

A CONSPECTUS OF PHYTOTAPHONOMY

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INTRODUCTION

The fossil record of plants principally results from individuals, variously sampled from one or more communities, that generally are associated with a depositional site. The processes responsible for the transfer of plant parts from the biosphere to the lithosphere may be biotic (e.g. physiological, animal herbivory, etc.) or abiotic (e.g. traumatic loss by wind and/or water; Krassilov, 1975) in nature. The factors ultimately responsible for the preservation of these plant parts are sedimentological and geochemical. The goals of the subdiscipline of Taphonomy, the study of processes of preservation and how they affect information in the fossil record (Behrensmeier and Kidwell, 1985), are to understand fossilization through necrology, biostratinomy, and diagenesis (Figure 1). The purpose of this chapter is to provide an overview of taphonomic factors responsible for the generation and preservation of plant macrodetritus. It is not meant to be an exhaustive dissertation or definitive discussion on phytotaphonomy.

NECROLOGY

Terrestrial plants, being anchored organisms, differ from most animals in that their ecology and growth habit greatly influence the chances of plant part burial and preservation (Figure 2). Taphonomic processes begin when plant death or loss of plant parts occurs (necrology). Different plant parts will undergo differing necrological processes (including organic decay). This will result in a variety of plant-organ assemblages incorporated under various sedimentological conditions within different depositional environments. These resultant plant-organ assemblages may be used to reconstruct the necrological processes responsible for burial and preservation, the degree of interaction between the plant parts and the sedimentological processes responsible for burial (biostratinomy), and the chemical alteration, lithification and preservation of the macrodetritus (diagenesis).

Lateral branches and ultimate plant parts (e.g. leaves, reproductive organs) are subjected to discard during the growth of canopy trees and understory trees/shrubs. Plants that are short and have a low growth stature are less likely to discard vegetative parts during growth, and they are less likely to be preserved. When encountered, these low stature plants are biased towards preservation in toto, although their occurrence is restricted to certain high-rate depositional settings (Kidwell et al., 1977; Van der Burgh, 1983/1984). Preservation in toto is not restricted to the herbaceous cover as evidenced by the fossilization of erect seedlings in alluvium (Crane and Stockey, 1985). The plant parts of canopy and subcanopy vegetation, discarded either physiologically or removed traumatically, are the most commonly encountered macrodetritus in the plant fossil record. This bias towards preservation of canopy elements has been demonstrated in various forested communities (Scheihing, 1980; Spicer, 1980; Ferguson, 1985; Gastaldo and others, in press).

