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Author(s): David A. Burney and Lida Pigott Burney

Source: *New Phytologist*, Vol. 124, No. 3 (Jul., 1993), pp. 523-535

Published by: [Blackwell Publishing](#) on behalf of the [New Phytologist Trust](#)

Stable URL: <http://www.jstor.org/stable/2558132>

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Modern pollen deposition in cave sites: experimental results from New York State

BY DAVID A. BURNEY AND LIDA PIGOTT BURNEY

Department of Biological Sciences, Fordham University, Bronx, NY 10458, USA

(Received 20 October 1992; accepted 22 February 1993)

SUMMARY

Results from two years of pollen trapping experiments in New York State show that pollen spectra inside the three caves studied are highly similar to the pollen rain outside the caves. Statistical comparisons of modern pollen spectra derived from Tauber traps, speleothems, moss polsters, and nearby pond sediments suggest that pollen deposition inside caves can provide a reliable index of the regional and local vegetation, directly comparable to the more conventional spectra derived from lake sediments and moss polsters. Because of the relatively low pollen influx inside caves, however, stochastic and episodic forms of particle transport may influence pollen deposition inside caves in proportions that are unique to each site. With careful attention to site parameters such as entrance size, pollen preservation, and modes of sedimentation, investigators could make greater use of caves in palynological studies.

Key words: Pollen analysis, caves, particle trapping.

INTRODUCTION

Cave sites have always been important in archaeology and palaeontology, but recent years have witnessed a major growth in the use of caves for palaeoecological studies. Much of this work has focused on the use of geochemical data (e.g. Farrand, 1979; Gascoyne, 1984; Talma and Vogel, 1992), packrat middens (e.g. Betancourt & Davis, 1984; Webb, 1986), and small animal bones (e.g. James *et al.*, 1987; Steadman & Kirch, 1990). Relatively few studies have utilized pollen analysis of cave sediments for climatic and vegetational reconstructions. Exceptions include Damblon (1974), Renault-Miskovsky & Girard (1978), Bastin (1978, 1982), Bastin, Dupuis & Quinif (1982), Davis (1984, 1989), Bastin *et al.* (1988), and Brook, Burney & Cowart (1990 *a, b*).

One major limitation to the use of pollen spectra from caves has been that pollen preservation is often poor, especially in cave sediments that are wet at least part of the time (Davis, 1990). A second limitation has been that cave sediments that might otherwise be suitable may be subject to considerable mixing, due to bioturbation and abiotic diagenesis of the sediments. These problems might be avoided, it would seem, by avoiding soft clastic fills and concentrating instead on pollen profiles from speleothems, when pollen-rich speleothems are available. Under ideal circumstances, it may be possible to recover well-preserved pollen in suitably high concentrations, with temporal resolution comparable to

moderately bioturbated lake and bog sediments, from stalagmites or other speleothems that can be dated by the $^{230}\text{Th}/^{234}\text{U}$ method back to 350 000 BP or more. This and other dating methods appropriate to cave environments but not ordinarily feasible in lakes and bogs make it possible to extend the dated palynological record an order of magnitude or more beyond the ^{14}C timescale in some karst areas (Brook *et al.*, 1990 *b*).

The third obstacle to the more widespread use of pollen analysis from cave sites has been the high degree of uncertainty associated with the interpretation of pollen spectra derived from such unconventional sources (Turner, 1985; Coles *et al.*, 1989). Unlike lakes and bogs, relatively little research effort has been devoted to comparing modern pollen spectra from caves to the present vegetation surround the sites, although some work has been done in Europe (e.g. Loublrier, 1974) and the southwestern United States (O'Rourke, 1985; Davis & Anderson, 1987).

A useful but little-explored avenue (but see Peterson, 1976) for evaluating the biases inherent in cave pollen spectra is to make detailed comparisons between modern pollen spectra and pollen influx in cave sites and similar pollen data derived from adjacent sites outside the caves. What is needed are studies utilizing pollen traps (Tauber, 1974), cave sediments (including speleothems), lake sediments, and moss polsters to sample the pollen rain from key sites in which these artificial and natural pollen

