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PATTERNS OF DISTURBANCE AND VEGETATION CHANGE
IN THE MIOCENE SUCCOR CREEK FLORA
OF OREGON-IDAHO

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PATTERNS OF DISTURBANCE AND VEGETATION CHANGE IN THE MIOCENE SUCCOR CREEK FLORA OF OREGON-IDAHO

By

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ABSTRACT

PATTERNS OF DISTURBANCE AND VEGETATION CHANGE
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Pollen analysis of 600 m of section in the Miocene Sucker Creek Formation shows three patterns of vegetation change that can be related to two kinds of disturbance.

1. A continuous pollen sequence through 70 m shows a pattern of repeated forest disturbance and secondary succession. Forest assemblages of mixed broadleaved evergreen, broadleaved deciduous, and conifer elements shift abruptly to an elm dominated broadleaved deciduous assemblage, apparently in response to cyclic disturbance that caused widespread damage, particularly to the evergreen elements. Possible disturbances included climate cycles that periodically killed vulnerable trees, or catastrophes such as fire, hurricane, or flood, that destroyed areas of forest. On such cleared sites deciduous species with early successional roles gained rapid dominance, then gradually yielded to mixed broadleaved-conifer dominance. In the time represented by this 70 m section, the forest did not attain steady state.

2. Discontinuous pollen sequences through the remaining section preserve a record of episodic disturbance by volcanism and of primary plant succession on an ash covered landscape. A pioneer herb-shrub complex is succeeded by an alder dominated broadleaved deciduous scrub. Alder quite probably improved the nitrogen content of the mineral ash for the other woody plants that followed, as it does today.

3. An aquatic vegetation succession is identified which developed concurrently with the terrestrial volcanic ash succession. A submerged, open water assemblage dominated by algae and aquatic fungi is succeeded by a *Glyptostrobus* swamp forest in which the aquatics were excluded. Volcanism apparently led to the blockage of drainage systems, creating shallow lakes with opportunities for aquatic and swamp plants.

The vegetation was constantly changing. The continuous pollen sequences provide a record of forest disturbances which occurred with a frequency that precluded the attainment of a steady state forest composition. The discontinuous pollen sequences provide a record of volcanism that destroyed the vegetation with a frequency that rarely allowed the development of forest. In both settings of disturbance, broadleaved deciduous trees dominated early successional stands.

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GEOGRAPHIC TERMINOLOGY

The Miocene flora and fauna and the creek for which they were named were spelled either "Succor" or "Sucker" prior to 1960 when the name "Sucker Creek" was officially adopted by the State of Oregon. Kittleman et al. (1965) used "Sucker" to name the formation exposed in the area, and Graham (1965) to publish a revision of the fossil flora. In 1966 the State Geographic Names Board reversed its earlier official ruling, changing it to the "Succor" form. "Sucker" must be retained for the formation, has been used for the fossil flora (Taggart 1971, 1973; Taggart and Cross 1974), and continues to be used for the fossil fauna (Shotwell 1968, Tedford et al. in preparation), but "Succor" has recently become the preferred spelling for the name of the fossil flora (Niklas and Gianassi 1977 and later, Taggart and Cross 1980 and later) and will be used here for consistency.

INTRODUCTION

Late Tertiary paleobotanical studies in the Pacific Northwest have documented broad trends in the modernization of the vegetation of the region. Evolutionary models of vegetation change and stratigraphic and climatic interpretations of the fossil floras have mostly been based on the assumption of long term climatic control of vegetation and thus on the assumption that the plant fossil assemblage preserved at any point in time is one of steady state, climatically controlled, climax vegetation.

Studies of Quaternary and recent vegetation history show ubiquitous patterns of disturbance and of continual vegetation change on the time scale of plant succession that have led to the conclusion that long term stability may be the exception and episodic disturbance the rule in the history of vegetation (e.g., Brubaker 1975, Davis and Webb 1975, Miles 1979, White 1979, Davis 1981). Extrapolated to pre-Quaternary forest vegetation, this concept has implications for models of evolution of Tertiary vegetation and for the biostratigraphic and climatic interpretations of Tertiary fossil plant assemblages.

A test of the concept of intrinsic disturbance in the pre-Quaternary history of vegetation requires the preservation of a stratigraphically continuous plant record in a sedimentary setting that allows resolution of vegetation change on a time scale of plant succession.

In the late Tertiary volcanic terrains of the Pacific Northwest pollen and spores provide the most abundant, continuous, and widespread plant fossil record. Many of the Neogene volcanic sections in the region were deposited very rapidly and are barren of plant fossils. In occasional sections, fine volcaniclastics were reworked into lake beds at a rate that allowed the incorporation of a more or less continuous pollen record with resolution of vegetation change on a time scale of plant succession. In such sequences in the Miocene Sucker Creek Formation of eastern Oregon and western Idaho, stratigraphically controlled palynologic studies have shown a record at disturbance and plant succession in the Succor Creek flora (papers by Taggart and Cross).

The present study involves the stratigraphic palynology of 600 m of volcaniclastic section in the Sucker Creek Formation. The results provide new insight into the patterns of both cyclic and episodic disturbances of the Succor Creek flora and into the processes of post-disturbance vegetation succession.

These findings contribute not only to ecological theory and models of vegetation evolution but also to biostratigraphy and the reconstruction of paleoclimate. Ecological and evolutionary assumptions form the basis of the application of fossil plant assemblages in biostratigraphy and in the reconstruction of paleoclimate. Thus, insight into the ecological significance of plant assemblages and the history of disturbance enhances effective paleoclimatic and biostratigraphic interpretation of late Tertiary plant assemblages in the Pacific Northwest.

Previous Studies of the Succor Creek Flora

The Succor Creek flora is one of the best studied in the region, including many contributions to classical macrofossil taxonomy and more recent intensive stratigraphic palynological studies. Historically, the Succor Creek flora is a complex of isolated florules collected from volcanic strata which outcrop in the Oregon-Idaho border area. Contributions to the macroflora include Knowlton (1898), Berry (1932), Brooks (1935), Arnold (1936a, 1936b, 1937), Smith (1938, 1939, 1940), and Chaney and Axelrod (1959). Graham (1963, 1965) undertook a thorough systematic revision of the flora based on approximately 2500 specimens from 15 localities. Included in the study was an examination of the leaf-bearing matrix for the occurrence of pollen and spores. This pioneering palynological study added an important dimension to our understanding of the flora by showing the presence of a significant conifer element in the pollen flora. *Picea* was shown to be the most abundant conifer pollen type, averaging 20% of total pollen and spores. *Abies* and *Tsuga* were also found to be consistently present. Shah (1968; Smiley, Shah, and Jones 1975) extended the regional record of the flora with collections from leaf-bearing localities in the Weiser area of southwestern Idaho assigned to the Sucker Creek Formation.

Taxonomic studies have generally considered the individual florules to represent a single contemporaneous flora consisting of a diverse deciduous forest complex growing under warm temperate conditions with moderate, evenly distributed rainfall.

An approach to study of the taxonomic affinities of some elements of the flora has recently been undertaken. Using well preserved material it has been possible to compare cell ultrastructure and chemistry of Miocene Succor Creek and living leaf genera (Gianassi and Niklas 1977, Niklas and Gianassi 1978, Niklas et al. 1978).

Paleoecological studies of the Succor Creek flora have been undertaken over the past decade by Taggart and Cross (Taggart 1971, 1973; Taggart and Cross 1974, 1980; Taggart et al. 1982; Cross and Taggart 1983[1]). The approach has involved continuous sampling of stratigraphically sequential sections for palynological study and collection of macrofossils from each horizon containing leaves, seeds, or wood. These studies have suggested patterns of vegetation dynamics of the flora in response to short term climatic oscillations, and to volcanic hydrologic, and fire disturbance.

The Present Study

The updated taxonomic treatment and stratigraphically-controlled palynologic perspective of the Succor Creek flora contributes significantly to the interpretative framework of the present study. The site for this study was selected because it provides a stratigraphic and topographic extension of previous studies in the formation. The measured and sampled section exceeds 600 m and is thus by far the thickest studied to date from the Sucker Creek Formation. The thickness of the section enhances the possibility of obtaining detailed data on the patterns of vegetation change and disturbance. The site is 10 km north of the type locality, previously the most northerly section documented by palynology, and thus provides a significant extension

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[1] Many references will be made to these studies. Where cited collectively, they will be referred to as "papers by Taggart and Cross" for brevity.

of the study area towards the Snake River. The site is here referred to as the "Devils Gate locality".

The study of the Devils Gate locality had the following objectives:

1. Describe the depositional units exposed at the Devils Gate locality and interpret their relative stratigraphic positions.

2. Identify the micro- and macrofossils preserved at the locality and compare the paleoflora with modern floras.

3. Document the stratigraphic palynology of the Devils Gate sequence.

4. Interpret the patterns and processes of vegetation change and the incidence and nature of disturbance, and derive insights for models of evolution of Miocene vegetation, and for biostratigraphic and paleoclimatic interpretation of Miocene plant assemblages.

METHODS

Field and Laboratory Methods

Description of the Collecting Locality

The Devils Gate section (Figure 1) is exposed on both sides of the Succor Creek Road, approximately 15 km south of the junction with Oregon State Highway 201 (Idaho 19). It is 10 km north of the type locality and 8 km north of the campground in the scenic Succor Creek Gorge. The location is in the Owyhee Ridge Quadrangle, Malheur County, Oregon (Sec. 31 S1/2 and Sec. 32 S1/2 R.46 E. and T.23 S.). It is referred to as the Devils Gate locality in this paper for the nearest named landmark, a prominent gap in the overlying Jump Creek Rhyolite situated about 1.2 km northwest of the site.

Measuring and Collecting Methods

Field work was conducted in the late summers of 1977 and 1978. The surface of most of the exposed sequence was covered with weathered bentonitic ash, the thickness varying with the slope. Continuous trenches were excavated to expose relatively less weathered rock for comprehensive sampling of the section. Each lithologic unit was sampled. Where lithologic change was imperceptible through extensive thicknesses, the unit was sampled in approximately 1.6 m increments. In three portions of the section particularly deep weathering precluded

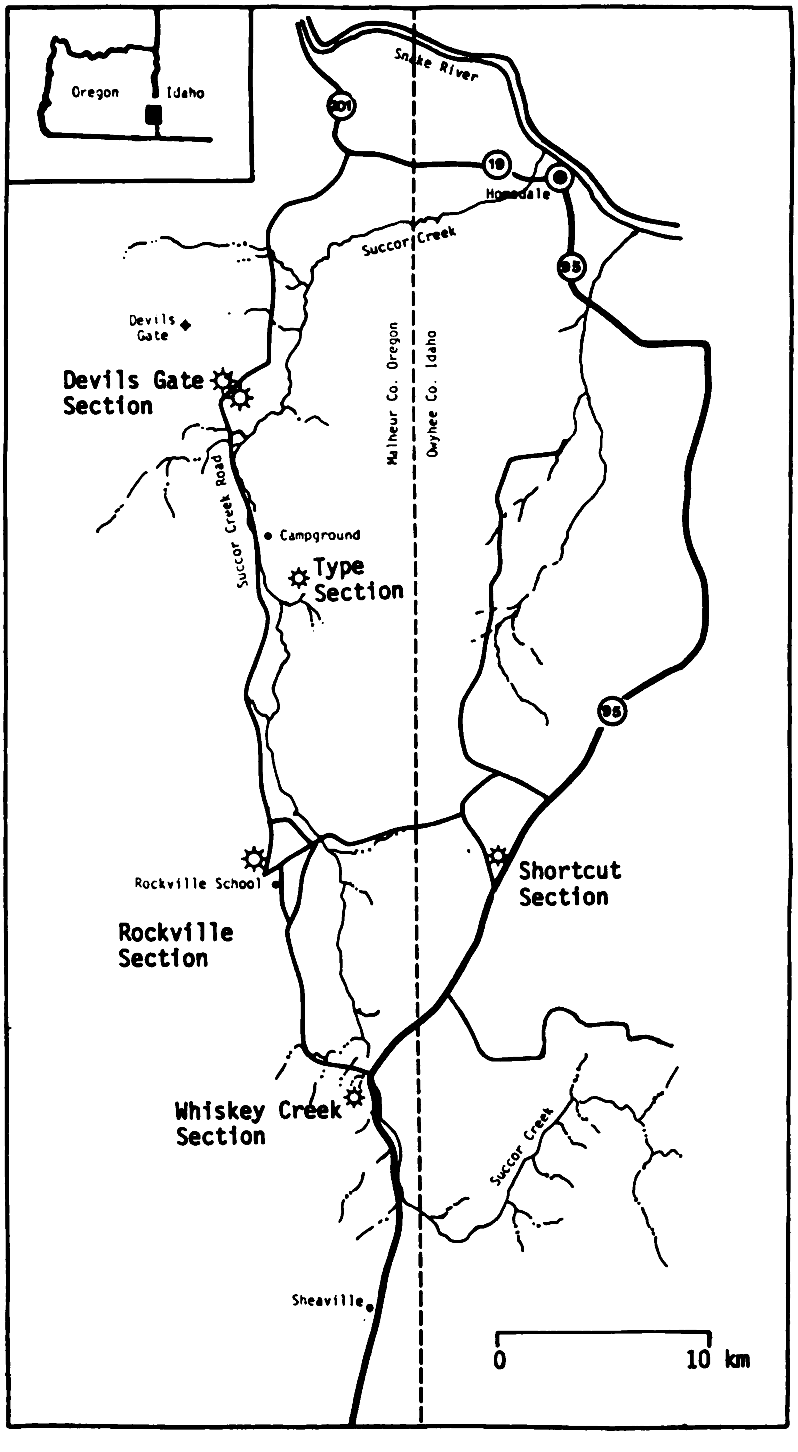


Figure 1. Locations of sampled sections in the Succor Creek area (after Taggart and Cross 1980).

the excavation of continuous sampling trenches. In these sequences holes were dug to somewhat less weathered rock. Samples were taken and a lithologic description attempted at measured intervals. Two hundred and fifty samples were collected from 630 m of section for palynological analysis. In the course of measuring and sampling the stratigraphic sequence, stumps were found at two horizons and two leaf beds were exposed and collections made. Fossil bone fragments were observed at seven horizons which were traced along the outcrop in a search for additional faunal remains.

Sample Preparation for Study of Palynomorphs

Initial trials were conducted to develop a standardized processing scheme which could be used routinely, with little modification. The aim was to develop a technique that would effectively macerate the range of volcanic rock types encountered in the sections while providing as uniform a processing schedule as possible. Cold HF treatment (after Taggart 1971) was employed to avoid possible destruction of palynomorphs caused by high temperature in the reaction of concentrated HF with these highly siliceous volcaniclastics. After HF treatment most samples required repeated washes in hot HCl to remove fluorosilicates. Many productive samples needed no further treatment except staining. A few samples containing excessive quantities of fine organic detritus were treated briefly with bleach prior to staining.

Details of Treatment.

1. A 20 or 30 g sample was crushed until the largest fragments were less than 10 mm.

2. A fragment was tested with HCl and the few samples containing carbonates received a preliminary treatment in 10% HCl for 4 to 8 hours. These were subsequently washed until all trace of the acid was removed.

3. A plastic beaker containing the crushed sample was placed in an ice water bath and crushed ice was added to the dry sample. Reagent grade HF (49%) was added very slowly and intermittently to keep the temperature of the reacting mixture cold. The sample was left to stand in HF for about 24 hours with frequent stirring for the first 8 to 12 hours and was then allowed to settle overnight.

4. The sample was centrifuged and washed repeatedly in hot, dilute HCl (10%) until all the fluorosilicate gel was removed. Need for subsequent treatment was determined by microscopic examination of the sample.

5. Fine, organic detritus was reduced by treatment with commercial bleach (5.25% NaOCl) until a color change was observed. This was followed by several washings.

6. Residues were stained with 1% safranin and stored in H.E.C. (hydroxyethyl cellulose WP-09, Union Carbide Corp.).

7. Four to six slides were prepared from each productive residue using H.S.R. (Harleco synthetic resin) as a mounting medium.

Analytical Methods

Methods of Morphological Study and Taxonomic Treatment of Palynomorphs

Most palynomorphs were assigned to living genera or families on the basis of comparison with modern reference material and published atlases.

Several atlases of north temperate airborne pollen with good generic descriptions and illustrations provided a useful supplement to the reference slide collections for this study:

Regional atlases - Martin and Drew 1969; Richard 1970 a,b; Huang 1972; Adams and Morton 1972, 1974; McAndrews et al. 1973; Lieux 1980 a,b, Lieux and Godfrey 1982. Systematic treatments - Ferguson 1977 (Cornaceae); Helmich 1963 (Acer); Sivak 1973 (Tsuga), 1975 (bisaccates), 1976 (Cathaya); Stone and Broome 1975 (Juglandaceae).

Two or more distinct morphotypes of some genera were found and each was assigned informal identifying codes for counting purposes. Some pollen types could not be identified. In part, these unknowns are probably due to the limits of scope of the search for modern equivalents. Further reference study and more detailed morphological study including scanning electron microscopy should resolve some of these taxonomic problems. Other unknowns probably represent the pollen of extinct taxa. All unidentifiable pollen types were found to be quantitatively insignificant in the subsequent pollen analytical study.

Photographs were taken of all pollen and spore types to document the range of variation of each type for constant reference during pollen counting. Succor Creek palynomorphs have been adequately treated systematically (Graham 1965, Taggart 1971, 1973); only the few new Devils Gate forms are described and illustrated here (Appendix and Plate 3).

Methods of Quantitative Analysis

Sampling and Counting. Counting was carried out along regular traverses of the slides at a magnification of 950X. Traverses were positioned evenly over the slide, and counts were divided between several slides. Five hundred palynomorphs of vascular plants were counted unless this was not possible due to the low productivity of a sample. Algal bodies and fungal spores were tallied outside of the basic pollen sum during the counting procedure. All the interpretations in a study of this sort obviously depend on accurate and consistent pollen identification. Care was therefore taken to assign to each pollen type a generic name, where an earlier assignment had been made, and also to a specific photograph. This allowed subsequent reassignments as more grains were examined and as observations and interpretations became more critical with experience. Where the essential morphological features of a grain were obscured it was assigned to one of several "indeterminable" classes indicating various levels of uncertainty. Morphologically determinable types which could not be assigned to a modern taxonomic group were referred to coded categories for counting purposes.

Presentation of Pollen Spectra. The basic pollen sum was the total number of higher plant spore and pollen grains counted in a sample. The relative abundance of each pollen type was calculated as a percentage of the basic pollen sum.

Pollen and spores of aquatic plants, algae, and fungi were excluded from this sum because their production is local and more or less independent of the factors influencing the sum of terrestrial plants. Their abundances were calculated as percentages of the basic sum plus their own sum, following the practice of Quaternary palynologists (Birks and Birks 1980, p. 168).

Relative abundances of groups of taxa were also calculated to elaborate broad trends through the section. Relative abundances were used to plot the pollen diagrams.

Interpretation of Relative Pollen Diagrams. The paleoecological interpretation of pollen diagrams is complicated by differential processes of production, dispersal, deposition, and preservation of pollen. These processes have been the subject of intensive study by Quaternary paleoecologists. A thorough recent review has summarized the significance of some of the principal factors (Birks and Birks 1980). Paleoecological reconstructions in this study are made within the accepted constraints of this body of information.

Through a single sequence of lake sediments, pollen assemblages are more or less controlled for many of the variables of pollen production and sedimentation so that major shifts in pollen floras through the sequence can be interpreted with some confidence as shifts in vegetation distribution or composition. Studies from lakes attest to the validity of pollen records for the purpose of reconstructing dynamics of vegetation through time (Janssen 1966, 1967, Davis et al. 1971, Webb 1974, Brubaker 1975). In a lake sequence, a major potentially distorting influence must be considered, that of local pollen input from lake margin vegetation which can change through time under local hydrologic control independently from the regional vegetation. This potential problem in the Devils Gate setting will be evaluated before interpretations are made of the pollen dynamics of continuous pollen sequences.

The significance of differences in pollen assemblages from different basins in space and time is much more uncertain than interpretation of changes through time in a single depositional setting, and comparisons made with other Succor Creek sections will be in very general terms.

STRATIGRAPHY

Sucker Creek Formation

The Sucker Creek Formation is in the Owyhee Upland physiographic region of the southern half of eastern Oregon. To the west and south are the northernmost extension of the Basin and Range and the High Lava Plains regions and to the east is the Snake River Plain, Idaho. The Owyhee Upland forms a broad plateau deeply dissected by many streams that drain toward the Snake River.

Stratigraphy

Surface Section in Southeastern Oregon. The Sucker Creek Formation, described by Kittleman et al. (1965), includes volcaniclastic sediments exposed along the general course of Succor Creek, in the vicinity of the Oregon-Idaho border. Kittleman described the type section of 180 m which was extended to about 200 m by Taggart and Cross (1980). The base of the unit is not exposed but Kittleman et al. (1965) estimated a total thickness of about 490 m. The formation lies unconformably beneath the Miocene Owyhee Basalt (equivalent of the Upper Yakima Member of the Columbia River Basalt) in the region of the Owyhee Reservoir and beneath the Pliocene Jump Creek Rhyolite (Kittleman et al. 1965) (equivalent of the Idavada Volcanics) to the east of the reservoir in the area under study.

Subsurface Extension into Southwestern Idaho. Clastic Miocene beds in southwestern Idaho have been considered to represent the Sucker Creek Formation (Shah 1968, Smiley et al. 1975). Outcrops are limited and are separated from Sucker Creek area at the surface by younger rocks in westernmost Idaho. Some authors, while considering the Idaho outcrops equivalent in age and stratigraphic position, mapped them separately as the Payette Formation (Newton and Corcoran 1963). While the outcrops in Idaho are limited, there is evidence from recent wells of an extensive subsurface distribution of the Sucker Creek Formation. Deep test holes in Owyhee County, Idaho (Warner 1977) indicate that Miocene volcaniclastic sediments (assigned to the Sucker Creek Formation) thicken markedly in a short distance north-northeast of the studied outcrops to an estimated 2000 m beneath the western end of the Snake River Plain.

Structural Setting

Miocene. The thickness of the Sucker Creek Formation requires a structural setting that provides for the enormous volume of volcaniclastic sediment and the rapid subsidence of the basin to accommodate up to 2000 m of sediment. The basin axis is interpreted to occur along the line of a rift zone (the Idaho rift) that was developing as a rapidly downwarping graben basin during Sucker Creek time (Warner 1976, 1977). The studied outcrop sections are placed along the southern flank of the basin with the Devils Gate section the nearest of the studied sections to the axis of the basin. Isopach projections indicate that the total thickness of the formation in the Devils Gate area is between 1000 and 2000 m. Alternate interpretations are reviewed by Cross and Taggart (1983).

Pliocene-Pleistocene. In the area of thickest development the Sucker Creek sediments are now deeply buried. The top of the formation appears to plunge to a maximum depth of about 3400 m below sea level along the line of the rift, not more than 50 km from where they outcrop at an elevation of 900 m above sea level. Such displacement indicates substantial post-Miocene downwarping or block faulting along the Plio-Pleistocene rift. In the area of downwarping the formation is overlain by late Miocene rhyolites and Pliocene to recent sediments (Warner 1977).

Age

Radiometric dates have not been successful in clearly establishing the age of the Sucker Creek Formation. An age of about 16 m.y. is tentatively assigned to the sediments, which is consistent with a Barstovian mammal age (Shotwell 1968) and places the formation in the uppermost Early Miocene on the Berggren (1972) Cenozoic time scale.

The radiometric age assignment is based on dates from clastics within the formation and from the overlying basalt. A vitric tuff from the Type section taken 119 m above the base (Kittleman, personal communication to A. T. Cross), is dated at 15.4 m.y. (sanidine) and 18.5 m.y. (glass shard) (Kittleman in Laursen and Hammond 1974). A basalt, thought to outcrop in the vicinity of the Whiskey Creek section, is dated at 16.7 m.y. (K/Ar) (Evernden and James 1964, and written communication to A. T. Cross). Collecting site and stratigraphic relationships of the basalt are unknown. The overlying Owyhee basalt is dated at 14.4 m.y. based on an average of 4 flows (Bottomly and York

1976), 13.1 to 13.9 m.y. on the basis of 16 successive lava flows (Watkins and Baksi 1974), and 24.6, 15.2, and 14.4 m.y. (Kittleman in Laursen and Hammond 1974).

Radiometric dates and macrofossil data indicate an older age for some outcrops east of the Whiskey Creek section. K/Ar dates between 36 m.y. and 22 m.y. and Sr/Rb dates with a mean of 22 m.y. are reported for leaf-bearing tuffs that also have distinctive floral components (Niklas and Gianassi 1978). Preliminary macrofossil data indicate an older age (possibly Oligo-Miocene) for exposures in the Coal Mine Basin now under study by Taggart and Cross.

Devils Gate Section

Structural Setting

The Devils Gate section is exposed in a 7 unit series of *en eschelon* fault blocks (Figure 2, Figure 3, Plate 1). The faults between the blocks extend more or less northwest-southeast. The blocks dip generally from southwest to northwest and the altitude of the strata vary from almost horizontal to about 20°. Internally, the blocks may be warped so that the dip varies across a single bedding plane. The prominent cliff (Unit V, Plate 1), for example, is essentially horizontal on the south end and dips 11° NNW at the north end, indicating that the block has dropped and rotated to the north. Internally, the blocks may also show minor faults that displace a part of the unit as on the south end of Unit V, for example. When erosion occurs along such a fault line, small valleys may develop and displaced portions of a unit may become isolated. These small-scale structural

Figure 2. Summary of measured and sampled units at the Devils Gate locality.

Number of samples collected in each unit, positions of productive samples, bone fragments, leaf and stump horizons and some lithologically distinctive beds are shown (modified after Taggart et al. 1982, fig. 1, p. 539.)