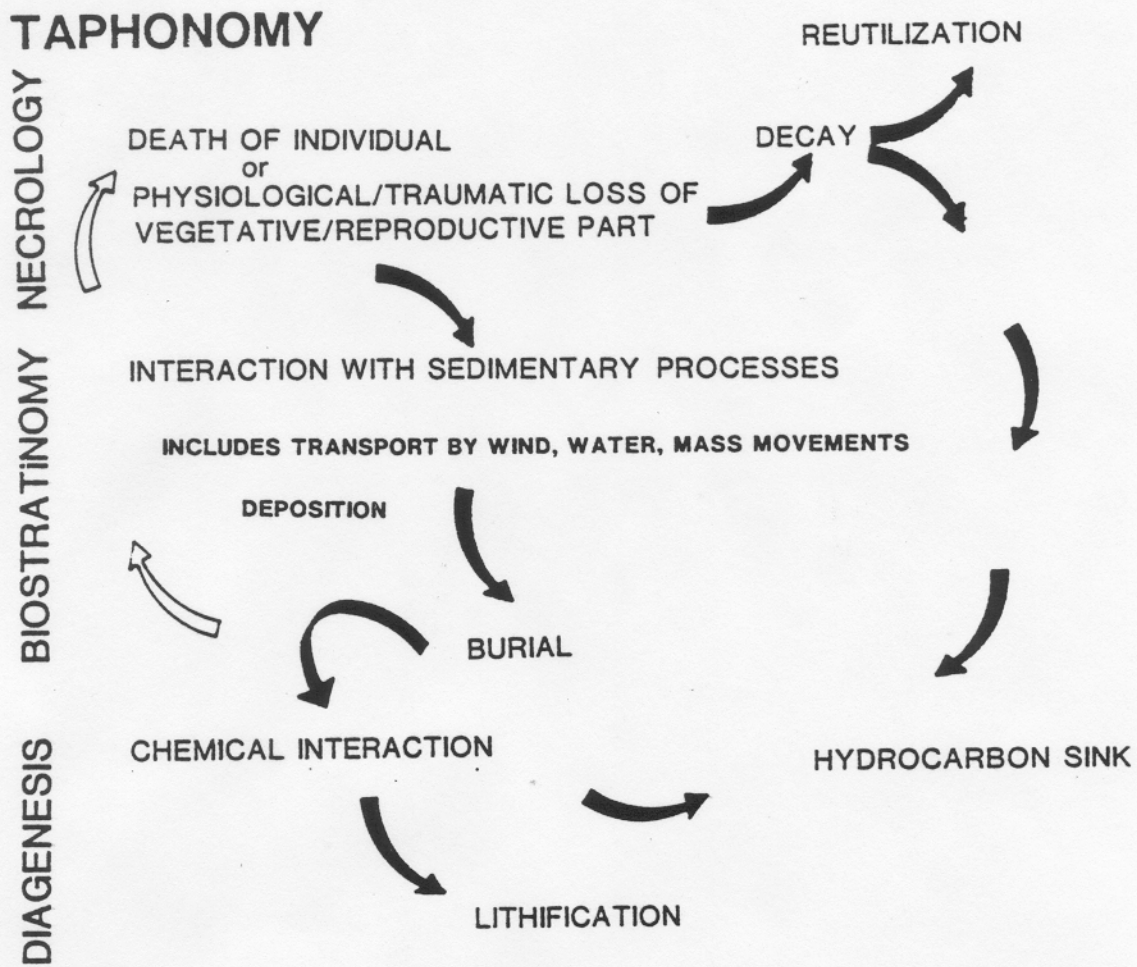


Figure 1. Diagrammatic illustration of the subdisciplines of Taphonomy and their relationships. (modified from Behrensmeyer and Kidwell, 1985)

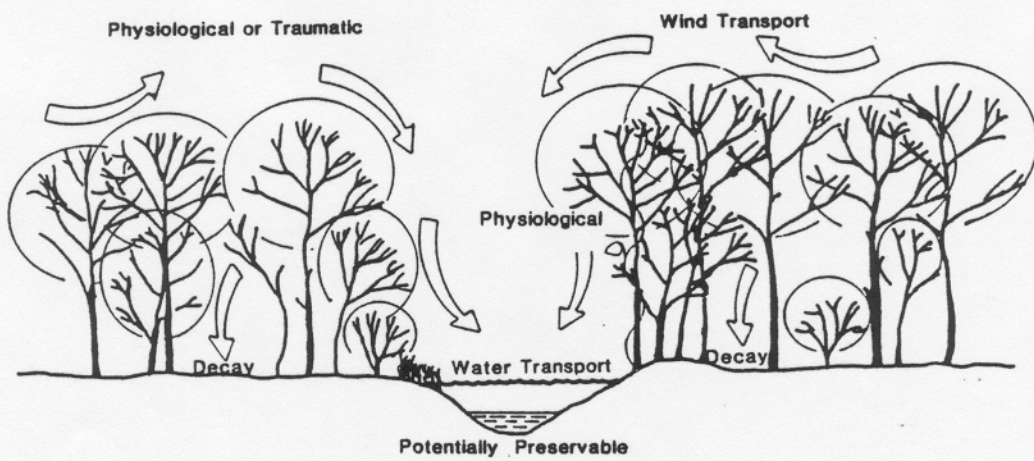


Figure 2. Transect through forested woodland depicting the fate of aerial plant parts and their potential for preservation under normal sedimentological and climatic conditions. (Modified from Ferguson, 1985).

Physiological mechanisms that are responsible for the production of potentially preservable macrodetritus include the abscission of assimilating leaves and shoots, loss of lateral and annual branches, bark shedding resulting from volumetric growth, and dispersal of reproductive structures. Differing climatic regimes affect the way in which a plant physiologically responds to the loss of assimilating leaves and shoots (see Spicer and Greer, 1986). These responses may affect the potential representation of a particular plant in the ultimate plant-part assemblage. For example, some vegetative and reproductive parts of plants (i.e. palms) growing in tropical climates tend to be retained on the parent during continued plant growth, but after completing the plant parts functional life, and rot on the stem. The potential of such a plant part to become incorporated into the fossil record via purely physiological mechanisms is poor. On the other hand, the number of plants in temperate/subtropical climates displaying this attribute is low. The tendency is to abscise assimilating leaves and shoots, increasing the probability of preservation of these taxa.

Various parts of a plant may be shed at different times of the year as the result of both growth-related phenomena and environmental factors. Although leaf fall in upper intertidal mudflat mangrove vegetation at Laguna de Mecocaca'an, Mexico, occurs throughout the year, increased leaf fall during April to September is directly correlative with the fluctuations in mean water level, insolation, temperature, and evaporation (Lopez-Portillo and Encurra, 1985). Local rainfall is not correlative with the physiological loss of leaves. The period during which flower fall occurs is offset by three months (July to September), whereas peak seedling fall occurs in December during a time when leaf fall is minimal. Branch loss is correlative with abscission of other plant parts, but is also found to increase 45 days after propagule fall.