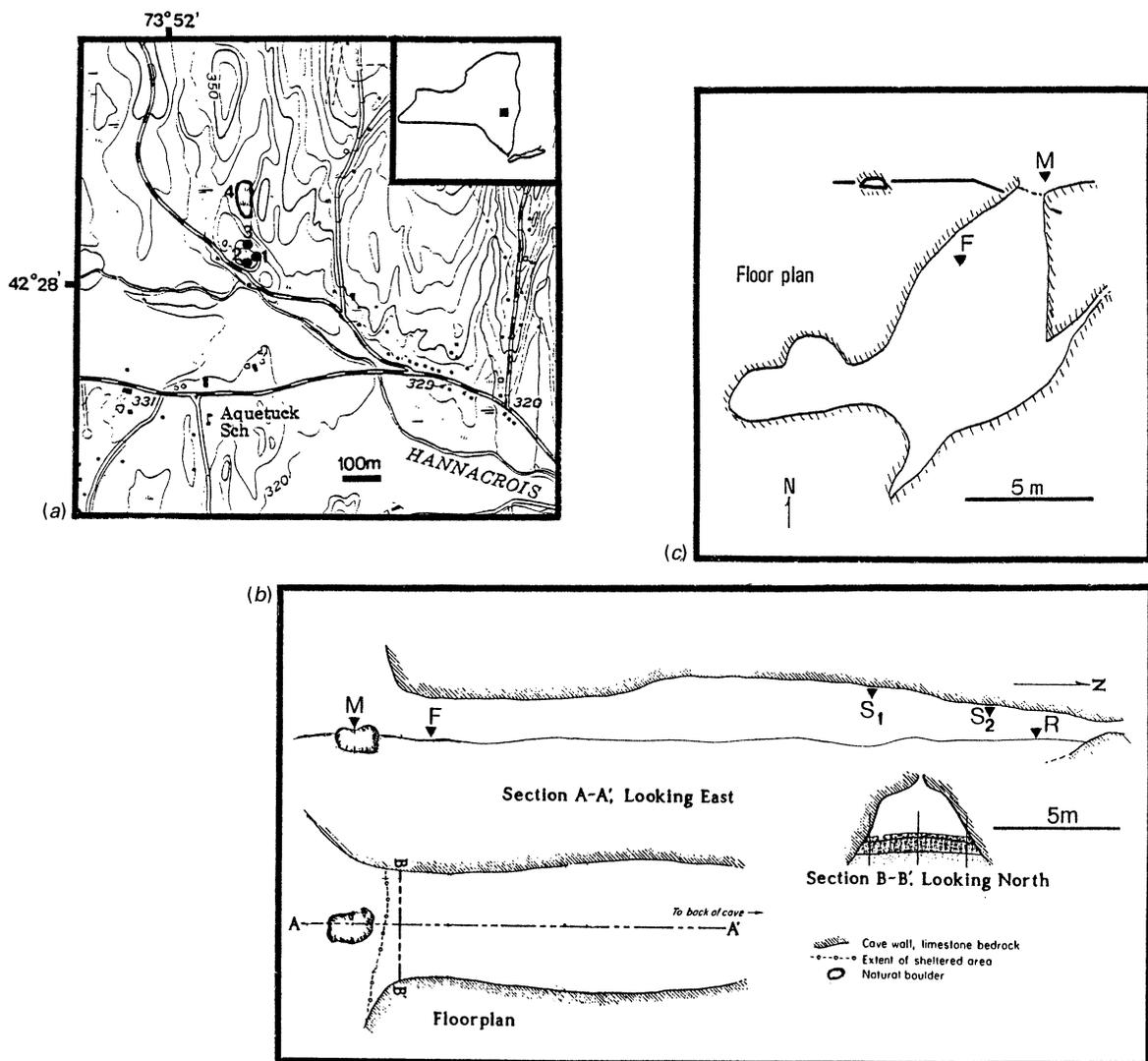


Figure 1. (a) Location map of Coeymans Hollow study site. Roofed and unroofed Tauber traps (no. 1), entrance to Joralemon's Cave (no. 2), entrance to Back Door Cave (no. 3), and a small shallow pond (no. 4) used in this study all lie within a radius of 100 m. (b) shows floor plan, longitudinal section, and cross section near entrance of Joralemon's Cave (after Funk, 1976). M = moss polster sample; F = Tauber trap inside front of cave; S₁, S₂ = speleothem samples; R = Tauber trap in rear of cave passage. (c) shows floor plan and cross section near entrance of Back Door Cave.

collectors have been arrayed according to the principles of experimental design. We present here the results from two years of experimentation of this type at three caves in southeastern New York State.

MATERIALS AND METHODS

Locations of study sites

Two rural locations in southeastern New York State were utilized for these experiments, one near Coeymans Hollow in southern Albany County (73° 52'W/42° 28'N, Fig. 1a) and the other near Croton Falls in northern Westchester and southern Putnam Counties (73° 39'W/41° 21'N, Fig. 2a). Both sites are in second-growth mixed mesophytic forest characterized by species of *Quercus*, *Carya*, *Fraxinus*, *Acer*, *Betula* and other trees typical of northeastern forests. The basic hydrology of the

caves was similar, in that vadose water drips in all of them, but none has an active stream inside.

The Coeymans Hollow site. The Coeymans Hollow site is in a small park located on limestone terrane, at an elevation of 110 m. A paved secondary road passes along the south edge of the site, with extensive grassy meadows and a dwelling within c. 200 m. Two Tauber traps, one roofed and the other unroofed (to separate wet vs. dry fallout components, as in Tauber, 1967), were placed at ground level in the forest (no. 1 in Fig. 1a), midway between the entrances to two caves. The two caves and a shallow pond of c. 0.5 ha that were used for the study are encompassed by a 100 m radius (no. 2, 3, and 4, respectively, in Fig. 1a).

The larger of the two caves (Fig. 1b) is known as Joralemon's Cave (Steadman, Craig & Engel, 1993)

or Fish Club Cave (Funk, 1976). At the single, south-facing entrance, it is 4 m wide, 2 m tall and roughly triangular in cross-section. The approx. level passage extends northward for *c.* 30 m, tapering to a small crack in the rock with a very small amount of air-flow. The ceiling of the cave has no large stalactites, but portions are covered with active 'straws' and nodules known to cavers as 'cave coral' (Moore & Sullivan, 1978). The floor is mantled with fine, moist sediments containing native American artefacts assigned to Archaic (mid-Holocene) and later periods by Funk (1976).

Tauber traps were kept in place on the cave floor for two years. In the first year (1989–90), traps were changed and the contents recovered at approx. monthly intervals throughout the pollen season and once at the end of the winter. During the second year (1990–91) traps were kept in place without monthly changes for the entire pollen season. One trap was placed 3 m inside the drip-line, about 30 cm from the wall of the cave. The other trap was placed in the rear of the cave, *c.* 27 m from the entrance and 30 cm from the wall. At the end of the study, pollen samples were collected from the tips of small active speleothems on the cave ceiling, 20 and 25 m from the entrance. A moss polster sample was collected from a large boulder located 1 m outside the drip-line of the cave. Surface sediment samples were also collected, but they yielded only a few poorly-preserved grains and were not included in the study. Two-litre bottles of drip-water were collected under large drips in the cave for 3 h periods once per month during the pollen season. Icicles were collected from the ceiling at the end of the winter. These two types of water samples were centrifuged and decanted, but no pollen was recovered in this way, suggesting that drip-waters in this cave are relatively pollen-free.

The other cave on the Coeymans Hollow site has a single north-facing entrance *c.* 60 m from Joralemon's Cave. Known as Joralemon's Back Door Cave or Back Door Cave, it has a SW-trending passage that extends *c.* 15 m from the entrance, and a smaller southern branch extending *c.* 12 m from the entrance (Fig. 1*c*). The cave opening is very small, 1 m wide and 40 cm high, semi-circular in cross-section. The floor descends *c.* 2 m from the entrance, and is covered with stony breakdown from the ceiling. The ceiling has a few small stalactite 'straws'.

A single Tauber trap was placed 3 m inside the entrance, 30 cm from a wall. It was serviced on the same schedule as the Joralemon's Cave traps and the exterior traps. A moss polster sample was collected *c.* 1 m outside the drip-line of the cave. Floor sediments and speleothems contained insufficient pollen for analysis.

About 50 m north of the entrance to Back Door Cave is a 0.5 ha natural pond. It is surrounded by forest, with some *Nyssa sylvatica* and *Acer rubrum*

trees and several aquatic macrophytes growing in the flooded portion of the littoral zone. A sample from the top 1 cm of the pond sediment was collected from approx. the centre with a long-handled scoop.

