DIFFERENTIAL SEDIMENTATION OF POLLEN GRAINS IN LAKES[1]

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ABSTRACT

Water circulation affects the sedimentation of pollen grains in lakes, sorting them according to morphological type. Pollen grains with rapid rates of sinking fall downward through the water and are deposited evenly onto the sediment throughout the lake. Those with slower sinking speeds in water, due to small size or low density, are kept in suspension in the turbulent waters of the epilimnion. They are carried across the lake in wind-driven water currents and are deposited preferentially onto littoral sediment. Preferential deposition distorts the original ratios in which pollen enters the lake from the air, causing variations in the pollen percentages in sediment from different parts of the basin. The process is thus of concern to paleoecologists, who seek to use pollen percentages as an index of regional vegetation.

Variations in the percentages of pollen grains in surface sediments of lakes in southern Michigan follow a pattern consistent from lake to lake (Davis et al. 1971). High ratios of herbaceous plant pollen to tree pollen occur in littoral sediment and low ratios in deep-water sediment. In Frains Lake the ratio of ragweed to oak pollen is three times greater in shallow-water sediment than in the deeper parts of the basin (Fig. 1). Within the tree pollen component, however, the pollen types occur in similar ratios to one another everywhere in the basin.

Variations in pollen percentages within lake basins are caused by differential input of pollen to sediment which occurs within a few days after the pollen enters the lake from the air. We here describe this process and discuss its effect on both absolute and relative rates of pollen accumulation throughout the basin.

Frains Lake, near Ann Arbor, Michigan, was the site of our most intensive investigation. The lake is 6.7 ha in area, with a single oval basin 9.5 m deep in the center. There are no permanent inflowing or outflowing streams. The lake was well suited for this study because it is surrounded by open fields: pollen from important forest trees, like oak, must be carried some distance—several hundred meters at least—before it enters the lake. Deposition of forest tree pollen from the air onto the water is therefore uniform over the lake surface, rather than higher nearshore. The same is true of pollen from ragweed, which is rare in the immediate vicinity of the lake but grows abundantly on roadsides and ploughed fields some distance away.

These two major pollen types (oak and ragweed) are emphasized because their abundance made them accessible to study, but the results can be generalized to the remaining pollen. Most of the larger pollen grains behave in a manner similar to oak, while ragweed is typical for the smaller grains.

We wish to express our appreciation to J. Beiswenger for encouragement and advice throughout the course of this study.

POLLEN MORPHOLOGY

Oak (*Quercus*) and ragweed (*Ambrosia*) pollen differ in morphology (Fig. 2). The oak pollen grain is prolate, about 28 μ in diameter, with 3 colpi (grooves) and a rough surface texture. Ragweed pollen is 18 μ in diameter, nearly spherical, with three short colpi (or pores) at the equator

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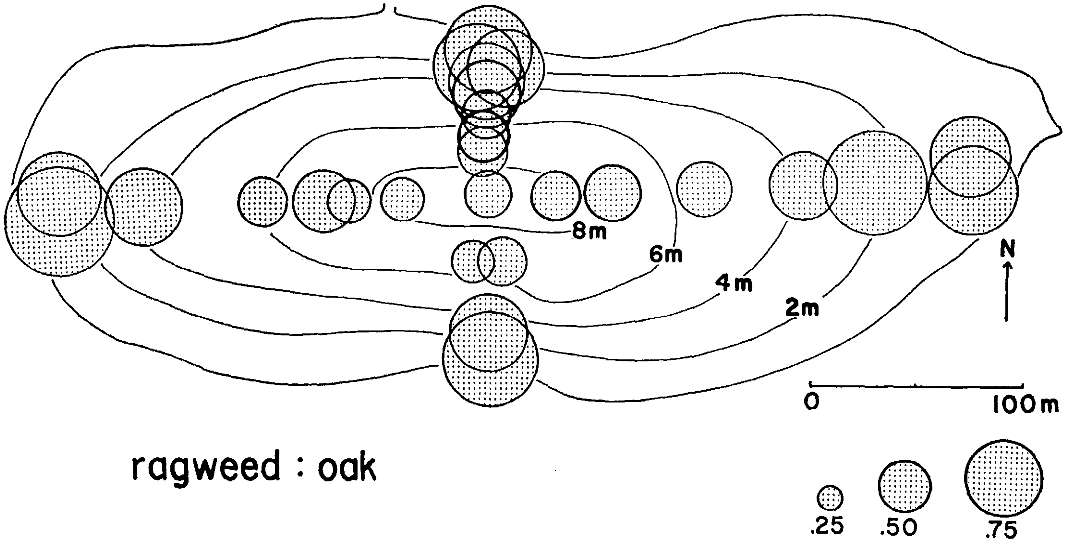

Fig. 1. Ratios of ragweed pollen to oak pollen in a number of samples of surface sediment (uppermost 2 cm) at Frains Lake, Michigan. The ratio is correlated with water depth.