The timing of plant part abscission in some taxa ultimately may be controlled by abiotic factors even when similar ecosystems are compared. For example, Briggs and Maher (1983) report in Eucalyptus swamps of New South Wales that the total leaf litter fall is similar to that reported in hardwood swamps of Louisiana (Conner and Day, 1976). In Eucalyptus swamps, though, litter fall was greatest following edaphic drying after prolonged flooding. Leaf abscission in the subtropical/temperate swamps of the southeastern United States follows a seasonal daylight-induced pattern, although some taxa (i.e. Quercus) may retain their leaves during the winter months (Gastaldo and others, in press; Gastaldo and others, submitted). Therefore, the contribution of a particular plant or plant community to a potentially preservable assemblage may vary depending upon the behavioral traits of different taxa. These subtle nuances in periodicity of natural canopy loss provide selective biases as to the potential fossil plant assemblage. As will become clear, a low probability exists that these assemblages would become part of the fossil record in clastic depositional sites due to normally low rates of burial.

Traumatic-induced loss, in contrast, may provide high quantities of biomass in geologically instantaneous events. The peak litter fall in the Louisiana hardwood swamps, noted above, coincided with Hurricane Carmen (Conner and Day, 1976). It is not uncommon that large geographic areas may be defoliated during hurricane force (cyclone) winds and rains. Numerous workers have assessed the defoliation, breakage of twigs, branches and trunks, tree fall and post-storm tree mortality in forested communities of various climates (Anderson, 1964; Dittus, 1985; and others). It has been demonstrated that the extent of canopy damage is a function of tree height, and that the energy of the storm is expended in the canopy rather than in the understory (Webb, 1958; Whitmore, 1974;

Scheihing, 1980). In a three-layered, moderately diverse, dry evergreen forest of Sri Lanka, Dittus (1985) reports that trees protruding above the closed subcanopy were totally or nearly totally defoliated (stripped of the majority of twigs and small branches) by winds in excess of 185 km/hr. The storm lasted for 48 hours and 20 cms of precipitation were recorded. Isolated trees were defoliated regardless of height, but minimal defoliation occurred in subcanopy and shrub layer trees. Crown damage in the subcanopy and shrub layer was approximately equal to that of the emergent canopy, though, as a direct result of falling emergent canopy crown debris. This subcanopy debris was encountered nearly in the site of growth, whereas canopy macrodetritus was transported for some distance from the parental plant.

Not only is the synusial aspect of the plant a consideration for selective sampling (Figure 3), but also the difference in histological and morphological features (size, shape and density) between taxa occupying the same geographical area. When Hurricane Diana ravaged the coast of southern Florida, up to 75% of mangrove populations were defoliated in some areas whereas marsh grasses were virtually untouched (Craighead and Gilbert, 1962).

Although canopy litter is continuously generated, the development of forest floor litters do not guarantee fossilization. Rather, the probability is extremely high that generated canopy litter will undergo decomposition (through bacterial, fungal and detritivore activity). The rate of decomposition is dependent upon climatic, as well as internal and external chemical parameters. Caro and Rudd (1985) demonstrated in Puerto Rico that litter decay rates in montane rain forest successional taxa differ after an initial rapid decay. Litter decay is quicker in the principal successional species found in the upper crown

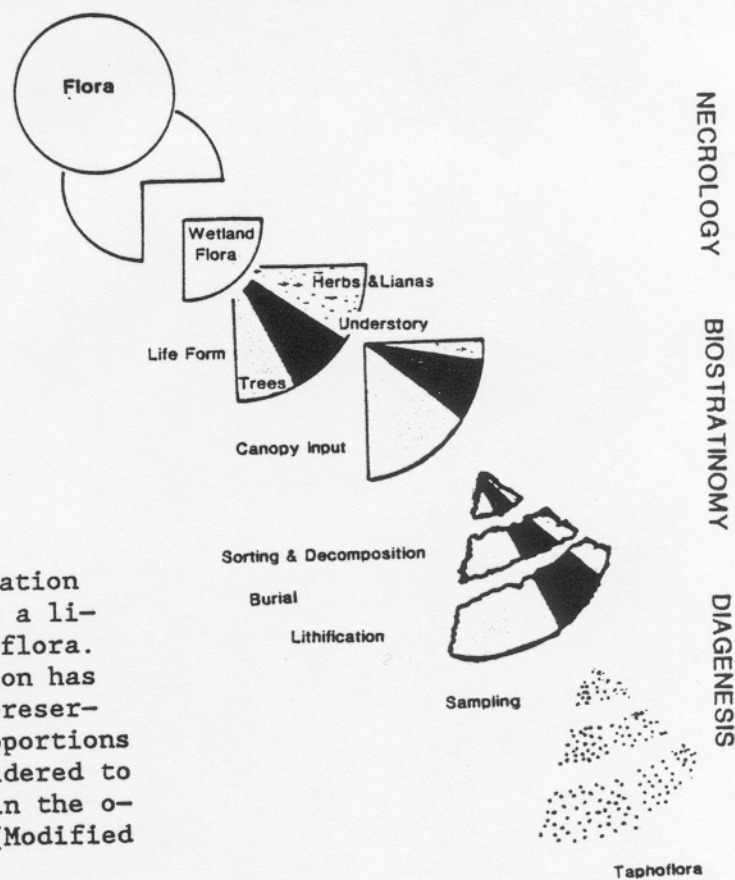


Figure 3. Schematic illustration of relationships between a living flora and a taphoflora. Since wetland vegetation has a higher potential for preservation, the relative proportions of life forms are considered to be approximately equal in the original vegetation. (Modified from Ferguson, 1985)