The Croton Falls site. The Croton Falls site is situated on metamorphic terrane at elevations ranging from 180 m at the cave, down to 140 m at the lowest pond (Fig. 2*a*). The site is *c.* 300 m from the nearest houses, roadsides and fields, in a heavily-wooded area, much of it in mature second growth. We named the feature 'Alec's Cave' for Alec Burney, who first drew this opening in the hillside to our attention. The 'cave' is actually a straight mine tunnel, roughly circular in cross-section and *c.* 2 m in diameter, excavated into solid crystalline rock, probably in connection with prospecting by an iron-mining interest several decades ago (Fig. 2*b*). It extends back into the hillside in a southerly direction for 8 m. The north-facing entrance is very small, 1.6 m wide \times 70 cm high, roughly elliptical in cross-section. The entrance to this mine shaft is slightly larger than the entrance to Back Door Cave, and the floor likewise slopes down from the entrance to a level *c.* 2 m below the opening.

A Tauber trap was placed 3 m inside the entrance, *c.* 30 cm from the wall, as in the two Coeymans Hollow caves. Roofed and unroofed Tauber traps were placed at ground level outside the cave, *c.* 30 m to the east. The Tauber traps were allowed to collect pollen for a full year (1990–91), on the same schedule as the Coeymans Hollow site.

Three ponds, located between 400 m and 500 m south of Alec's Cave, were sampled as described above for the pond in the Coeymans Hollow site. Pond no. 1 is *c.* 1.0 ha in area. It is surrounded by forest but supports an extensive growth of *Typha*, *Sagittaria*, and other macrophytes over much of its shallow bottom.

Pond no. 2 is immediately W of no. 1. It is a permanently-flooded hollow *c.* 10 m in diameter, in deep shade, with few macrophytes. Pond no. 3 is a permanently wet hollow about 15 m in diameter, likewise in deep shade and with few macrophytes, at slightly higher elevation (150 m *vs.* 140 m).

Pollen analysis

The static non-overload pollen collectors used in this study were modified from the design of Tauber (1974) to accommodate the constraints imposed by work in caves. To minimize condensation and breakage when changing the traps in the moist, rocky environs of caves, soft plastic (Nalgene) was substituted for the original plexiglas containers. The airfoil, like the container, maintains the approximate dimensions and aerodynamics of Tauber's design, but substitutes a less breakable, less condensation-prone commercial plastic airfoil (sold in toy stores

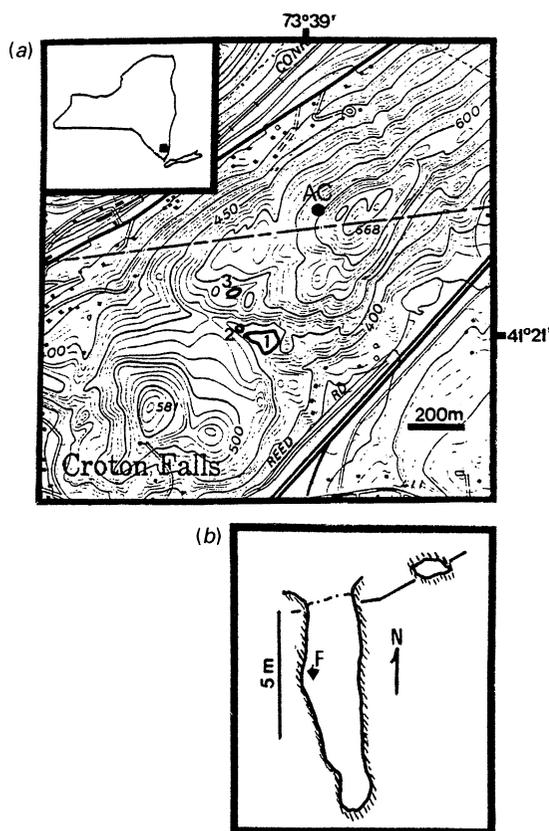


Figure 2. (a) Location map of Croton Falls study site. AC = location of Alec's Cave (mine shaft). Roofed and unroofed Tauber traps located 30 m E of entrance. Pond no. 1 was site of pollen sample N92S-1; no. 2, N92S-2; no. 3, N91S-1. (b), floor plan and cross section near entrance to Alec's Cave. F = Tauber trap inside front of cave.

under trade names such as 'Frisbee'). The traps were cleaned before each deployment with strong (laboratory decontaminant) detergent, rinsed, oxidized to remove any residual pollen with 30% H_2O_2 , and rinsed thoroughly in deionized water. Traps were mounted on a 70 × 70 cm base with silicone aquarium cement to discourage tipping by cave animals, loaded with 100 ml of 100% glycerine (pollen-free) and placed in the locations described above. This 'cave-adapted' trap design was also employed for the exterior trapping for consistency. The traps were deployed according to the specifications in Tauber, except all traps inside and outside the cave were situated with their openings 30 cm above the ground surface (or cave floor) at each sampling site. All traps inside caves were located the same distance from a wall (30 cm) to control for centre-to-edge differences in pollen deposition rates (Davis, 1990).

In a laboratory environment with positive pressure and electronically-filtered air, trap contents were washed through a 275 μm screen with deionized water, and fine solids were concentrated by centrifugation at 4000 rpm and decantation.

Speleothem pollen samples were extracted from the calcite matrix with 37% HCl as described in

Brook *et al* (1990a). Pollen from moss polsters was extracted by washing down with deionized water as described in Prentice (1986).

Samples thus derived from traps, speleothems and moss polsters were then processed to concentrate the pollen residues according to the standard methods described in Faegri & Iversen (1975). Pond mud samples were also processed this way. At the beginning of the pollen processing, a tablet containing a known quantity of exotic *Eucalyptus* pollen was added to each sample to facilitate concentration and influx calculations (Benninghof, 1962; Stockmarr, 1972).

Pollen slides were counted at ×400 (×1000 for difficult pollen identifications) on a Zeiss Axioplan microscope. All counts used in the analysis ranged between 400 and 600 grains per sample. Pollen sums were calculated on the basis of total terrestrial pollen. Plant nomenclature follows Gleason & Cronquist (1963).

Pollen diagrams and dendrograms were plotted using TILIA 1.09 software developed by Eric Grimm. Cluster analyses of the spectra were generated by comparing the percentages for all terrestrial pollen types represented by 2% or more in at least one sample. *Ulmus* and *Ailanthus* pollen were excluded from this analysis, for reasons described in more detail in the following section, as were trees and shrubs such as *Acer*, *Nyssa* and *Alnus* which grow in the littoral zone of some of the ponds analyzed. The clustering routine consisted of unconstrained incremental sum-of-squares calculations based on the square-root-transformed data, using Edwards and Cavalli-Sforza's Chord Distance as the dissimilarity coefficient. This technique yields a good 'signal-to-noise' ratio by up-weighting minor taxa and down-weighting major taxa to a moderate degree (Overpeck, Prentice & Webb, 1985; Prentice, 1986).