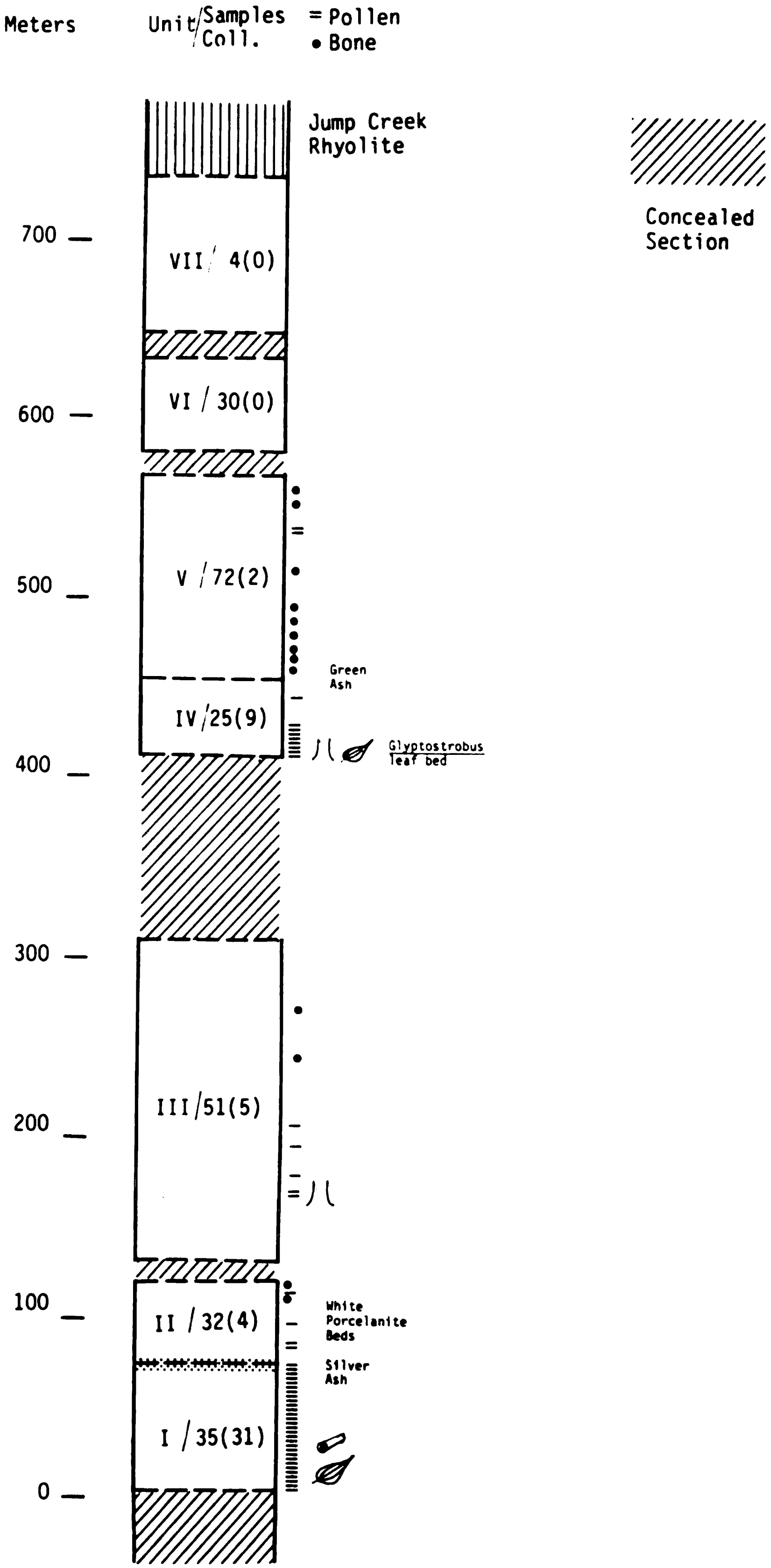

Meters
Unit/Samples Coll.
= Pollen
● Bone
Jump Creek Rhyolite
Concealed Section
700
VII / 4(0)
600
VI / 30(0)
500
V / 72(2)
Green Ash
IV/25(9)
Glyptostrobus leaf bed
400
300
III/51(5)
200
100
II / 32(4)
White Porcelanite Beds
Silver Ash
I / 35(31)
0

Plate 1. View of the Devils Gate locality showing locations of sampled units. Looking west, the Jump Creek Rhyolite caps the section and forms the skyline.

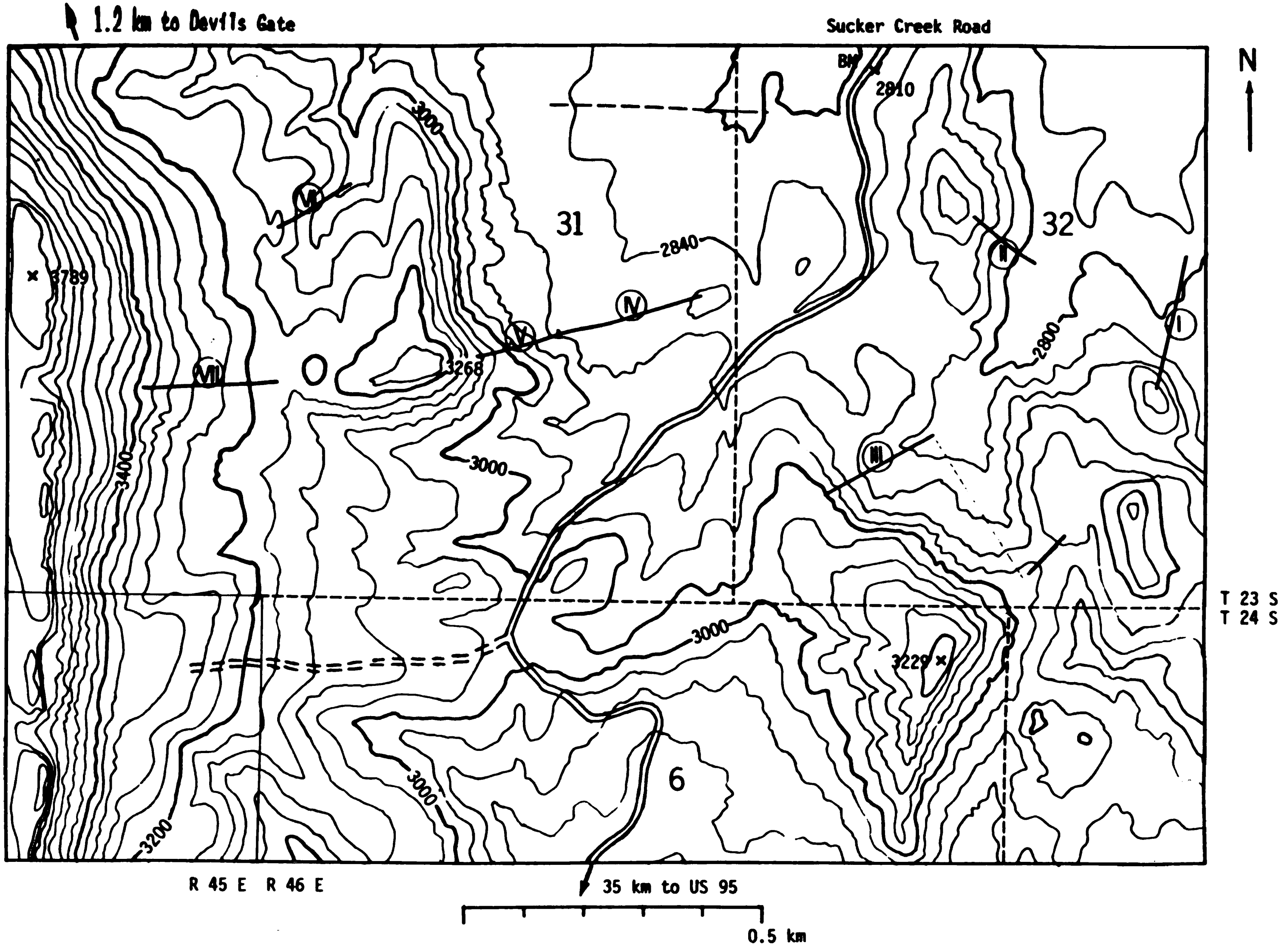


Figure 3. Approximate positions of measured and sampled units at the Devils Gate locality. Enlargement of Sec. 31, Owyhee Ridge Quadrangle and Sec. 32, Graveyard Point Quadrangle--U.S. Geol. Survey topographic maps (1/24,000).

features of the section make it difficult to measure and establish relative positions and stratigraphic correlations of the 7 units.

Lithology

Sediments of the Devils Gate section include massive yellowish-gray to drab-olive volcanic sandstones which often contain pumiceous fragments and glass shards; fine, drab-olive to brown tuffs, buff platy tuffs, white opaline shales, occasional thinly-bedded paludal lignitic shales, and calcareous shales. Both fluvial and airfall volcanic sediments are present. Depositional environments recognized at the Devils Gate site include fluvial, lacustrine, and occasionally paludal.

The more massively bedded, coarse, light-colored, volcanics are relatively resistant to erosion and form bare, low cliffs. Darker, fine, tuffs are poorly indurated and form low, deeply weathered, slopes. The weathered bentonitic clays swell when wet and shrink when dry to give a characteristic granular ("popcorn") surface to the outcrops.

Descriptions of Units

Seven exposed units with a combined thickness of 629 meters have been measured, described, and sampled (Figure 2). Intervening concealed section adds a minimum of 106 meters to the section making a total measured thickness of about 735 meters, perhaps 183 meters less, if a duplicated section is demonstrated as will be discussed later. The units lie on an approximately east-west transect along 1.75 km of northwest trending faulted terrain. The base of the measured section lies to the east. The upper contact is with the overlying Pliocene Jump Creek Rhyolite at the western edge of the area under consideration

(Figure 3 and Plate 1). The sampled units are exposed primarily on east to northeast facing slopes with beds dipping generally northwest to southwest. The measured units are numbered from the base of the section, in the order of their inferred stratigraphic positions. Generalized descriptions of the sampled units will precede a stratigraphic interpretation of the 7 units.

Unit I. The base of Unit I is concealed. The exposed sequence of 74 m faces northeast. It consists of alternating series of dark (brownish-gray and grayish-brown) weathered claystones and siltstones and light (pinkish-gray to pale yellowish-brown) indurated platy claystones and siltstones that weather to an even lighter color on the surface. At about 12 m above the base is a macrofossil zone yielding leaves, seeds, twigs, and fish scales. Throughout several meters of light colored platy beds above the main leaf zone occasional Glyptostrobus fragments are found. Permineralized wood fragments are found weathering out at two levels, about 24 m and 39 m above the base. The uppermost bed of this unit is a distinctive light gray, silvery, poorly consolidated, granular ash (6 m) containing purplish-tinted plant fragments, mostly twigs. Unit I is distinguished in the Devils Gate section by the alternation of deeply-weathering, dark beds and resistant, indurated, platy, light-colored beds. The sequence is mostly fine-grained and is extraordinarily productive of pollen. It appears to have been deposited in an uninterrupted lacustrine setting.

Unit II. The base of Unit II is marked by a massive, light gray, silvery, poorly consolidated ash with lenticular inclusions rich in purplish twig fragments. The bed is apparently indistinguishable from the uppermost bed of Unit I. The measured block is exposed on a southwest- facing slope and is internally faulted with 24 m of repeated section recognized by marker beds. The unit consists of 52 m of non-repeated section. Above the gray ash about 30 m of distinctive white and light- gray opaline shales occur. Within the evenly and thinly-bedded opaline series are found some thin dark earthy sandstone layers. The upper 14 m consists of yellowish-gray to pale olive volcanic sandstones and siltstones which become increasingly pumiceous towards the top. A few bone fragments were recovered in the upper third of the unit. Unit II is distinguished in the Devils Gate section by the basal ash and the white opaline series. This sequence can be traced to the northwest across the Succor Creek road where they are useful in relating Units I and II to the younger units in the section. The basal ash probably represents an airfall. The evenly bedded opaline series appears to be a lake deposit and the overlying volcanic sandstones are mostly fluvial. Only 4 of 32 pollen samples were productive. These occur at irregular intervals through the unit.

Unit III. The base of Unit III is marked by a north trending, steeply dipping, fault plane that juxtaposes Unit III against the white opaline series of Unit II to the south of the measured face described above. The lowest 37 m of Unit III was measured from the fault line in a southwesterly direction across a saddle to a stump horizon. The attempt was made to trace the stump bed along its strike (mostly concealed but inferred horizontal extension) northward across the small valley, using intermittent wood fragments weathered out on the surface to mark its position. In the north end of the valley the (inferred equivalent) wood-bearing horizon was taken as a starting point to continue measuring the section in a west southwesterly direction across a deeply weathered, low slope for 65 m stratigraphically, and up a steeper, less weathered, rock face for another 85 m. The total measured section was 184 m thick. The low slope consists of deeply weathered, banded, olive to olive-brown to yellowish-brown, sandstones and siltstones, some pumiceous, and most poorly indurated. The cliff face comprises a series of light yellowish-gray thickly bedded, volcanic sandstones and siltstones, some flecked with angular fragments of yellow pumice or dark glass shards, and several prominent ledge-forming beds. Bone fragments weather out along the strike of a horizon near the cliff base. The upper series consists of drab yellowish-gray and light olive-gray sandstones and siltstones, often pumiceous. The section is concealed by deep weathering and vegetation to the top of the hill. Apart from some swamp and lacustrine beds in the lower third, most of the unit is probably fluvial. Unit III yielded 5 productive pollen samples from the lower 40 m of section at the stump zone and above.

Unit IV. Unit IV is informally named the "*Glyptostrobus* unit" for the *Glyptostrobus* stump and leaf beds near its base. It is separated from Unit III by an uncertain amount of covered section on both sides of the main road. Unit IV consists of dark, organic siltstones and sandstones, largely concealed by deep weathering on very low slopes. The unit (as estimated) is 55 m thick from the base of the exposed beds below the stump horizon to the base of the green ash series of Unit V.

Unit V. The unit forms a broad cliff that faces approximately east and is clearly seen from the Succor Creek Road. Thickness, measured from the base of the green ash series, to the covered section at the top of the cliff is 116 m. Above the green series (10m), Unit V was measured up the cliff face through a sequence of light-colored, mostly yellowish-gray, volcanic sandstones including two ledge forming horizons (22 m); series of mostly coarse volcanic sandstones often with pumice fragments in colors of dusky yellow and light olive-gray (47 m); and an upper light colored series with persistent ledge forming horizons (37 m). Fossil bone fragments weather out at several levels in the lower third and at one level in the upper third. Only 2 samples of 72, from a zone at about 74 m from the base, yielded pollen. Most of the sediments were apparently rapidly deposited by fluvial processes and are little altered, coarse volcaniclastics.

Unit VI. Unit VI can be seen looking west from the top of Unit V. It is a down-faulted block and the amount of concealed section at the base separating the exposed sequence from the top of Unit V cannot be determined. The outcrop consists of 61 m of volcanic sandstones and siltstones with several ledge forming pumiceous sandstones. It has no distinguishing lithologic features. The top is covered. All 30 pollen samples were barren.

Unit VII. The unit was measured from the covered section in the saddle above Unit VI up to the Jump Creek Rhyolite that unconformably overlies the Succor Creek Formation in the area and forms the prominent ridge across the skyline (Plates 1 and 2). Unit VII is comprised of

88 m of mostly yellowish-brown, coarse volcanic sandstones and siltstones. The four pollen samples were barren.

Stratigraphic Interpretation

Relative stratigraphic positions are reasonably clear in the several blocks of measured section and, for the most part, sampling gaps occur where strata have been buried by down-faulting or where strata are concealed by deep weathering on slopes with low relief. The amount of missing section is uncertain. The major stratigraphic problem is the possibility of repeated section in Units III to V. In the following discussion I will describe the stratigraphic uncertainties in detail and present an alternative Devils Gate section. However, it should be mentioned here, that because of the pattern of occurrence of samples with significant pollen content these stratigraphic uncertainties appear to be of little consequence in the interpretation of vegetation dynamics through Devils Gate time.

Relationship of Unit I and Unit II. In the field, the outcrops of Unit I and Unit II are adjacent with a small valley separating them. The two blocks dip in different directions and beds cannot be traced across the small valley. A stratigraphic relationship of the two adjacent blocks can be reasonably inferred lithologically. The lowest beds in Unit II are lithologically distinctive, including a light gray or silver gray ash bed and overlying white opaline shale series. Such a sequence of beds is found at the top of Unit I, indicating that Unit II is stratigraphically above it. If this is correct, the valley between the 2 blocks may mark the position of a fault line along which the two blocks were vertically displaced, laterally separated, slightly rotated, and eroded, to bring them into adjacent positions with differently dipping beds. (Figure 4).

Repeated Section on Unit II. Where a minor fault has occurred on the face of a tilted block, the faulted portion may have slumped resulting in a repeated sequence of beds. Such a situation is found in Unit II where 28 m of section is repeated. In this case, marker beds, interpreted as repetitive, have been used to make the stratigraphic correlation.

Stratigraphic Position of Unit III. The relative position of Unit III is the most uncertain. The exposed block is bracketed by a major fault plane below and by concealed section above. At the base, a fault plane, which extends approximately northward above the opaline shale beds, juxtaposes Unit III against the eroded (?) surface of the opaline beds of Unit II. A concealed section and possible unrecognized faults occur between the top of Unit III and the Glyptostrobus stump zone at the base of Unit IV. It has not been possible to trace Unit III to the northwest across the Succor Creek Road.

Two independent sets of measurements of the section and lithologic comparisons of Unit III with Units IV and V suggest that Unit III may be repeated in part in Units IV and V in exposures to the north of the road. Although Unit III has not been located west of the road, the lower Devils Gate section (Units I and II) can be related to the upper part of the section (Units IV to VII) by the white opaline series (of Unit II) with its basal silver ash bed. This pair of distinctive

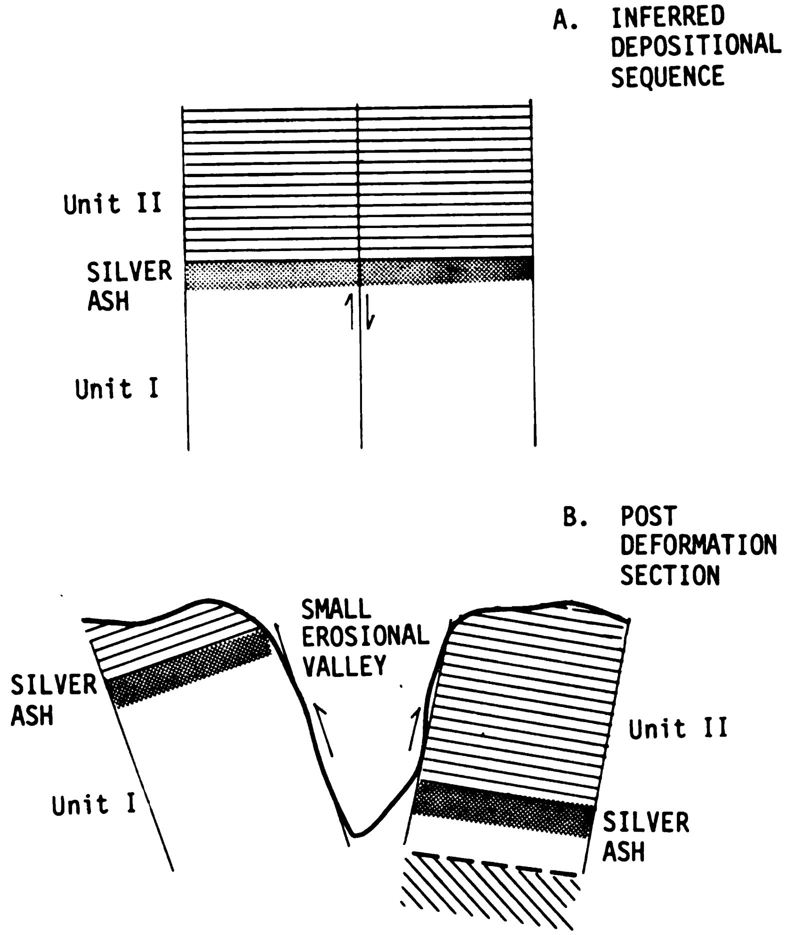


Figure 4. Stratigraphic relationships and present positions of Units I and II.

lithologic units can be traced continuously along the outcrop across the road into the valley below the Glyptostrobus stump zone. This correlation allows a second measurement of the interval between the silver ash bed (base of Unit II) and the Glyptostrobus stump bed (base of Unit IV) at a location several hundred meters north of the section just described (Figure 5). The brunton-pace traverse measurement of 177 m for the section to the north indicates a consistently thinner interval than the measurement of Unit III to the south which is 324 m. This difference of 183 m between the top of the silver ash bed up through the opaline beds to the base of the Glyptostrobus stump layer is too great to be explained by sedimentary deposition.

In these measurements, consideration must be allowed for uncertainty concerning the presence, location and magnitude of concealed faults, changes of dip of strata, and the possibility of repeated section in concealed strata. However, the magnitude of this discrepancy (147 m) and its approximation to the thickness of Unit III (183 m), require an alternate interpretation of the section such as in Figure 5C where Unit III is excluded and is considered to be a duplicate of a large portion of Units IV and V. This interpretation of repeated section based on comparison of the two measured sections is further supported by a lithologic comparison of Unit III with Units IV and V.

Several similarities are found. The two sequences (Figure 6 and Plate 2) have a basal horizon of silicified stumps or logs that outcrop in drab-olive and brown banded, deeply weathered, poorly exposed valley sediments. At about 65 m above the stump zones the two sequences are comprised of prominent cliffs with indurated light-colored, yellowish-gray, coarse, pumiceous sandstones. Both have distinctive

Figure 5. Alternate interpretations of the Devils Gate section.

A. Total measured section Units I to VII.
B. North section between silver ash bed and stump zone.
C. Interpreted section with Unit III equivalent to Units IV-V.

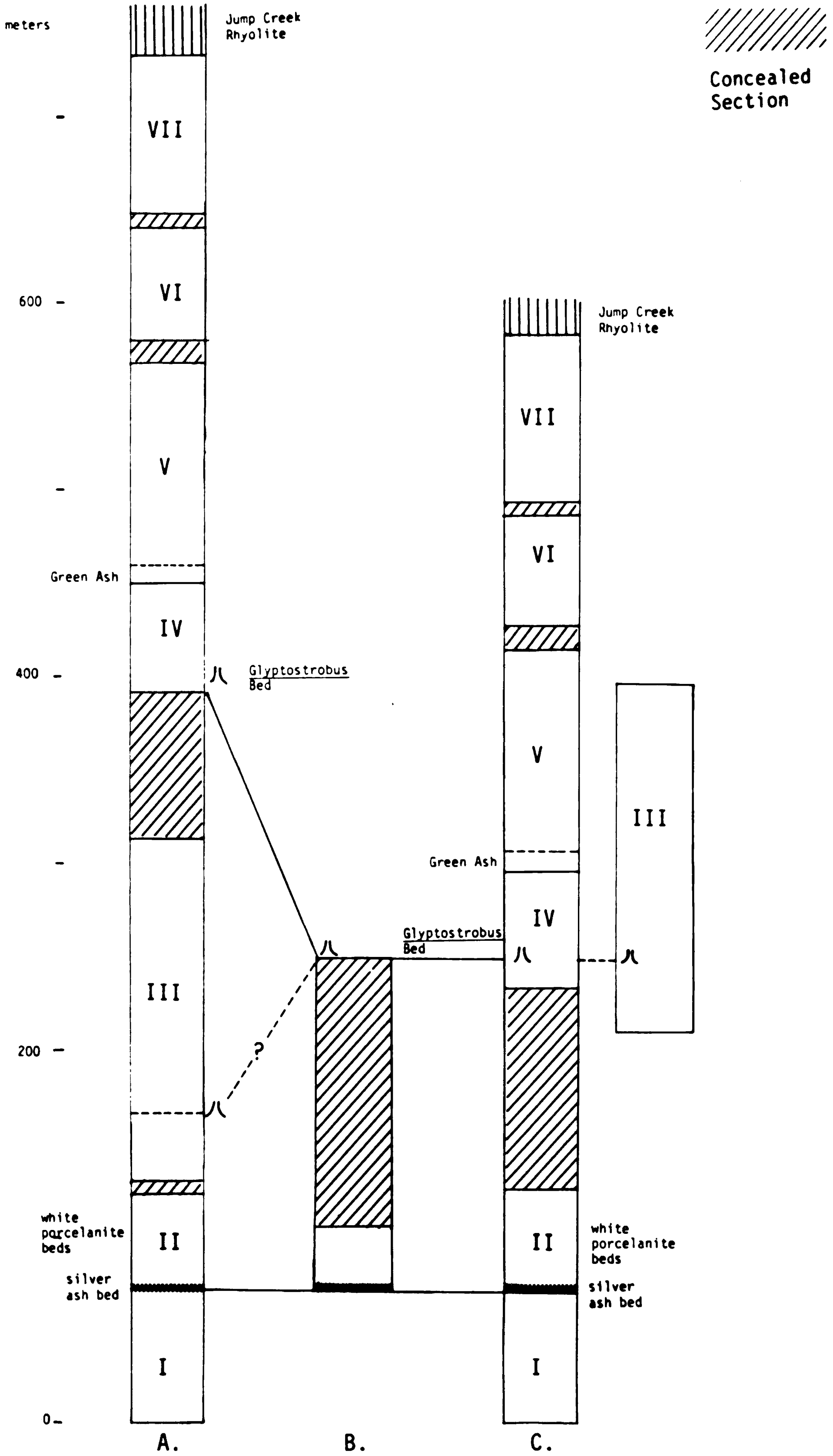

meters
600
400
200
0
Jump Creek Rhyolite
VII
VI
V
Green Ash
IV
Glyptostrobus Bed
III
?
white porcelanite beds
II
silver ash bed
I
A.
B.
C.
Concealed Section

Plate 2. View of Devils Gate Units III, IV, and V. Arrows at right indicate two locations of the stump zone; arrows near center indicate two locations of bone beds and ledge. (See Figure 6 for stratigraphic sections.)

