by soluble carbonates in young dune soils. More importantly, the return of these elements in surface litter of this and other mesophytic species listed earlier should retard leaching of these elements.

Probably also because of the high base status of this litter, rapid bacterial decomposition develops mull-type humus instead of duff-mull or even mor types of humus like that found in the black oak-blueberry forest floor (36, 63). For any given nutrient capital present in the system, a larger fraction is probably available in or to plants at any time. An ion might circulate several times through the cycle of soil-plant-animal-micro-organism in the time that it might circulate once in a sluggish ecosystem.

Incidentally, on lee slopes, fresh sand may occasionally slip down in thin layers for many years after the initial basswoods have grown into full-size trees and have been joined by other high-calcium species. This buries the soil a little at a time, dispersing nutritious humus through a great depth of soil—a "super-mull" humus profile condition. Carbonates in such fresh sand would further offset whatever tendency rainwater had for leaching.

An additional source of nutrient elements in protected dune pockets and on lower slopes is found in the leaves that are blown off the more exposed upper-dune slopes. This is a bonus, gained at the expense of other ecosystems, aggravating the losses which the latter suffer from leaching in ground water. Thus rich systems may get richer, while poor ones get poorer, as time goes on.

Together, these circumstances probably explain the typically less acid character of these richer dune soils. The percentage of exchange acidity generally lies below the level for the main black oak series (points *M* on fig. 19*B*). Cation exchange capacity is consistently higher (fig. 19*A*), along with general level of organic matter. Both of these differences combine to make the exchangeable bases conspicuously higher than in the normal soils for all ages sampled. No very old dunes that represent this relatively favorable nutritional condition were found in Indiana, but in Warren's Dunes State Park, Michigan, a surface soil of a dune believed to be of Tolleston (or Algonquin) age had an exchangeable

base estimate of 11 me/100 gm, two or three times as high as that on the black oak dune soils (fig. 19C). Although a detailed discussion of these mesophytic dunes is beyond the scope of this paper, it is interesting that the one just mentioned is one of the nearest examples of the sugar maple-beech dominance in the dunes that can be found upon leaving Indiana for Michigan.

The most recent soil survey (54) recognizes the Bridgman fine sand as a less acid soil than the usual Plainfield fine sand, including both young profiles which have not had time to be thoroughly leached and some older profiles of moderate acidity.

General conclusions

DUNE ECOSYSTEM DEVELOPMENT

The sand dunes thus show how the ecosystem concept means more than just a name for the biological community and its habitat. The concept of a dynamic, physical-biological system was clearly involved in the interaction of vegetation and physical forces which built the dune. It is especially well shown by the chemical transformations and circulations of the elements in the course of succession and soil development on stabilized dunes.

Succession describes the changing state of this ecosystem, for example, as a function of time since stabilization of the surface. Figure 13 (*top*) suggests the rise and decline of successive waves of populations of herbs, shrubs, and trees. Probability predictions can be made for the state of the system, but these are naturally subject to considerable variability inherent in biological populations and additional variability arising from differences in factors other than dune age. Various alternative pathways of succession are summarized in figure 12. Following the main Indiana succession from grasses through shrubs and pines to black oak-blueberry in figure 13, the increase in basal area of trees and in weight of fresh and partly decomposed litter is rapid at first and slow or irregular later on.

Along with general changes in the nature of the soil profile, a rapid initial rise occurs in soil organic matter and nitrogen, cation exchange capacity, and related soil variables, which eventually seem to approach some upper limit. Mathematical estimates suggest that roughly a thousand years are required to attain about 95% of the theoretical limiting value estimated for these variables (figs. 17, 19; eqs. [3] and [4]).

In the meantime the initial content of calcium-magnesium carbonate is lost from the surface soil within the first few hundred years and is no longer detectable within 2 meters depth after a thousand years. Probably this irreversible loss helps explain why the acid (pH 4.5) A₂ horizon becomes conspicu-

ous about this time—about the time that a blueberry-huckleberry undercover is becoming widespread. The A₁ and successively greater depths of B horizon become more acid, and exchange acidity continues to rise for several thousand years. This presumably occurs at the expense of exchangeable bases.