Influx calculations on the spiked samples from the Tauber traps could be calculated at approx. monthly intervals during the pollen season and for the entire winter for the Coeymans Hollow site. At the Croton Falls site, only the total annual influx could be calculated, since monthly sampling was not done at this site.

RESULTS AND DISCUSSION

Coeymans Hollow site

Figure 3 shows the pollen percentages for major types occurring in the samples from the Coeymans Hollow site. Major wind-pollinated types (e.g. *Betula*, *Quercus*, *Carya* and *Pinus*) have similar percentages in all the samples from Tauber traps, speleothems, moss polsters and the pond sediment. The most evident distinction among these taxa is that the traps, both inside and outside the caves, seem to under-represent *Quercus* and *Pinus* relative

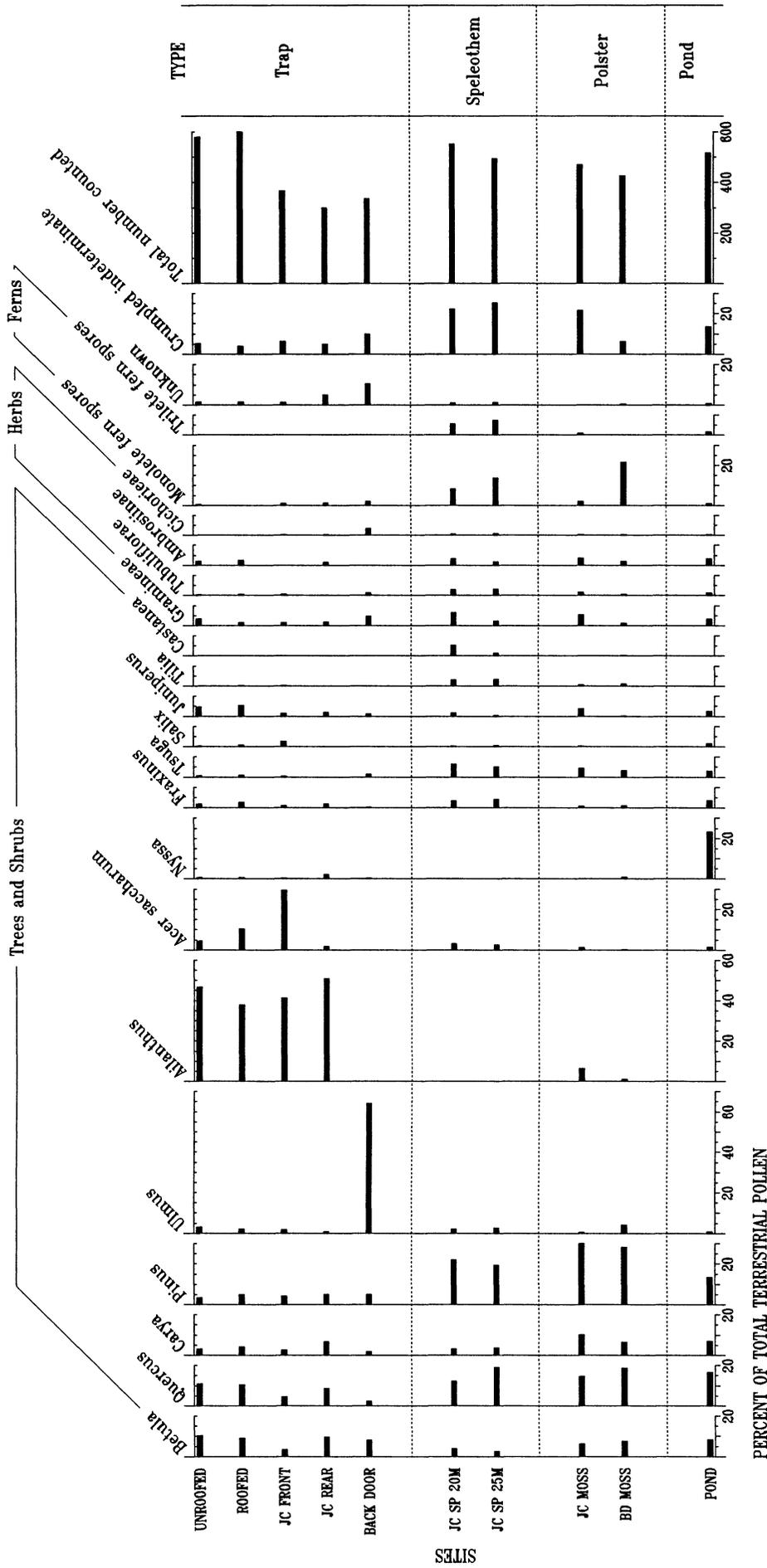


Figure 3. Pollen spectra in and near cave sites, Coeymans Hollow, New York. Diagram shows percentages for major types, defined as 2% or more in at least one sample. Samples are, top to bottom: unroofed exterior Tauber trap, roofed trap at same location, trap inside front of Joralemon's Cave, trap in rear of same cave, trap inside front of Back Door Cave, speleothem from 20 m inside Joralemon's Cave, speleothem from 25 m inside, moss polster at entrance to Joralemon's Cave, moss polster at entrance to Back Door Cave, pond adjacent to the caves.

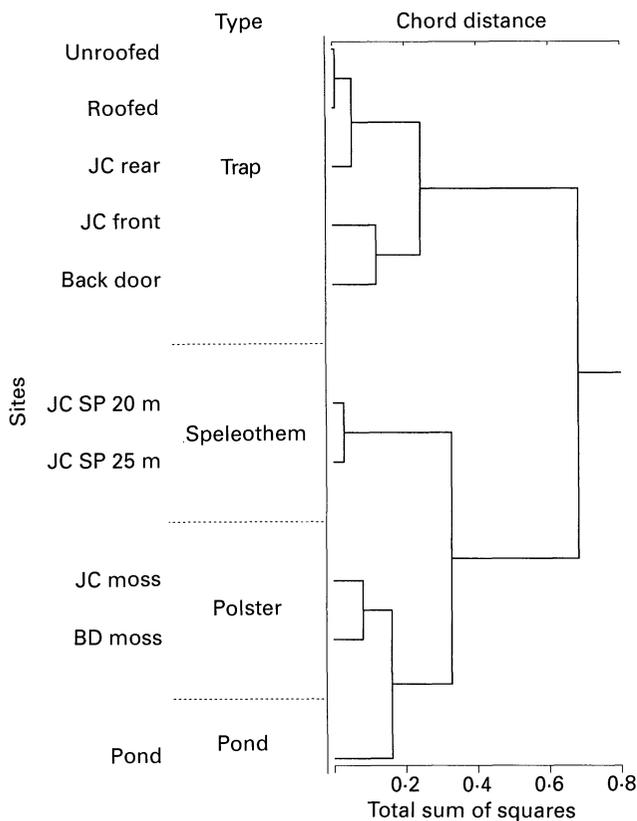


Figure 5. Unconstrained incremental sum-of-squares cluster analysis based on major types from Coeymans Hollow pollen diagram. See text for inclusion criteria and description of statistical methods. Sample designations as in Fig. 3.

to all other types of sample. The values for these taxa in the speleothems were generally closer to the values for these taxa in the pond and polster samples than in the traps.