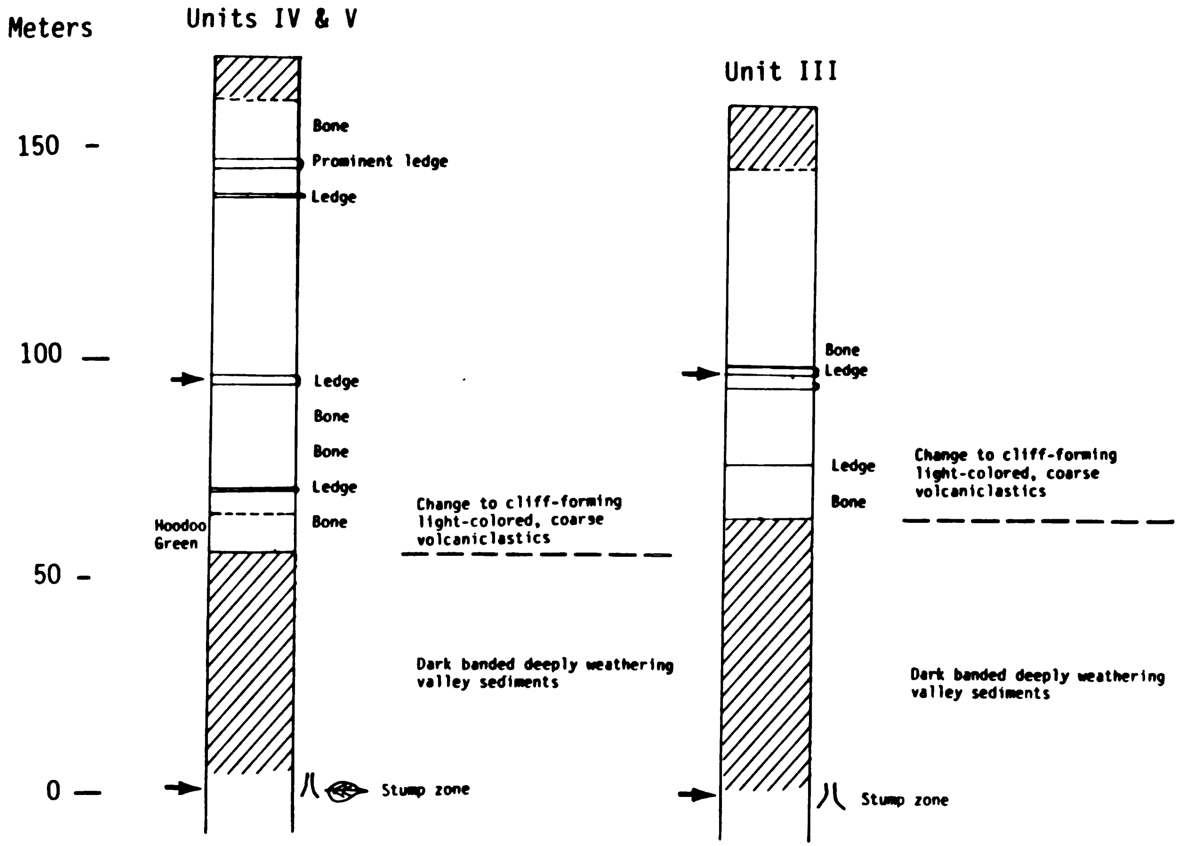


Figure 6. Stratigraphic comparison of Unit III and Units IV-V. Arrows refer to marker beds corresponding to those in Plate 2.

ledges at about 96 meters. Bone beds are present in this part of each sequence.

However, two distinctive features of Units IV-V have not been found in Unit III. One is a Glyptostrobus dominated leaf bed found above the stump zone in Unit IV which may be due to a slight difference in swamp environment between the two locations. The other is a conspicuous lithologic feature well exposed at the prominent Unit V cliff base at about 55 m. Bright green ash beds occur at this level which, as will be discussed later, may have correlative value even beyond the Devils Gate locality. They have not been found in Unit III but since the supposed equivalent horizon is deeply weathered and extensively covered and has been sampled only at intervals where some exposure by digging was successful, there is some possibility of their occurrence in the unit. One green-colored sample of somewhat comparable appearance and lithology was collected from Unit III at 32.4 m.

The palynology of the two units has not produced sufficient evidence to resolve this correlation question. In both sections, the lower beds sampled were deeply weathered and samples were taken only at intervals where less weathering and vegetation cover permitted excavation to sufficient depth to obtain satisfactory samples. Thus, comparable or continuous sets of pollen samples were not obtained and, as demonstrated elsewhere in this paper, pollen assemblages may change markedly in very short vertical intervals through a stratigraphic unit. Nevertheless, two features of the pollen profiles compare favorably. First, the general composition of the mixed forest pollen assemblages is similar in both sets of samples. Second, the composition of both sets of samples are distinctly different from those in the underlying Unit I, particularly in having high abundances of Abies, Tsuga, and Alnus, and in the absence of Lithocarpus. Third, the sequence of pollen assemblages is comparable:

Unit III (m)	Pollen Assemblage	Unit IV (m)
39.9	herb-shrub	32.4
28.8	alder-dominated woody	13.5
12.9	herb-shrub	10.2
0.6	mixed forest (abundant montane conifers)	1.8 to 6.9
0	herb-shrub	0

The consequence of correlating Unit III with Units IV-V is to reduce the total Devils Gate composite section to approximately 445 m (Figure 5C). The following sections on stratigraphic palynology will discuss the attributes of Unit III along with the treatment of the other units. This approach is adopted for the sake of completeness but it should be kept in mind that the evidence for regarding Unit III as a repeated section is persuasive.

Stratigraphic Relationships of Sucker Creek Sections

The four previously published sections (Figure 1) are the Whiskey Creek ("Valley" section of Taggart 1971, Taggart & Cross 1974), Rockville, Shortcut, and Type section (type locality of Kittleman et al. 1965). Their stratigraphic relationships are discussed by Taggart and Cross (1980). On the basis of lithology they fall into three separate depositional settings: Whiskey Creek, Rockville-Shortcut, and Type section. Stratigraphic palynological interpretation indicates that the sections have some overlapping time relationships. This is based in part on similarities in the pollen spectra, particularly the montane conifer element interpreted in a setting of inferred relative topographic positions of the sections with respect to the axis of the basin. A palynologic comparison of the Devils Gate section with previously studied sections is included in later discussion. However, at this point it is appropriate to describe an apparent lithologic similarity between the upper Devils Gate section (Units IV and V) and the Type section that indicates a possible correlation of the two.

Despite the difficulties of correlating Sucker Creek outcrops in the area, the lithologic characteristics of color, texture, and induration of some of these sedimentary rocks are so striking that they allow recognition of unique combinations and sequences which permit correlation with some confidence. Taggart (1971) correlated the Rockville-Shortcut sections across 12.8 km of terrain. This lithologic correlation was later supported by palynologic interpretation of vegetation shifts. The Type section and the Devils Gate section are 10 km apart, a correlative distance that is not unreasonable by comparison with the Rockville-Shortcut correlation. The similarity of the two cliff-forming blocks is apparent from a marker bed of unique lithology, correlative sequential combinations of several distinctive rock units, and their positions relative to the marker bed.

Lithologic Comparison of Upper Devils Gate Units and Type Section

On the basis of lithology (Figure 7), each section can be divided into two parts, separated by the distinctive green ash series that is not recognized at any other level in the two sequences or in any other Succor Creek outcrops studied. In the Type section it is conspicuous at or near the base of the lower cliff face where it weathers to a "hoodoo" type of feature. In the Devils Gate section, the green series occurs at the cliff base but has not been eroded to such conspicuous geomorphic character.

Below the "hoodoo" green beds, dark, relatively fine, thinly-bedded sediments with several prominent lignitic shale zones are present. A stump or wood zone occurs about 50 m below the "hoodoo" green beds near the base of each exposed unit. These sediments form low, deeply-weathering slopes (Type section) and valley floor (Unit IV Devils Gate section) and yield some productive pollen samples.

Above the green beds, each section is well exposed on relatively steep cliffs. Each section is comprised of vari-colored, coarse, volcanic sandstones alternating with light gray volcanic sandstones of angular, pumiceous fragments, and glass shards which generally form resistant ledges. The two cliff sequences (125 m) are barren of palynomorphs. Both sections contain fossil bone fragments. Type section mammalian material has been studied by Shotwell (1968).

In summary, this lithologic comparison is largely made on the basis of the equivalent positions of thick, light colored cliffs with resistant ledges and bone beds, and the equivalent positions of fine, dark, deeply weathered ashes, lignites, and wood zones. In both

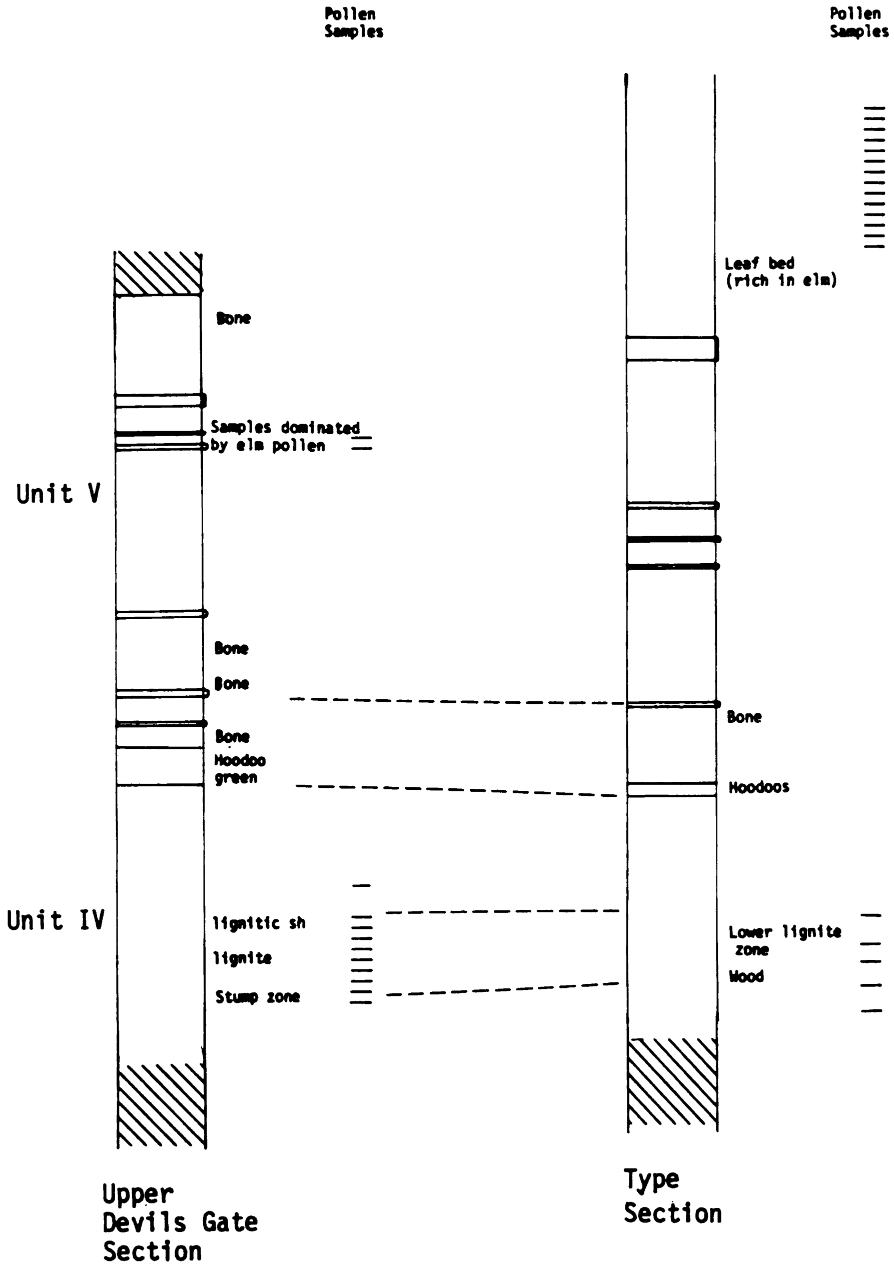


Figure 7. Stratigraphic and paleontologic comparison of the Type section and Devils Gate section Units IV-V.

sections the positions of these beds are established relative to the green beds. Additional support for placing such correlative value on the green beds comes from subsurface wells. Warner (1977) describes a marker bed used in subsurface correlation as a green chloritic ash, the "Green Hornet Ash". This bed occurs above his second marker described as a white porcelanite, the "Snowbird Shale" which fits the description of the white opaline shales of the Devils Gate Unit II. In the "average" subsurface section the green and white beds are separated by approximately 150 m, and in the Devils Gate section they are separated by approximately 200 m.

Summary

This section has presented descriptions of the seven measured units that comprise the sampled Devils Gate section and a stratigraphic interpretation that places Units I and II, and IV to VII in stratigraphic sequence with some uncertainties concerning the amount of concealed section. Unit III is considered to be a repeated section of the main portion of Units IV and V. A correlation of Units IV-V with the Type section is postulated which, if true, would place most of the productive pollen samples at Devils Gate below the Type section. The stratigraphic palynology of the Devils Gate section may therefore represent a valuable extension, in time as well as space, of the study of Succor Creek vegetation dynamics.

THE DEVILS GATE FLORA

This section reports additions to the Succor Creek flora, analyzes some biases in preservation in an attempt to determine the relative importance of some genera in the Succor Creek vegetation, and proposes an emphasis for the reconstruction of the vegetation and climate. The purpose of this floristic and climatic analysis is to provide a setting for interpretation of the stratigraphic changes in pollen assemblages through the Devils Gate section.

Additions to the Succor Creek Flora

Additions to the Palynoflora

The taxonomic study of the Devils Gate palynomorphs (Table 1) added very few pollen genera to the well-studied Succor Creek flora. New pollen records are *Keteleeria*, *Pseudotsuga*, *Fraxinus*, and *Platanus*. All have been previously reported as macrofossils. The other pollen genera were quite abundant and their floristic and ecological significance will be discussed in due course.

Zygospores of an aquatic alga, *Ovoidites* (Zygnemataceae), spores of an aquatic fungus *(Chytridaceae)*, and several acritarchs of unknown botanical affinity are also reported here. They occur together and in only a few samples at Devils Gate but when present are generally very abundant. Descriptions of new forms are contained in the Appendix.

Table 1. Families and genera recognized in the Devils Gate section. S-seed, C-cone, W-wood, L-leaf.

		MACRO-FOSSIL	MICRO-FOSSIL
FUNGI	Phycomyceta		
	Chytridaceae		+
	Imperfecti		+
ACRITARCHS	Undifferentiated		+
	Psophosphaera		+
	Micrhystridium		+
	Sigmapollis		+
ALGAE	Chlorophyta		
	Zygnemataceae		
	Ovoidites		+
	Chrysophyta		
	Botryococcaceae		
	Botryococcus		+
LYCOPSIDA	Lycopodiaceae		
	Lycopodium		+
SPHENOPSIDA	Equisetaceae		
	Equisetum	St, C	+
PTEROPSIDA	Polypodiaceae		+
	Osmundaceae		+
GYMNOSPERMS	Cupressaceae		+
	Thuja?	S	
	Pinaceae		
	Abies		+
	Cedrus		+
	Keteleeria	L?	+
	Picea	L?	+
	Pinus	L	+
	Tsuga		+
	Podocarpaceae		
	Podocarpus		+
	Taxaceae		+
	Taxodiaceae		+
	Glyptostrobus	L, C, W	
	Ephedraceae		
	Ephedra		+

Table 1. (continued)

		MACRO-FOSSIL	MICRO-FOSSIL
ANGIOSPERMS	Aceraceae		
	Acer	L, S	+
	Aquifoliaceae		
	Ilex		+
	Berberidaceae		
	Mahonia	L	+
	Betulaceae		
	Alnus	L	+
	Betula		+
	Carpinus-Ostrya		+
	Corylus		+
	Caprifoliaceae		+
	Chenopodiaceae-Amaranthaceae		+
	Compositae		+
	Artemisia		+
	Eleagnaceae		
	Shepherdia		+
	Fagaceae		
	Castanea		+
	Lithocarpus		+
	Fagus	L	+
	Quercus	L	+
	Hamamelidaceae		
	Liquidambar		+
	Juglandaceae		
	Carya		+
	Juglans		+
	Pterocarya	L, S	+
	Lauraceae		
	Persea	L	
	Malvaceae		+
	Meliaceae		
	Cedrela	S	
	Nyssaceae		
	Nyssa		+
	Oleaceae		
	Fraxinus	S	+
	Onagraceae		+
	Platanaceae		
	Platanus	L	+
	Rosaceae		+
	Crataegus	L	

Table 1. (concluded)

	MACRO-FOSSIL	MICRO-FOSSIL
Salicaeae		
Salix	L	+
Tiliaceae		
Tilia		+
Ulmaceae		
Celtis		+
Ulmus	L, S	+
Gramineae		+
Potamogetonaceae		
Potamogeton		+
Typhaceae		
Typha		+

Additions to the Macroflora

Collections were made from two leaf beds. One bed is a light colored tuff that contains sparse but well preserved leaves and seeds of diverse conifers and angiosperms. The other is a dark, lignitic, bentonitic clay bed that has preserved numerous Glyptostrobus leaf shoots.

Unit I Mixed Leaf Bed.

The leaf bed is found at about 12 m above the base of Unit I (Figure 2 and Plate 1) in a pinkish-gray to pale yellowish-brown tuff. The collection is notable for three features:

1. Additions to the Succor Creek record for the Juglandaceae. Here specimens of Pterocarya (leaf and seed) were found, the only such fossils reported in extant Succor Creek collections. Pterocarya pollen has been reported by Graham (1965) and Taggart (1971). A leaf specimen was cited by Chaney and Axelrod (1959) but it could not later be located (Graham 1965). The leaf collected from Unit I is a fine specimen with seven large, attached leaflets.

2. The assemblage is mixed, with five conifer genera, four broadleaved evergreen genera (Quercus, Mahonia, Cedrela, and Persea), and seven broadleaved deciduous genera (Table 1).

3. Some genera are represented by more than one species. The most diverse genus is Acer with at least 5 species differentiated.

Macrofossil genera are represented by pollen in the same sediment, with only two exceptions, Cedrela and Persea. These are both tropical to warm temperate, evergreen trees, with insect pollinated flowers whose pollen is typically not released and incorporated in the pollen rain.

Furthermore, even when deposited, the pollen of the Lauraceae (including *Persea*), deteriorates rapidly and is generally not preserved.

Unit IV Glyptostrobus Bed. This leaf bed occurs in association with a *Glyptostrobus* stump zone. It contains innumerable *Glyptostrobus* twigs, both sterile and fertile, cones and stems of *Equisetum*, and broadleaved angiosperm leaves which are poorly preserved and unidentifiable and are overlain by *Glyptostrobus* leaves. Leaves are preserved in a volcanic ash mudstone which deteriorates upon exposure. The bed is noteworthy because it is the richest *Glyptostrobus* leaf bed found to date in the Sucker Creek Formation. These sediments also contain the highest percentage of taxodiaceous pollen found in the Devils Gate section (45%). It is apparently the record of a *Glyptostrobus* swamp forest. Graham's collections of 2500 specimens included only 50 of *Glyptostrobus* representing 2% of the flora. His most productive locality yielded only 10%, leading to the conclusion that swamps were a rare development in the Succor Creek setting (Graham 1965).

Contribution to Floristic Analysis

The few new plants recorded here complement previous records but provide little new floristic insight. However, with the addition of this study to the record of the Succor Creek flora, a pattern of co-occurrence of macrofossils and pollen in leaf beds and a pattern of pollen dynamics through time in the Devils Gate section can be to suggest an emphasis for reconstruction of the Succor Creek vegetation.

In the Succor Creek flora (72 gymnosperm and angiosperm genera and families) 28 taxa (39%) are preserved as both macrofossils and microfossils, 25(36%) as macrofossils alone, and 19 (25%) as pollen alone (data from Graham 1965, Taggart and Cross 1980, and this study). The two sets of data are thus complementary and reconstructions of vegetation have been strongly aided by considering both macrofossils and microfossils (Graham 1965, papers by Taggart and Cross).

The flora includes diverse genera of three major physiognomic subdivisions of forest vegetation based on leaf characteristics: coniferous, broadleaved deciduous, and broadleaved evergreen. A comparison of the relative abundances of the physiognomic elements represented by both macrofossils and microfossils in the same beds in Succor Creek localities (Graham 1965) shows that broadleaved taxa, important as macrofossils, are underrepresented by pollen. Broadleaved elements constitute 94% of the total leaf flora and 60% of the pollen flora. Particularly notable is the relative representation of oak leaves (48%) and oak pollen (7%). *Acer*, *Populus*, *Salix*, and *Platanus* are also consistently more abundant in macrofossil assemblages. Other broadleaved taxa are more abundant in pollen assemblages from the leaf beds including *Alnus*, *Carya*, *Celtis*, *Fagus*, *Fraxinus*, *Liquidambar*, and *Ulmus*. As a group the conifers are much more strongly represented by pollen (26%) than macrofossils (6%). In particular spruce leaves and seeds are very rare or absent in the leaf beds where pollen assemblages average 20% spruce.

Interpretation of Inconsistencies of Macrofossil and Microfossil Records

Discrepancy between pollen and leaf representation of a taxon is to be expected because of a large number of obvious factors that differentially bias the record of the two classes of fossils. Factors include differences in production, time and modes of dispersal, modes of transport, and durability of the two classes of fossils. The significance of the discrepant recovery of pollen and leaf fossils is, however, sometimes difficult to assess and interpretations of relative populations in the original vegetation are largely a matter of judgment and intuition. Studies of leaf taphonomy are few (Birks 1973, Spicer 1981) and not particularly applicable to the Succor Creek leaf flora for either leaf types or the depositional setting. In general, studies show that leaf material is transported relatively short distances and indicate that macrofossil assemblages are thus biased strongly towards representation of local vegetation. By contrast, many pollen assemblages are representative of the regional vegetation and their significance on a regional scale is rather well understood on the basis of many studies of temperate forests that show overall good correspondence between a pollen assemblage and the vegetation of a region (Birks and Birks 1980, Davis and Webb 1975, Webb and McAndrews 1976).

In the Succor Creek flora, two genera with discrepant records, the broadleaved evergreen oaks (represented by leaves) and the conifer spruce (represented by pollen), particularly merit evaluation because of their dominance in the Succor Creek fossil record, their dominance of two of the vegetation elements, and apparent ecological disparity.

Previous studies have emphasized the significance of spruce (papers by Taggart and Cross) in the regional vegetation. The following discussion will attempt to support the position that both the oaks and spruce had important roles in the regional vegetation and that zonation was indistinct. The lines of support will include modern studies of dispersal and deposition of the pollen; comparison with the structure of modern, temperate forests in regions where both evergreen oaks and spruces are prominent; and an analysis of the pattern of occurrence of forest elements in more or less contemporaneous Miocene floras of the Pacific Northwest.

Interpretation of the Role of Evergreen Oaks in the Flora. In the Succor Creek leaf beds that yield pollen as well as leaves, evergreen oak leaves are much more abundant than oak pollen (Figure 8). Yet, North American oaks are known as good pollen producers that tend to be overrepresented in modern pollen rain relative to their importance in the vegetation (e.g., Davis and Goodlet 1960, Webb 1974). On this basis an interpretation of the discrepancy is that the oaks were unimportant regionally, that they dominate the leaf assemblages only because they grew on the immediate margin of the basins, and thus that their relative abundance in pollen spectra reflects dilution of a local riparian element in the regional pollen rain. Two factors can be used to argue for more than a limited riparian role. First, the presumed living equivalents of three of the leaf species (*Q. consimilis*, *Q. dayana*, *Q. hannibali*) are not necessarily restricted to riparian or lake margin habitats (Graham 1965) and some have very wide altitudinal ranges. The fourth species, *Quercus simulata*, has uncertain affinities. Second,

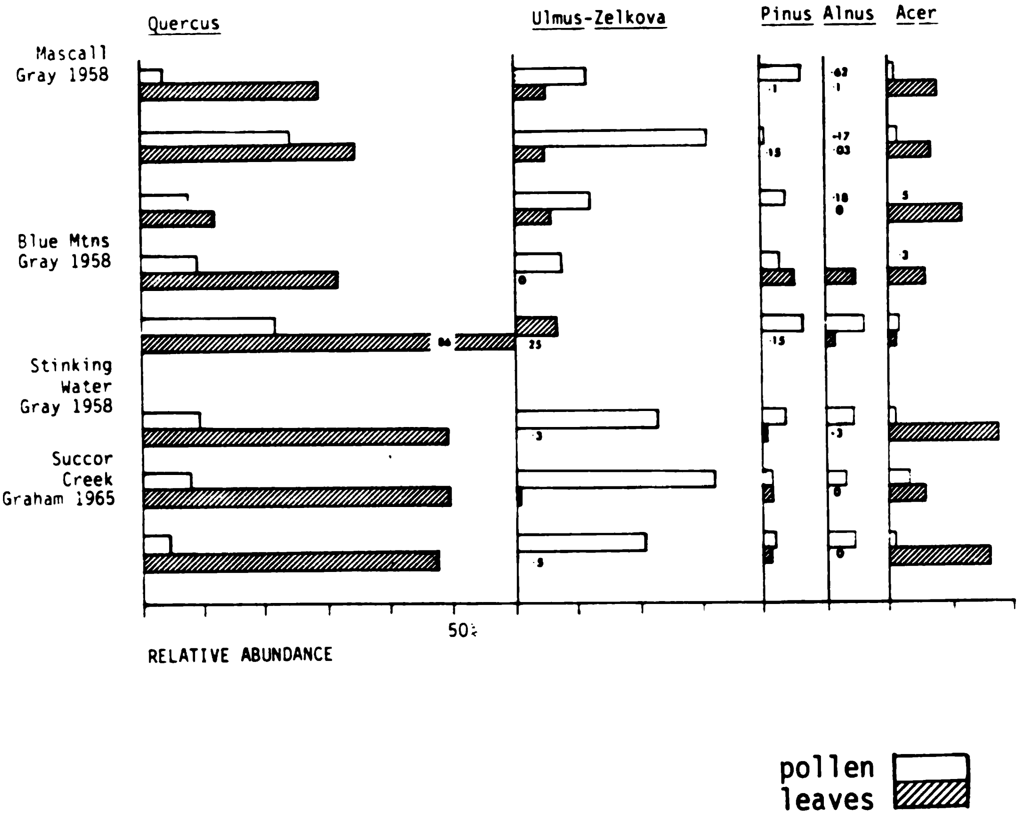


Figure 8. Comparison of pollen and leaf abundances from some Oregon Miocene leaf beds.

three or all four oak leaf species occur at most localities in fairly stable proportions in association with a diverse assemblage of other broadleaved evergreen, broadleaved deciduous and coniferous taxa. The present day setting in which three or four species of evergreen oaks are found together with diverse broadleaved evergreen, broadleaved deciduous and coniferous taxa is in broad regional mixed forests of East Asia (Wang 1961).