than those of the secondary taxa, yet after 16 weeks (113 days) of exposure only 10-20% of the composite litter remained. Even when litter is resident in an aqueous environment degradation may proceed quickly (Kaushisk and Hynes, 1971). In acidic waters of *Eucalyptus* swamps of New South Wales, the half life of submerged leaves was only 80 days (Briggs and Maher, 1983). In less acidic waters (i.e. lakes), the decay rates are dependent on the histology and chemistry of introduced taxa (Spicer, 1981; Ferguson, 1985).

BIOSTRATINOMY

In order for plant parts to be preserved, they must reside within or be moved to a depositional setting in which either anoxic (reducing) conditions prevail or are created as a result of rapid burial or alteration in pore water chemistry. The interaction of plant parts with sedimentary processes and the ultimate burial and incorporation of macrodetritus in clastic sediments comprise the second taphonomic phase, biostratinomy. The following discussion will be centered around macrodetritus of canopy and subcanopy vegetation since herbaceous and understory cover is infrequently preserved (Figures 2,3). Biostratinomic factors responsible for the generation of peats will be discussed separately.

Autochthonous burial, or burial in growth site, provides the most accurate documentation of original vegetational relationships. Autochthonous burial in clastic environments of deposition may be reflected by either the preservation of subterranean rhizome or rooting structures, or the subaerial burial of either low-stature plants or basal parts of erect trunks. Additionally, forest floor litters may be preserved by event sedimentation (e.g. flooding, volcanoclastic deposition) and represent preservation of canopy parts in growth site. The aerial parts of plants may be preserved either in vertical orientation (e.g. Gastaldo, 1986a) or, when displaced from the vertical by sediment-laden flood waters, horizontally in a parallel to subparallel orientation (e.g. Johnson, 1984).

Preservation of subterranean rooting structures is associated with soil formation primarily in which gleyed or organic-rich soils may preserve plant parts in or around the upper soil horizons. In lowland or depressional settings, these sites of deposition (as opposed to sites of erosion in which most soils develop) may allow for standing waters to develop. This may generate localized reducing chemistries establishing the conditions requisite for the potential preservation of rooting structures. Fossilized rooting structures are rarely identifiable in oxidizing soils, but forest soils may retain oxidized phytoliths (endocarps of fruits that are already mineralized) or rhizoliths (Retallack, 1983). Haloing of root traces by oxidized iron, in addition to traces of slender roots within B-horizon soils, may aid in the identification of paleosols. Geochemical data, though, provide the most accurate means of identifying oxidizing soil horizons.

The processes responsible for preservation of erect plants are linked to anomalous, catastrophic, high-rate sedimentological events. Catastrophic burial may occur via flooding or breaches of the channel levee in fluvial systems (i.e. crevasse splays; Brzyski and others, 1976; Gastaldo, 1986a), mudflows in mountainous terrains (Fritz, 1980), valley infilling (Hall and Lintz, 1983), volcanoclastic eruptions (Burnham and Spicer, 1986), and so forth. These events introduce large quantities of primarily fine-grained clastics into an area within a geologically instantaneous period of time allowing for the preservation of vertically oriented lifeforms. Another mechanism that may provide conditions

suitable for the preservation of erect autochthonous burial includes the development of limnic systems, by the damming of fluvial channels, and their subsequent infilling (Horie and others, 1976). Once the main river channel has been blocked, potentially by log jams, and the waters are backed up upstream, the newly created lake system overflows onto the alluvial floodplain and extends over the lowland vegetation. In situ vegetation may be preserved depending upon the rate of sedimentation vs. the rate of organic decay.

Burial in a vertical orientation is a good indication, but not always a definitive one, of preservation in original growth site. As noted by Spicer (1980) and others, trees may enter a river by bank collapse and thereafter be transported down gradient. In estuarine systems various authors have reported vertically floating trees as the result of their bases being weighed down by soil and/or rock, or a greater horizontal: vertical ratio of the trunk (see Stevenson, 1912). Erect floating trees may be transported into open ocean waters. In 1885, for example, the Challenger Expedition reported upright floating plant debris off the coast of New Guinea. In Spirit Lake, Washington, Coffin (1983) notes that 2 1/2 years after the eruption of Mt. St. Helens, rafts of trees covered the lake's surface and vertically oriented stumps were still floating. Some of these stumps had grounded in shallow waters.