Two other pollen types, *Ailanthus* and *Acer saccharum*-type, have high values in four and two traps, respectively. Several specimens of the exotic *Ailanthus altissima* grow directly over the exterior traps and in the vicinity of the entrance to Joralemon's cave. These plants contribute very high *Ailanthus* values (40–51%) to the spectra from the external traps and both traps inside Joralemon's Cave. The moss polster in the entrance to the cave showed the next highest value (6.4%), and *Ailanthus* was absent from all other samples except for 1% in the moss polster at the front of Back Door Cave. This insect-pollinated tree, although it produces a large amount of pollen, fails to disperse the pollen very far.

The reason for high values for *Acer saccharum*-type in two trap samples is not known. It is likely that some of the insects that occasionally were drowned in the traps may have been dusted with this pollen type. Like *Ailanthus*, this pattern seems to reflect a peculiarity of the Tauber traps *vs.* the natural pollen traps (including speleothems), rather than a depositional feature unique to cave environments.

One of the most peculiar values in the trap data from the caves was the extremely high *Ulmus* percentage in the Back Door Cave trap. Although the value for *Ulmus* in all other samples ranged from 0.6 to 4.1%, it made up 64.2% of this cave sample. Since no other pollen types are anomalously high in this sample (including others that flower in late winter–early spring as *Ulmus* does), it seems unlikely that some peculiarity of air exchange in a cave of this configuration accounts for the high percentage. A possible explanation, not easily tested, however, is that *Ulmus* pollen was being brought into this cave by the animals that use it as a den. Of the three caves studied, this was the only one used as a den by animals on a regular basis. No fresh animal sign was seen in the other caves, but the investigators observed a woodchuck (*Marmota monax*) in Back Door Cave on two occasions, and a porcupine (*Erethizon dorsatum*) has been seen inside in recent years. (D. Steadman, personal communication). Relatively fresh racoon (*Procyon lotor*) bones occur on the surface of the cave floor, as do scats of coyote (*Canis latrans*), woodchuck, porcupine and rat (*Rattus* sp.) (personal observations). There was no evidence of bats roosting in any of the caves studied, however. Perhaps because of its small entrance, convoluted interior, and the relative infrequency of human visitors to this cave, it is frequented by various animals that might bring particular pollen types into the cave in connection with feeding, defecation, or den construction. At any rate, both the full-year trap sample used in this analysis and the winter–early spring samples from the seasonal influx study conducted in the previous year show the anomalous *Ulmus* values, suggesting that the high percentage is not peculiar to one year's pollen deposition only. It is also unlikely that the high *Ulmus* value is a reflection of the local abundance of the tree at this site, as the moss polster just outside the drip-line of this cave yielded only 4% *Ulmus* pollen.

Most other pollen types shown exhibit no distinct differences between sampling sites and types of samplers, except the percentage of *Nyssa* is much higher in the pond than in all other samples. The tree grows in the shallow waters of the littoral zone. Aquatic and paludal pollen types are also more prevalent and more diverse in the pond sample (Fig. 4).

Tauber traps seemed to under-represent fern spores, as compared with other samples. This pattern was not determined by whether the sample was taken inside or outside a cave, as all Tauber taps were low in spores and the two speleothem samples were among the highest in both monoletes and triletes (Fig. 3).

A survey of all major and minor types (Figs 3 and 4) shows that samples from inside caves registered virtually all pollen types recorded from the outside,