An alternative interpretation of the fossil discrepancy, in light of the taxonomic diversity of the Succor Creek oaks and the ecological diversity of their living equivalents, is that they were a regional component of the vegetation that was being underrepresented by pollen in the regional pollen rain. Despite their usual overrepresentation in the North American pollen rain, there is indication from modern studies of pollen underrepresentation in some circumstances.

Pollen is underrepresentative of oak trees in some vegetation types. While overrepresentation is reported for eastern North American studies generally (e.g., Davis and Goodlet 1960, Webb 1974) and for some European studies (e.g., Wijmstra 1978), other European studies show oak and vegetation to be about equally represented (Janssen 1966, Faegri and Iversen 1975). A study from central Taiwan in a mixed vegetation that includes evergreen oaks shows that the pollen was more abundant than oak in that vegetation by a ratio of 1:1.7 (Tsukada 1967). The Taiwan study may be particularly relevant to the problem under consideration because the vegetation and pollen rain is similarly of mixed evergreen oaks, broadleaved deciduous genera, and conifers. It appears that oak is either not necessarily an overproducer or that other factors are operating in some settings to affect its relative abundance in the pollen sum.

There are no studies of the deposition and preservation bias of these entire or serrate margined, coriaceous, evergreen oak leaves in a mixed vegetation. It might be expected that in this mixed flora, these leaves would have distinct advantages in their availability for transport and burial by winter storm, in their transportability, and in burial. Thus one might expect that the fossil leaf/pollen discrepancy would be greater than the tree/pollen discrepancy.

The question of the role of oaks in the flora is not resolved by these observations but they leave open the possibility that disparate representation of oak pollen and leaves in the flora does not necessarily mean a limited local occurrence for the four oak species in a mixed fossil assemblage. The possibility of a regional role will be further supported with discussion of modern East Asian vegetation that have several evergreen oaks in important regional roles in mixed forests.

Interpretation of the Role of Spruce in the Flora.

In this case the discrepancy in the fossil record is the inverse of that for the oaks. Spruce macrofossils are rare in Succor Creek leaf beds. Only a few seeds have been found whereas pollen is consistently abundant (averaging 20%) in the pollen assemblages of the same leaf-bearing beds (Graham 1965). Spruce pollen represents more than 50% of samples in other horizons in the formation and the conclusion has been reached that these pollen abundances reflect an important role for spruce in the regional vegetation removed from the immediate basins (papers by Taggart and Cross). This interpretation is based on modern pollen studies that show spruce pollen abundance to be a fair representation of spruce trees in the vegetation.

Studies of spruce pollen in both moss and lake samples show a general pattern of relatively poor dispersal capacity and some show underrepresentation of the vegetation at local as well as regional levels (Janssen 1966, 1967, Webb and McAndrews 1976. Hicks 1977, Prentice 1978). Webb and McAndrews (1976) found the occurrence of pollen to be generally a good indicator of the regional distribution of spruce in the vegetation in eastern and central North America. But when they compared relative abundances of pollen and trees they found the "relative abundance of spruce trees to be somewhat greater than that of pollen; this fact indicates the general underrepresentation of spruce in the pollen record". Values exceed 20% only in the boreal forest and tundra.

Caution may be indicated in comparing relative abundances of spruce from these modern pollen studies with those in Succor Creek samples because of the substantial difference in the representation of pine pollen. Pine is an associate in modern spruce dominated forests. In pollen spectra from spruce forests pine is the dominant pollen type with the consequence that all other relative abundances (including spruce) are relatively lower. By contrast, pine pollen frequencies are relatively low in the Succor Creek assemblages that show high spruce pollen. Pine was probably not abundant in the Succor Creek forests and consequently less a factor in the distortion of other pollen percentages than it is in the modern pollen spectra. Nevertheless, 20% spruce pollen in evergreen oak leaf dominated sediments (Graham 1965) strongly indicate that spruce was an important regional component.

Other conifers are similarly disparately represented by pollen and macrofossils in the Succor Creek flora. In the Devils Gate section hemlock pollen abundance peaks at 10% and fir pollen abundance at 8%. In modern sediments the pollen of hemlock and fir are even more strongly underrepresentative of their regional contribution to the vegetation than is spruce. Maximum values of fir pollen (20%, mean 1.6%) are found in small pockets in the boreal forest of North America (Webb and McAndrews 1976). Hemlock pollen abundance is highest in pollen spectra from the mixed conifer hardwood forests of eastern North America (maximum abundance 15%, mean 2.4%). These comparisons also suggest important roles for hemlock and fir.

In the mixed forest vegetation of central Taiwan, Picea, Abies, and Tsuga dominate stands 1600 m above an evergreen oak dominated site where lake sediments were sampled for pollen. In this setting total pollen abundance for the three conifers did not exceed 5% (Tsukada 1967). Such evidence lends strong support to the placement of these conifers close to the Succor Creek basins as a regional dominant where their combined contribution may exceed 50% of the total pollen (papers by Taggart and Cross, this study).

The evidence from modern pollen studies supports the interpretation that spruce was a major component of the Succor Creek vegetation at least somewhat removed from the margin of the basins (based on the paucity of fossil seeds in the leaf beds) but not restricted to limited areas of high elevation. Substantial populations of hemlock and fir also occurred regionally. Similarly, they could not have been confined to distant sites of high elevation.

Vegetation Reconstruction

Summary of Characteristics of the Succor Creek Flora

1. The preceding discussion focused on an interpretation of the relative abundance in the Succor Creek flora of two genera that have disparate but important representation in leaf or pollen assemblages and argued for regional roles for spruce and (presumably evergreen) oaks.

2. The oaks were represented by four species of coriaceous, entire, or sparsely serrate-margined leaves. Three or four oak leaf species occur together at most macrofossil collecting localities and apparently were closely associated in life. They are thought to have been evergreen on the basis of the habit of the living equivalents (Graham 1965). However, it should be noted that uncertainties surround this designation. The systematic treatment of entire-margined and irregularly-serrate fossil leaves of three of the genera of Fagaceae is very difficult. Uncertainties surround even the distinction of entire-margined species of *Quercus* from the genera *Lithocarpus* and *Castanopsis* (Graham 1965). Furthermore, the large suite of modern oaks with entire to serrate-margined leaves exhibit a range of habit from evergreen to semi-evergreen to deciduous. In the diverse Mexican oak flora, for example, entire-margined and serrate-leaved types are more commonly deciduous than evergreen.

3. Other evergreen broadleaved trees, shrubs, ground-covers, and vines are represented as macrofossils including: *Castanopsis*, *Lithocarpus*, *Cedrela*, *Oreopanax*, *Arbutus*, *Mahonia* (3 species), *Hiraea*, *Ilex*, and *Anoda*.

4. Diverse deciduous genera occur. Some genera are represented by several species that often occur in the same deposit: *Acer* (6 species), *Betula* (3 species), *Platanus* (2 species), *Populus* (3 species), *Ulmus* (4 species).

5. Diverse conifer macrofossil remains have been found, though their occurrence is mostly erratic, with the exception of *Glyptostrobus*. Conifer genera are: *Glyptostrobus*, *Taxodium*, *Thuja*, *Cephalotaxus*, *Picea*, *Keteleeria*, and *Pinus*. Diverse conifer pollen is found, some types in great abundance: *Abies*, *Cedrus*, *Keteleeria*, *Picea*, *Pinus*, *Tsuga*, *Pseudotsuga*, Taxodiaceae-Cupressaceae-Taxaceae, and *Podocarpus*. *Glyptostrobus* apparently developed locally pure stands in swamp conditions and also occurred in mixed stands on drained slopes.

These characteristics will be compared to modern East Asian temperate forests to suggest a Succor Creek vegetation of mixed physiognomic and floristic diversity where evergreen oaks, diverse broadleaved evergreen and deciduous trees and shrubs, and diverse conifers grew either in overlapping stands or in a blurred mosaic of stands, with an increasingly strong representation of conifers in the regional vegetation at higher elevations.

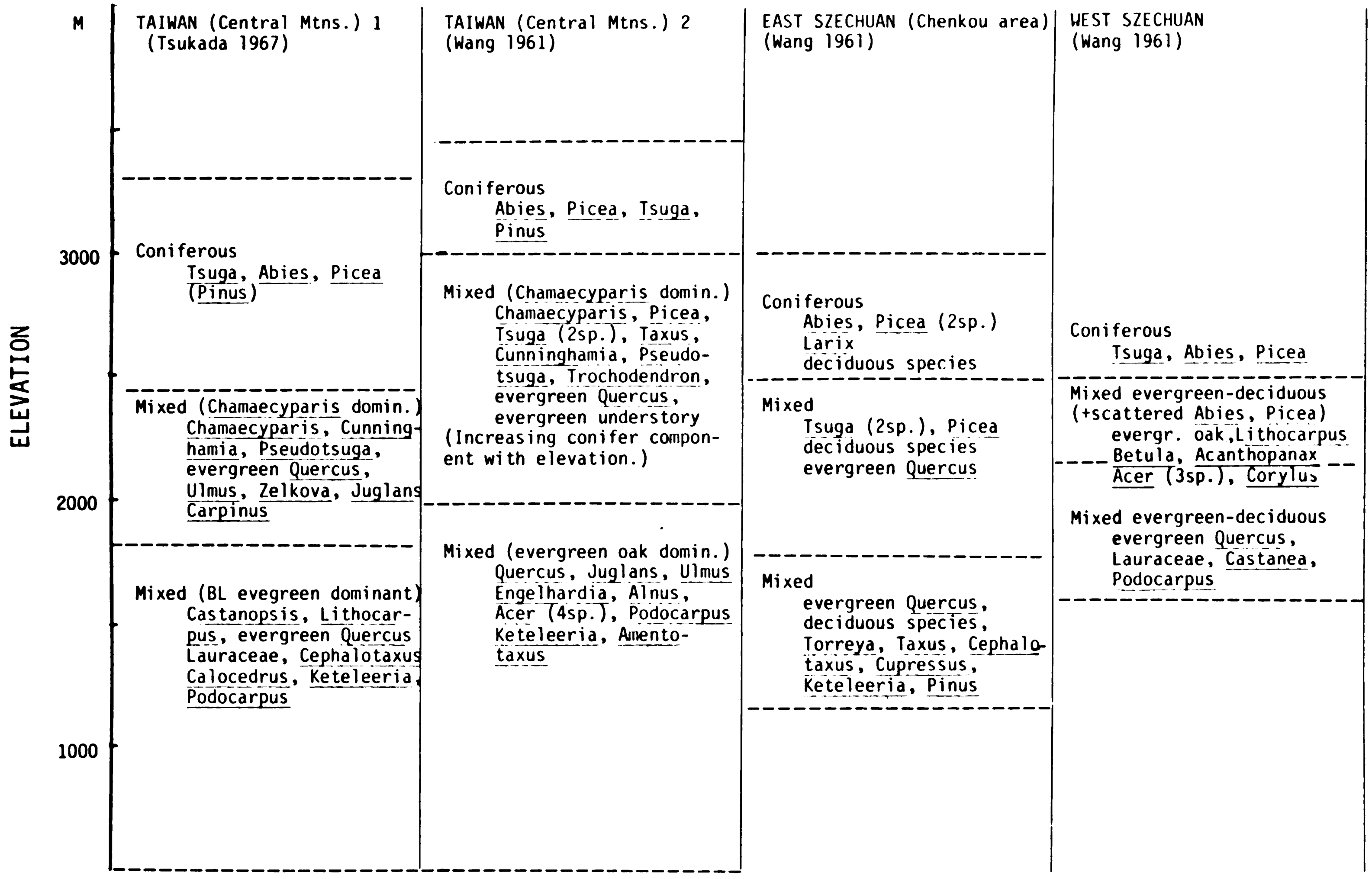
This emphasis differs from Graham (1965) in suggesting the lack of clear zonation of the conifers and an association of broadleaved evergreen and deciduous elements of the flora. It differs from Taggart and Cross (papers) in recognizing the broadleaved evergreen component of the flora and in proposing a significant role for that element at lower elevations in a mixed vegetation. The regional importance of conifers in the Succor Creek vegetation has been cogently stressed (Taggart and Cross 1980, Cross and Taggart 1983).

In the following discussion comparisons will be made with temperate East Asian mixed forests and climate. Then comparisons will be made with some North American forests that show strong floristic similarity to elements of the Succor Creek flora but do not show the association of elements. They provide a test for the proposed reconstruction of the Succor Creek environment by identifying the environmental parameters that causes one element or another of the mixed vegetation to be eliminated. Finally, the discussion will summarize regional trends in the association of broadleaved evergreen and conifer elements of the vegetation of some well studied, more or less contemporaneous Miocene floras in Oregon and Idaho.

Floristic and Climatic Comparisons:

Mixed Temperate Forests of East Asia

The striking feature of temperate East Asian forests is that many associations can be characterized as "mixed", with broadleaved evergreen, broadleaved deciduous, and conifer elements. The floristic composition of each element is largely shared by adjoining forest types and it is only the proportional representation of each element and its position in the forest mosaic that changes (Table 2). Wang's treatise (1961) is used here as the primary source of data on the composition of the mixed forests of China.



TAIWAN (Central Mtns.) 1 (Tsukada 1967)	TAIWAN (Central Mtns.) 2 (Wang 1961)	EAST SZECHUAN (Chenkou area) (Wang 1961)	WEST SZECHUAN (Wang 1961)
Coniferous *Tsuga*, *Abies*, *Picea* (*Pinus*)	Coniferous *Abies*, *Picea*, *Tsuga*, *Pinus*	Coniferous *Abies*, *Picea* (2sp.) *Larix* deciduous species	Coniferous *Tsuga*, *Abies*, *Picea*
Mixed (*Chamaecyparis* domin.) *Chamaecyparis*, *Cunninghamia*, *Pseudotsuga*, evergreen *Quercus*, *Ulmus*, *Zelkova*, *Juglans*, *Carpinus*	Mixed (*Chamaecyparis* domin.) *Chamaecyparis*, *Picea*, *Tsuga* (2sp.), *Taxus*, *Cunninghamia*, *Pseudotsuga*, *Trochodendron*, evergreen *Quercus*, evergreen understory (Increasing conifer component with elevation.)	Mixed *Tsuga* (2sp.), *Picea* deciduous species evergreen *Quercus*	Mixed evergreen-deciduous (+scattered *Abies*, *Picea*) evergr. oak, *Lithocarpus* *Betula*, *Acanthopanax* *Acer* (3sp.), *Corylus*
Mixed (BL evegreen dominant) *Castanopsis*, *Lithocarpus*, evergreen *Quercus* Lauraceae, *Cephalotaxus* *Calocedrus*, *Keteleeria*, *Podocarpus*	Mixed (evergreen oak domin.) *Quercus*, *Juglans*, *Ulmus* *Engelhardia*, *Alnus*, *Acer* (4sp.), *Podocarpus* *Keteleeria*, *Amentotaxus*	Mixed evergreen *Quercus*, deciduous species, *Torreya*, *Taxus*, *Cephalotaxus*, *Cupressus*, *Keteleeria*, *Pinus*	Mixed evergreen-deciduous evergreen *Quercus*, Lauraceae, *Castanea*, *Podocarpus*

Table 2. Temperate mixed forests of Taiwan and Szechuan (China).

Two mixed forest mosaics encompass the broadleaved evergreen and deciduous components as well as all the conifers of the Succor Creek flora. One is dominated by broadleaved elements with a diverse admixture of conifers, except *Picea* and *Abies*. The other is dominated by *Picea* and *Abies* with an admixture of broadleaved elements. Under specific climatic regimes these two mixed associations are juxtaposed and interdigitate.

Broadleaved evergreen dominated mixed forests. Characteristics can be compared in detail with the Succor Creek flora:

1. These forests include evergreen oaks with several species (up to 6), sharing dominance in a particular area. The supposed living equivalent of one of the Succor Creek oaks, *Quercus myrsinaefolia* (*Q. consimilis*) is one of the most wide ranging in this forest type.

2. Many other evergreen taxa are present in this complex with genera of Lauraceae being among the most important.

3. Many of the deciduous genera of the Succor Creek flora are widely distributed in such forests. Some of these genera are notable for having from several to many species growing together. They include the same genera that had several species growing in this Miocene forest (e.g., *Acer*, *Alnus*). Some of the important genera of the Devils Gate deciduous element (e.g., *Liquidambar*, *Celtis*) are actually more common associates of mixed evergreen forest than of a deciduous dominated forest.

4. The forest includes many conifer genera. Wang (1961) lists 4 families and 17 genera in some associations including: Pinaceae (*Cathaya*, *Keteleeria*, *Libocedrus*, *Pinus*, *Podocarpus*, *Pseudolarix*,

Pseudotsuga, Tsuga), Cupressaceae (5 genera), Taxaceae (2 genera), Cephalotaxaceae (2 genera). Pines are rare except on some disturbed sites.

5. Glyptostrobus has a relict occurrence on drained slopes in this mixed association in the hilly regions of Fukien Province together with eight other conifers including Tsuga and Pseudotsuga.

Conifer dominated mixed forests. The mixed forest dominated by evergreen oaks may grade directly into a mixed coniferous forest which is characterized by dominance of conifers particularly Picea, Abies, Pseudotsuga, and Tsuga, while retaining the evergreen oak and laurel component and the deciduous genera notable in the Succor Creek flora (especially genera of Betulaceae, Aceraceae and Ulmaceae). The conifer dominants are the same genera that constitute the conifer pollen component in Succor Creek pollen assemblages (with the exception of Pseudotsuga which has a very poor pollen record). In some areas a transitional zone may be found in which other conifers such as Chamaecyparis and Tsuga, or deciduous genera may dominate (Table 2).

Broadleaved deciduous dominated mixed forests. Broadleaved evergreen and coniferous mixed forests grade into deciduous mixed forests. Included in this category are the "mixed mesophytic forest" (Wang 1961), characterized by its particularly high diversity, and other mixed deciduous forests of lower diversity. The mixed mesophytic forest of East Asia differs from the eastern North American mixed mesophytic forest in having greater physiognomic diversity including diverse broadleaved evergreen oaks and diverse conifers (Wang 1961).

Discussion. Within this mosaic of mixed forests can probably be found close equivalents of the Succor Creek flora and other Miocene forests of the Pacific Northwest. The characteristics shared by the East Asian and Succor Creek forests that have been considered important in this comparison are that several species of evergreen oaks grow together in mixed stands with other broadleaved evergreen genera, diverse broadleaved deciduous genera often with several species of a genus, and diverse conifers, and with gradational change to conifer dominance with moderate change in elevation.

Climate Requirements of East Asian Mixed Temperate Forests

There are several considerations in determining the climatic requirements of East Asian mixed broadleaved-conifer forests.

1. The boundaries of such mixed forests with strong floristic overlap are difficult to establish. Indeed, the mosaic can be viewed as a broad ecotone between the belts of "simple" broadleaved evergreen forest and "simple" coniferous forest. In an ecotonal setting the controlling conditions shift gradually in relation to critical ranges of environmental parameters so that shifts in dominance of broad plant groups within the ecotonal belt reflect small shifts in those parameters across critical limits. Thus any classification scheme for broadly overlapping (ecotonal) mixed forests is necessarily somewhat arbitrary.

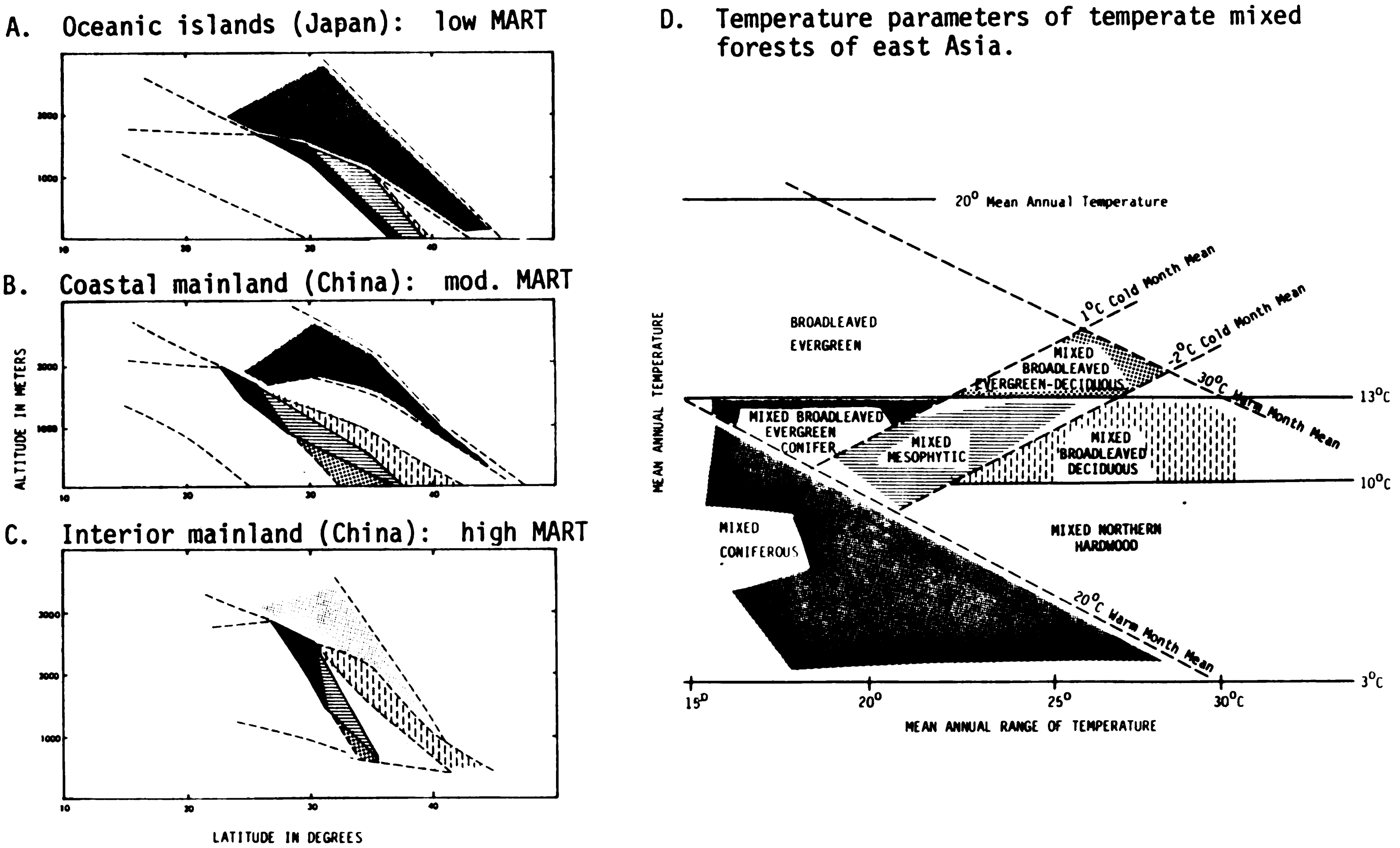
2. Similarly, attempts to delimit the environmental parameters critical to shifts in dominance must involve a degree of uncertainty. Such attempts are particularly difficult in a region such as temperate east Asia where the forest vegetation has been disturbed so extensively

and continuously by cutting and agriculture, and where records of climate data and field study of natural vegetation have been limited.

3. In addition to the limitations of the data base in climate analysis of forest requirements, the question has been raised as to the appropriateness of using recent climatic data to circumscribe forest requirements. Present mature forest composition is the product of eighteenth and nineteenth century conditions since the mean life span of hardwoods is 150 years and of conifers is 300 years (Brubaker 1981). But it is now known that twentieth century climate data, especially from 1930 to 1960, is anomalously warm and atypical of the period of the life spans of existing forests (Brubaker 1981). Thus the floristic composition of present forests may not be in equilibrium with present climate.

Despite these difficulties the results of climate analysis have proved instructive and show trends of value to an understanding of climate and vegetation shifts in the Sucker Creek flora. The available forest data (modified from Wang 1961) and temperature data from temperate East Asia have been compiled by Wolfe (1979) with interesting insights concerning mixed forest associations.

Altitude and Latitude. It is at higher elevations that the mixed assemblages with a strong evergreen oak component are found at the same latitude, adjacent to and interdigitating with mixed conifer assemblages where *Picea*, *Abies*, and *Tsuga* dominate (Figure 9A-C). The broadleaved deciduous component tends to be less widely distributed with increasing elevation. At low elevation, a band of deciduous dominated forest separates mixed evergreen from mixed coniferous forests except in an



A. Oceanic islands (Japan): low MART

B. Coastal mainland (China): mod. MART

C. Interior mainland (China): high MART

D. Temperature parameters of temperate mixed forests of east Asia.

Figure 9. Topographic and thermal fields affecting distribution of temperate mixed forests of East Asia. After Wolfe 1979. (MART - Mean Annual Range of Temperature)

oceanic climate. On the islands of the western Pacific the broadleaved evergreens and conifers intergrade at low elevation (Figure 9A). In the continental interior of China they are adjacent only above 2000 m and are separated by a wide latitudinal belt of deciduous dominated forest at low elevations (Figure 9C).