In order to ascertain the potential degree of transport prior to the preservation of an erect stump and, hence, the associated biostratigraphic inferences, Fritz and Harrison (1985) suggest that two critical features of the trunk base be assessed. The condition of the large diameter roots at the base of the trunk provide some indication as to transport history. Those trunks in which principal root systems are intact have a higher probability of being preserved autochthonously than those in which the large diameter roots are broken. Additionally, the trunk height to root width ratio is a useful indication to infer transport. Those erect trunks in which the trunk height:root width ratio is less than 1 are more likely to have been transported.

Most plant fossils, though, have been transported some distance from the parental plant prior to their incorporation into a depositional setting. Plants that live adjacent to or within a depositional site may lose their aerial parts directly into the system. The plant parts may be moved away from the growth site to various distances depending on the abiotic processes affecting the environment of deposition. In lowland swamps, for example, canopy litter resident on the forest floor may be redistributed within the swamp either by tidal influence (Scheihing and Pfefferkorn, 1984) or flooding (Gastaldo, 1985; in prep.). This minimal degree of transport (designated by me at less than 0.5 km distance from the parent plant) is termed hypoautochthony. On the other hand, in fluvial channels macrodetritus can be carried 10's to 100's of kilometers away from the original growth site (Gastaldo and others, in press). Plant parts transported greater than 0.5 km from the parental plant are allochthonous. Macrodetritus may be transported by either wind, water, or a combination of both. Within certain depositional settings, plant parts may be moved by mudflows and other mass movements.

FACTORS INVOLVED IN PLANT PART TRANSPORT

Wind is one principal abiotic mechanism transporting plant parts by suspension load, although tumbling may play a minor role in certain depositional settings. The distance any particular plant part will travel is dependent on its weight and its surface to volume ratio. Leaves that are comparatively light and

abscise late in the season in temperate or subtropical systems can be optimally disseminated after drying (Ferguson, 1985). The prevailing wind speed at the time of abscission (or denudation) will greatly affect the dissemination of the canopy part. Leaf size heterogeneity of the original plant must be taken into consideration when attempting to discern whether or not any size sorting of the canopy litter has taken place after loss. Some taxa produce both small sun and larger shade leaves on the same tree and it has been demonstrated that sun leaves can be transported farther than the shade leaves (Roth and Dilcher, 1971; Spicer, 1975). In other plants, a unimodal distribution of leaf size occurs. It is often difficult to assess whether or not the resultant litter accurately represents the morphometric variability of the original taxon, or whether it has been size sorted by wind (Ferguson, 1985). In general, the less surface:volume ratio that exists in a plant organ, the greater probability of transport of that organ over greater distances by wind. The distances that wind-borne leaves are carried is slight when compared with pollen, spores, and small seeds (Ridley, 1930).

Plants living adjacent to bodies of water may contribute aerial detritus to the aquatic system as a response to either traumatic or physiological mechanisms. In most instances, water movement provides the impetus to transport plant detritus great distances from the site of growth. This is especially true in fluvial systems where, during extreme climatic conditions (e.g. surface runoff caused by heavy rainfall, floodwaters), flow rates are increased. This, in conjunction with the buoyancy of water-logged wood and leaves, are mitigating factors in the duration of time a plant part remains resident in suspension load. Hence, the distance any particular organ can be transported is a function of these two parameters. It must be noted that under these conditions, plant detritus transported in suspension load may actually reside beneath the surface of the waters, rather than floating on the water's surface (personal observation). A decrease in the water velocity will allow for the settling of the suspended litter to the sediment-water interface. Macrodetrital burial or decay, or a combination of both, at the sediment-water interface may follow.

In fluvial systems, branch and stem material may be transported alternately in suspension load and bedload before final burial occurs. Their orientation within the channel bedload is dependent on the plant part asymmetry (MacDonald and Jefferson, 1985). Those fragments in which length is greater than width tend to be aligned parallel to the direction of flow. Where woody detrital fragments are equidimensional, alignment may be perpendicular to the current direction. A more positive correlation exists between eccentric wood fragments and the channel orientation when waters are flowing at a faster rate. But, large fragments may be deposited over a wider range of current velocities and, therefore, adopt a wider scatter of orientations.

Not all woody material in the bedload may have been resident for the same amount of time prior to burial. Differences in the extent of rounding in allochthonous wood fragments recovered from a crevasse splay system suggest several biostratinomic processes have affected their morphology. It appears that similar-sized fragments may undergo preferential rounding depending on systematic affinities. Also, the ultimate assemblage can be comprised of wood fragments introduced into the bedload over a period of years imparting an aspect of heterogeneity in the rounded wood fraction (Gastaldo and others, in press).