As a result of these trends, nutritional conditions for the more exacting mesophytic tree and undercover species probably become less favorable in time, instead of more favorable, as COWLES thought should happen. This conclusion and the inherently low moisture reserve of these well-drained, moderately exposed dunes, as well as repeated disturbance by fire, help to explain the lack of any strong field evidence for improvement of old black oak forests to oak-hickory and sugar maple-beech.

By contrast with the preceding pine-oak succession, COWLES recognized a basswood-red oak-sugar maple succession that develops rapidly on some lee slopes and protected dune pockets, without usually passing through pine or black oak stages. Soil and nutrient conditions improve here very rapidly. Probably the high base content of foliage tends to maintain calcium and other elements in the surface soil more efficiently than in the black oak-blueberry ecosystem.

SHELFORD (50:233) recognized the significance of site, at least as far as to note that in certain moist sands the black oak community "passes more or less rapidly into the next [black oak-red oak], the rate of change depending on the height above ground water." Following COWLES, he found still other sites where black oak-red oak was changing to mixed oak-hickory (on moraine clays) or where this community was changing to beech or sugar maple (certain ravines and moist lowlands). He inferred that this meant that it was only a matter of time until even the drier black oak dune communities would also give way to the "stages" just listed. "Theoretically at least the [beech-sugar maple] climatic type of community rapidly displaces the communities of all the varied kinds of soil of a newly uplifted area which is only a few hundred feet above the sea. In these situations the climatic communities dominate sterile soil by process of successional development extending over a few score or hundreds of years" (50:311).

As far as the dunes are concerned, probably the most striking vegetational change occurs in the first few hundred years, although organic matter, moisture equivalent, and exchange capacity continue to increase fairly rapidly for a thousand years or so. But presumably the succession would lead toward mesophytic forest only on a few inherently favorable sites, while it would lead toward variations of black oak communities on most other sites. COWLES'S

original writings and the conclusions of the present study are both in disagreement with the distortion of the different dune successions into a single linear sequence leading *from* pine and black oak *to* oak-hickory and beech-sugar maple, even if such a scheme concedes that rates vary widely and that some stages may be skipped. Successions in the dunes are going off in different directions and have different destinations according to the many possible combinations of independent variables which determine the original site and subsequent conditions for development; this seems more like a general rule than like an exception, a rule worth emphasizing rather than obscuring by pedagogical oversimplifications.

PRINCIPLES OF SUCCESSION AND CLIMAX

COWLES concluded that "the condition of equilibrium is never reached, and when we say that there is an approach to a mesophytic forest we speak only roughly and approximately. As a matter of fact we have a variable approaching a variable rather than a constant. These conditions do not destroy the validity of a physiographic classification, but rather they require an enlargement of the conception" (14:81).

Such an enlargement emerges naturally if we attach a quantitative interpretation to these two variables. Then this statement nicely summarizes present conclusions on COWLES's own classic area and on the principles which he derived from it.

The first variable, which we earlier abbreviated E_d , describes the state of the ecosystem—with the various particular dependent variables as components. Equation (1a) abstractly describes succession, or at least its expected ideal pattern. We saw how exponential functions provided instructive models for changes of several soil variables, though further research will no doubt lead to more refined models. One interesting thing about the exponential function is that it does indeed tend to approach a limiting value. It is this limit which should describe the theoretical "climax community" and the "mature soil."

This limiting condition of equilibrium, of course, would never quite be reached, even mathematically; it is only an asymptote. Furthermore, in nature many kinds of deflections could repeatedly displace the actual state of the ecosystem away from the very close approach that might ultimately be followed if the system continued for a very long period without disturbance.

In the case of variables like soil nitrogen, we saw how an approach *toward* equilibrium might gradually be achieved by gradual shifts in rates of income and loss from the soil or the whole ecosystem until the nitrogen budget, for example, became nearly bal-

anced. A displacement like that mentioned above would automatically disturb the near-equality of these two rates. But the unequal rates should then automatically lead to changes in nitrogen that would tend to remedy the sudden change.