Temperature. On the Asian continent the parameter that keeps the mixed coniferous forest, the mixed mesophytic forest, and the mixed broadleaved evergreen and conifer forest from descending to low elevation is the mean annual range of temperature (MART). Annual temperature range is lowest in the oceanic climate of the islands and highest in the continental interior. Within the zone of temperate mean annual temperatures it is a high MART that allows expansion of broadleaved deciduous forest (Figure 9D). The broadleaved evergreen component is eliminated in the lower end of the temperature range by winter cold, and some of the conifers (especially Picea and Abies) are eliminated in the upper end of the temperature range by summer heat. In east Asia the areas of dominance of the broadleaved evergreen trees have a mean cold month temperature not less than 1°C. The mixed mesophytic forest with the most equable balance of forest components and highest diversity has a mean cold month temperature of not less than -2°C. Below -2°C the evergreen broadleaved component is eliminated. The mixed coniferous forest is constrained by a mean warmest month temperature of 20°C. Thus, for the two components, broadleaved evergreen oaks and Picea (with Abies and Tsuga) to grow in juxtaposition, the thermal limits of the region encompassing the two are constrained at both ends of this -2°C to 20°C range. This is consistent with the cool, equable temperate climate suggested by Taggart and Cross (papers) and differs from the warm temperature reconstruction of Graham (1965).

Discussion. The striking feature of Wolfe's temperature data is the narrow thermal fields that define the areas occupied by these East Asian forests of mixed broadleaved evergreen, broadleaved deciduous, and coniferous elements. This is reflected in narrow altitudinal and latitudinal ranges (Figure 9). Steep slopes and steep temperature gradients are not needed to move from, for example, a mixed broadleaved evergreen-conifer forest to a mixed coniferous forest. Critical temperature shifts may even be effected by local differences such as the aspect of a slope at the same elevation (papers by Taggart and Cross).

By contrast with the narrow thermal limits and strong overlap of these mixed forests, simple broadleaved evergreen forests and simple conifer forests occupy broad areas on the altitudinal-latitudinal plots (Figure 9) and broad geographic belts. They extend in directions away from critical temperature parameters and are not sensitive temperature indicators until they approach their respective subtropical and subarctic limits of tolerance.

The sensitivity of mixed forests at the thermal limits of each physiognomic element suggests that differences in dominance of elements of the mixed forests of the Miocene should be sensitive indicators of differences in paleotemperature. A problem with this potential tool is that at present the modern vegetation and pollen information are not available that are needed to interpret the relationship between vegetation and pollen in these mixed assemblages. It is thus possible that major shifts in micro- or macrofossil plant assemblages may be erroneously interpreted as reflecting significant climatic shifts. Another problem is that the same shifts in dominance of forest elements can be seen through successional stages following disturbance in modern forests. This study will show that disturbance also caused marked shifts in dominance of forest elements in the Succor Creek vegetation.

Floristic and Climatic Comparisons:

Mixed Temperate Forests of North America

North America has no equivalent of this East Asian forest vegetation today. The mixed mesophytic forest of eastern North America has neither the evergreen oaks nor the high conifer diversity. The mixed evergreen forest of the southeast has two evergreen oaks, a semi-evergreen oak, and a broadleaved deciduous element similar to the Succor Creek flora but lacks the diversity of the broadleaved evergreen element and lacks the conifers with the single exception of pine. The live oak forest of western North America includes several oaks and a few conifers but not the deciduous component. The mixed conifer forest North Pacific coast has diverse conifers including *Picea*, *Abies*, and *Tsuga*, a low diversity deciduous understory, and minor evergreen shrub component, but does not include evergreen oaks.

Mixed Mesophytic Forest. Wang (1961) points out that the eastern North American mixed mesophytic forest is a relatively simple broadleaved deciduous dominated forest and thus unlike the "mixed mesophytic forest" of East Asia or the Miocene forests of the Pacific Northwest in that it lacks both the significant broadleaved evergreen element and the diverse conifers. Wolfe (1979) points out that in being almost exclusively deciduous this forest is anomalous, because the plotted temperature parameters (MAT and MART) for the region should support evergreen oaks. He suggests that it is winter extremes during brief cold snaps, not detected in mean annual temperature data, that eliminate the broadleaved evergreen trees.

Mixed Evergreen Forests. Only two species of evergreen oak occur in southeastern North America along the broad coastal plain and only one is important (*Quercus virginiana*). A "semi-evergreen" species also occurs in the same area, it is deciduous for only a few weeks in early spring. In the southeast and the Mississippi River embayment two mixed associations are found with a broadleaved deciduous component that shows striking generic correspondence with that of the Succor Creek flora.

1. Evergreen oak forest: evergreen oaks, evergreen magnolia, semi-evergreen and deciduous oaks, *Liquidambar*, *Ulmus*, and *Celtis* (Braun 1950, p. 303).

2. Beech-Magnolia forest: evergreen magnolia, evergreen oak, semi-evergreen and deciduous oaks, beech, *Liriodendron*, *Liquidambar*, *Acer*, *Carya*, *Tilia*, *Juglans* (2 species), *Celtis*, *Ilex*, *Carpinus*, *Ostrya*, *Cercis*, *Fraxinus*, *Castanea*, *Prunus*, and *Persea* (Braun 1950, p. 301). Relict stands include two conifers, *Torreya* and *Taxus*.

Locally distributed swamp conifers, *Taxodium* and *Chamaecyparis*, add to the conifer element regionally. Of course, the most striking difference from the Succor Creek flora is the paucity of conifers and the great distance of this lowland plain mixed broadleaved association from elevations where spruce, fir, and hemlock grow. Summer high temperatures on the plain and the lack of elevation where cooler summers would prevail are probably major factors in eliminating the conifers.

North Pacific Coast Forests. The interesting characteristic of these forests is the diversity of conifers including species of *Picea*, *Abies*, and *Tsuga* that are found together in the coast ranges at low elevation and down to sea level near the coast. Near sea level grow the most luxuriant conifer forests in the world with the largest and longest living species of several genera: *Abies* (4 species), *Picea*, *Tsuga* (2 species), *Pseudotsuga*, *Larix*, *Chamaecyparis*, *Libocedrus*, *Thuja*, and *Taxus*, with *Sequoia* in the southern limits of the forest range (Harlow et al. 1975). The broadleaved deciduous element has low diversity of genera, most genera have only one species and its distribution is restricted to wet sites on the coast (Franklin and Dyrness 1973, Daubenmire 1978). Genera include *Acer*, *Alnus*, *Fraxinus*, and *Populus*. The broadleaved evergreen component is limited to understory shrubs including *Arbutus*, *Berberis*, and *Rhododendron*, and the ground cover *Mahonia*.

This conifer dominated mixed forest grows in a region where the temperature parameters are approximately the same as in the mixed evergreen-coniferous forest of East Asia (Wolfe 1979). It is believed that the precipitation regime involving limited summer rainfall is the major factor in conifer dominance and broadleaved restriction (Waring and Franklin 1979).

In conclusion, these modern forest comparisons suggest that East Asian temperate forests of mixed broadleaved-conifer elements may be more useful than any North American temperate forest for interpreting the Succor Creek flora and climate.

Floristic and Climatic Comparisons:
Miocene Mixed Forests of Oregon and Idaho

Miocene floras of Oregon and Idaho that are considered more or less contemporaneous with the Succor Creek flora show a pattern of dominance of each mixed forest that helps to place the Succor Creek flora in a dynamic mixed regional forest mosaic. Along a west to east transect a trend can be inferred from broadleaved deciduous dominance (presumably at low paleoelevation in central Oregon) to mixed broadleaved-conifer dominance with increasing conifer abundance and diversity, and increasing representation of evergreen oak (presumably at higher paleoelevation in southeastern Idaho).

Mascall, central Oregon (Gray 1958, Chaney and Axelrod 1959). These Columbia Plateau leaf localities to the west of the Succor Creek area have lower conifer pollen abundance than Succor Creek, with *Picea* not exceeding 9%. The deciduous component is much more abundant and includes deciduous lobed oaks. It is interesting to note, within the Columbia Plateau localities, an apparent correlation of abundance of evergreen oaks and spruce. In Gray's studies (1958) of 4 localities in the Mascall and Blue Mountains floras, the two with the highest percentage of evergreen oak leaves (17% and 28%) show much higher spruce pollen (8% and 9%) than the deciduous dominated localities.

Trout Creek, southeastern Oregon (Graham 1965). The evergreen oaks are even more important than at Succor Creek (63% of the macrofossil flora) and they occur with a more abundant and diverse suite of conifers. Four species of oaks occur together and are the four most abundant leaf types in the flora. *Quercus consimilis* is by far the most important oak at Trout Creek and its presumed modern equivalent, *Q. myrsinaefolia*, is one of the most widespread in the East Asian mixed broadleaved-conifer forests today (Wang 1961). These oaks occur with diverse deciduous trees and shrubs similar to those at Succor Creek. This stronger dominance of evergreen oaks occurs with a more diverse suite of conifers than at Succor Creek (8 genera and 10 species including 3 species of *Picea*), although abundance is low (2.5%). No productive pollen samples have been recovered to date.

Trapper Creek, southeastern Idaho (Axelrod 1964). Conifer macrofossil representation is high (30%) and the most diverse of the floras considered here (10 genera and 17 species). Evergreen oaks dominate the macrofossil assemblages (53%) with *Q. consimilis* overwhelmingly dominant (50%). The conifer assemblage includes 5 species of *Abies*, 2 species of *Picea*, 2 species of *Pinus*, and 2 species of *Pseudotsuga*. A pollen sample from one leaf horizon has yielded high *Abies* pollen (11%) and *Picea* pollen (8%) (unpublished data).

It is in the mixed broadleaved evergreen-coniferous forests where *Quercus myrsinaefolia* is most important and widespread and where conifers are most diverse (Wang 1961). Further pollen studies of the flora may clarify the role of broadleaved elements and particularly *Q. consimilis* in the Trapper Creek area. The diversity of the coniferous element and the abundance of _Q. consimilis_ may allow the interpretation of a mixed conifer-broadleaved forest.

Discussion. The vegetation trend, along a west to east transect, is from broadleaved deciduous dominance (Mascall) to mixed broadleaved evergreen-deciduous-conifer forest dominance (Succor Creek and Trout Creek) and to conifer dominated mixed forest (Trapper Creek). A pattern in physiognomic composition can be suggested for these Miocene mixed floras. Macrofossil assemblages in which abundant, presumed evergreen oaks occur also have diverse conifers and abundant conifer pollen, particularly of _Picea_. On the other hand, assemblages in which broadleaved deciduous taxa dominate have low abundances of evergreen oaks and conifer macrofossils and pollen. The highest diversity of conifers is found together with the highest abundance of evergreen oak in the Trapper Creek flora. This trend lends support to the interpretation that both the broadleaved evergreens and diverse conifers may have had regional dominance and may have been juxtaposed in the regional forests as in East Asian temperate forests of mixed physiognomy.

Summary

In this vegetation analysis patterns of occurrence of macrofossils and pollen have been used in a complementary way to characterize the Succor Creek vegetation. The characterization has emphasized the physiognomic diversity of the vegetation with a strong conifer component growing in proximity to, and possibly interdigitated with, broadleaved evergreen and deciduous elements. It has considered the flora as a whole but has been based primarily on the patterns of occurrence and abundance of plant fossils that are found repeatedly at the localities that preserve both leaves and pollen. The next section will present the stratigraphic changes in composition of pollen assemblages of the Succor Creek flora at the Devils Gate locality. The reconstruction of Succor Creek vegetation made here and the modern mixed broadleaved-conifer forests with which it is compared will be used as a basis for the interpretation of stratigraphic shifts in Succor Creek pollen assemblages.

STRATIGRAPHIC PALYNOLOGY

Of the 250 samples that were collected and macerated, 53 samples were sufficiently productive to justify quantitative pollen analysis. Productive samples occur at intervals through the lower 450 m of section Figure 2) however 31 of the 53 samples are found in continuous sequence in the lowest 67 m of Unit I. All samples from the top 380 m were barren (upper Unit V, Unit VI, and Unit VII). This section describes the stratigraphic changes in pollen assemblages through continuous and discontinuous sequences and interprets the pollen dynamics in terms of vegetation changes and possible causal factors.

Description of the Continuous Sequence Unit I

Unit I, lowest in the Devils Gate section, produced a continuous pollen record through 31 consecutive samples and 67 m of section. A distinctive, poorly indurated, silver gray, vitric ash bed above sample 31 is barren. A sample from the top of the ash bed contains a low concentration of palynomorphs of distinctly different composition from those in the 67 m continuous sequence below it.

In analyzing the quantitative data it was immediately apparent that the pollen assemblages were quite variable throughout, changes in individual taxa were complex, and patterns obscure. In an attempt to reveal patterns, pollen assemblages have been organized into the broad physiognomic plant groups that have proved helpful in characterizing the vegetation. Pollen groups were organized as follows.

Trees and Shrubs

Conifers - 3 groups

1. Saccate types (less Pinus): Abies, Cedrus, Keteleeria, Picea, Tsuga, Podocarpus.
2. Pinus.
3. Taxodiaceae-Cupressaceae-Taxaceae complex.

Broadleaved - 2 groups

1. Quercus: assumed to be mostly evergreen oaks on the basis of leaf analysis.
2. Other broadleaved trees and shrubs: mostly deciduous.

Herbs and Shrubs

Chenopodiaceae-Amaranthaceae, Compositae, Gramineae, Malvaceae, and Onagraceae.

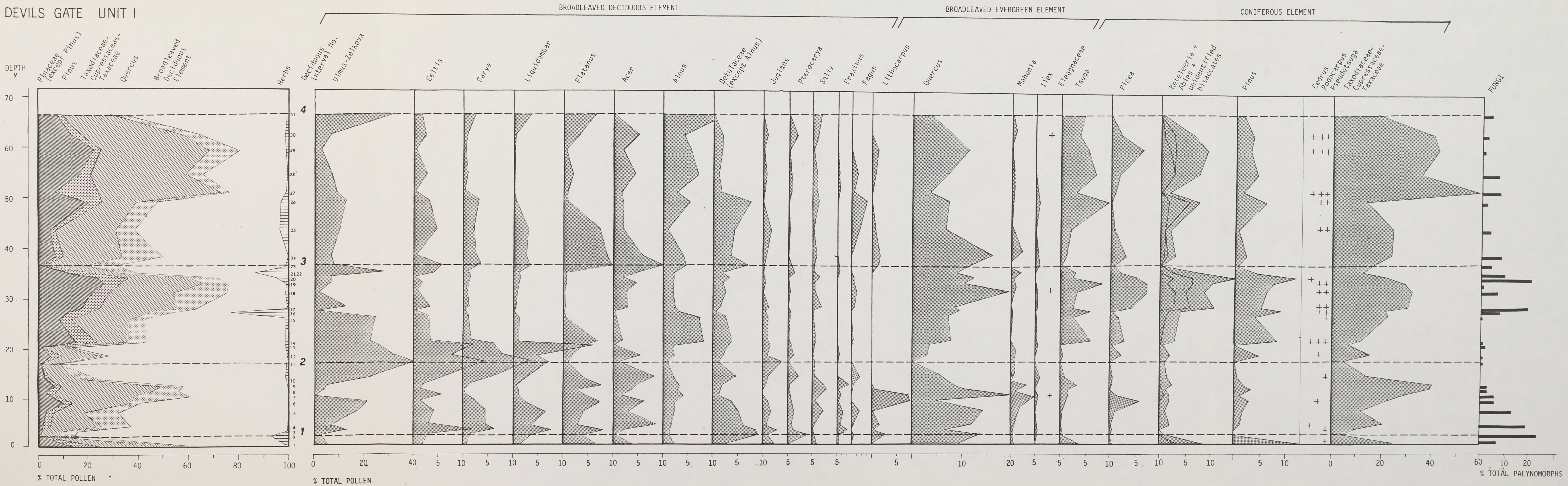
General Patterns

When the data are organized in this manner and presented graphically, a striking pattern is apparent (Figure 10A). Four assymetric shifts in the composition of pollen assemblages occur followed by more gradual changes. The pattern of change within each of the four fluctuations is similar, involving oscillations in dominance of the tree and shrub groups. The shift involves:

1. A sudden decline in the conifers at the same time as the broadleaved deciduous group becomes strikingly important. The decline to minimum conifer values occurs through an interval of 2 samples in each cycle.

Figure 10. Pollen diagram from Unit I.

DEVILS GATE UNIT I



2. This sudden shift to deciduous dominance is followed by a steady return of the conifers to levels with fairly equitable representation of all groups. The return of a mixed assemblage occurs through an interval of 7 or 8 samples in each cycle.

3. The most balanced representation of each major element occurs immediately before each sudden shift to deciduous dominance. After the shift, the conifer groups are each reduced by at least 50%, Quercus is reduced, and the broadleaved deciduous group constitutes the balance (Table 3A).

A dramatic shift away from this vegetation oscillation occurs above the barren silver ash at the top of the section. The uppermost shift is from tree groups to the herb and shrub group (Table 3B).

1. Conifers, oaks, and other broadleaved trees are all reduced, together totalling only 6% of the pollen.

2. Pine increases to 20% of the total pollen.

3. Composites and Cheno-Ams overwhelmingly dominate (78%) the pollen assemblage.

Dynamics of Individual Taxa

This summary diagram of the dynamics of the broad groups provides a perspective for looking at the dynamics of individual taxa (Figure 10B).

Broadleaved Deciduous Group. Individual taxa in this group have brief but striking intervals of dominance. The pattern is more or less repeated in each succeeding interval. Ulmus-Zelkova (elm[1]) is the

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[1] Although these two genera were not separable on the basis of pollen, I will commonly refer to this pollen type as "elm" due to the abundance of Ulmus leaves relative to Zelkova in the macrofossil record.

Table 3. Composition of pollen assemblages from selected levels in the Devils Gate section.

A. Comparison of mixed broadleaved-conifer forest and overlying deciduous- dominated assemblages. Relative abundance is expressed as percentage of total pollen.

	Mixed	Deciduous	Mixed	Deciduous
	Level 19	Level 21	Level 29	Level 31
Conifers[1]	27	13	22	7
Pinus	8	4	3	2
TCT[2]	30	13	43	19
Quercus	11	8	12	4
Broadleaved deciduous	23	48	19	65
Herb-Shrub	1	13	1	3

B. Comparison of forest (level 31) and overlying herb assemblage (level 32) separated by barren ash bed.

	Forest	Herb-Shrub
	Level 31	Level 32
Conifers	7	1
Pinus	2	20
TCT[2]	19	1
Quercus	4	3
Broadleaved deciduous	65	1
Herb-Shrub	3	74

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[1] Saccate conifers except pine: Abies, Cedrus, Keteleeria, Picea, Tsuga, Podocorpus.

[2] Taxodiaceae-Cupressaceae-Taxaceae complex

most important pollen type in each deciduous interval. It peaks early (21% to 42%) and declines rapidly from dominance with subsequent low values of 2% to 7%. _Celtis_, _Carya_, and _Liquidambar_ follow a similar course to elm. _Platanus_ and _Acer_ lag a little in the two lower deciduous intervals. In the two higher intervals they peak earlier and with higher percentages, partly replacing elm, _Celtis_, _Carya_, and _Liquidambar_ in the assemblages. The Betulaceae (other than _Alnus_) are particularly important in the first and third shifts. _Alnus_ is more important in the second and fourth shifts. _Ulmus_-_Zelkova_ is always the most abundant pollen type in deciduous intervals while the abundance of the other deciduous genera vary. The five most important genera in each deciduous interval are:

Interval 1: Elm (21%), _Celtis_, _Acer_, Betulaceae (excluding _Alnus_), _Liquidambar_
Interval 2: Elm (42%), _Liquidambar_, _Carya_, _Celtis_, _Alnus_
Interval 3: Elm (28%), _Platanus_, _Acer_, Betulaceae
Interval 4: Elm (32%), _Alnus_, _Platanus_, _Liquidambar_

Conifer Groups. Each conifer group shows its lowest abundance coincident with the peaks of deciduous types and all the conifer groups subsequently increase steadily to a more or less coincident peak. However, the peaks of importance of individual conifer taxa do not coincide, nor do they follow the same sequence through each interval. Overall, _Tsuga_ and _Pinus_ curves show closest correlation. The section shows some alternation between the importance of _Tsuga_ and _Picea_. The diversity of the conifers increases in direct proportion to their total abundance. Small numbers (less than 1%) of *Pseudotsuga*, *Cedrus*, and *Podocarpus* occur in the samples with high conifer pollen abundance.

Quercus. Like the conifers, the dynamic pattern for oak is different in each sequence. While the trend is not as clear, it tends to peak with the conifers and to fluctuate inversely with the broadleaved deciduous element. Like all other taxa, the curve is smoothest in interval 2, peaking with *Tsuga* and the TCT group and immediately before the other conifers.

Herbs and Shrubs. Three peaks of dominantly herbaceous and shrubby types occur. Those peaks show no obvious correlation with the dynamics of tree and shrub groups.

Details of Patterns in Each Deciduous Interval. The vegetation shifts to deciduous dominance are dramatic, abrupt, and very similar in pattern. The subsequent changes towards mixed assemblages are gradual and are also more or less similar in each sequence. While the overall pollen changes are strikingly repeated through the sequence the details of change through each interval have some distinct features.

The first deciduous interval is unusual in that elm is not the first deciduous pollen type to peak although it is still the most important taxon. Betulaceae, with smaller amounts of *Juglans*, *Pterocarya*, and *Fagus* peak first, followed by *Celtis*, *Carya*, *Liquidambar*, and *Platanus*. The curves for some taxa are smooth (elm, Betulaceae, *Carya*) but other taxa oscillate through the interval. Peaks of these deciduous types alternate with peaks of oak and various conifers (Picea, Pinus, and Tsuga). Strong peaks of Lithocarpus (10%) and Quercus (23%) coincide. The third interval is somewhat like the first in showing oscillations of some types (Quercus, Celtis, Acer, Alnus, other Betulaceae). The second interval begins with the most dramatic expansion of deciduous types and the smoothest sequence of changes through it. The interval is marked by the virtual absence of Fagus, Lithocarpus, and Fraxinus. They return in the third interval. The vegetation change following the fourth shift to deciduous dominance is aborted after one sampling interval. This is the last of a continuous pollen record through 31 samples. The sequence is terminated by the silver ash bed that caps Unit I. The fourth interval is marked by the relative importance of Alnus (15%).

Descriptions of the Devils Gate Units II to V

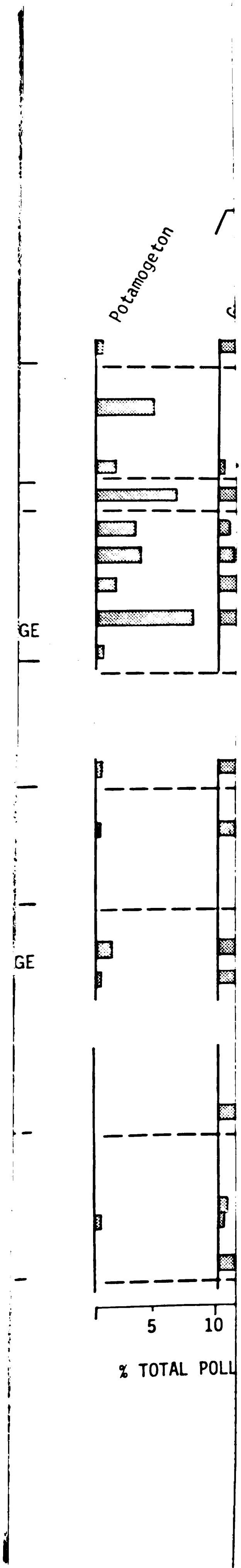
Above the continuous pollen record of Unit I, 550 m of strata sampled continuously throughout, yielded only 21 pollen rich samples at irregular intervals through Units II, III, IV, and V and only one short continuous sequence comprised of 6 samples in Unit IV (Figure 11).

Continuous Sequence (Unit IV)

The continuous pollen record of 6 samples occurs through 7 m of section that also contains a stump zone, a Glyptostrobus leaf bed, and an aquatic palynomorph assemblage stratum. The lowest sample (level 42) yielded a herb and shrub assemblage. Above it is a mixed forest pollen assemblage with high conifer representation (35% conifers including 10% Tsuga and 8% Picea), 6% oaks, and diverse broadleaved deciduous taxa.

Figure 11. Pollen diagram from pollen sequences from discontinuous sample levels in Units II to IV.

As discussed in the stratigraphy section, Unit III quite probably repeats Unit IV.


Potamogeton
GE
GE
5
10
% TOTAL POLL

In the next two samples TCT expands relative to all other pollen groups, followed by a shift back to a forest assemblage of mixed elements including 45% conifers (exclusive of the TCT group). Earlier high frequencies of Betulaceae (excluding Alnus), Acer, and Quercus occur before the TCT increase. Pollen peaks of Pterocarya, Platanus, and Liquidambar follow the TCT dominated samples. Finally an abrupt shift to deciduous dominance with an expansion of herbs, particularly grass (7%) occurs before the sequence is terminated by a 3 m stratum of barren sediment. This deciduous interval shows strong representation of Liquidambar (14%), Platanus, (7%), Ulmus (6%), and Pterocarya (5%).

Some differences in composition of the pollen assemblages of forest vegetation between this sequence and Unit I are noted (Table 4). Pinaceae conifers are much more important than at any level in Unit I. Abies and Tsuga are dominant relative to Picea and Keteleeria. Dominance within the broadleaved deciduous group has also changed. Alnus, Liquidambar, Pterocarya, and Platanus are more abundant than in any sample through Unit I. Ulmus-Zelkova and Carya are much reduced and Fraxinus is rare. Quercus is less abundant and Lithocarpus was not identified at any level.