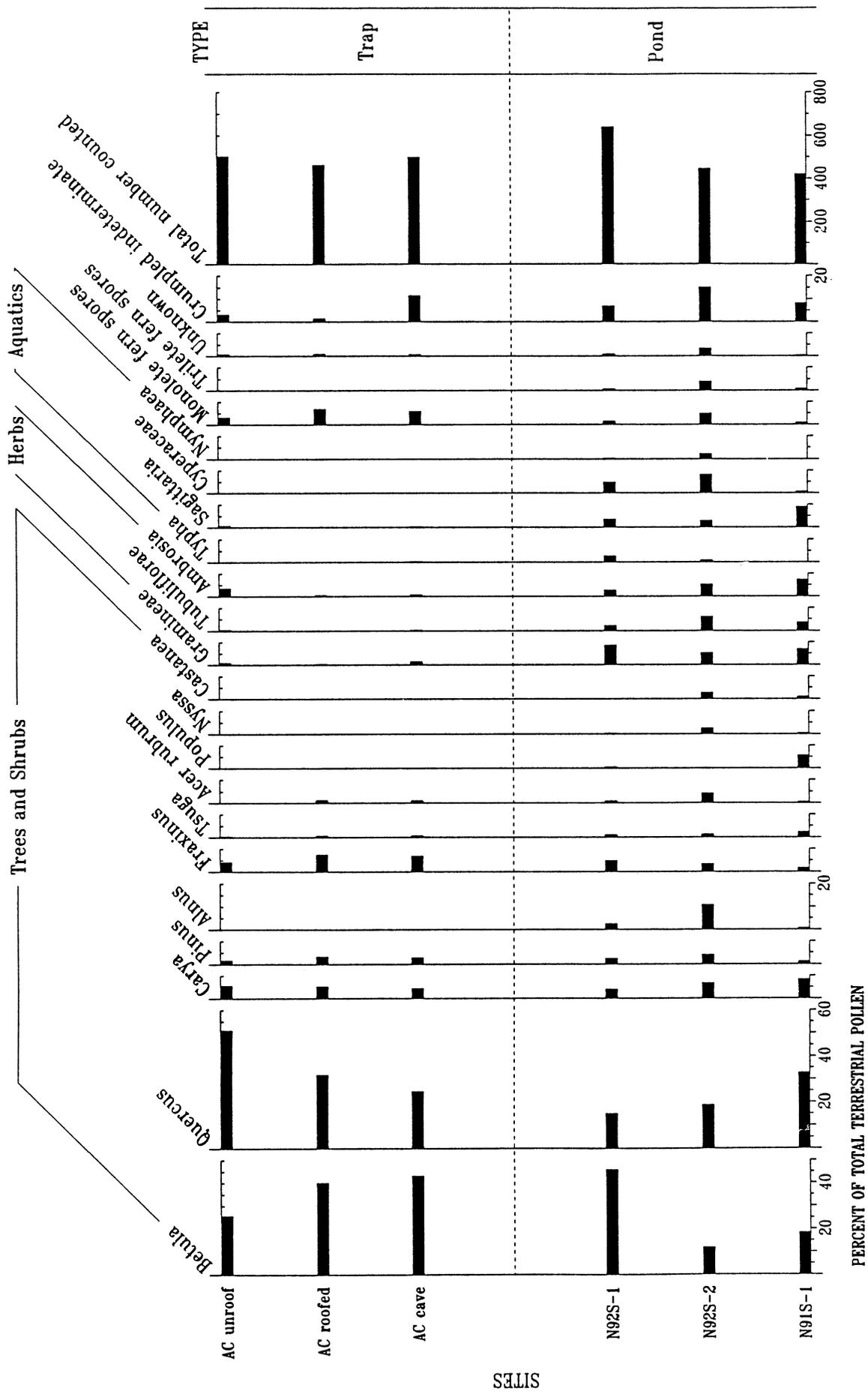


Figure 6. Pollen spectra in and near Alec's Cave, Croton Falls, New York. Diagram shows percentages for major types, defined as in Figure 3. Sample designations, from top to bottom, are: unroofed exterior Tauber trap located near cave entrance, roofed trap located near cave entrance, trap inside entrance to Alec's Cave, sediment sample from ponds no. 1, no. 2, and no. 3.

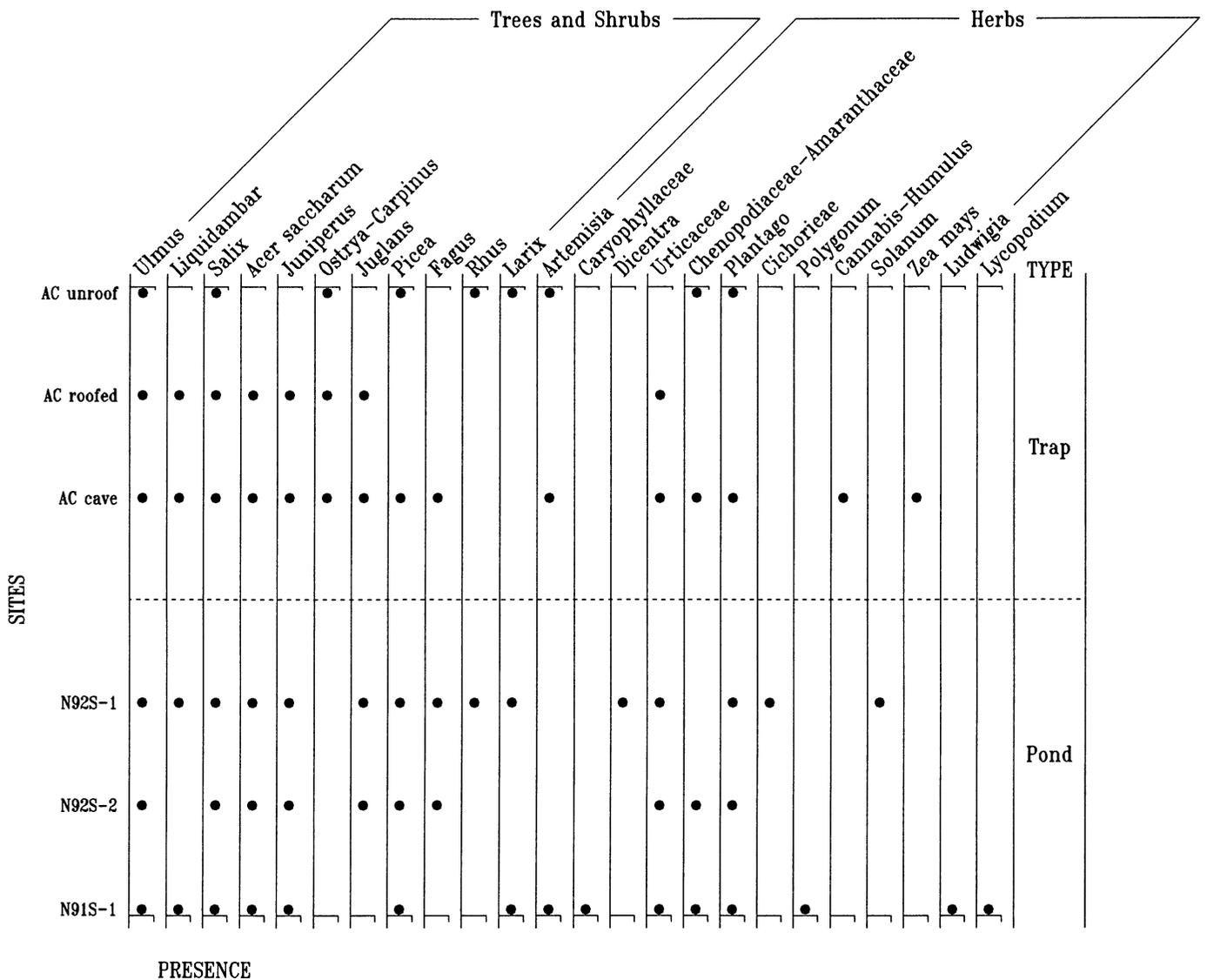


Figure 7. Minor types (< 2% in all samples) in and near Alec's cave. Dot indicates presence in pollen spectrum. Sample designations as in Fig. 6.

the main exception being that the pond includes more aquatic and paludal types than any other samples in or out of the caves.

Clustering of the pollen spectra from the Coeymans Hollow site (Fig. 5), yielded synoptic results that reflect clearly the major trends in the data and the key differences between sites and types of sampler. It should be noted that, although the clustering behaviour of the data invites tentative conclusions regarding differences, the overall differences are minor. The total sum-of-squares derived from the dissimilarity coefficients shows a dispersion of only 0.68.

The clustering of the data in Figure 5 shows the following patterns.

(1) The roofed and unroofed samplers (on the exterior form the first cluster. These are joined by the sample from the rear of Joralemon's Cave and these join with the samples from the front of each of the two caves. These form a cluster distinct from all

other samples, suggesting that, in terms of pollen spectra, those derived from Tauber traps inside or outside caves are more similar to each other than to any other type of sample inside or outside the caves. All trap percentages have been lowered to various degrees by 'swamping' of the pollen sum by *Ailanthus*, *Acer*, or *Ulmus*. As a mathematical experiment, we also ran the clustering algorithm with these taxa arbitrarily excluded from the pollen sum. The value of total dispersion in the cluster analysis increased slightly, from 0.68 to 0.81, but the clusters remained stable, including the high-level separation of trap samples from all others.