and regularly spaced spines over the surface. The inner layer of its exine (intexine, visible as a thin layer in the photograph) is continuous with the intine and protoplasm. It is attached to the outer layer (ektexine) only at the pores and along the meridians extending from each pore to the poles. When the protoplasm loses water and shrinks, the intine and intexine pull away from the outer wall, leaving a cavity which fills with air. Under these conditions the density of the entire grain is only 0.82 g cm^{-3} (Harrington and Metzger 1963). When exposed to humid air or to water, the protoplasm swells again to fill the cavities, and the density of the complete grain increases to 1.20 or 1.28. Harrington and Metzger made their measurements of density by weighing samples of pollen grains whose volume had been determined in a gas pycnometer. We attempted to measure density by suspending grains in sucrose solutions and found that most of the ragweed grains had densities close to 1.20. Microscopic inspection of the grains revealed that some still contained air bubbles in one or more of the internal cavities, effectively reducing their density. However, grains filtered from lake water appear fully expanded, with all air expelled from the internal cavities. We expect therefore that the density of ragweed grains in lake water is closer to 1.28 than to 1.20. We are unable to explain the discrepancy between these results and those of Brush and Brush (1972) who measured wet ragweed pollen in a pycnometer and found a density of 1.5.

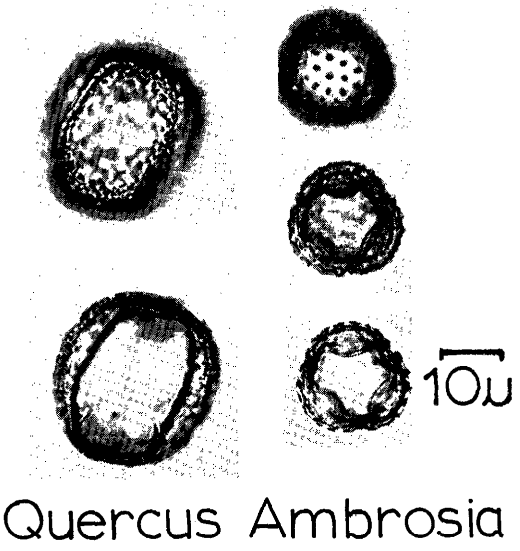

Fig. 2. Photomicrographs of the exines of oak and ragweed pollen grains. The exine is the part of the grain that is preserved in the sediment.

The density of the solid portion of dry ragweed pollen, excluding air in the internal cavities, was found by Harrington and Metzger (1963) to be 1.31. This is the maximum density possible, even when more water is included, unless the grains shrink appreciably after long submergence.

The average density of our sample of *Quercus macrocarpa* pollen using sucrose solutions was 1.16, which agrees with the measurement of 1.2 obtained by Brush and Brush (1972) who used the gas pycnometer on wet oak pollen.

Spherical particles in the size range of pollen grains are expected to fall as predicted by Stokes' law, which should be useful for predicting the sinking rate of one type of grain relative to another, but the extent to which it predicts behavior of these particles, which are not spherical and have surface roughness, is debatable. Brush and Brush (1972) found that pollen grains in a laboratory flume displayed differences in their tendencies to settle that could not be explained by differences in fall speed calculated from Stokes' law and speculated that grains shrink or swell or develop protuberant swellings after long submergence, departing from Stokesian conditions. The sinking speed of oak pollen should be at most twice that of ragweed (Table 1). It may be as little as 36% greater; Brush and Brush (1972) calculate only a 4% difference. Whatever the real difference in sinking speed, it is sufficient, as we shall demonstrate, to cause sorting of these two types of pollen in turbulent lake water.

Table 1. Calculated velocity of fall in still water

Oak	
Diam 28 μ, density 1.16, 20°C	0.0068 cm sec^{-1} 24.6 cm hr^{-1}
Diam 29 μ, density 1.2,* 15.5°C	0.0081 cm sec^{-1}
Ragweed	
Diam 18 μ, density 1.2, 20°C	0.0035 cm sec^{-1} 12.7 cm hr^{-1}
Diam 18 μ, density 1.28, 20°C	0.0035 cm sec^{-1} 18 cm hr^{-1}
Diam 18 μ, density 1.5,* 15.5°C	0.0078 cm sec^{-1}*

*Determination by Brush and Brush (1972).

DEPOSITION OF RAGWEED AND OAK POLLEN

Deposition of ragweed pollen in Frains Lake was measured directly by sediment traps placed in the lake water for 3 weeks in August and September 1968. The sediment traps were half-gallon (2 liter) plastic bottles, with mouth area 54 cm^2, surrounded by wire mesh cages (mesh size 1.3 cm) (Davis 1967). The traps were tied in vertical series. The lowest was attached by rope to an anchor; the highest had a flotation collar sufficient to hold the series upright in the water. Four traps, at 1-, 3-, 5-, and 7-m depth were placed in this manner in water 8 m deep near the center of the lake. Two traps, at 1- and 3-m depth, were placed in water 4 m deep, and a single trap at 1-m depth was placed in water 2 m deep near the south shore. Additional single traps were placed in water 2 m deep near each end of the lake.

After 3 weeks of exposure the traps were brought back to the laboratory where the contents were concentrated by centrifugation. Portions were used for dry weight and ash weight measurement and for pollen analysis. Pollen content was determined by the aliquot slide method (Davis 1966) after samples had been treated by standard sediment preparation procedures (Davis et al. 1971). *Eucalyptus* pollen, which is distinguishable from all native pollen types, was added in known amounts to the samples as a control for pollen loss; 100% recovery was observed in all cases.