Disjunct Samples (Units II, III, and IV)

Apart from the Glyptostrobus sequence all samples through Units II, III, and IV are separated by barren sequences. The pollen record represents two distinct floristic assemblages:

1. Herb-shrub assemblages. Herbs and shrubs range from 70% to 85% and pine from 10% to 20%. Cheno-Ams and composites dominate.

Table 4. Comparison of the composition of the mixed broadleaved-conifer pollen assemblages of Unit I and Unit IV. (The two levels were selected for having the highest conifer abundances in each sequence.)

	Unit I Level 20	Unit IV Level 47
Saccate Conifers (- *Pinus*)	24	45
Abies	(2.5)	(10.2)
Cedrus	(2.8)	(0)
Keteleeria	(4.6)	(0.4)
Picea	(5.6)	(3.3)
Tsuga	(2.5)	(6.9)
Undifferentiated bisaccates	(6.3)	(21.2)
Pinus	13	4
TCT[1]	24	14
Quercus	12	2
Broadleaved deciduous	22	32
Alnus	(2.1)	(8.8)
Carya	(1.4)	(0.4)
Liquidambar	(1.4)	(7.0)
Platanus	(0.7)	(7.3)
Pterocarya	(0.4)	(5.5)
Ulmus-*Zelkova*	(7.0)	(5.9)
Herb-Shrub	5	3

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[1] Taxodiaceae-Cupressaceae-Taxaceae Complex

2. Deciduous dominated assemblages. They contain 50% to 90% deciduous taxa and differ from the deciduous dominated intervals in Unit I in being more strongly dominated by one pollen type. In Unit II, as in Unit I, the dominant is elm (45% and 77%) with strong representation of *Celtis* (5% and 12%). In Units III and IV *Alnus* is the overwhelming dominant with 25% to 80% abundance, with elm 1-2%, *Celtis* 0-2%, and *Carya* less than 1%. This deciduous assemblage occurs above a herb-shrub assemblage at 4 levels, though always with intervening barren ash beds. An assemblage intermediate between the herb-shrub and deciduous tree dominated assemblages occurs in sample 36 with 70% herbs, 10% pine, and 20% deciduous pollen of elm, *Celtis*, *Carya*, and *Liquidambar*.

Patterns of Occurrence of Other Palynomorph Groups

Fungi. The abundance of pigmented fungal spores is variable through the Devils Gate Section (0 to 41% of total pollen and spores), nevertheless a pattern in evident. Fungal spores tend to be much more abundant in herb dominated assemblages than in forest assemblages. Through Units II to V, is herb assemblages the mean is 15% fungi (range 0-41%, n=10), and in forest assemblages is 1.6% (range 0-5%, n=9). Through the forest dominated Unit I the mean is 6.5% fungi (n=31).

Aquatics.

1. Unpigmented aquatic fungi. Unpigmented spores of the aquatic family Chytridaceae (Phycomycetes) occur in strong pulses in levels dominated by aquatic assemblages.

2. Algae. Through Unit I small numbers of algae (less than 2%) are found. Through the higher units surges of abundance of Ovoidites are recorded at 5 horizons (11% to 54%). This is a green alga of the family Zygnemataceae. Other thin walled, psilate, spherical algal cysts (2% to 23%), and acritarchs are also found.

3. Potamogeton. Pollen peaks of Potamogeton, a submerged aquatic angiosperm, coincide with peaks of occurrence of spores of green algae and aquatic fungi.

These aquatic assemblages occur in the stump zone of Unit III, in the stump zone and in two higher levels of Unit IV, and at the only productive horizon in Unit V. They occur in strata overlying sediments dominated by herb assemblages.

Ferns. Through most of the section fern spores are neither diverse nor abundant. With 2 notable exceptions they do not exceed 2%. In Unit III, 2 levels show high percentages of Polypodiaceae spore types (9% and 16% of total pollen and spores). Both levels of high fern spores are in alder dominated deciduous pollen assemblages (26% and 80% alder abundance respectively) that follow herb-shrub assemblages.

Patterns of Disturbance and Vegetation Change

Stratigraphic palynology of the Devils Gate section has shown four patterns of change in pollen assemblages. The first two of these pollen shifts occurs in a sequence of disjunct samples separated by barren sediments and the last two occur in continuous sequences.

1. Shift from forest to herb-shrub dominated pollen assemblage, in some cases followed by a deciduous assemblage dominated by *Alnus*.

2. Significant increase of aquatic plants and fungi.

3. Important increase of Taxodiaceae-Cupressaceae-Taxaceae pollen coincident with diminished abundances of other conifer groups and broadleaved groups.

4. Broadleaved deciduous and mixed broadleaved-conifer forest oscillation involving marked shifts in the relative abundance of forest pollen groups; from mixed forest assemblages with conifers, oaks, and deciduous elements, to deciduous dominated pollen assemblages with pronounced increases of elm and other deciduous taxa. These relatively abrupt shifts to deciduous dominance are followed by a relatively gradual return to mixed forest pollen assemblages producing an asymmetric pollen curve.

These pollen shifts are abrupt, repeated, and of large magnitude. Such shifts imply major changes in the composition or distribution of the source vegetation. Such changes in source vegetation are presumed to have been caused by major disturbance. Previous studies (papers by Taggart and Cross) in the Succor Creek area have documented two of these vegetation changes and made interpretations regarding the nature of the disturbances. The following discussion will briefly consider these two types of vegetation change, the replacement of forest by a herb-shrub assemblage and the expansion of TCT. It will include additional insights from the Devils Gate study and evidence that links the herb-shrub, alder, aquatic assemblages, and the TCT expansion in a common pattern of disturbance. Discussion will then consider in detail the characteristics of the deciduous-mixed forest oscillations and possible causes.

Shift from Forest to Herb Assemblages

Vegetation shifts to herb-shrub dominated assemblages have been documented from three previously studied sections in the Succor Creek Formation (Shortcut, Rockville, and Type sections). The herb-shrub assemblage is in each occurrence identified above thick, coarse, barren ash sequences in the Devils Gate section. It has not been found to date as the dominant element in the pollen record of a continuous lithologic sequence. In each herb dominated interval the total abundance of forest tree and shrub pollen (except pine) is reduced to less than 10%.

The Devils Gate study provides the first record of a subsequent deciduous succession stage on such disturbed terrains. The herb assemblage is followed by a deciduous pollen assemblage which is overwhelmingly dominated by elm (levels 33 and 34) or by alder (levels 38, 40, and 50) with ferns (levels 38 and 40).

The vegetation shift recognized in this study and in the previous studies of Taggart and Cross is apparently linked to large scale volcanic events that repeatedly resulted in thick, coarse, clastic deposits which covered the landscape with ash and pumice, and essentially devastated the vegetation of the area.

Characteristics of the Ash as a Growth Surface. As noted by Taggart and Cross (1980, Cross and Taggart 1983) volcanic ash is a harsh surface for plant growth.

1. It is a mineral soil, low in nitrogen. A nitrogen content of about 60 ppm in fresh ash (Tagawa 1964) contrasts with an average content of around 550 ppm in temperate forest soils (Schreiner and Brown 1938). Furthermore, the volcanic soil accumulates leaf litter very slowly due to the sparse nature of successional scrub and high soil temperatures with consequent high rates of degradation (Tagawa 1964).

2. Ash and pumice do not hold moisture and are strongly insolated with consequent wide temperature fluctuations (Tagawa 1964). Thus they have been called ash and pumice "deserts" because they simulate, in a mesic climate, the dry, hot edaphic conditions of a desert.

3. The surface is unstable, subject to erosion, and successful biotic invasion is very slow (Moral 1981).

Plant Succession on a Modern Volcanic Terrain. The pattern of plant change on such a surface is one of primary succession. The recent volcanic fields in the south of Kyushu Island, Japan provide a useful site for comparison with the Succor Creek setting, because of similarity of vegetation and climate. The island has a mesic, equable, temperate, oceanic climate that supports mixed evergreen and coniferous forests. Natural forests on the island include evergreen forest (evergreen Quercus-Lauraceae) below 500 m; mixed evergreen-coniferous forest (evergreen Quercus, Ilex, Abies, Tsuga, and Cephalotaxus) between 500 m and 1150 m; and mixed deciduous-evergreen-coniferous forest (Fagus, evergreen Quercus, and Tsuga) above 1150 m (Tagawa 1964).

The area studied by Tagawa has been extensively disturbed by volcanic flows and ashfalls that have produced a series of surfaces dating from 1476 to the present. It has thus been possible to observe in detail the patterns of establishment of vegetation on ash and lava. The sequence of stages of primary succession have been reconstructed as follows: lichen-bryophyte, herb, Alnus scrub, pine forest? (since pine has been planted in the area the natural role of pine is not clear), mixed broadleaved evergreen forest.

Primary Succession in the Devils Gate Section. Primary succession on ash terrains in the Devils Gate record appear to represent the same herb and Alnus scrub stages as the Kyushu setting. In most sequences, the vegetation was then interrupted by further barren ash layers except in Unit IV (levels 43 to 48) where a mixed forest developed.

Herb stage. Among the aggressive pioneer plants in the Devils Gate "edaphic desert" were Compositae, Chenopodiaceae-Amaranthaceae, Gramineae, Malvaceae, and Onagraceae. These are families with species tolerant of the high light, wide temperature fluctuations, and drought conditions that also characterize the climatically controlled desert of the Succor Creek area today.

In Devils Gate herb assemblages, pine shows abundances of about 20%. Its role in the Devils Gate area is not clear. In modern environments of herbaceous vegetation (prairie and tundra) absolute pollen input is low with the consequence that pine pollen may be found in relatively large numbers miles removed from the nearest trees (Webb and McAndrews 1976). The average pine pollen abundance in tundra is 20% (Webb and McAndrews 1976), which suggests that abundances of 20% in the Devils Gate herb assemblages could also have been transported from outside the area of devastation. In other Succor Creek sections higher pine levels (Taggart and Cross 1980) indicate a role for pine in some vegetation recovery sequences.

Alnus scrub stage. The first undisputed woody immigrants were broadleaved deciduous successional genera. In this setting the deciduous dominated assemblage is less diverse than in the deciduous dominated intervals in the continuous forest sequence of Unit I and other constituents are apparently subordinate to Alnus. Alder is especially adapted for a successional role on inorganic soil because of the nitrogen-fixing capacity of its root nodules (Harlow et al. 1975, Franklin and Dyrness 1973). It improves a nutrient-poor soil for associated and subsequent species in several ways: by building up a humus layer, increasing the nitrogen content of the soil by both N-fixing root nodules and high nitrogen leaf litter, and improving nutrient cycling and soil microbiota. It has been shown that the growth of other pioneering shrubs on glacial debris is stimulated by their association with alder (Miles 1979).

At two alder dominated levels (38 & 40) fern spores show increase in abundance synchronous with the high levels of alder pollen. Ferns apparently also played a role in primary successional vegetation. It is interesting to note that such a limited successional role for ferns in the Succor Creek flora is supported by the macrofossil record as well as by observation of their role on recent volcanic terrains. On the volcanics of southern Japan ferns are actually the dominant pioneer in the initial herb stage of colonization on the ash (Tagawa 1964).

The macrofossil record of ferns comes from only one locality in the Succor Creek area (Smith 1938, Graham 1965) but at this locality

Woodwardia dominates the assemblage, contributing 54% of the macrofossils recovered. Graham concluded that *Woodwardia* evidently formed a dense stand on the edge of this depositional site but was not common in plant communities of the many sites where the mixed forest vegetation was preserved.

Summary. The initial pioneering role for herbs and shrubs on volcanic ash has been demonstrated in earlier studies (papers by Taggart and Cross). The Devils Gate study complements the earlier findings with the documentation of important roles for alder and ferns in a subsequent woody successional stage.

Development of Taxodiaceae

A marked increase in the level of TCT pollen occurs in Unit IV synchronously with the reduction of other conifers and broadleaved taxa (except *Alnus*). This is in contrast to the Unit I sequence where TCT increases in concert with the pollen of other conifers. Such a TCT pollen shift has been observed in other Succor Creek sections and is interpreted to indicate the areal expansion of a local *Glyptostrobus* swamp environment with most of the TCT pollen being locally derived (papers by Taggart and Cross). Several lines of evidence strongly support such an interpretation for the pollen shift in Unit IV.

1. The macrofossils from the sampling site appear to be the remains of a *Glytostrobus* swamp. At this site a number of permineralized, standing, taxodiaceous stumps in a single stratum can be traced for hundreds of yards along the outcrop and the associated leaf horizon is dominated by twigs of *Glyptostrobus*.

2. High TCT pollen percentages, similar to those found in Unit IV, have been found in modern sediments where swamp forests are dominated by trees of the Taxodiaceae (Cohen 1975).

3. When the TCT element is deleted from the pollen sum, the pattern of pollen change through Unit IV (levels 43 to 48) is like that found repeatedly through Unit I (Figure 12). Levels for individual taxa fluctuate but there is an overall trend toward an increase in conifers (to a peak in level 47), followed by an abrupt shift to deciduous dominance (level 48) before the sequence is terminated by barren ash. Thus it appears that the pollen record of a local _Glyptostrobus_ dominated vegetation is superimposed on a pollen record of regional mixed forest change.

4. The environment of a _Glyptostrobus_ dominated horizon can be inferred by comparison with the environment in which the living trees form dominant stands. _Glyptostrobus_ (Chinese water pine) is the East Asian ecological equivalent of _Taxodium_ (bald-cypress). Both genera show morphologic adaptation to high, fluctuating water levels, i.e., the development of pnematophores (conical "knees") on the roots. Both genera face little competition and can form almost pure stands in standing water, though on drained soils their occurrence is scattered because of competition from the many forest trees that also thrive in these conditions (Harlow et al. 1974). Thus it is reasonable to infer that such high TCT pollen abundances in levels that preserved dominantly _Glyptostrobus_ leaves and stumps was one of more or less permanent standing water.

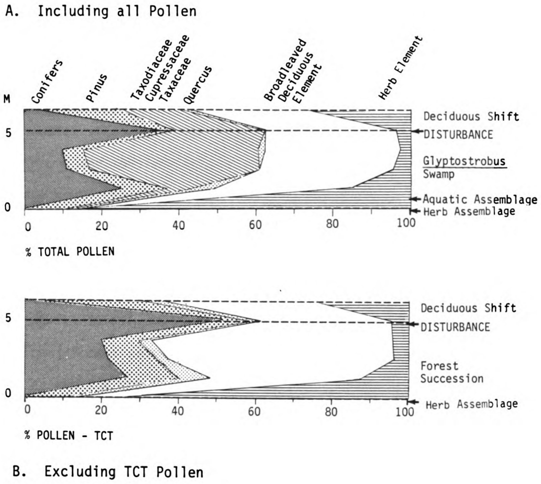


Figure 12. Summary pollen diagrams for the Unit IV *Glyptostrobus* sequence.

Disturbance. Clearly, the control of Glyptostrobus forest swamp expansion is hydrologic. It has been suggested (papers by Taggart and Cross) that in the Succor Creek setting volcanic disturbance was one of the causes of hydrologic changes that allowed the expansion of a swamp environment and vegetation. They envisaged the creation of lakes and swamps due to disruption of drainage systems by earthquakes and volcanic ejecta. In Unit IV it is apparent that a volcanic disturbance initiated the vegetation sequence. The same event may well have established the standing water swamp environment that allowed the expansion of Glyptostrobus and the lake environment in which an open water aquatic assemblage developed (level 44). The first productive sample in the sequence (level 43) occurs above a series of barren ash beds and is the typical pioneering herb complex that colonized volcanic ash horizons repeatedly through Succor Creek time. The assemblage is succeeded in subsequent levels (45 to 47) by the coincident development of two successional forest sequences. One is the development of a swamp vegetation and the other is the development of a drained slope vegetation, first with the alder dominated woody stage that succeeds the herbs on volcanic sites, and then with forest succession from deciduous to mixed broadleaved-conifer dominance. The first appearance of a herb pollen assemblage occurs on a volcanic ash surface. This ash accumulation probably disrupted patterns of drainage and allowed the subsequent development of lake and swamp.

Development of an Aquatic Element

Aquatic palynomorph assemblages are preserved at several levels through Units III, IV, and V, including the stump zones at the bases of

Units III and IV. The assemblage includes an aquatic flowering plant (Potomogeton), a green alga (Ovoidites), other thin-walled, spherical algal cysts, acritarchs, and a fungus (Chytridaceae, Phycomyceta).

Ovoidites is the zygospore of Spirogyra (Zygnemataceae, Chlorophyta), the common green alga and is reported to be a good environmental indicator of open "stagnant, shallow, warm, and more or less mesotrophic, fresh water habitats" (van Geel 1978). The pattern of occurrence and abundance for the algae (especially Ovoidites) is strikingly duplicated by the spores of Chytridaceae. These fungi are known to be generally aquatic, of parasitic and saprophytic habit, and most commonly parasitic on freshwater algae (Ainsworth, 1971).

Disturbance. Development of this aquatic assemblage apparently represents intervals of relatively shallow, sunny, open water conditions that supported aquatic flowering plants, an algal bloom, and a bloom of saprophytic and parasitic fungi. In the Unit IV Glyptostrobus stump zone the development of this environment (level 44) follows a xeric interval (level 42) that occurs above a barren ash sequence and precedes expansion of the Glyptostrobus dominated swamp sequence (levels 45 to 47). This implies that the shallow body of water in which the aquatics grew was possibly dammed by the volcanic ash on which the herb assemblage became established. The aquatics eventually yielded to swamp forest as they were possibly excluded by shade or by shallowing. Thus all three assemblages are apparently a result of the volcanism that deposited the ash on which the herbs pioneered, and created the impoundment in which aquatic plants and swamp trees flourished.

Deciduous-Mixed Forest Dynamics

The nature of the vegetation shift, i.e., from mixed broadleaved-conifer forest to broadleaved deciduous dominance, appears to be the result of disturbance. In many temperate mixed forests, whether conifer, broadleaved evergreen, or broadleaved deciduous elements dominate in undisturbed stands, it is found that the deciduous element has a major successional role following disturbance (Braun 1950, Wang 1961, Tagawa 1964, Franklin and Dyrness 1973, Van Cleve and Viereck 1981). The notable exception to deciduous dominance is pine dominance in some types of post-disturbance vegetation (Braun 1950, Christensen and Peel 1981).

Although such a pattern of pollen dynamics has not been previously described from Miocene studies in the Pacific Northwest, the pattern is so clearly repeated through continuous section in Unit I that it is possible to establish some characteristics of the disturbance. The following analysis will consider four characteristics that can be reconstructed from the pollen diagram: the geographic relationship of the disturbance to the basin of deposition; the effects of the disturbance on the vegetation and its response; the frequency of disturbance; and the magnitude. By comparison with the characteristics of present day disturbances and known vegetation responses, an attempt will be made to determine the most likely cause of the Devils Gate forest disturbances.

Characteristics of the Disturbance

Position of the Disturbance Relative to the Basin of Deposition.

At the outset it is important to determine whether the vegetation changes were local or regional. It is important to know whether disturbance was affecting the regional forest or merely the lake margin vegetation and superimposing a local disturbance cycle on a background of regional environmental and vegetational stability.

Hydrologic changes around the margin of a depositional basin can superimpose a local dynamic component on a regional pollen profile in at least two ways:

1. Variations in the distance of the shoreline from the sampling site cause variations in the influence of local plants on the pollen assemblage. The greater the distance of the sampling site from the lake margin, the more regionally representative is the pollen sample (Janssen 1967, Davis et al. 1971).

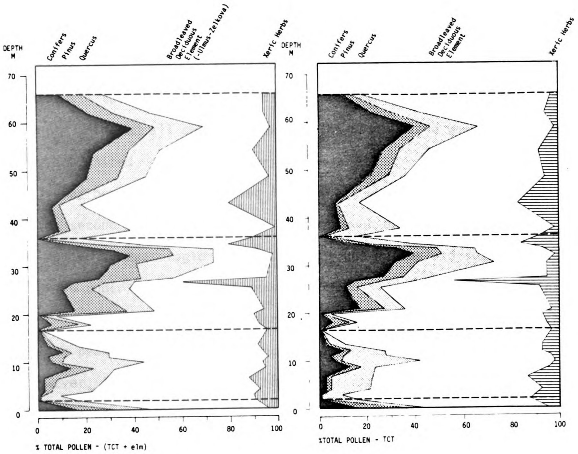
2. Variations in the water table and lake level around the lake margin, cause changes in the composition of the lake margin community independent of the regional environment or vegetation.

Recognizing the local or regional origin of pollen is difficult. One method is to omit a suspect taxon from the pollen sum and evaluate the residual pollen dynamics. In the Unit I pollen sequence there are at least two taxa that warrant evaluation for possible local overrepresentation on the basis of their present day ecological tolerances that includes swamp habitats and the dynamics of their pollen abundance in the section. The two pollen types are Taxodiaceae-Cupressaceae-Taxaceae ("TCT") and Ulmus-Zelkova ("elm").

TCT pollen may be considered to be a local component for several reasons. In some levels it is the most abundant pollen type. Through Unit I it fluctuates strongly between 4% and 45% of the total pollen. At least part of the TCT pollen group represents Glyptostrobus since the leaves are found in the same beds. Glyptostrobus is a lake margin tree. It grows as a swamp tree that may form pure stands on permanently inundated sites. Such stands thrived from time to time around the depositional basins, periodically dominating the pollen and macrofossil record as in Unit IV. When the pollen sum in Unit IV was recalculated without TCT pollen, the shape of the residual curve was changed. A pollen curve more typical of a regional forest succession was revealed. This had been masked by the local TCT abundance (Figure 12). TCT pollen fluctuation was independent of other conifers and its exclusion from the pollen sum brought out a pattern of change of the other conifers and broadleaved deciduous types similar to that in Unit I.

Through the Unit I sequence (unlike Unit IV) the abundance of TCT pollen is found to fluctuate directly with the other conifers and inversely with the broadleaved deciduous group. The effect of excluding TCT from the pollen sum is to accentuate the dynamics of the other pollen groups (Figure 13A).

TCT pollen is probably partly locally derived in the Unit I sequence, but it may also reflect abundant trees from mixed stands on drained slopes. Even Glyptostrobus has a scattered occurrence in mixed upland forests (Wang 1961) and other genera of Cupressaceae and Taxaceae are common, including Thuja and Cephalotaxus that are rarely found in



A. Excluding TCT and elm pollen. B. Excluding TCT pollen.

Figure 13. Recalculated summary pollen diagrams from Unit I.

the macrofossil record. Much of the TCT pollen in Unit I can be tentatively assigned to Cupressaceae and Taxaceae on the basis of morphology. Its omission from the pollen sum shows that its pattern of abundance is not simply the expression of hydrologic dynamics acting on the margin of a relatively stable regional landscape. The same disturbance that influenced the pollen rain of TCT affected the input of pollen of all the other upland conifers. The same disturbance apparently affected all conifer groups. The disturbance was followed by their synchronized, gradual recovery.

Elm may be suspected of being local for the same reasons as TCT. It is the second most common pollen type through Unit I and could also be controlled by hydrologic factors. _Ulmus_ has bottomland species today that thrive under conditions of seasonal inundation around lake margins. It shows a highly variable occurrence and a pattern of alternation with TCT pollen peaks through the sequence. To exclude elm from the pollen sum, however, leaves the residual pattern of change unaffected (Figure 13B). Peaks of abundance of elm follow the event that disturbs the conifers. Peaks coincide with those of other deciduous genera with apparently similar strategies that allow them to achieve prominence rapidly following disturbance.

Correction for suspected local sources of pollen does not damp or alter the pattern of pollen dynamics but serves to emphasize a reciprocal pattern of dominance of two pollen groups and indicates that disturbance affected the forests at some distance from the lake margin.

Patterns of Pollen Change. Several patterns of pollen change (and inferred vegetation change) occur:

1. Changes are cyclic and strongly asymmetric.

2. All the conifer groups are markedly affected by each event and are rapidly replaced by broadleaved deciduous genera. The conifer groups that appear to have been similarly affected have mixed climatic indications.

3. From the broadleaved deciduous peaks subsequent change involves gradual replacement by conifer groups and oaks.

4. Not only is the composition of the vegetation change similar in each interval. The rate of change of the vegetation is also very similar. In intervals 1 and 2 the rate of change is almost identical (Figure 15), approximately 6% per meter of sediment decrease in the relative abundance of pollen of broadleaved deciduous trees. The trend in interval 3 is more difficult to interpret, in part because the sampling was necessarily discontinuous. Through this interval the curve connects 10 to 20 cm samples taken at approximately 2 m intervals. By contrast, the lower part of the section was sampled continuously in 1 to 2 m increments. The trend in interval 3 may be drawn several ways (Figure 14). Line "a" suggests a slower rate of change, or a higher rate of sedimentation, than the lower part of the section. If the trend reversal at approximately 40 m is interpreted as a minor disturbance, then line "b" may be drawn parallel to line a of intervals 1 and 2, i.e., with the same rate of replacement. Line "c" emphasizes an apparent slowing rate of replacement of the broadleaved deciduous element towards the top of interval 3, the thickest of the three post-disturbance sequences. Such a pattern of decreasing rate of vegetation change with time is noted in modern ecosystems in the course of succession (Whittaker 1975).