Leaf and branch detritus transported in suspension load may be deposited along the channel margins when velocities decrease in response to channel shallowing. Scheihing and Pfefferkorn (1984) note that plant materials incorpo-

rated into channel forebank point-bar deposits are confined to parallel-laminated and cross-stratified sequences. It appears that the recovered assemblages are biased towards the overrepresentation of two local riparian taxa. Burnham (1985) reports matted leaf horizons in fine flood-deposited forebank muds in paratropical rivers of central Mexico.

In quiet water limnic condition, where wind-generated surficial waves are the primary currents responsible for movement of macrodetritus, aurally deposited plant parts may be transported across the water surface prior to settling out of the water column. Those plants living either fully submerged at the lake's edge or along the shoreline are more apt to be over-represented in the lake assemblage (Birks, 1973; Spicer, 1981).

The amount of litter and the degree of macrodetrital transport into the lake are a function of many variables. Factors that must be taken into account include the number of debouching streams and the relationships between debouching streams and the regional geomorphology. Variance in the regional topography will affect the vegetational communities adjacent to the contributing stream (Spicer and Wolfe, 1987) and, hence, the allochthonous contribution to the system. The extent of wind-generated surficial currents, along with the size and geometry of the lake, tend to play a role in the sorting of introduced plant parts (Wilson, 1980). In those instances where hydrophytes colonize lake margins, a filtering of transportable macrodetritus by these aquatics may subjectively bias the movement of plant parts to the open water (McQueen, 1969). These controls, in conjunction with variance in flotation times of different types and systematic affinities of plant detritus, dramatically alter the distribution and eventual incorporation of plant litter. As Spicer (1981) noted, there is no direct relationship between deposited remains and the source vegetation.

In open large bodies of water and coastal environments, deposited macrodetritus may be remobilized and redistributed by a number of processes. In estuaries, for example, tides can reentrain litter deposited in shallow waters and move it to other depositional sites (Dame, 1982; Gastaldo, 1985), or alter the distribution of plant parts within a deposit (Gastaldo and others, in press). In addition, tidal activity can affect the movement of plant parts from nearshore sites of deposition to offshore basins where they may accumulate as hydrocarbon precursors. Risk and Rhodes (1985) report on the ebb tidal flushing of mangroves in Missionary Bay, Australia, via anoxic tidal creeks. The biomass (2-10 grams/m²/day) is deposited onto shelf environments in which the resistant lipid content of the cuticle may become altered to kerogen precursors. It is known that terrestrial plants are responsible for the principal hydrocarbon contribution in various deltas (i.e. Mahakam Delta, Kalimantan; Durand, et al., 1986), and these organic rich delta front accumulations are, in part, redistributed by daily tides.

Tidal currents and long shore drift currents may play a major role in the redistribution of macrodetritus, introduced into the nearshore waters by fluvial processes, along the coast. Quite often these deposits display sorting not only by plant type (i.e. seeds), but also by size. Scheihing and Pfefferkorn (1984) discuss the development of extensive seed banks along the chenier plains of the Orinoco delta. The hydrodynamically sorted assemblages are dominated by palm seeds, but logs with attached roots, leaves of the mangrove *Rhizophora*, and branches are common components. The buoyancy of any particular plant part will affect the resident time in the water, as well as the distance to which it can be transported by oceanic currents. Gunn (1972) records the presence of tropical

Caribbean seeds and fruits along the eastern U.S. coast. The northern-most limit of tropical disseminules has been reported to be on Nantucket Island, Massachusetts, where a viable legume, Hymenaea courbaril was recovered. These disseminules are most commonly deposited as the result of sea storms.

Mass movements are another geological process that may move and/or bury plants, initiating the possibility for their incorporation into the rock record. Due to the energy expenditure involved with mass movements, there is a tendency towards large woody parts being preserved. Fritz (1986) notes that in Mount St. Helens, the mudflows and hyperconcentrated stream flows were the most important processes for transporting and burying plant remains. These mechanisms are typical of many Tertiary volcanoclastic terrains that contain abundant fossil plant detritus. Small scale earth movements, such as slumps, may also provide a means for plant part incorporation (Scheiing and Pfefferkorn, 1984).

PEATS

Macrodetrital accumulations, with little or no clastic component, are composed of plant parts that may be deposited either autochthonously (including hypoautochthonous contributions) or allochthonously (Gastaldo, 1986c). Autochthonous peats form in a number of depositional settings (alluvial floodplains, lakes, deltaic wetlands, coastal mangroves), but all share the common feature of being derived from contributions of in situ vegetation. The peat forest soils are vegetated by a variety of water and nutrient stress-tolerant plants, and most of the aerial macrodetritus decays into a brown mush to black amorphous soupy matrix within the first 10 cm of the swamp's surface. The woody litter (roots, trunks, crown branches) has a higher probability of being preserved once it has been buried below the level of the water table (usually 10-20 cm below the peat surface). Peats may accumulate to depths of 10's of meters. Hypoautochthonous elements may be introduced by traumatic winds. These plant parts would be derived from nearby vegetation inhabiting non-peat soils.