The lake water was strongly stratified throughout the experiment. The surface water was 20.5°C. The metalimnion extended from 3.5- to 6-m depth; near the bottom the temperature was 10.5°C. Under these conditions the epilimnion is turbulent and subject to currents driven by the wind across the lake. Water returns in eddies along the shores, or in countercurrents at depth near the thermocline. Below the thermocline the water is relatively still (Hutchinson 1957).

Deposition of ragweed pollen was highest in traps 1 m below the water surface (Fig. 3A). The traps in the lake center collected 75 ± 18 ragweed grains per square centimeter each day, while traps at 1-m depth at the ends of the lake collected 143 ± 24

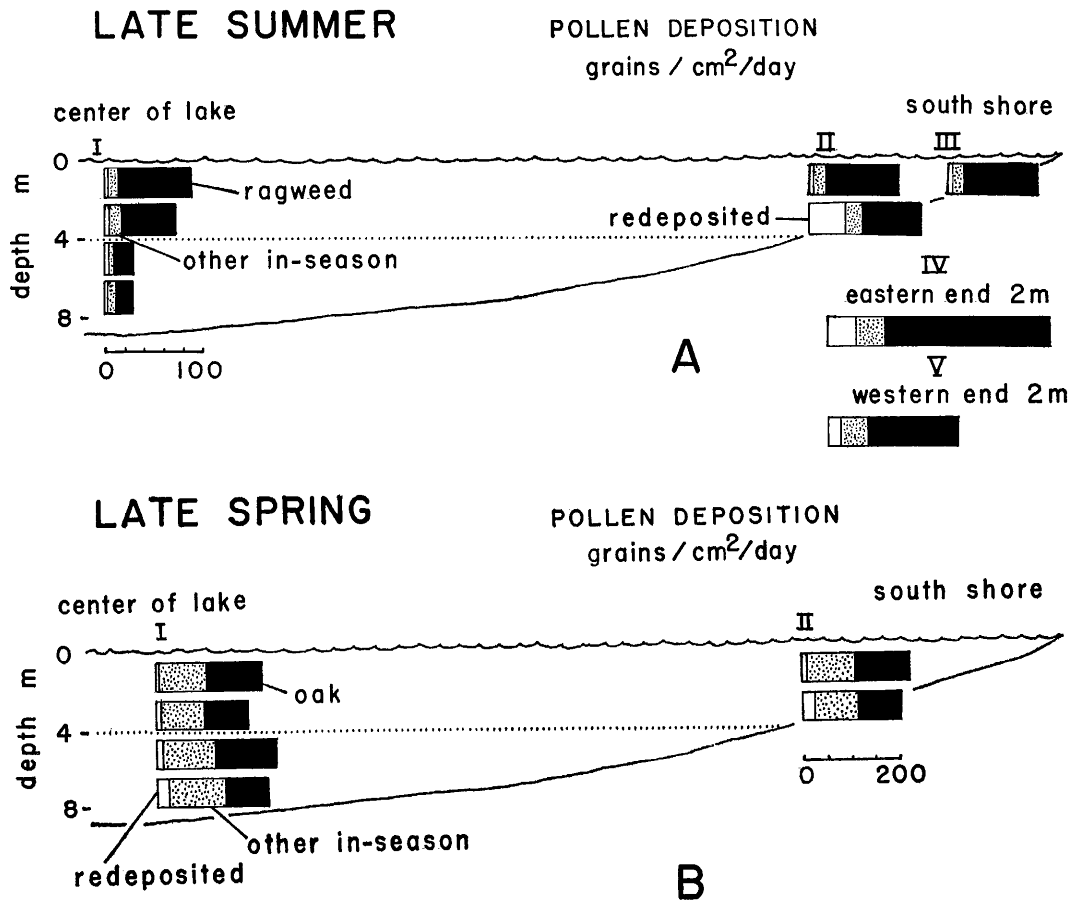

Fig. 3. Numbers of grains deposited in sediment traps at various stations in Frains Lake. The diagram depicts half of a cross section of the lake. The dotted line indicates the depth of the top of the metalimnion. A. Ragweed—late summer. B. Oak—late spring.

and 170 ± 26. Fewer grains fell through the water at depth. We measured 60 ± 16 ragweed cm^{-2} day^{-1} at 3 m, but below the thermocline deposition rates were only 18 ± 9.

The sinking rate of ragweed pollen in turbulent lake water is apparently sufficiently slow that the pollen is swept across the lake by wind-driven currents before it sinks deeply in the water column. Wind-driven currents are known to affect the distribution of plankton. For example, *Daphnia*, which maintains a constant depth, becomes concentrated where water currents converge in Lake Mendota (Ragotzkie and Bryson 1953). Our measurements of the concentrations of pollen in the water support the idea that a similar process affects the concentration of ragweed pollen.

We collected water samples with a Kemmerer sampler on 21 August 1970, filtered them, and counted pollen directly on the filters. The surface water on the upwind side of the lake contained many fewer grains than water on the downwind side (Fig. 4). The numbers were higher among the *Nuphar* plants at the west end of the lake than in open water outside them. We found pollen at the surface and at 1-m depth, but on the day of sampling only a trace at 3, 6, and 8 m. On days when the water is less turbulent the pollen may penetrate deeper in the water column before it is moved to the side of the lake; this would explain the

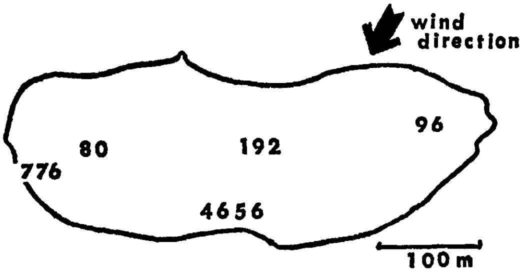

Fig. 4. Numbers of ragweed pollen grains per liter of surface water at Frains Lake on a day during the flowering season for ragweed.

presence of pollen in traps at 3-m depth over a 3-week interval.