(2) The pollen data from the two speleothems from 20 and 25 m inside Joralemon's Cave are practically identical. They cluster first, not with the other cave samples (Tauber traps) but with the pollen samples from moss polsters and the pond. A slowly-accreting speleothem is more likely to contain a pollen spectrum reflecting 'average' pollen de-

position over several years (like shallow ponds and moss polsters), whereas Tauber traps sample a discrete time interval, in this analysis one full annual cycle of pollen deposition. The annual cycle is subject to all the inherent interannual variation that might arise from the year-to-year variations in pollen production of the component species.

Croton Falls site

Data from the Croton Falls site (Figs 6 and 7) were collected in the second year of the study in order to provide a second test of some of the inferences gathered from the Coeymans Hollow study. In particular, we wished to evaluate another cave with a small entrance comparable to Back Door Cave, but in a different vegetational and geological setting.

Analysis at this site was restricted to three Tauber traps and three ponds. As with Coeymans Hollow spectra, the major wind-pollinated types (*Betula*, *Quercus*, *Carya*, *Pinus*, and *Fraxinus*) showed very similar percentages for traps inside and outside the cave, and three ponds were likewise similar to the cave spectrum. A few types associated with littoral zones (e.g. *Alnus*, *Nyssa* and many herbs and aquatics) showed higher values in one or more pond spectra than in the Tauber traps as would be expected. This difference was not a reflection of the cave environment, as the external traps showed the same differences from the pond samples. Likewise, pond spectra varied among themselves as a probable reflection of the relative abundance of various aquatic and paludal types in their respective littoral zones.

The data for fern spores in Figure 6 indicate that monoletes are represented inside and outside the cave in similar percentages, and this percentage was comparable to one pond and slightly higher than the other two. Trilete fern spores occurred in all the ponds at low percentages, but were absent from all the pollen traps.

The presence diagram for all trace types (Fig. 7) shows clearly that the number of minor types represented in a comparable pollen sum from the cave was higher than from the external traps, and practically identical to the list of terrestrial types

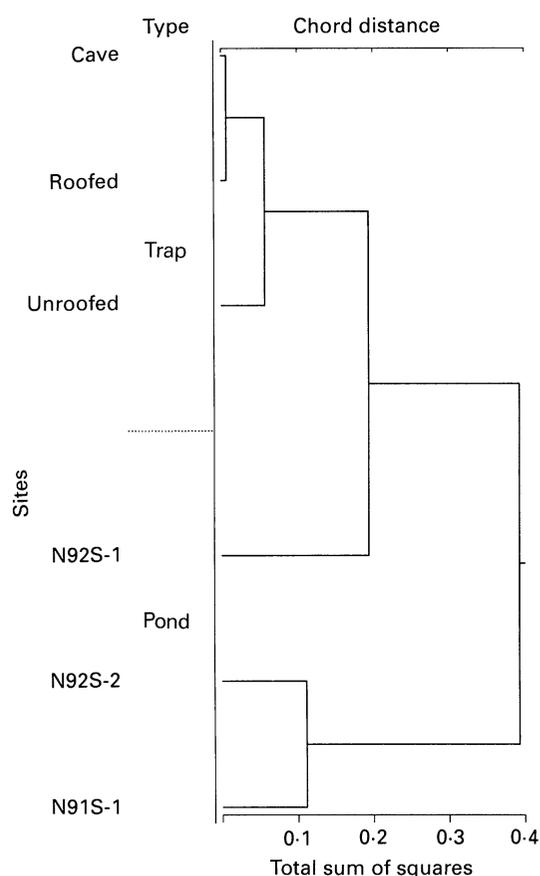


Figure 8. Unconstrained incremental sum-of-squares cluster analysis based on all the major types from the Croton Falls pollen diagram. See text for statistical methods. Sample designations as in Fig. 6.

derived from the ponds. The same trend was evident in the Coeymans Hollow data, but it is somewhat more convincing here because the taxon list is derived from not one but three ponds, and these ponds and the cave site are arrayed over a geographic area more than an order of magnitude larger than the Coeymans Hollow site.

The dendrogram generated for this site with the same criteria as Coeymans Hollow (except that all terrestrial taxa $> 2\%$ in at least one level were included in the Croton Falls analysis) show many of the same patterns (compare Fig. 8 with Fig. 5). The total dispersion in the cluster analysis was even lower

Table 1. Pollen influx data from Tauber traps, Coeymans Hollow, New York

Trap sites	Annual influx (grains $\text{cm}^{-2} \text{yr}^{-1}$) Mean/range	Mean daily influx (grains $\text{cm}^{-2} \text{day}^{-1}$)					
		22 Mar.– 21 Apr.	21 Apr.– 24 May	24 May– 26 June	26 June– 12 Aug.	12 Aug.– 5 Oct.	5 Oct.– 24 Mar.
Unroofed	28,403/8,605–48,200	4.0	10.6	35.8	969.0	12.6	1.9
Roofed	4,314/2,343–6,285	15.0	25.3	8.8	2.4	3.0	2.9
JC front	726/391–1,061	—	0.4	0.4	0.02	1.5	1.7
JC rear	126/61–192	0.2	0.3	0.2	0.04	0.5	0.05
BD front	1,389/1,093–1,685	0.6	0.1	0.4	2.8	5.4	3.8

JC, Joralemon's Cave; BD, Back Door Cave.

(total sum-of-squares = 0.39), indicating high similarity between all the spectra. The trap inside the cave produced an almost identical spectrum to that derived from the roofed trap outside. The unroofed trap joins this cluster, exhibiting relatively slight differences from the other two traps. All the traps form a cluster with the largest of the ponds, and these four form a cluster at the highest level of dispersion with the cluster formed by the other two ponds, which are much smaller in area. One of these small ponds (sample N92S-2) is adjacent to the larger pond, and the other is more than 200 m away.

The cluster analysis shows that the pollen spectra derived from traps inside and outside this cave are more similar to each other than spectra from three ponds in the area are to each other. Remarkably, the largest and smallest ponds are adjacent, yet the difference between their spectra is several times greater than the difference between the spectra inside and immediately outside the cave, and is somewhat greater even than the difference between the spectrum derived from the larger pond and that derived from inside the cave.