Allochthonous peats are generally comprised of highly fragmented plant parts (fruits and seeds, leaves, branches, stems) that have been redistributed by water currents. These may occur within lake systems (i.e. sapropelic channel coals), open coastal estuarine systems (Gastaldo and others, in press), or along deltaic coastlines (Allen and others, 1979). In the Mahakam and Mississippi deltas, for instance, ridges of allochthonous peat are deposited along several kilometers of the delta fronts by tidal reworking. Allen and others (1979) have noted the accumulation of detrital organics as beach ridges occurring within headlands between distributaries. These ridges may be up to 7 km along the coast with accretion 2 km inland. The peats may accumulate to depths of several meters.

DIAGENESIS

The third subdiscipline of Taphonomy addresses the processes responsible for the ultimate preservation of the organic remains after incorporation into a depositional environment (Figures 1,3). This not only includes the alteration of the original part in response to compaction, but also what affects cementation, replacement, and metamorphosis may have on preservation. Schopf (1975) elucidated the principal modes in which plant macrodetritus can be fossilized. These include coalified compressions - impressions, authigenic cementation, permineralization, molds and casts, and duripartic preservation.

Oxidizing environments promote plant part degradation, but depending upon the timing of decay in relation to burial, impressions of incorporated macrodetritus may occur if sediment grain size and other factors permit. The oxidation or reduction of organic matter is dependent on the pore volume to water movement ratio. Early diagenesis occurs in most sands as the result of maximum percolation of oxygenated waters. It appears that maximum compaction accompanies this initial phase of alteration which may account for the preponderance of impressions of trunks and logs in channel bedload sands. Argillaceous muds, although composed of 50-80% water, provide a minimum of interclast space through which oxygenated waters can pass. Additionally, the close proximity of reactive clay minerals to the organic matter can allow for rapid chemical interaction with an increased propensity towards preservation. Spicer (1977) reports in lake environments that an iron-rich encrusting layer can be precipitated on the surface of a leaf shortly after burial. These factors can insulate macrodetritus from decay and, when followed by compaction, help to ensure their preservation.

The deformation of any plant part is temporally controlled by differing phases of sediment compaction. Rex and Chaloner (1983) have demonstrated experimentally that distortion during the compression of plant parts is unidirectional, in the vertical plane. Depending upon the morphology, histology, degree of degradation, etc. of the original plant part prior to compaction, various alterations in the morphology of the part may result. These include the potential for external topography to be translated to the internal infilling, the imprinting of internal characters to the exterior surfaces, differential preservation of appendages (e.g. spines, hairs), and the development of a compression border approximating the original thickness of the plant structure (Rex, 1983; Rex and Chaloner, 1983).

Biochemical alteration by bacteria and fungi affect the original organic composition of the plant part by decreasing the cellulose component by hydrolysis and increasing the lignin component (humification; Barghoorn, 1952). The chemical path through which any piece of litter it then follows is dependent upon the chemical microenvironment in which it is deposited. Humification of cellulose in an aerobic environment will ultimately alter the organic material to polymerisates and humic acids. Under anaerobic conditions, though, the high molecular weight molecules will be altered by various bacteria to monomers, fatty acids, and acetate after which methane may be formed. No enrichment in carbon is noted to occur during biochemical degradation. Coalification is a subsequent geochemical process in which the remaining volatiles are expelled and the fixed carbon is increased. The organic materials are metamorphosed to a black, highly lustrous, coal maceral termed vitrinite (Stach and others, 1982), and the result is an anthracolemma (Schopf, 1975).

If chemical conditions are appropriate in argillaceous clastic depositional environments, organic detritus may act as the nucleating agent for the precipitation of encrusting carbonates. The exact cause for crystallization of these chemicals around the macrodetritus is not known, but may be related to the cellular senescence of the plant part buried within the clays.

An increased production of CO_2 , as the result of respiration pathways dominating cellular processes, would quickly react with available Ca^{++} , Mg^{++} , or Fe^{++} . It is also possible that the CO_2 is evolved in the degradation by bacteria (Curtis, et al., 1975). If these cations were abundant in the pore water supply, both calcite (calcium carbonate) and siderite (iron carbonate) would form. This

is a common diagenetic process in black shales and other organic-bearing muds (Tourtelot, 1979; Woodland and Stenstrom, 1979). The resultant fossilization mode is termed authigenic cementation (Schopf, 1975), commonly referred to as concretions or nodules (e.g. Mazon Creek).

The conditions requisite for cementation include the initial clay mineralogy, a specific range of Eh and pH conditions, a water supply that is high in available CO_2 and Fe^{+2} but having a Ca/Fe ratio lower than seawater, and the absence of bacterial reduction of SO_4 (Tourtelot, 1979; Woodland and Stenstrom, 1979). Curtis, et al., (1975) noted that there are two distinct phases of precipitation. Siderite, a Cl_3 -rich carbonate, is deposited proximal to the nucleating zone, whereas in the distal zones pistomesite, a Mg^{++} -rich carbonate, occurs.