The end result of high deposition rates for ragweed pollen at shallow depths is preferential deposition onto littoral sediments, since these are the only sediments exposed to epilimnetic water containing large quantities of ragweed pollen. Rates of deposition are especially high where emergent aquatic vegetation slows down the movement of water currents, allowing the pollen to fall out of suspension.

We measured deposition of oak pollen by traps placed at various depths during May 1969, when oak was in flower. The experiment was set up in the same way as the ragweed experiment reported above, but the results (Fig. 3B) were quite different. Oak pollen was deposited more or less equally at all depths and at all stations. The lake was thermally stratified throughout the experiment, with the surface 16°C on 1 May and 24°C on 30 May; the metalimnion extended from about 3.5 to 6.5 m; the hypolimnion was 6°C. Although May has frequent storms with high winds, the wind-driven water currents and turbulence associated with the epilimnion of the thermally stratified lake failed to affect oak pollen deposition, and oak pollen input was the same to profundal and littoral sediment.

REDEPOSITION OF OAK AND RAGWEED POLLEN IN SEDIMENT

Distribution of pollen within the lake basin is also affected by movement of sediment from one part of the basin to another. Large amounts of sediment are redeposited each year in Frains Lake (roughly 4 times the annual increment), mainly during spring and fall mixing. Sediment is resuspended in greatest quantity from the littoral zone, but it is mixed in the water throughout the lake and deposited again everywhere within the basin. The net result is movement of sediment from the littoral zone to the profundal regions of the lake. The transport is equal for all the different kinds of pollen in the littoral sediment (Davis 1973).

We observed deposition and redeposition of oak and ragweed pollen for 1 year (1965–1966) in sediment traps placed 2 m above the bottom in the hypolimnion near the center of the lake. New pollen input from the air was separated quantitatively from redeposited pollen by using out-of-season pollen as an index to the total amount of redeposited pollen, assuming a constant ratio within the redeposited component (Davis 1968).

Oak pollen was found in the air during May and June (Fig. 5A), the time of year when new input of oak pollen reached the sediment traps. It was also deposited in fall and early spring, when pollen-bearing sediment was stirred up from the lake bottom and redeposited into the traps, but only a fourth of the total oak pollen collected in the traps in the hypolimnion came in the form of redeposited sediment.

Ragweed deposition into the traps followed a somewhat different pattern (Fig. 5B). Input of pollen to traps in the hypolimnion was low during the flowering season in August–September, despite the large amount of ragweed pollen in the air. This corroborates our earlier observation that little ragweed pollen entering the lake from the air penetrates the water deeply enough to be deposited onto the profundal sediment. But as soon as thermal stratification disappeared in October, redeposition of the sediment began. This sediment is very rich in ragweed pollen, since it comes largely from the littoral zone, and constitutes a major source of ragweed pollen to the profundal zone; in 1965–1966, 11 times more ragweed entered the traps as redeposited sediment than as primary input.