Influx studies

Studies of pollen influx rates in and outside the caves were undertaken, but the data presented in Table 1 should be viewed with caution. Total pollen concentrations in Tauber traps measured over the relatively short time-interval of this study are complicated by interannual variation. The traps were also subject to stochastic events that blur the picture somewhat. The annual influx for the unroofed Croton Falls sample, for instance, could not be accurately measured because some of the sample was apparently lost through a bullet hole contributed to the trap by an unknown assailant. This is not likely to affect the pollen percentage calculations, but loss of any of the sample of course makes influx calculations impossible. In the same way, the early spring sample for the front of Joralemon's Cave was lost because someone removed the sampler from the cave. A few other traps contained flowers, leaves, insects, or small frogs that could certainly raise the measured influx. Despite these caveats, the influx data show some interesting and apparently robust trends.

(1) Total annual exterior influx, which was measured for two years at Coeymans Hollow, showed extremely high interannual variance. Nevertheless, it is apparent that the unroofed sampler has the highest influx rate (mean: 28403 grains $\text{cm}^{-2} \text{yr}^{-1}$, range: 8605–48200). This trap presumably receives pollen from aerial dry fallout, from wet fallout (pollen in the precipitation), and from the considerable amount of pollen on flowers and leaves that fall in directly (mostly *Ailanthus* in this case). The roofed trap at the site received less pollen (mean:

4314 grains $\text{cm}^{-2} \text{yr}^{-1}$, range: 2343–6285), in this case most likely all from aerial dry fallout (see Tauber, 1974, for a discussion of the physics of Tauber trap sampling).

(2) Influx inside the caves was much lower. The traps in the front of both caves received roughly one-fourth the influx measured in the roofed sampler. The cave with the smaller entrance showed a slightly higher influx, but this difference appears to be driven primarily by the high influx of *Ulmus* in Back Door Cave, as demonstrated above in the percentage diagram for this cave. As discussed previously, this may be a reflection of animal-mediated pollen deposition. This impression is strengthened by the annual influx data for Alec's Cave in the Croton Falls Site. This cave, which has similar volume and entrance size to Back Door Cave (but no evidence of animal use, by contrast), showed an annual influx of only 372 grains $\text{cm}^{-2} \text{yr}^{-1}$ for the one year measured, roughly one-fourth the mean influx to Back Door cave. This value is quite low compared to the roofed-trap value for the same period from the exterior of Alec's Cave: 11,349 grains $\text{cm}^{-2} \text{yr}^{-1}$.

(3) The annual influx data from the rear of Joralemon's Cave, compared with the front, shows that influx decreases considerably at greater distance from the entrance, from a mean of 726 to 126 grains $\text{cm}^{-2} \text{yr}^{-1}$. This would be expected if the primary mode of transport were aerial dry fallout. If drip waters or animals were the primary mode of pollen transport into the cave, influx might increase toward the back of the cave, where dripping is more prevalent and where animals could find more secure hiding places.

(4) The daily influx data, partitioned at approx. monthly intervals during the peak pollen season, show similar trends to the annual data regarding the lower influx inside caves. The only exception is Back Door Cave in the period from mid-August to late March, when it receives pollen influx comparable with the exterior traps. Once again, this points to denning mammals as a possible pollen source in this cave. In general, too, it appears that the difference between influx inside and outside is smaller during this same period. Whether this is a reflection of animal transport, or merely a delayed transport effect produced by saltative pollen movements across the cave floor (refloatation, *sensu* Tauber, 1967), or by changes in air-movement patterns driven by seasonal temperature differentials between cave environments and the outside air (Tuttle & Stevenson, 1977), cannot be determined with certainty from this study.

(5) The extremely high influx for the period 26 June–12 Aug. in the unroofed sampler (969 grains $\text{cm}^{-2} \text{d}^{-1}$) can be explained by the highly localized input of *Ailanthus*, as mentioned before. If this input is disregarded, the overall trend for the site is for pollen influx to peak on the exterior in late

spring-early summer, with a less pronounced peak inside the caves that comes about two months or more later in the season.

CONCLUSIONS

Results of two years pollen trapping presented in this paper show that the pollen spectra inside the caves studied are similar to those obtained by traps in the exterior environment, especially roofed traps that sample the aerial dry fallout. These spectra are also similar to spectra derived from the tips of active speleothems from one of the caves, from moss polsters at the cave entrances, and from modern sediments of ponds located in the vicinity. The potential for increased use of fossil pollen profiles derived from speleothems with acceptable temporal resolution or from unmixed clastic cave fills with good pollen preservation should be obvious.

The results also give some clues as to what types of caves would yield pollen spectra most easily interpreted in terms of the local and regional vegetation. Caves with large entrances and strong air circulation are likely to have higher pollen influxes than caves with smaller entrances and minimal air circulation. Pollen sampling sites in caves should be as near to an entrance as possible, since influx rates decline rapidly at greater distances from an entrance. Caves that have characteristics that attract denning animals may show stronger local biases of pollen brought in by the animals. Because of the relatively low pollen influx inside caves, and the generally low sedimentation rates associated with limestone accretion and clastic infilling in most caves, stochastic and episodic forms of particle influx, such as transport by animals, periodic flooding and human activities, may influence pollen deposition inside caves in proportions that are unique to each site. Caves with bat roosts, multiple entrances, or streams that bring contemporary sediments in from the cave exterior may pose additional interpretive problems. The differences between sedimentation regimes, if taken into account, are not likely to be insurmountable obstacles to the greater use of caves as palynological sites. Such variations could be useful for developing fine-scale interpretations of regional paleoecological trends, for instance. Multi-disciplinary studies integrating pollen studies from lakes and bogs with cave pollen studies could help clarify regional *vs.* local trends, and extend dated pollen records well beyond the radiocarbon timescale. Likewise, cave pollen studies combined with other types of cave-derived data from paleontological, archaeological and geological investigations could play an important role in paleoecology by linking paleovegetational changes temporally and spatially to the faunal, human, and abiotic changes elucidated by these other methodologies.

ACKNOWLEDGEMENTS

We thank Dave Steadman for suggesting the Coeymans Hollow caves as a good site for our experiments, and for guiding us to them. George Brook, Jean Maley, Helen James, Merlin Tuttle and P. S. Martin encouraged us to think about the advantages, disadvantages, and uncertainties associated with the use of caves in palynology. Thompson Webb III, Helen James and Dave Steadman provided helpful comments on the manuscript. Tom Engel provided a draft map of Back Door Cave. Mara Burney assisted with the deployment and servicing of the pollen traps. This work was supported by NSF grants SES-8912867 and BSR-9025020.

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