When mineral-charged waters infiltrate plant tissues, and the cells act as templates for crystallization, permineralizations result (Schopf, 1975). Although over 40 minerals have been identified as contributing to the process, four primary minerals are often encountered. These are hydrous silica, microcrystalline calcite, microcrystalline quartz, and pyrite. The chemical processes leading to silicifications and calcifications have been studied in some detail. Leo and Barghoorn (1976) speculated that a hydrogen bonding between soluble silica and ligno-holocellulosic complexes may be responsible for the onset of crystallization. Opaline silica lithomorphs were experimentally formed under a low geothermal gradient, low atmospheric pressure, and near-neutral conditions. Submerged wood, kept swollen and maintained in a plastic state, would allow for maximum permeability of low molecular silicic acid-rich groundwater. Silicic acid is a potential derivative from volcanic ash devitrification and clay mineral diagenesis (Siever, 1957).

The generation of permineralizations by precipitation of microcrystalline calcite may be more complex. A wide variety of processes ultimately may be responsible and these appear to be dependent upon the depositional environment. In any case, pore fluid impregnation by calcium carbonate allows for the retention of plant histology.

When the internal organization of a plant part is degraded and a void develops, this void may act as a mold. If the mold is subsequently infilled with either clastic sediments or crystals, a cast may be formed. The most conspicuous casts are those of large plant parts (e.g. trunks, branches), although casts of more delicate structures can be found. Experimentally, the formation of casts has been attempted in an effort to document the mechanisms responsible for the infilling of prostrate, hollowed canopy parts and erect stumps (Rex, 1985). The sedimentological processes and sedimentary structures generated within the prostrate molds are dependent on the length and diameter of the stem, the depth of burial in the bedload, and the velocity and sediment capacity of the flume. Infilling of upright stems occurs via suspension load sedimentation during low current velocities. The state of degradation of the stump, and the sedimentological regime may affect the ultimate configuration of a molded erect stump (Gastaldo, 1986b).

Duripartic preservation is the result when a plant part is able to withstand the effects of an oxygenated depositional site. The resistant parts are preserved without alteration.

Diagenetic processes and the sequence of alteration of the organic-bearing

sediments with continued burial are intergradational and interrelated. The homogeneity or heterogeneity of the sediments will play a major role in the amount of compaction following increased depth of burial. This tendency towards differential compaction as a result of differing sediment mixtures may dramatically alter the appearance of any particular plant part. Often, two identical plant parts preserved in differing matrices have been assigned separate taxonomic status. The strongest effects are noted in fine-grained sediments. Compaction can be accompanied by cementation. The deposition of minerals within the interstices of a sediment is the result of intraclast chemical reactions. These reactions are controlled by the Eh and pH of the sedimentary environment, as well as, the initial chemical and physical states upon burial of both the organic and inorganic components. The most common cementing minerals are calcite, dolomite, siderite, and silica. These may originate from within the sedimentary body (entrapment between clasts), or may be introduced by solution from an outside source.

Lithologic conditions may be altered at any time during its burial and post-burial history. Differential solution may occur between sediment clasts as well as along bedding planes. This selective solution process may dissolve and alter (by recrystallization) particular preservational modes. In some instances, new minerals may develop from reactions between the original clasts and percolated chemicals introduced from external sources. New minerals may develop within the space occupied by the original mineral (replacement). In the case of some permineralized woods, this effectively destroys any structural attributes of the original plant material.

The tendency towards loss from the fossil record is not restricted to the phase of lithification. In many instances, the alteration of lithologies occurs after exposure to weathering elements. Percolation of groundwaters ultimately may be responsible for the loss of paleontological data. Dissolution, hydrolysis, hydration, and oxidation of minerals (particularly clays) in shales cause these mudrocks to disaggregate, destroying any preserved fossil that may be present. Indeed, the outcrop may hide as much as it reveals (S. Wing, personal communication).

CONCLUSIONS

Phytotaphonomy is an emerging and important subdiscipline of paleobotany. It is evident, even from the brief discussion herein presented, that taphonomic processes place a variety of limitations on the paleontologist because of their multiplexity. The necrological, biostratigraphic, and diagenetic phases through which a plant part must pass prior to being recovered for study selectively filter the available data that ultimately can be assessed. Differing depositional environments, and the same environment of deposition in different climatic regimes, have unique conditions under which these taphonomic phases operate. Phytotaphonomists have recently begun to identify the potential filtering mechanisms within taphonomic subdisciplines and have attempted to use these analogs in ancient environments. Once we are able to understand the principal mechanisms responsible for the preservation of a taphoflora under specific environmental (including climatic and biogeochemical) and geographical constraints, we will be better able to interpret plants and plant-part assemblages in the Phanerozoic.

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