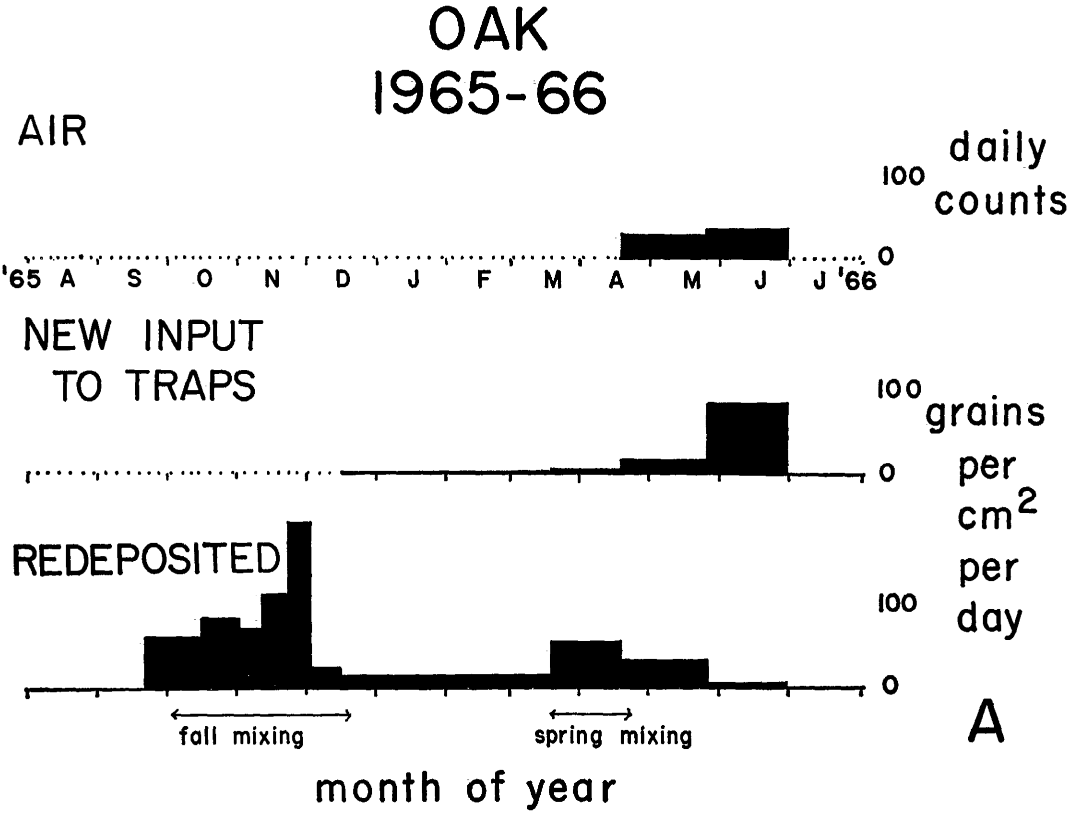

Fig. 5. Pollen in the air and deposited in sediment traps (as estimated new input and as estimated redeposited pollen) in Frains Lake during the course of a year. The traps were in the hypolimnion about 2 m above the lake bottom near the center of the lake. A. Oak pollen. B. Ragweed pollen.

FINAL PATTERN OF ACCUMULATION IN THE LAKE SEDIMENT

Models for the deposition of the two kinds of pollen in Frains Lake are shown in Fig. 6. Oak pollen is deposited evenly over the lake floor during the flowering season. Later, sediment from the littoral zone is resuspended more extensively than sediment from deep water, the material mixed in the water, and redeposited evenly over the entire basin. A net movement of material thus occurs from shallow to deep water. The final absolute accumulation of oak pollen in sediment is greater in the deeper parts of the lake.

The initial input of ragweed pollen is mainly to littoral sediment. Redeposition moves littoral sediment into the profundal zone. The moving of sediment rich in ragweed pollen to the center of the lake tends to equalize the absolute amounts of ragweed in all parts of the basin.

To test the validity of this model of pollen deposition, we measured net accumulation of oak and ragweed pollen on the lake bottom. Short cores of sediment, about 0.5 m long, were collected at 11 stations. The cores were from various depths, excluding the deep hole in the lake center. The deep hole comprises only 2% of the area of the basin. Its depth makes it immune to erosion and removal of sediment; the sediment accumulation rates there are atypical and 10 times the rates measured elsewhere in the basin (Davis 1973). In each core a sharp change in pollen percentages could be identified, usually about 40 cm below the surface; this is the decrease in the percentage of tree pollen and increase