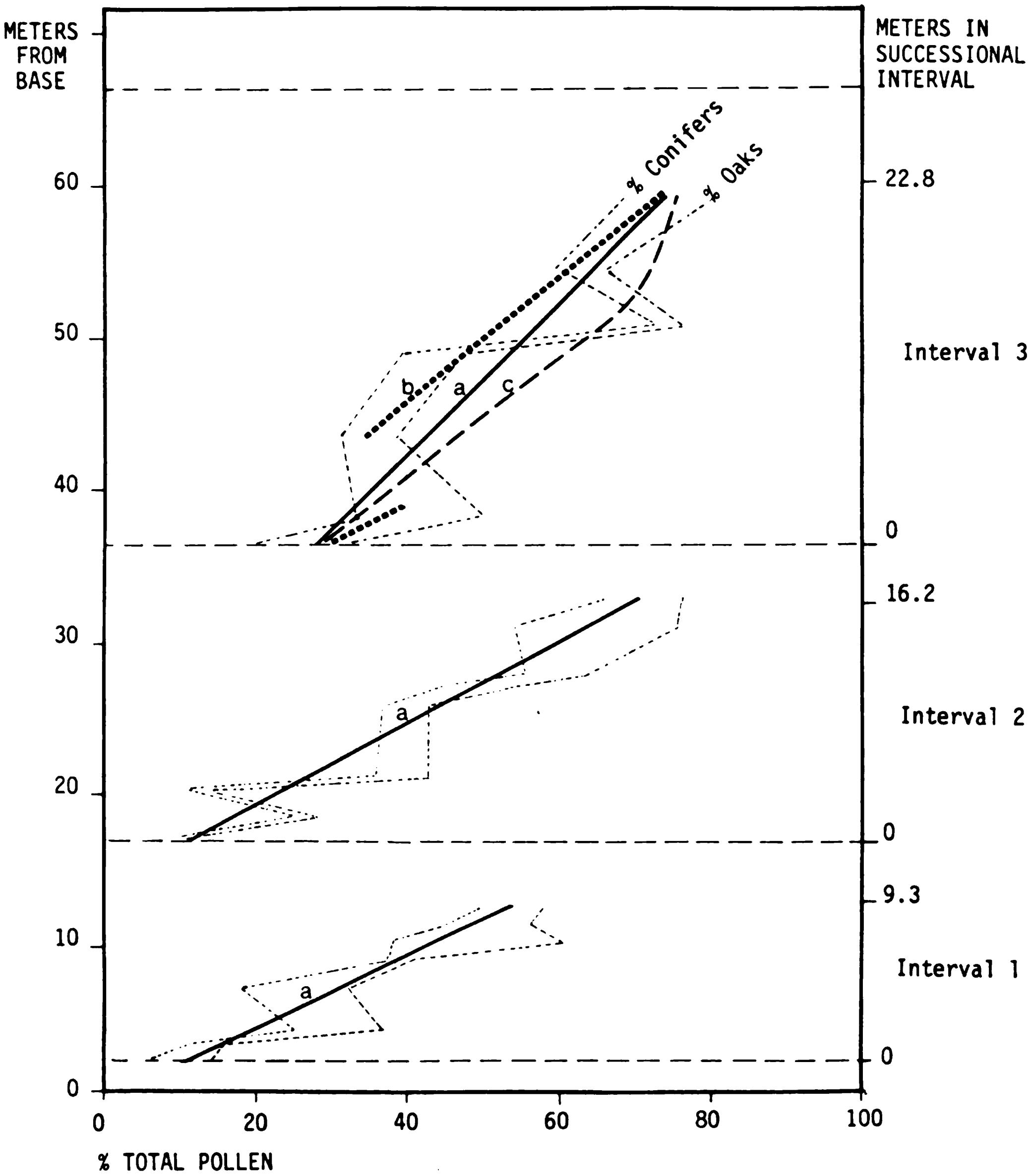


Figure 14. Summary pollen diagrams of Unit I showing trend in recovery of dominant evergreens (conifers and oaks) following disturbance.
Line a connects the midpoints of the two curves.
Lines b and c are possible interpretations of the trend in interval 3.

5. Each of the deciduous genera that show pulses of dominance during post-disturbance intervals has species with early successional strategies that enable them to exploit disturbed sites in temperate forests today (Table 5). The strategies of successional deciduous trees include:

a. Shade-intolerance. Each of the genera in Table 5 has shade-intolerant species that are short-lived in a closed forest unless they are released by a disturbance which opens the canopy and allows direct sunlight onto the forest floor.

b. Rapid early growth in direct sunlight. Intolerant species show a dramatic ability to respond to release. In the direct sunlight of a forest clearing their seeds germinate immediately. Their early growth is rapid so that they quickly shade slower growing tolerant species. _Alnus_ _rubra_, for example, can attain a height of 40 feet in 10 years. _Platanus_ can grow 8 feet in the first year. They are fast maturing, i.e., they flower at a relatively young age so that their presence is recorded in the pollen rain without significant delay.

c. Production of numerous light seeds. They produce enormous numbers of light, wind-carried seeds with very high germination rates. Thus they compete successfully with the local source of heavier seeds of the tolerant canopy trees. Despite the distance of the seed source from other disturbed sites such as clearings, the edge of the forest, or stream banks, they have a high probability of arriving at a disturbed site.

Table 5. Some ecological characteristics of deciduous genera that dominate the post-disturbance intervals. (Includes range of tolerance[1] of the genus and other comments on successional strategies (from Harlow et al. 1975). Genera are arranged in order of abundance in the Unit I sequence and order of presentation in Figure 10).

GENUS	SHADE-TOLERANCE[1]	Other Characteristics
Ulmus	intermediate	Numerous seeds, moist to dry conditions.
Celtis	variable	Depends on site conditions, common on limestone and droughty sites.
Liquidambar	intolerant	Germinates on any soil, aggressive pioneer on old fields.
Platanus	intermediate to intolerant	Pioneer in nearly pure stands, low seed viability, only on moist mineral soil in open sites.
Acer	tolerant to intolerant	Some species are pioneers on disturbed sites including logged and burned land (e.g. A. rubrum and A. macrophyllum).
Alnus	intolerant	A. rubra is the first tree following fires and logging. Improves soil for subsequent species. Numerous seeds germinate on organic or mineral soils.
Betula	some intolerant	Seedlings of B. populifolia and B. papyrifera live less than 1 year in closed forest. B. populifolia covers large areas on abandoned and burned-over land, grows on poorest, sterile soils.

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[1] The tolerance rating refers to level of tolerance of shade of seedlings or saplings.

d. Soil preference. Many of the species have seeds that will germinate on a wide variety of soils.

e. Vigorous sprouting from roots and stems. Sprouts from established stumps are capable of much higher growth rates than seedlings and are less vulnerable to erosion on exposed soil.

These patterns of vegetation change suggest that the pollen sequence is a record of: (1) repetition of a sudden disturbance event that particularly affected conifer groups and oaks; (2) subsequent more or less unhindered forest recovery (seen in intervals 1 and 2), but with the possibility of a setback as seen in interval 3 (Figure 14); and (3) early exploitation of disturbed sites by vigorous deciduous genera with competitive successional strategies. It appears that a sudden disturbance event repeatedly reset a successional vegetation "clock" at each point of abrupt pollen shift to deciduous dominance and, that after each disturbance event, similar conditions for forest recovery apparently existed and succession proceeded at a similar rate and with a similar pattern of change in each cycle.

Frequency of Disturbance. In these sediments it is not possible to establish an independent chronology. However, a rough estimate can be attempted on the basis of the biological argument that has been made above, that the record of pollen change is one of forest succession following disturbance. Thus the time represented by a successional interval can be compared to the known (or estimated) period required for vegetation of similar aspect and climatic requirement to shift from an early successional deciduous stand to a mixed broadleaved-conifer forest. From such a biological time estimate, an approximate sedimentation rate might be calculated. This estimated sedimentation rate can be compared to known rates for lakes and thus provide one comparative check on the time scale of vegetation change that has been proposed here.

Estimated sedimentation rate for Unit I: The estimate assumes relatively stable conditions of sedimentation with comparatively steady and continuous rates of deposition through the sequence. Lakes are the most constant of sedimentary environments and the most likely to preserve a continuous fossil record (Schindel 1980). The Unit I sequence was interpreted in the field as a lake setting; sedimentation was at least sufficiently constant to deposit a relatively continuous pollen record that shows a constant rate of change of pollen assemblages through three intervals (Figure 15).

Rough time estimates for recovery of disturbed sites in mesic temperate forests vary from 200 to 1000 years (Henry and Swan 1974, McAndrews 1976, White 1979, Franklin and Hemstrom 1981). The upper end of the range is estimated for Pacific Northwest conifer forests where many of the conifers are particularly long-lived. These estimates assume an uninterrupted recovery from a single disturbance event. Any mild disturbance during the course of recovery requires an increase in these estimates.

A figure in this range can be taken as the time estimate for post-disturbance interval 3. A 1000 year estimate for the successional sequence of 22.8 m yields an average depositional rate of 22.8 mm per year. A 200 year interval yields a rate of 114 mm per year.

Depositional rates in modern lakes: A compilation of available data on lake sedimentation rates presents a range of 0.15 to 31.7 mm per year and a mean of 5.8 mm per year (Schindel 1980). The 1000 year recovery interval yields a depositional rate within this range (22.8 mm) but a 200 year interval requires a depositional rate 3 to 4 times greater than the upper limit (114 mm). The outcome of this comparison is not surprising. The Unit I depositional setting has some unusual features not found in the modern lakes for which data were compiled by Schindel (1980) which indicate that Unit I deposition rates were unusually high for a lake setting.

1. The lake filled with mostly silt-size reworked volcanic ash with a relatively low organic content and relatively coarse grain size for lake sediments.

2. While the sediments are evenly bedded, they are rather thick by comparison with typical lake sediments.

It was apparently a setting in which easily erodable volcanic ash was carried into the lake at a fairly steady rate that allowed the incorporation of adequate amounts of pollen. The sediment content of the inflowing water was relatively high, not because of the eroding force of torrential rain, but because of the erodability of the ash.

A useful comparison for such a sedimentary setting may be made with post-settlement sedimentation rates in modern lakes. Cleared and ploughed forest lands provide a highly erodable substrate that may be somewhat comparable to an ash sediment source. Records from mesic temperate North American site illustrate the sedimentation consequences of the availability of an easily erodable sediment source. Immediately following settlement of the areas around Frains Lake, Michigan, a

30-fold increase in the accumulation rate of sediment occurred (Davis 1976). It later stabilized at about 10 times the pre-settlement rate. Experimental deforesting of the Hubbard Brook area, New Hampshire, produced a 15-fold increase in sedimentation rate (Bormann and Likens 1979). Swain (1973) and Cwynar (1978) have also demonstrated increased sedimentation rates following episodes of natural forest disturbance that opened up areas of forest floor.

Comparison of the two sedimentation rates: The rate of 22.8 mm per year was calculated on the basis of a forest recovery time of 1000 years. This figure falls within the upper range for lake sedimentation of 0.15 to 31.7 mm per year (Schindel 1980). At the other end of the range of estimated forest recovery rates (200 years) a 5-fold increase in the rate of accumulation of the sediment (114 mm per year) would have to be assumed if the pollen sequence is to be interpreted as a simple successional recovery. The values for sediment influx from cleared, erodable land indicate that it would not be unreasonable to expect such rates of sedimentation in the Devils Gate setting.

Conclusion: These comparisons at least do not exclude the interpretation that the Unit I sequence was deposited at a rate that recorded vegetation dynamics on a successional time scale. At the average rate of 22.8 mm per year, Unit I could have been deposited in about 3000 years in which case sampling intervals represent an average of about 90 years. At this rate, catastrophic disturbances resulting in major vegetation shifts occurred at intervals of about 400, 700, and 1000 years (average frequency 700 years). At this rate the average time represented by the shift from the peak of mixed broadleaved-conifer forest to the peak of deciduous forest was about 200 years, but this interval could have been relatively shorter than the recovery part of the cycles. If it was the record of a disturbance event that destroyed a large area of the forest vegetation it might well have been accompanied by an increased erosion rate like that shown in the cleared Hubbard Brook forest (Bormann and Likens 1979) and thus represent a much shorter period of time than that following the subsequent revegetation by deciduous trees.

Scale of Disturbance. The scale of disturbance can be estimated by comparing the Unit I pollen shifts with the pollen record from modern forests for which the magnitude of the disturbance is known.

In the Algonquin National Park, Ontario, fire has occurred in the conifer forest every 80 years on an average. The destroyed conifer stands are replaced by broadleaved deciduous trees, yet the pollen record preserved in lake sediments has been quite unvarying for the last 1200 years (Cwynar 1978). A similar history of fire (every 60 to 70 years) in a conifer forest (of northern Minnesota) showed some increase after fire in the broadleaved deciduous pollen in lake sediments though not markedly and not consistently (Swain 1973).

These disturbances occurred on a relatively modest scale and with sufficient frequency that at any point in time the forest was a mosaic of areas in various stages of regeneration. Since the pollen rain derived from such a mosaic landscape is a highly integrated regional record of vegetation it tended to vary through time in a manner independent of discrete disturbance events. By contrast with these studies the scale of pollen shift in the Unit I sequence was dramatic with 42%, 40% and 40% increases in the broadleaved component in the three sequences. If, as assumed here, the abrupt shifts are taken to represent shifts in regional pollen rain, then the Devils Gate Unit I pollen shifts appear to be reflections of disturbance of great magnitude. Further, if the percentage increases in the broadleaved component across the intervals of abrupt shift (42%, 40% and 40%) can be taken as a rough measure of the magnitude of each disturbance, then the events appear also to have been strikingly similar in their effects.

The magnitude and frequence of disturbance in forest vegetation is usually modest (Woods & Whittaker 1981) but can vary widely. Interesting is the finding that disturbance frequency is often inversely related to magnitude (White 1979). Not only were the Unit I disturbances of much greater magnitude than those cited above but they were also apparently much less frequent, as estimated above (150 to 1000 years). The Devils Gate sequence may reflect a pattern of disturbance at one end of a continuum of possible sizes and frequencies in the Succor Creek flora, a fortuitous combination for insight into Miocene vegetation dynamics. At more modest scales and more frequent occurrence the detail of disturbance and vegetation change would not necessarily have been detected in the pollen record.

This interpretation of the scale of disturbance has been based on the assumption that the pollen dynamics are not exaggerated by shifts in pollen productivity significantly greater than shifts in vegetation composition. The possibility cannot be ruled out that the disturbance was of more modest magnitude and that the pollen rain of disturbance vegetation was somewhat exaggerated. Such bias can arise where flowering and pollen production in successional stands are much greater than in the trees of the undisturbed closed canopy (Birks and Birks 1980).

Summary of Characteristics of the Disturbance.

1. The disturbance affected the regional vegetation. It was not a local, lake margin event superimposed on a steady state regional environment.

2. The effects of disturbance on vegetation were cyclic, relatively abrupt, apparently selectively damaging to the conifers and evergreen oaks. The early post-disturbance vegetation was dominated by broadleaved deciduous genera all of which have species with early successional strategies. The subsequent expansion of conifers and oaks was relative slow; thus the cycles of vegetation change were strongly asymmetric.

3. Disturbances probably occurred on a time scale of hundreds of years following substantial change in forest dominance.

4. The magnitude of disturbance was apparently relatively large.

Natural Disturbances

In mixed forests two classes of natural disturbance can effect a shift from mixed to deciduous dominance. One is climatic. The other is the class of disturbances that destroys tracts of trees and opens areas of forest. Such catastrophic disturbances include fire, windfall, and certain volcanic phenomena in an active volcanic terrain. Whether the mixed forests are dominated by broadleaved evergreen, broadleaved deciduous, or coniferous types, such disturbed sites are dominated by successional species of deciduous genera (Wang 1961, Tagawa 1964). The following discussion will compare the characteristics of each type of disturbance with those of the Devils Gate Unit I disturbance in an attempt to determine a likely cause of the Devils Gate disturbance.

Climate

Both precipitation and temperature can vary in a cyclic manner. Where data are available, their effects on vegetation, as recorded in pollen sequences through time, can be compared with the Unit I sequence. Their effects along climatic gradients, on the composition of standing vegetation, can also be compared.

Temperature Fluctuations. Substantial fluctuations of mean annual temperature (MAT) are well documented in the Pleistocene. 0^{18} - derived temperature curves have been correlated with dated pollen curves of similar composition to the Devils Gate assemblages (Fuji 1980, Fuji and Horie 1972, 1976).

The changes that occurred in the pollen assemblages in response to temperature fluctuations are substantially different from the Devils Gate pollen curve. The warmer intervals are dominated by a mixed assemblage, including broadleaved evergreen (Quercus), deciduous (Fagus), and coniferous TCT (Metasequoia) elements, and cooler intervals by a conifer dominated assemblage (Picea and Tsuga). In other words, pollen assemblages oscillated between mixed (warmer intervals) and conifer dominated (cooler intervals). In contrast, the Devils Gate conifers with mixed climatic indications do not segregate following disturbance. Picea and Tsuga, TCT, and Quercus, are all elements of a diverse, mixed assemblage, are all affected by the disturbance, and are all replaced by a deciduous element.

This documented effect of MAT cycles on mixed pollen assemblages could also be predicted from analysis of vegetation along MAT gradients. The broadleaved deciduous element is eliminated by winter lows below a temperature parameter critical for the group, a mean for the coldest month of less than -2°C (Figure 9). To reduce spruce at the same time requires also an increase in summer temperature mean for the warmest month above approximately 20°C. Thus, to allow expansion of the broadleaved deciduous element at the expense of both the broadleaved evergreen and coniferous elements of a mixed flora requires a cyclic change in the mean annual range of temperature (MART) across critical temperatures at both ends of the range. The history of MART changes is not well known and Pleistocene pollen studies were not found that could be compared to the present study. Such cycles of seasonality cannot be ruled out, but it seems that they would need to be rather specific to effect the pattern of vegetation change reflected in the Devils Gate pollen curve.

A second difference between the Pleistocene pollen diagram cited above and the Unit I pollen diagram is the shape of the curve. The temperature cycles did not produce sharp asymmetric response cycles in vegetation, with an abrupt shift in composition followed by a gradual return to the original assemblage. The pollen curves tend to be rather smoothed reflections of temperature cycles (Fuji and Horie 1972, 1976; Tsukada 1967). Apparently the magnitude of fluctuation was not sufficient to have the immediate effect of killing established trees that would be needed to produce a dramatic change in vegetation dominance. If climatic change is not killing in its effect, then with the life spans of individual trees averaging 150 years for hardwoods and 300 years for conifers, change in vegetation composition is gradual. In such situations replacements are generally be made as openings become available in the forest, either by death of aged individuals or by disturbance of a catastrophic nature that kills trees in large areas (Westman 1968).

If climatic change is not killing in its effect then the time scale of climatic cycles that can be detected on a pollen curve is on the order of 10^3 to 10^4 years, a chronology that is well established by radiometric dating. On this time scale Pleistocene pollen changes have been a good reflection of climate.

Climatic cycles on the time scale of 10^2 years, such as are postulated to result from cycles of earthquakes and corresponding tsunamis that overturn the ocean water causing heat transfer between the ocean surface and depth and global cooling, are commonly detected in tree-ring width variation (Tairo 1982) precisely because, once established, the trees have continued to grow. Eventually senescence or catastrophe takes its toll and provides opportunities for establishment of other species. The composition of the replacement species depends on many factors including the climate at that point in the short term climatic cycle.

Precipitation Fluctuations. Precipitation fluctuations cause disturbance by flooding and drought. Drought has consequences for regional vegetation, flooding for bottomland vegetation particularly.

The lowland effects are caused primarily by change in water level of the swamps, lakes, and rivers. In wet years flooding creates and destroys sites for tree colonization by changing stream course, soil removal, and deposition. In dry years low water level exposes sites for colonization and drains swamps.

Many of the broadleaved deciduous genera of the intervals in Unit I dominated by deciduous trees have flood tolerant species adapted for early colonization of spring flooded sites (Bell 1974, Bell and del Moral 1977, Harlow et al. 1975, White 1979). In the Devils Gate Unit I sequence, intervals dominated by the broadleaved deciduous trees may be interpreted as relatively wet periods that caused frequent and widespread flooding, erosion, and deposition. Such flood cycles favored expansion of flood tolerant, successional, deciduous genera in the bottomland and restriction of intolerant mixed forest to the upland. Dry periods favored the expansion into the lowland of intolerant mixed broadleaved conifer forest. A pollen group that appears to not fit into this scenario is Taxodiaceae-Cupressaceae-Taxaceae (TCT). At least some of this group would be favored in periods of high rainfall and water level (especially Glyptostrobus and Taxodium) yet through Unit I its abundance varies inversely with the broadleaved deciduous element.

The upland regional effects of precipitation variation are often not catastrophic, affecting growth rates and effecting changes in composition of the vegetation only by replacement as individual trees die or a catastrophe opens sites. However, a severe drought can kill broadleaved trees (at least vulnerable individuals) outright.

Drought tends to favor conifers. In the Pacific Northwest where conifers are dominant and broadleaved groups are restricted to protected sites and stream banks, it is thought to be summer drought (annual cycles of precipitation) that favors conifers.

With this in mind, an attempt to fit drought cycles to the Unit I pollen curve may relate the conifer peaks to intervals of relatively low annual rainfall or of relatively rainless summers. However there are at least two problems with such an interpretation. First, the conifer group includes genera with various precipitation requirements and conifer peaks include genera that grow today in mixed broadleaved associations, in mesic habitats with adequate summer rain. Second, it is difficult to fit a precipitation cycle to the asymmetry of the pollen curve. If drought cycles are correlated with conifer peaks then it is necessary to envisage the subsequent, relatively abrupt and synchronous reduction in conifer abundance following amelioration of the drought cycle. But in more mesic intervals the established and relatively long-lived conifers would be expected to continue to thrive with only very gradual displacement of some genera.

Summary. In this discussion of climate it is concluded that simple temperature (MAT) fluctuations do not adequately account for the disturbance of both broadleaved evergreens and the suite of conifers. Discussions of seasonality and drought were inconclusive, in part for the want of suitable comparative data and for an inability to envisage the asymmetry of the pollen curve due to these disturbances. However, precipitation fluctuations involving cycles of extensive flooding suggest a mechanism for the sequence of pollen changes in Unit I.

Catastrophic Disturbances

Catastrophic disturbance that destroys tracts of trees can cause relatively abrupt vegetation shifts that may produce the patterns of change noted in the Devils Gate Unit 1 pollen record. On such cleared sites, early successional deciduous genera are favored that later yield to vegetation that may be of mixed association or dominated by broadleaved evergreen, broadleaved deciduous, or coniferous elements depending on environment. Disturbances that can cause sudden clearing of areas of forest include volcanism, fire, and windfall. The objective of the following discussion will be to attempt to determine which catastrophic disturbance best accounts for the observed patterns of change.

Volcanism.

Volcanism may destroy a forest by burial and create a new ash covered landscape on which a course of primary succession proceeds. By contrast with such devastation, volcanic phenomena can cause more modest disturbance by killing areas of trees without burying the forest floor. Trees may be killed by:

1. Volcanically-induced fire. Fires are started by incandescent volcanic bombs thrown out of a volcano. In the volcanic region of southernmost Japan, fire bombs attain sizes up to 1 m, are propelled for a considerable distance, and may be very common. Over a six year period an observatory recorded 70 bomb-induced fires in the vegetation of the area within view (Tagawa 1964).
2. Gassing. Trees may be killed by sulphur dioxide and other noxious gases emitted during volcanic outbursts.

3. Ash damage to foliage. Physical damage of ashfall on leaves may result in death. Broad leaves are more susceptible to damage than needle leaves and deciduous leaves more than evergreen. The ash acts in several ways. The acid pH of the ash damages the leaves (Tagawa 1964), clogs stomates interrupting gas exchange and thermal control (del Moral 1981), and forms a light barrier reducing photosynthesis by as much as 90% (Cook et al. 1981).

The fine ash that was deposited through the Unit I sequence attests to volcanic activity through Unit I time. If such volcanic disturbance is infrequent and widespread, it might cause the pattern of forest change seen through Unit I. If such disturbance is too frequent, as may happen in a volcanically active region, the effect is to inhibit forest change and perpetuate early successional, depauperate, deciduous, woody stands (Tagawa 1964). With very frequent disturbance the course of change may even be retrograde, from a woody to a herb stage.

The consequences of infrequent disturbance by fire will be discussed in more detail below. Whether fire is initiated by an incandescent bomb or by lightning, the consequences are similar. A problem with attempting to relate ash damage to the Devils Gate pattern of forest change is that susceptibility is highest in the broadleaved deciduous group. The Devils Gate disturbance apparently was most damaging to the evergreens.

Wind. In temperate forests wind damage frequently occurs but the scale is generally modest, involving single vulnerable trees or small patches. Exposed wind-prone sites may suffer more intense catastrophic damage from windstorm (Spurr 1956, Raup 1964, Henry and Swan 1974).

Less frequent but even more severe damage is caused in sheltered sites (Vitousek and White 1981). But even on these vulnerable sites the magnitude of damage is modest, on the order of hectares. For the most part such a modest scale of wind damage would preclude its recognition in the regional pollen rain for two reasons:

1. Often, when single trees or small patches are felled, the tree replacements are by tolerant seedlings of the same taxa that formed the canopy. Site modification is minimal.

2. Local changes are averaged over regional pollen rain and over sampling intervals representing many years and are not detected in the pollen record.

Thus, it is probable that most storms would have caused damage on too small a scale to be detected in the pollen record.

Fire. Fire is a well-studied natural disturbance. Three characteristics are of particular interest in the setting of the present study. They are elaborated here for the purpose of suggesting that the Succor Creek mixed forest, with abundant conifers on a regional scale, would have been highly susceptible and suffered widespread damage by fire. They also suggest a mechanism for a cyclic pattern of infrequent fire that is related to maturation in a mixed forest.

1. Forest composition is a factor in its potential vulnerability to ignition and in the magnitude of the effect. Evergreens are more susceptible than deciduous trees and conifer dominated forests are the most susceptible and most widely disturbed by fire (Heinselman 1973, 1981; Wright and Heinselman 1973).