This leads to consideration of changes in the second of COWLES's variables—the asymptote itself. Probably COWLES assumed that, after the early rapid changes of succession were over, there would still be a slow but sure improvement in soil conditions and hence in the potentialities of future succession. Almost certainly changes of this type occur somewhere. But it is necessary to consider the possibility that the limit for some variables might even decline in time. The optimistic American spirit has perhaps given this possibility less attention than it deserves, although the idea has long been commonplace in European studies (e.g., 3, 33, 48, 58). Instead of rigid *convergence* to a single climax and a mature zonal soil, one might find a *divergence* of different ecosystems on different sites as a natural outcome of ecological succession.

Combined effects of many factors may explain why a climax community or mature soil varies from place to place as it may from time to time. If we go back to equation (1b) and consider the special case in which the ecosystem is already so old (and free from recent disturbance) that the changes due to time are negligible as compared with effects of other independent variables, then an equation for the climax ecosystem would be:

$$E_d = \sum \frac{\partial E_d}{\partial E_i} \Delta E_i + \epsilon + f(t)_{E_i}. \quad (1c)$$

For now, $f(t)_{E_i}$ is merely some constant reference condition, and one is interested in considering the amount that the ecosystem differs from this condition with changes in each of the independent variables of parent-material, topography or other conditions affecting ground-water, climate, or biotic factors (25, 26, 37). Ideally, a series of conditions could be found that would permit separation of the effects of each of these independent variables, so that an estimate could be made of the partial derivatives $\partial E_d / \partial E_i$ against varying background combinations of the other independent variables. Then specifying how much difference there actually was in a particular case of interest, namely, the increment ΔE_i , would specify how much this climax ecosystem would differ from the comparative standard. In actuality, one would have to be content with the more strikingly important independent variables which could be classified or measured on a quantitative scale and dispose of some minor or inscrutable factors as additional components of chance variability, like ϵ .

Equations like (1b) and (1c) are merely first-order

(Taylor series) approximations to a more complete equation of state for an ecological system, which can presumably be evaluated much more completely in favorable circumstances as additional information becomes available:

$$E_d = f(E_i, t) + \epsilon. \quad (1d)$$

Because the independent variables in this equation are mostly continuous, some concept involving a continuum of communities or ecosystems provides the most natural and general basis for classification. Yet we still may find it convenient to speak of different segments of this continuum *as if* they differ sharply where there are correspondingly abrupt changes in the values of certain independent variables or where two contrasting states of the system are more stable than transitions between them.

Similarly, the concept of a gradational "climax pattern" (62) is more general than that of a poly-climax mosaic of discrete climates on contrasting sites (51) or of a single regional climax (11), although there may be places where these approximations provide very useful bases for discussion.

Summary

1. Geological dating of the Great Lakes shorelines and other methods now provide approximate absolute age estimates for many dune systems in Indiana.

2. Plots on these dunes provide estimates of rates of change in COWLES's classic succession from dune grasses (*Ammophila*, *Calamovilfa*, *Andropogon*) to pine (*Pinus banksiana* or *P. strobus*) and black oak (*Quercus velutina*).

3. Soil analyses of carbon, nitrogen, moisture equivalent, carbonates, acidity, and cation exchange relations show how most soil improvement of the original barren dune sand occurs within about a thousand years after stabilization. The pattern of change on older dunes promises little further improvement and perhaps even deterioration of fertility.

4. Low fertility favors vegetation with low nutrient requirements. But such vegetation probably is relatively ineffective in returning nutrient to the dune surface in its litter and thus aggravates low fertility. Leaching of nutrients out of the sand-dune ecosystem and the low moisture reserve of most dune surfaces help account for the poor prospects for successional replacement of the black oak-blueberry community by the more exacting species of the mesophytic forests.