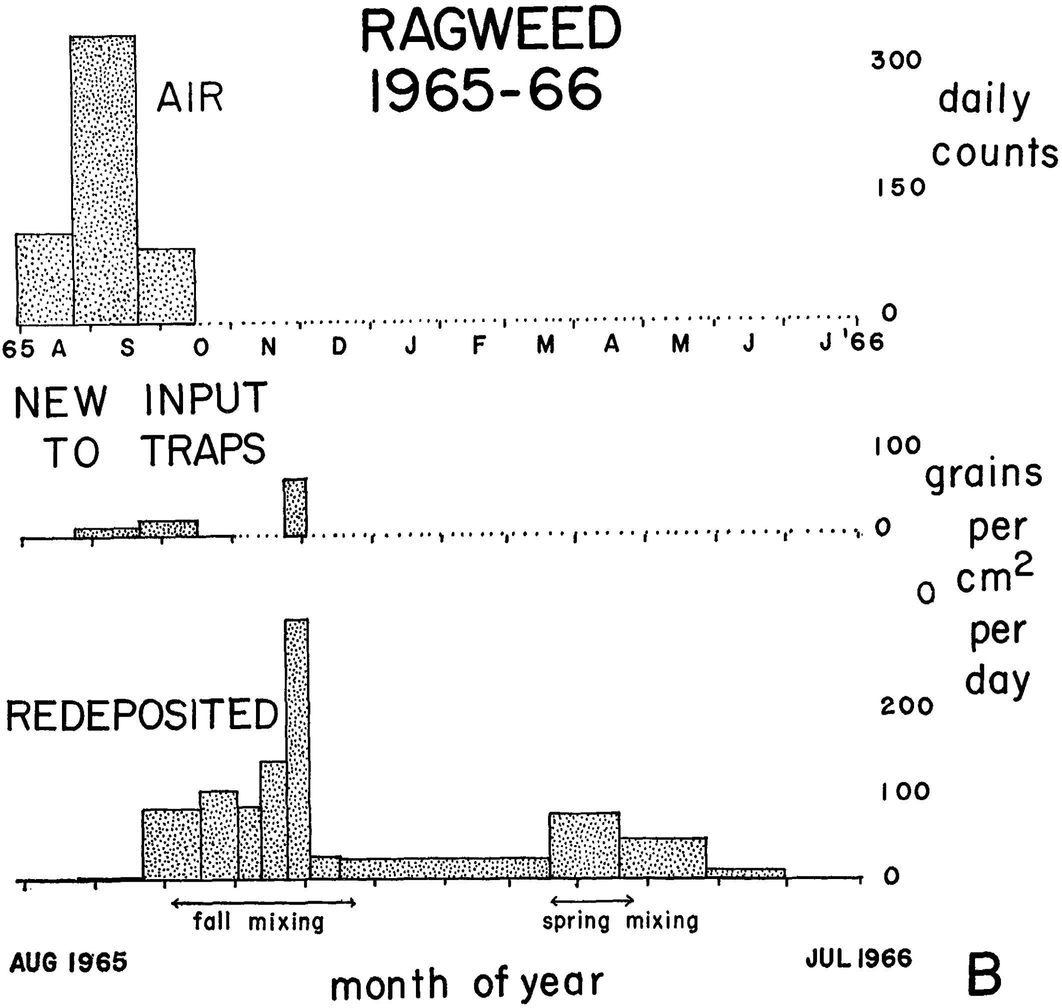

Fig. 5. *Continued.*

in the percentage of ragweed that records the clearance of forest for farming in 1830 A.D. (Davis et al. 1971). Once this time horizon has been identified, pollen grains can be counted in the core above it. It is then easy to calculate the numbers of each kind of pollen grain that have accumulated at that sampling station since forest clearance 140 years ago.

The results, expressed as average annual rate plotted against water depth, are shown in Fig. 7. Average yearly accumulation of oak pollen varies from less than 1,000 to about 8,000 grains cm^{-2} yr^{-1}, with the highest deposition in deepest water. This fits our model, entailing even input of new pollen followed by lateral movement into the deeper parts of the basin and hence greater rates of accumulation there. Average yearly accumulation of ragweed pollen is about 2,000 grains cm^{-2} yr^{-1}. The accumulation is independent of water depth. This corresponds to our model of initial input preferentially to shallow-water sediment, with subsequent movement to deeper water equalizing the amounts accumulating everywhere in the lake.

The differences in the patterns of absolute accumulation for ragweed and oak pollen result in a different ratio between

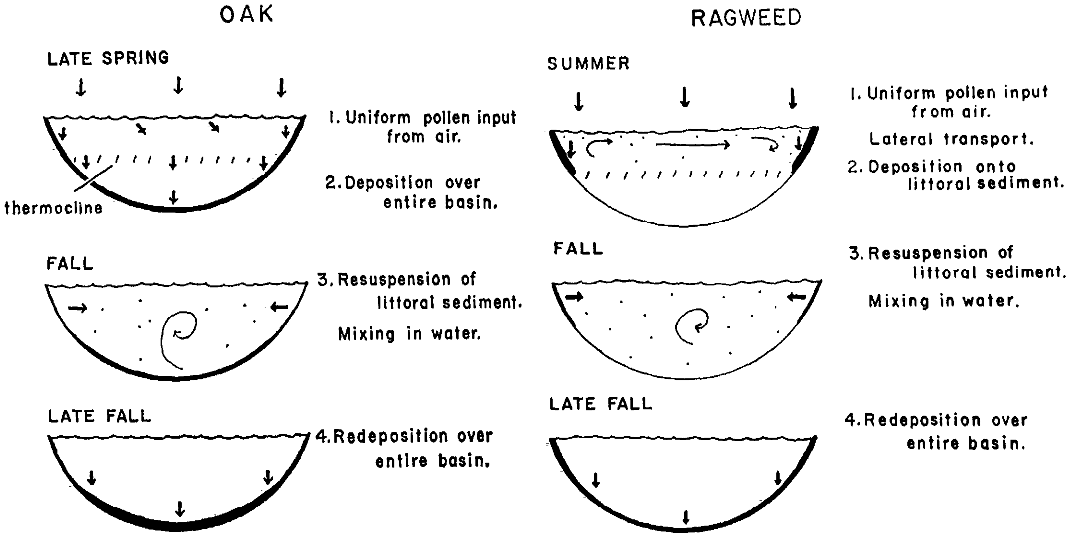

Fig. 6. Left—model for oak pollen deposition in Frains Lake. Net accumulation is greatest in deep water. Right—model for ragweed pollen deposition in Frains Lake. The dashed line indicates the position of the top of the metalimnion (thermocline) in the summer when ragweed pollen enters the lake. Net accumulation is more or less uniform at all water depths.

the two in shallow water and in deeper water. This is important, because the relative frequencies of pollen are used for interpretation by paleoecologists. The ratio of ragweed to oak pollen, calculated from the ratio of the two least squares lines shown in the upper two graphs, is highest in shallow water and lowest in deep water, with a curvilinear relationship between ratio and depth (Fig. 7).

We corroborated this relationship by measuring the ratio of ragweed to oak pollen in 28 surface samples (Fig. 8) comprising the uppermost 2 cm of sediment. They included deposition over the last 5 or 10 years, a shorter time interval than the sediment cores. As predicted, the ratio of ragweed to oak is highest in shallow water, decreasing in curvilinear fashion in deep-water sampling stations.

DISCUSSION

Ratios of ragweed and oak pollen vary in Frains Lake sediment because oak pollen input is similar in amount everywhere in the lake, while ragweed input is preferential for shallow-water sediment. We have explained the difference in input as the result of different sinking speeds for the two kinds of pollen. Different settling rates for these two types of pollen have been observed in a laboratory flume (Brush and Brush 1972), and slight differences are predicted by Stokes' law because of differences in size and density. A difference in sinking speed is the only obvious explanation, as the temperature profile, and presumably the turbulence of the lake water, was similar in late May when oak was in flower and in late August when ragweed shed pollen. We have no direct measurement, however, of water turbulence, nor of the pattern and velocity of wind-driven water currents crossing the lake. We are simply assuming that the general pattern of water circulation is similar to that in other lakes (generally somewhat larger) where measurements have been made.