2. Fire can act on a regional scale and exhibits an inverse relationship between magnitude and frequency of disturbance. In recent history many forests have burned as often as every 50 to 100 years (Loucks 1970, Taylor 1973, Swain 1973, Wright and Heinselman 1973, Henry and Swan 1974, Cwynar 1978, Heinselman 1981), although other forest types have shown much longer fire rotation periods, 650 to 2000 years (New Brunswick; Wein and Moore 1977) and 100 to 1000 years (North Pacific: Franklin and Hemstrom 1981). Conifer forests of the Pacific Northwest have a consistent pattern of relatively infrequent but catastrophic fire, by contrast with a more modest scale of relatively frequent fire in other forests. A study in the Mount Rainier National Park (Franklin and Hemstrom 1981) has reconstructed a history of fire occurrence only every 430 years on an average but the effect is described as "holocaustic" and the scale may be enormous (10^4 to 10^5 hectares). The scale of destruction may be increased even further by the climatic component in fire vulnerability. Since fire is most likely to occur during dry periods, geographically separate fires may be synchronized over a broad region.

3. Forest susceptibility to fire (both the probability of ignition and the magnitude of destruction) increases with time. The potential for destruction by fire can increase directly with the accumulation of organic matter through time. In some settings it increases for a limited period, in other settings indefinitely, depending on climate (Bormann and Likens 1979, Wright and Heinselman 1973, Heinselman 1981).

Of particular interest are the susceptibility of conifers, the potential for damage on a large scale, and a mechanism for the development of a cyclic pattern of infrequent, widespread disturbance. It is also interesting that the characteristics of the Devils Gate forest; its mixed composition and successional trend involving an increasing conifer component, promote the development of a cyclic pattern of disturbance by fire with feedback from the changing forest itself. As such a forest matures and the abundance of conifer trees and litter increases, so does the probability of ignition and the magnitude of destruction, to the point that with a drought season and lightning, fire may be readily initiated. Thus forest succession is repeatedly "reset" to an earlier stage of deciduous dominance and low fire risk and as the forest develops the risk builds until fire is triggered again. Thus an interplay of endogenous biotic factors, in a mixed forest of changing structure and composition, and exogenous factors including an ignition source and favorable weather conditions can account for the cyclic pattern of disturbance, the scale of the damage to vegetation, and thus the magnitude of the pollen shifts in the section.

Pattern and Process in a Disturbed Forest

The pollen record shows a post-disturbance pattern of early deciduous dominance followed by gradual recovery of broadleaved evergreens and conifers. The process of that shift can be reconstructed by comparison with the process of successional change in the modern forest.

Disturbed and cleared forest sites retain the soil surface although its condition depends on the type of disturbance and the extent of erosion soon after. In fire disturbance some of the nutrient content, including at least part of the nitrogen, may be lost by volatilization.

There is no lag in the establishment of woody species. Most of the species and individuals of trees that become established on the disturbed site do so in the first few years after disturbance (Franklin and Hemstrom 1981, Heinselman 1981) so that much of the apparent succession through time is a reflection of different growth and maturation rates rather than of a series of plant replacements. Trees are reestablished either by vegetative growth or by seed germination. Those that establish vegetatively have a substantial lead in maturation. Evergreen oaks, many deciduous trees and shrubs, and perennial herbs sprout vigorously from underground roots and stems that have not been killed. Their initial growth, spurred by established root systems and of released minerals, may be spectacular. Many of them flower early, producing surges of pollen (Swain 1973, Vitousek and White 1981). Conifers, which do not sprout from old stumps or roots, and broadleaved trees that were not present on the site or did not survive the fire vegetatively, may also become established quickly by seed germination.

Conifer and tolerant broadleaved seedlings lag markedly in growth and maturation and thus in pollen production (Swain 1973). Much of the apparent succession shown in the Devils Gate pollen sequence may reflect a similar succession of maturation rates of trees that had been established at more or less the same time. The sprouting vigor and rapid growth of intolerant broadleaved trees resulted in their early maturation and pollen production ahead of slower growing, suppressed, tolerant trees.

The early bloom of herbaceous plants that is characteristic of cleared land is only weakly detected in the Devils Gate sequence in two of the disturbance intervals. There are at least two possible reasons for this. One is suggested by a modern study (Swain 1973). On fire disturbed sites in Minnesota the herbaceous bloom was not detected in lake sediment pollen samples. The finding was attributed to averaging of a short-lived pulse of herbaceous pollen in composite samples representing 10 year intervals. This explanation is equally applicable to the Devils Gate samples which represent even longer sampling intervals and longer time averaging. A second possible reason is suggested by the Devils Gate forest structure. Disturbance was probably more extensive in the vegetation somewhat removed from the lake margin where conifers were more abundant and slopes more susceptible to environmental perturbations, with the consequence that a herbaceous pollen pulse might have been somewhat screened from the site of deposition.

Several factors contributed to the fortuitous record of forest disturbance and secondary succession in Unit I:

1. The depositional setting that preserved a continuous pollen sequence through 67 m.

2. The depositional rate and time scale of disturbance that allowed the resolution of successional vegetation change within the lithologic sampling interval used.

3. The large magnitude of disturbance that was not masked by pollen input from surrounding undisturbed vegetation.

4. Forest vegetation of mixed physiognomic elements where succession involved a shift from broadleaved deciduous dominated assemblages to mixed broadleaved-conifer assemblages that could be readily detected in the pollen record.

The Devils Gate Unit I pollen record may be unusual but it suggests that disturbance may not have been. Having established in Unit I the post-disturbance significance of abrupt shifts to broadleaved deciduous dominance and the dominant roles of some deciduous genera in secondary succession it has been possible to infer similar forest disturbance and succession in more ambiguous pollen records in the previously studied Succor Creek sections (Cross and Taggart 1983).

Conclusion

It is concluded that cycles of temperature seasonality or rainfall, or infrequent and widespread disturbance by ash fall, windstorm, or fire, could account for the asymmetric, cyclic pattern of pollen change in Unit I. It is concluded that fire, in particular, provides a mechanism for cyclic disturbance on the time scale of forest succession. In a forest of mixed evergreen and deciduous elements, increasing fire vulnerability accompanies successional change from deciduous to mixed dominance to the point where lightning and drought trigger another widespread fire.

A pre-Quaternary history of fire has been inferred from other lines of evidence including charcoal (e.g., Harris 1958), fire scarred wood (Jefferson 1982), and reconstructions of climate and vegetation types (e.g., Kemp 1981). The latter approach argues that fire prone forests, in lightning and drought prone climatic regimes, must have had a long history of fire. The Quaternary record of forest fire, showing that forest fire has been normal in many temperate forests, strongly supports such an extrapolation in time. While the Devils Gate disturbance record may be fortuitous, the Devils Gate disturbance pattern may have been a common one in the Succor Creek Flora and in other temperate Tertiary forests.

Study of vegetation change in other Tertiary floras is needed to understand the incidence, nature, and role of natural disturbance in temperate forest history.

SUMMARY AND CONCLUSIONS

This section presents two sets of conclusions. The first summarizes the specific findings of the Devils Gate study that contribute to an understanding of the Succor Creek flora. The second set of conclusions are more general insights for Neogene floral studies derived from the Devils Gate study.

The Devils Gate Study

1. The depositional setting and stratigraphic and lithologic frequency of sampling interval in the Devils Gate section of the Sucker Creek Formation has made possible new insights into the dynamics of the Succor Creek flora on a time scale of successional plant change.

2. Characterization of the Succor Creek flora is based primarily on the significance of the co-occurrence of diverse broadleaved and coniferous groups. The vegetation comprised a forest with mixed broadleaved evergreen, broadleaved deciduous, and coniferous elements growing in proximity and interdigitation. The conifer component was increasingly important in the regional vegetation removed from the immediate basin margin. Elevational zonation may have been less distinct than in modern, temperate, mesic North American forests.

In composition and spatial overlap of elements, the vegetation may have resembled the temperate East Asian mixed broadleaved-conifer forests that grow in mesic climates of high equability.

3. Three patterns of vegetation change are reconstructed from the pollen record that can be related to two orders of disturbance.

  a. Episodic volcanism repeatedly devastated the vegetation and left a mineral ash surface on which was initiated a process of primary vegetation succession from a pioneer herb-shrub stage to a woody alder dominated stage and, when conditions permitted, to a forest stage.

  b. Hydrologic changes allowed the local expansion of a shallow, open water, aquatic assemblage that yielded to a *Glyptostrobus* swamp forest. The stratigraphic association of the herb-alder scrub succession with the aquatic-swamp forest succession links hydrologic disturbance to the volcanism.

  c. Cyclic disturbance periodically damaged or killed large areas of mixed broadleaved-conifer forest. On the cleared sites a process of secondary succession was initiated with early dominance held by the broadleaved deciduous element. With time the forest again became increasingly mixed in composition as broadleaved evergreen and coniferous elements matured. Possible causes of the cyclic disturbances include climatic cycles of seasonality or rainfall, modest falls of volcanic ash, windstorm, or fire.

4. The two orders of disturbance that destroyed forest vegetation were contrasting in occurrence and effects. That which promoted secondary succession occurred in a cyclic pattern, possibly involving feedback from the forest itself. On the disturbed forest site, diverse trees were evidently reestablished in a relatively short period. Fast growing, intolerant, deciduous types initially developed dominance ahead of slower maturing, tolerant trees.

In the particular case of disturbance by fire, the forest would have become increasingly vulnerable as litter accumulated and the forest returned to a semblance of its ignitable pre-fire composition (of mixed dominance with abundant broadleaved and coniferous evergreens) until it was readily ignited again by lightning in a season of drought. Thus a cyclic pattern of fire disturbance could have involved factors of the forest itself that promoted it as well as factors of the environment that then initiated it. Each disturbance reset the process of secondary forest succession to an earlier stage of deciduous dominance.

By contrast, the volcanic disturbance which initiated primary succession was erratic in occurrence and scale, entirely external to the vegetation, and often more devastating in effect. It created harsh, ash soil surfaces on which the establishment of a primary vegetation succession was slow and determined by the condition of the ash. Herbs and shrubs, then a deciduous alder assemblage contributed humus, nitrogen, and other nutrients to the soil.

5. The lower 67 m (Unit I) contrasts with most of the Devils Gate section in vegetation and disturbance regime. Unit I was dominated throughout by forest vegetation with a cycle of disturbance

and secondary succession. Fine sediments preserved a continuous record of forest pollen assemblages. The top of Unit I coincides with the onset of a period of intense volcanism (Figure 15) that was to persist through the time of deposition of the remainder of the section. The upper 550 m has many coarse, barren ash sequences with a discontinuous pollen record; recurring pioneer herb pollen assemblages, deciduous alder assemblages, aquatic assemblages, and a sequence of forest swamp development. Only one sequence has been identified in which a mixed broadleaved-conifer forest assemblage developed. Volcanism was an intense pressure on vegetation through much of Devils Gate time.

6. The vegetation was ecologically complex and flexible. In response to disturbance it showed a resilience that was similar in pattern and degree to modern north temperate forest communities. Deciduous genera that today have species with successional strategies apparently filled the same roles on disturbed sites in these Miocene forests. The implication is that the genera had evolved complex ecological strategies before the Miocene that they have retained to the present.

7. Disturbance was an integral factor in the history of the vegetation. A diagrammatic summary of vegetation history through Devils Gate time (Figure 15) shows that there was no period when the vegetation was stable, no point where succession could be seen to have attained steady state.

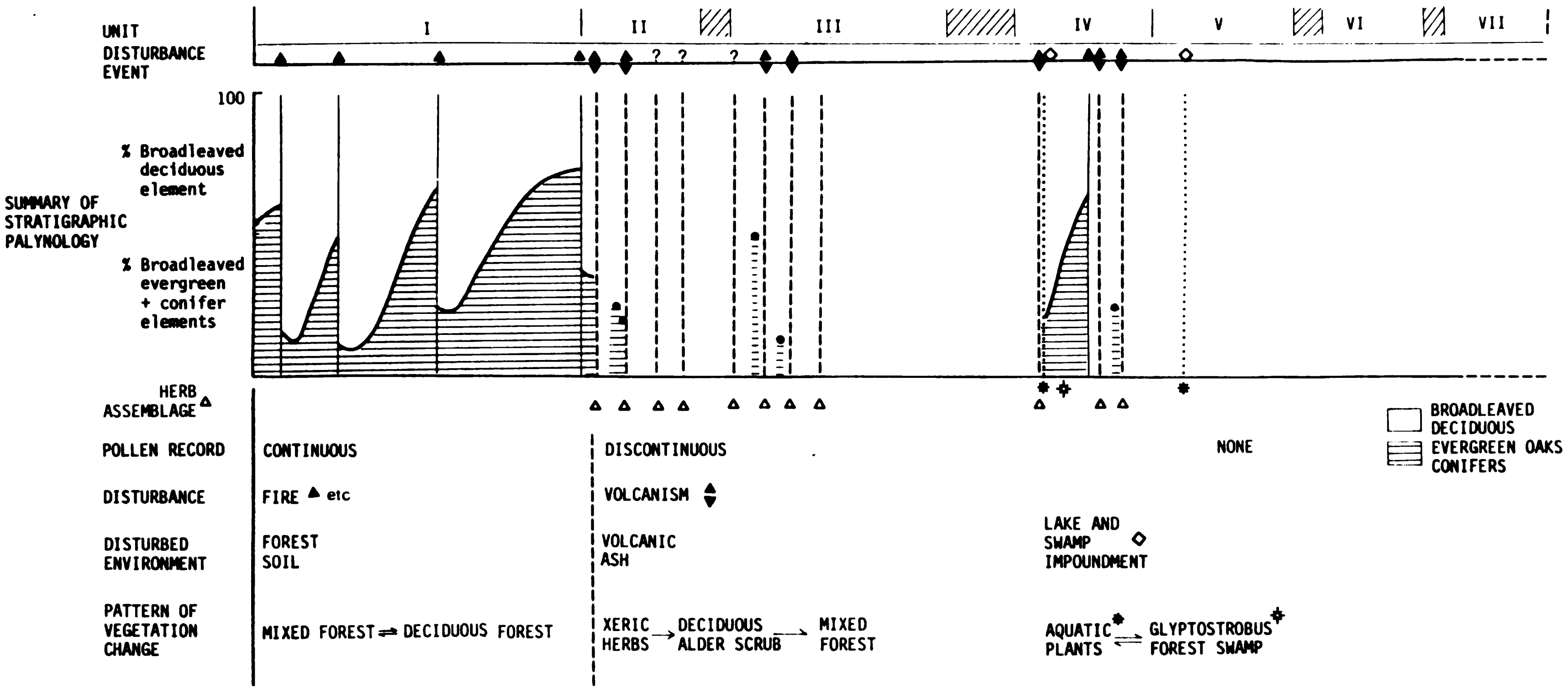

Figure 15. Summary of disturbance and vegetation change in the Devils Gate section. Section is not to scale.

General Conclusions

The time scale of this vegetation study is much shorter than that at which pollen assemblages show evolutionary or climatic trends and thus have biostratigraphic application. However, the time scale of the study has made it possible to recognize the ecological roles of some of the plants contributing to Miocene pollen assemblages and the patterns of disturbance and successional change in a forest of mixed composition (i.e. mixed broadleaved evergreen, broadleaved deciduous, and coniferous elements). The findings have contributed to a view of Tertiary forest vegetation in which disturbance on a time scale of successional forest change may be the rule, and stability on a time scale that would allow a forest to attain steady state may be the exception. This view has implications for climatic and biostratigraphic interpretation of Miocene pollen assemblages and for evolutionary models.

Climatic and Biostratigraphic Interpretations of Neogene Floras.

Tertiary leaf floras have been used in reconstructions of Tertiary climatic change (e.g., Axelrod and Bailey 1969; Wolfe 1971, 1978, 1980; Wolfe and Hopkins 1967). A useful approach has involved comparing physiognomic composition of fossil leaf floras with modern vegetation for which the temperature parameters are known (Wolfe 1978, 1980). In the Pacific Northwest climate interpretation of leaf floras have been frustrated by uncertainties concerning stratigraphic relationships and paleoelevation. This study illustrates another problem that has been expressed (Wolfe 1979). Disturbance regime is another variable that can affect floral composition and thwart interpretation of fossil assemblages. The ratios of broadleaved evergreen, broadleaved deciduous, and coniferous elements may be a function of disturbance as well as of climate, stratigraphic position, and paleoaltitude. The deciduous component may be particularly misleading.

The role of disturbance relative to establishment of a herb dominated assemblage has been identified previously and this same caution for biostratigraphy and paleoclimatic reconstruction expressed (papers by Taggart and Cross).

Roles of Volcanism and Climate in the Evolution of Miocene Floras. Volcanism was intense and sustained and of short duration in eastern Oregon during the Miocene. K/Ar and paleomagnetic analyses of the Columbia River basalts that bracket the ash beds in which the floras are preserved show that most of the volcanics were produced in a relatively short period of about two million years (Watkins and Baksi 1974). It has thus been called an event, the "Columbia Volcanic Episode".

Thus, it appears that the floras of the region, preserved in the volcaniclastic sequences, are a record of the vegetation of thousands or hundreds of thousands of years of intensely disturbed periods of time, and not, as earlier thought, of many millions of years of more modest volcanic disturbance (e.g., Gray and Kittleman 1967). Thus, it can be inferred that such intense and sustained nature of volcanic activity had profound, immediate effects on vegetation. It was a pressure that repeatedly devastated vegetation with a sustained intensity that has no demonstrated present day analogue. The primary, physical consequence of volcanism on the vegetation was an immediate disturbance of far greater impact than the effects of volcanism on global temperature.

Nevertheless, to the immediate primary effects of widespread disturbance of the vegetation must be added the effects of a profound climatic deterioration. Oxygen isotope ratios from benthic foraminifera in the North Pacific Ocean show two temperature plateaus in the Miocene, a warmer one in the Early Miocene and cooler in the Late Miocene with a pronounced cooling event from about 15 m.y. to 13 m.y. (Savin 1977). The "Columbia Volcanic Episode" and the global cooling event may well have been coincident and causally related (Axelrod 1981). Thus the flora that occupied eastern Oregon after the volcanically disturbed Succor Creek interval was the product not only of the physiographic and floristic changes that had occurred during the period of maximum volcanic disturbance, but also of a substantial climatic deterioration.

Role of Disturbance in Evolution and Survival. The record of forest instability suggests an ecological setting for evolution of the vegetation in which disturbance played an important role. It is a normal pattern of cyclic disturbance that creates and maintains ecological diversity with an array of successional strategies, and thus the species diversity, that enables vegetation to respond to episodic disturbance (Holling 1973, White 1979).

Volcanism was more extensive and disrupting to the Succor Creek vegetation than cyclic disturbances had been. Yet the vegetation showed a remarkable resilience. In the Succor Creek setting, then, it may have been a long history of normal disturbances--fire, wind, flood, temperature cycles, etc.--that ensured the evolution and maintenance of ecological variety and flexibility which were to enable the vegetation to respond to the unexpected disturbance--volcanism and climatic deterioration.

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APPENDIX

APPENDIX

Additions to the Succor Creek Palynoflora

ALGAE

Zygnemataceae

Ovoidites Potonie 1951 emend, Potonie 1966 (Plate 3, figures 8-11)

An elliptical body, with a distinct line of weakness extending around the broad dimension, along which it usually splits. Specimens preserved in the Devils Gate section range in shape from very broadly to narrowly elliptical and in size from 50-120 x 20-40um. Sculpture is psilate or rugulate.

Van Geel (1978) established its botanical affinity and ecology. *Ovoidites* is the zygospore or aplanospore of the common green alga *Spirogyra*. The zygospores are produced in open, shallow, relatively eutrophic lakes and marshes (Van Geel 1978, Rich et al. 1982). In the Devils Gate section *Ovoidites* occurs in samples dominated by an aquatic plant assemblage. The acritarchs and fungi described below were co-dominants in these aquatic plant horizons. *Ovoidites* is known from fresh water deposits of Cretaceous to recent age.

ACRITARCHS

Sigmapollis Hedlund 1965 (Plate 3, figures 5-7)

An unpigmented, more or less spherical cyst ca. 25-30 um, with regularly but sparsely spaced spines ca. 1.5-3 um in length. The cyst is distinguished by a sigmoidal aperture.

The genus was first described from a Nevada Miocene lignite, apparently in a similar aquatic assemblage (Hedlund 1965). The Devils Gate specimens differ from them in the angle of curvature of the aperture and the density of spines. The Devils Gate cysts appear to be identical to specimens from the Paleogene of Germany (*Monogemmites pseudosetarius* of Takahashi and Jux 1982) also in a dominantly algal assemblage including several species of *Ovoidites*, it is reported from the Nebraska Miocene Kilgore flora (*Micrhystridium*, MacGinitie 1962). *Sigmapollis* occurs in aquatic assemblages in the Devils Gate section.

Micrhystridium Deflandre I937, emend. Downie & Sarjeant 1963
(Plate 3, figure 4)

Acritarchs assigned to this genus are small, spherical, unpigmented cysts, less than 20 um in overall diameter and ornamented with long spines ca. 5um. They are relatively uncommon in aquatic dominated assemblages through the Devils Gate section.

Psophosphaera Naumova 1939 ex Ischenko 1952 (Plate 3, figures 12-13)

Various more or less psilate spheroidal cysts with thin walls (not more than 1 um) that are commonly folded. Size is variable, generally ca. 25-80 um.

Cysts are common in aquatic-dominated assemblages but also occur in small numbers with the alga Botryococcus in dominantly forest pollen assemblages through Unit I.

GYMNOSPERMS

Pinaceae

Keteleeria (Plate 3, figure 14)

Large (90-120 um), bisaccate grains with a pronounced angle of attachment of the sacs. The cap is thin, 2-4 um in the median, proximal zone where it is widest, tapering gradually toward the margins.

Keteleeria is similar to Abies in size and form with distinct attachment of the sacs. It is distinguished from Abies by the thinner cap lacking a median, proximal zone of thinning (Sivak 1975). In the Devils Gate section Keteleeria is more common than Abies through the Unit I sequence of continuous forest pollen assemblages. Abies is more common in the Unit IV continuous forest sequence.

Macrofossils are not common in the Miocene floras of the region. They are easily confused with those of other members of the Pinaceae. Leaves in the Devils Gate Unit I bed may be Keteleeria, having a raised circular scar and length exceeding 5 cm, but assignment cannot be made with confidence until complete specimens with leaf tips are recovered. Pollen is reported from the Early Miocene Clarkia locality (Wu and Gray 1980).

Pseudotsuga-Larix? (Plate 3, Figure 15)

Grains are 65-90 um in diameter, wall thickness is about 1 um. They are folded and split and poorly preserved.

With so few characters for identification and few specimens preserved, the two genera cannot be distinguished and may even be confused with some algal cysts (Leiosphaeridia). It is thus no surprise that they are rarely reported from Tertiary sediments in the region. The Devils Gate record (Figure 10) consists of a few specimens from few levels in Unit I. Other Miocene reports in the region are from central (Piel 1977) and western (Martin and Rouse 1966) British Columbia where they are reported as "fairly common".

ANGIOSPERMS

Fagaceae

Lithocarpus? (Plate 3, figures 22-23)

Tricolporate with a small, indistinct pore, slightly thickened colpus margin, prolate to more commonly perprolate, faintly granular, size range ca. 13-18 x 5-12um. Castanea-Castanopsis pollen and Lithocarpus pollen have been distinguished on the basis of shape, size, and pore.

Lithocarpus is recognized as having a higher P/E ratio, smaller size, and a less distinct pore. Devils Gate specimens appear to fit this description. Fossil Lithocarpus leaves are taxonomically difficult and could not be satisfactorily distinguished from Quercus hannibali or Castanopsis in the Succor Creek flora (Graham 1965).

Oleaceae

Fraxinus (Plate 3, figures 16-18)

Tricolpate (rarely 4-colpate), colpi of medium length, not clearly defined, fine, fairly regular reticulum to more coarse, angular, irregular, reticulum, sub-spherical to sub-rectangular, size 18-26 x 16 x 23um.

Fraxinus is distinguished from Platanus by the more closed colpi with sharp apices lacking a persistent membrane, by the usually larger size, and the commonly sub-rectangular shape. Where the colpus membrane is lacking in Platanus some grains may be misidentified. Seeds and pollen of Fraxinus are found in small numbers at many Miocene localities in the region, the leaves occur less commonly. Both seeds and pollen occur in the Devils Gate section.

Platanaceae

Platanus (Plate 3, figures 19-21)

Tricolpate, more or less spheroidal, 18-23 um in diameter, finely reticulate. Colpi are of moderate length, gaping with rounded apices and diffuse margins and filled with a persistent verrucate membrane.

The furrow membrane allows ready identification. Where destroyed, Platanus may be confused with some grains of Fraxinus with a fine reticulation. In many specimens the distinction is still clearly on the basis of the round colpal apex. The leaves are common in Neogene floras of the Pacific Northwest and the pollen is reported (Gray 1958, Wu and Gray 1980). In the Devils Gate Unit I, pollen shows cycles of abundance synchronous with other deciduous genera (Figure 10).

PLATE 3

Additions to the Succor Creek Palynoflora

Figure	
1,2,3	Chytridaceae
4	Micrhystridium
5,6,7	Sigmapollis
8,9,10,11	Ovoidites
12,13	Psophosphaera
14	Keteleeria X500
15	Pseudotsuga-Larix? X500
16,17,18	Fraxinus
19,20,21	Platanus
22,23	Lithocarpus?

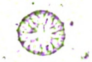
Magnifications X1000 unless otherwise noted.

Plate 3


1


2


3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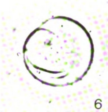
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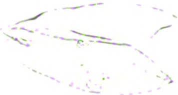
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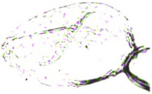
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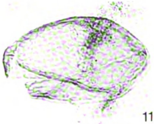
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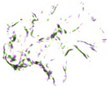
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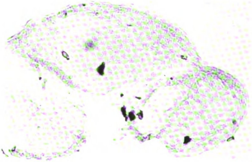
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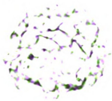
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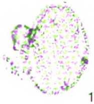
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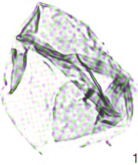
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