5. Fire history probably (a) helped keep black oak in some areas that could otherwise have supported a richer forest; (b) aggravated the normal loss of nutrients from the black oak-blueberry community;

and (c) helped favor persistence or return of grass undercover in prairie-margin areas and probably slowed soil acidification here.

6. A succession of basswood → red oak → sugar maple (*Tilia americana*, *Quercus rubra*, *Acer saccharum*) develops in moister sites, on lower lee slopes and dune pockets that are protected from drying and burning, usually without passing through stages like those leading to black oak-blueberry communities. These and associated species seem to have higher nutrient requirements; the higher nutrient content of their litter apparently helps maintain the fertility of soils in these local areas at a higher level than in the surrounding pine and oak dunes.

7. These conclusions fit into a mathematical framework for analyzing ecological succession and climax. Vegetation, soil, and other properties of an ecosystem usually change rapidly at first and more slowly later on. If they approach some limit asymptotically or fluctuate around it, this limit should describe the climax community or mature soil. In some cases like the soil nitrogen or cation exchange relations discussed here, this limit might be computed theoretically from rates of gains and losses.

8. The limit itself may vary with time and place. Ideally it describes a gradational "climax pattern" of communities or ecosystems in any region—generally not a uniform "climatic climax."

9. These points follow simply from assuming a quantitative meaning for COWLES's own statement of the fundamental principle of ecological succession: that it represents a "*variable approaching a variable rather than a constant*."

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LEAF ANATOMY IN GRASS SYSTEMATICS

WALTER V. BROWN

Introduction

Although the subfamilies and tribes of the Gramineae are generally distinguished by morphological characters of the spikelet and inflorescence (4, 11), it has been known for seventy-five years or more that additional characters may contribute to a more natural and phylogenetic arrangement of the major taxa. AVDULOV (1) was the first to organize the results of such studies and to use them in conjunction with a number of new characters, especially those of chromosome size and basic number, as a basis for characterizing major groups within the family. PRAT (20, 21) continued the use of microscopic characters (leaf epidermal cells) as reflecting true relationships more exactly than spikelet characters. From time to time since 1936, additional characters of many sorts useful in the systematics of the Gramineae have been discovered, and others have been subjected to restudy or extension. At the present time characteristics of chromosomes, root hairs, stem apices, the first seedling leaf, embryo structure, physiology, reserve carbohydrate, nucleoli, geographical distribution, leaf epidermis, and leaf anatomy have been found useful in characterizing the major taxa within the family (1, 5, 6, 15, 23, 25, 28, 35, 38).

Grass leaf anatomy, as revealed by transverse sections, has been emphasized as a very fundamental character (1, 15, 21, 35). DUVAL-JOUVE (10) was the first to attempt to use it for systematics. The character used was the position of the bands of bulliform cells in relation to the nerves: for example, the pres-

ence of bulliform cells over the tertiary nerves in the Paniceae and Andropogoneae and the existence of bulliform cells in both upper and lower epidermises of Paniceae. SCHWENDENER (26) discussed the nature of the two sheaths that surround each vascular bundle. The inner, the mestome sheath which has characters of an endodermis, has been reported to be present in all grasses (10) or present in some grass groups but absent from others (26). External to the mestome sheath when that layer of cells is present, or in contact with the metaxylem vessels when there is no mestome sheath, is the parenchyma sheath. The cells of the latter vary greatly in size and thickness of walls. External to the parenchyma sheath, the chlorenchyma tissue shows various cellular arrangements.

SCHWENDENER considered the distribution of sclerenchyma between the vascular bundle and the upper and lower epidermises to be of systematic importance also. He arranged the grasses studied in two groups, those with (I) and those without (II) a mestome sheath. In the latter group he included the Andropogoneae, the Maydeae, and some of the Paniceae. All others were included in group I. He further noted the large, clear parenchyma sheath cells of the Arundineae and felt that the peculiar arrangement of the sclerenchyma of the Bambuseae indicated that no close relationship existed between that tribe and the Festuceae.

Subsequent anatomical studies of grass leaves (16-18) have added little of importance to the systematic significance of leaf anatomy. PÉEL-LABY