A critical test of the importance of sinking speed in controlling deposition could be made for pollen grains of different sizes or densities that enter the lake water at the same time of year. The test is not easily made, as most of the herbs that shed pollen in the summertime, when ragweed is in flower, produce small grains. Herb pollen

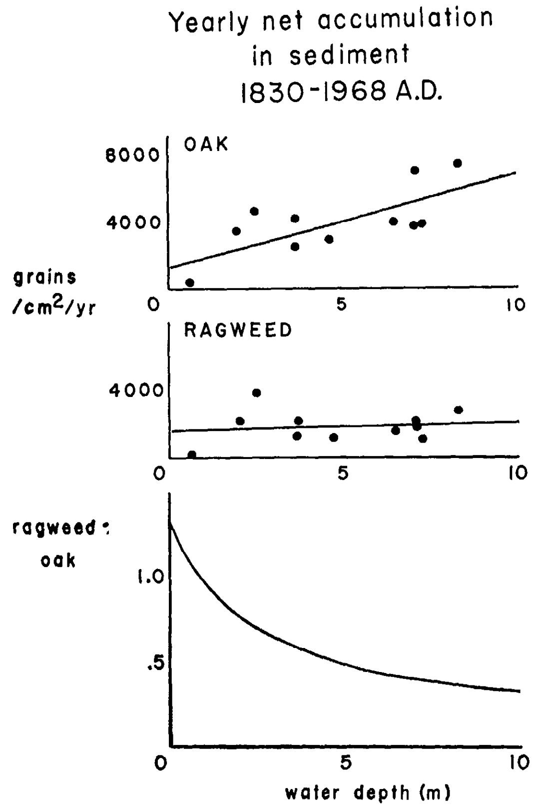

Fig. 7. Net accumulation of oak and ragweed pollen (average yearly influx cm^{-2} since 1830) in 11 cores from water depths 0–9 m in Frains Lake. The ratio of the two least squares lines is shown in the lowermost graph.

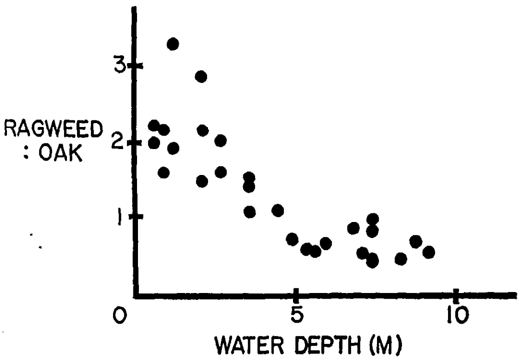

Fig. 8. Ratio of ragweed to oak pollen in surface sediments from Frains Lake plotted against water depth (after Davis et al. 1971).

follows ragweed, with high ratios to oak pollen in shallow-water sediment, falling off to lower values in deep-water sediment (Davis et al. 1971). These ratios reflect differential deposition of small grains by the same mechanism affecting ragweed, demonstrated by high deposition rates for herb pollen in traps in the epilimnion (Fig. 3A).

Pollen from other trees in southern Michigan is of similar size to or larger than oak pollen. The only small grains are sycamore (*Platanus*, about 18 μ), ash (*Fraxinus*, 20–24 μ), juniper (*Juniperus*, 22 μ), and willow (*Salix*, 17 μ). Willow is produced along the shores of the lake and therefore cannot be used to assay differential deposition; in any case, its pollen is shed early, when the lake water is still mixing. Sycamore pollen is also shed quite early; its ratio to oak pollen is variable, with some tendency for preferential deposition in shallow water. The numbers are low and the data show too much scatter, however, for a definite conclusion. Juniper pollen is rare in Frains Lake. Ash pollen occurs in the same ratio to oak pollen everywhere in the lake, showing that differential deposition does not occur (data from Davis et al. 1971).

The only test in our data for the importance of sinking speed is from pine pollen. Pine pollen floats until water fills the air bladders, increasing the density of the grains. In the laboratory this will happen when the grains are treated with acetone or alcohol. In the field it may happen after mechanical breakage, or attack by bacteria or fungi, after the grains have been deposited on the beaches or littoral sediments. Once the bladders fill with water, pine grains, which are large, tend to settle rapidly (Brush and Brush 1972). Samples of lake water collected while pine is in flower contain pine pollen, most with air still in the bladders. Turbulence has apparently carried these grains below the surface, but their tendency to float will keep them high in the water, where they can be moved against the shore and deposited onto sediment. The pine:oak ratio in shallow water relative to deep water in Frains Lake is high, as would be predicted by our model of pollen sedimentation.

Earlier (Davis et al. 1971) we noted that deciduous tree pollen percentages are remarkably similar from one sampling station to another within southern Michigan lakes. We are now in a position to explain this. Some of the tree pollen enters the lake in very early spring when the water is mixing, is mixed throughout the basin, and deposited evenly everywhere. The remaining tree pollen is large enough or sufficiently dense to penetrate the thermocline before being carried across the lake to the littoral zone; this is deposited evenly everywhere in the basin. Pine and perhaps sycamore are exceptions, but they are both so infrequent in Frains Lake that their uneven distribution has little effect on the percentages of other tree pollen types. After the initial input of tree pollen to the sediment surface, tree pollen grains are moved into the deep basin of the lake by redeposition in the manner described for oak. Because transport and redeposition of sediment occurs without sorting (Davis 1973), the initial ratios in which the tree pollen entered the lake are preserved, even though the total numbers of grains accumulating are different in different parts of the lake.

Differential distribution of birch pollen in Lithuanian lake sediments has been reported by Kabaleine (1969). We did not observe this, perhaps because the numbers of birch grains are too low for accurate observation. Birch pollen shows a tendency to remain suspended in water in the laboratory according to Brush and Brush (1972); they speculate that it swells into a triangular shape that causes a slower fall speed than predicted from Stokes' equation. Kabaleine reports higher percentages on the downwind sides of lake basins, suggesting behavior similar to that of ragweed pollen.

We ascribe the differential deposition of pollen grains to eddies and water currents carrying small particles across lakes to the downwind shore where they are deposited onto littoral sediment. Pollen grains are a useful tracer, showing that the eventual fate of at least some particles deposited uniformly onto the lake surface is preferential deposition onto littoral sediment. High ragweed pollen ratios occur on all sides of Frains Lake (Fig. 1), suggesting that the wind blows with equal frequency in all directions. Alternatively, return currents carry material around the shores of the lake to the leeward side again, exposing all shores to pollen-rich water. Meriläinen (1969) also found that water movements affect deposition patterns. Currents in the epilimnion cause uneven distributions of diatom frustules in sediments of the three meromictic lakes he studied.

Small differences in sinking speed seem to have a great effect. An explanation is apparent in Stommel's (1949) theoretical treatment of the behavior of particles in Langmuir vortices (wind-driven water currents that form series of vortices with the long axes parallel to the water surface and to the wind direction). Stommel's calculations show that small differences in sinking velocity can cause sorting of particles, if the sinking velocity of the particles is close to the maximum upward velocity of the water. Two cases are shown: in one all the particles settle out although they are deflected from a vertical path; in the other a large proportion are retained within the vortex. The sinking velocity of the particles in the first case is twice that in the second. This model helps to explain how a difference in settling velocity as small as that between oak and ragweed pollen could be sufficient to cause very different sedimentary behavior, with oak analogous to the first case and ragweed the second. Stommel's model also shows that in the first case concentrations of the settling particles will form beneath the vortices in the regions of convergence; it is, therefore, conceivable that concentrations become great enough to permit vertical density currents to form along the thermocline. Bradley (1965, 1969) points out that the settling velocities of many particles in lake water, such as diatoms, are too low to permit them to reach the bottom of deep lakes in the same year they are formed. Yet banded sediments provide evidence for rapid deposition, within a few weeks or months of a diatom bloom. He postulates that density currents form where particles become concentrated enough to increase the specific gravity of the particles and the enclosing water to the point where it sinks as a dense body through the surrounding, more dilute water. Vertical density currents forming along the thermocline would carry oak pollen down rapidly into the hypolimnion, accounting for its appearance in sediment traps during the flowering season (Fig. 5A).

Our results might be generalized to plankton or other kinds of particles held in suspension in lake water. Before this can be done we need more accurate information on sinking velocities. The predictions based on Stokes' equation are inconsistent, partly because they are based on measurements of size and density that change when pollen grains are immersed in water. We need empirical laboratory observations of fall velocity of fresh pollen under controlled conditions.

Palynologists should be aware that uneven deposition may occur for pollen from any plant that flowers after lake waters become stratified, unless the pollen has a rapid sinking speed. Before stratification, mixing of the lake water will distribute the pollen throughout the water column (Davis 1973). After stratification sets in, however, currents in the epilimnion will carry the pollen horizontally, unless it sinks rapidly enough to penetrate the thermocline before lateral transport takes place.

Deposition early in the spring during water mixing, rapid fall speed, or both, explain the uniform ratios of deciduous tree pollen types in lake sediments in southern Michigan (Davis et al. 1971); since any sample collected anywhere in the lake is typical, sampling problems for these pollen types are much reduced. However, the concentrations of grains that are preferentially deposited, like ragweed, are so variable relative to tree pollen that sampling problems are acute, and precise interpretations of fossil data will not be possible. What is worse, the variation will affect all pollen percentages, unless the variable types are excluded from the pollen sum (Davis et al. 1971). For this reason it is important to know which types are subject to preferential deposition. Deposition patterns should be studied in all regions; systems that include birch and pine pollen, which sink slowly, should be studied in particular.

Patterns of pollen deposition correlated with water depth can be expected in all thermally stratified lake basins. The strength of the pattern, i.e. the amount of distortion of the input pollen ratios, will depend on the extent of both differential input and redeposition. These processes are antagonistic, one producing differences and the other smoothing them out; each process varies from lake to lake. As a result even adjacent lakes of similar size, both showing a pattern of high ratios of ragweed:oak in shallow water, can have different pollen ratios in deep water (Davis et al. 1971). We suspect that similar deposition patterns may exist for other microfossils, such as diatoms and microcrustaceans. Paleoecologists who express microfossil data as percentage abundances should be aware of this possibility and study the distribution of fossils in modern lakes before interpreting their results.

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