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PHANEROZOIC TERRESTRIAL ECOSYSTEMS

Convened by Robert A. Gastaldo and William A. DiMichele

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PHANEROZOIC TERRESTRIAL ECOSYSTEMS

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WELCOME TO THE C₄ WORLD

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THERE ARE TWO principal mechanisms of photosynthesis amongst the plants of the world. One produces a 3-carbon compound as the primary photosynthate and is called C₃ photosynthesis. The other produces a 4-carbon compound as its primary photosynthate and is called C₄ photosynthesis. This latter method is of rather recent origin, and its inception had important consequences for the flora and fauna of the world. The C₄ plants make up a significant portion of global net primary productivity, especially in low latitudes. C₄ plants are predominantly warm-season grasses, while C₃ plants include most dicotyledons and cool-season monocotyledons. In this review we answer the questions about how C₄ photosynthesis differs from C₃ photosynthesis, where C₄ plants are found, and review the paleoecological history of C₄ photosynthesis.

WHAT IS C₄ PHOTOSYNTHESIS?

In the late 1800s it was known that a small fraction of plants, particularly some monocotyledonous plants, possessed a Kranz ("wreath") anatomy, a different anatomy than most dicotyledonous plants (Haberlandt, 1884). Photosynthetic carbon reduction (PCR) to produce sugars occurs in the bundle sheath cells of Kranz anatomy plants, instead of in dispersed mesophyll cells as in C₃ plants. Further distinctions were observed in water-use efficiencies (Shantz and Piemeisel, 1927) and even in ¹³C/¹²C ratios (Wickman, 1952; Craig, 1954). However, it was not until the 1960s that it was recognized that these Kranz anatomy plants used a different photosynthetic pathway than most plants (Kortschak et al., 1965; Hatch and Slack, 1966).

The first photosynthetic pathway known to

have appeared on Earth is the "C₃-pathway," one in which CO₂ is fixed into the three-carbon molecule phosphoglyceric acid (PGA; Table 1 for terms used in the text); hence, the name "C₃-photosynthesis" or "C₃-plants." In this process CO₂ molecules diffuse through the stomata in the leaves where they are reduced by the enzyme Rubisco (ribulose-1,5-biphosphate carboxylase/oxygenase) in the chloroplasts of mesophyll cells (Fig. 1). This occurs in an "open system" that results in the internal CO₂ concentration being lower than atmospheric CO₂.

In C₄ photosynthesis, CO₂ is catalyzed initially by PEP-carboxylase in mesophyll cells where it is fixed temporarily as oxaloacetate, which is a 4-carbon acid, from which the name "C₄-photosynthesis" originates. The oxaloacetate is converted to malic or aspartic acid, which diffuses to the bundle sheath cells where CO₂ is released by decarboxylation. Because the CO₂ cannot escape by gaseous diffusion (i.e., a closed system), the internal CO₂ concentration within the bundle sheath cells is higher than that of the atmosphere. In the bundle sheath cells virtually all the CO₂ is reduced by Rubisco to produce sugars. Figure 2 shows a schematic diagram comparing these two pathways.

How carbon isotopes distinguish between the C₃ and C₄ photosynthetic pathways.—The natural abundance of ¹³C is about 1.11%. The relative ratios of ¹³C and ¹²C are expressed as:

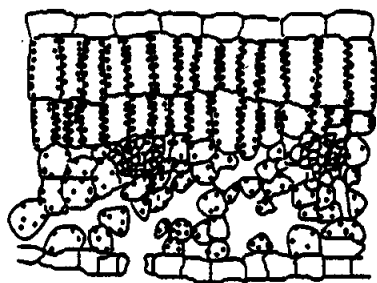
$$\delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$$

where R_{sample} and R_{standard} are the ¹³C/¹²C ratios in the sample and the isotope standard PDB, respectively. Isotope enrichment is expressed as:

$$e_{\text{AB}} = (R_{\text{A}}/R_{\text{B}} - 1) * 1000$$

Leaf cross sections

C₃ plants



C₄ plants

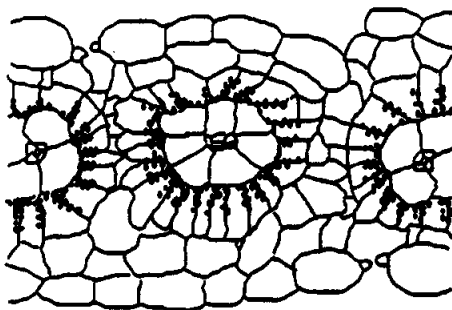


FIGURE 1.—Cross sections of C₃ versus C₄ leaves. Dark areas are sites of PCR, which occurs in the mesophyll cells of C₃ plants and in the bundle sheath cells of C₄ plants.

where R_A and R_B represent the $^{13}\text{C}/^{12}\text{C}$ ratios in A and B, respectively.

The difference in the “open” or “closed” nature of CO_2 reduction results in a large difference between the $\delta^{13}\text{C}$ of the fixed carbon. In an “open system,” there is a 4.4‰ effect due to diffusion as well as discrimination against ^{13}C by the enzyme Rubisco (Farquhar et al., 1982). The net discrimination for C₃ plants averages about 19‰, but ranges from about 14 to 24‰ (Bender, 1968). The modern atmosphere has a $\delta^{13}\text{C}$ value of -8‰ (the “normal” pre-industrial revolution value of the atmosphere of -6.5‰ is diluted by fossil fuel burning) so that this discrimination results in an average $\delta^{13}\text{C}$ value for plants of about -27‰ for the late 20th century. As C₃ plants reduce their stomatal diameters to prevent water loss, CO_2 exchange is reduced and the discrimination is reduced. Therefore, C₃ in water stressed regions can be several ‰ enriched in ^{13}C compared to “average” C₃ plants (Ehleringer and Cooper, 1988). Likewise, recycling of CO_2 from soils, along with reduced photosynthetic rates in light-poor closed canopy environments, can result in $\delta^{13}\text{C}$ values as negative as -36‰ (van der Merwe and Medina,

1989). In the “closed system” photosynthesis that occurs in C₄ plants, only the diffusion isotope effect is important because all the assimilated CO_2 is consumed, and the mean $\delta^{13}\text{C}$ value for C₄ plants averages about -12.5‰ (Fig. 3). It is important to note, however, that even within C₄ plants there is a slight difference in $\delta^{13}\text{C}$ values due mainly to slight differences in the details of C₄ photosynthesis, discussed below.

WHY C₄ PHOTOSYNTHESIS?

Enzymes are needed to catalyze biochemical reactions in photosynthesis. The most abundant enzyme on Earth is ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco), which catalyzes the reduction of CO_2 to form phosphoglyceric acid in the Calvin cycle. This photosynthetic reaction results in the synthesis of sugars, carbohydrates, and ultimately all the products produced during photosynthesis.

However, Rubisco has significant oxygenase activity along with the carboxylase activity. This oxygenase activity consumes oxygen and produces CO_2 so that each oxygenase reaction offsets a

TABLE 1.—Glossary of terms used in the text.

TERM	DEFINITION
<i>angiosperms</i>	flowering plants; more derived than gymnosperms
<i>aspartic acid</i>	HOOC-CH ₂ -CH(NH ₂)-COOH
ATP	Adenosine triphosphate
C ₃	photosynthetic pathway where the first photosynthetic product after assimilation is the 3-carbon compound 3-phosphoglycerate
C ₄	photosynthetic pathway where the first photosynthetic product after PCA is the 4-carbon compound oxaloacetate
<i>carboxylase</i>	enzyme that catalyzes addition of a carboxyl group to an organic compound
<i>cofactor</i>	ion or molecule needed by an enzyme to act on a substrate
<i>dicotyledons</i>	angiosperms having two seed leaves
<i>enzyme</i>	a protein that catalyzes biochemical reactions. The suffix "-ase" indicates an enzyme that acts on a particular substrate
<i>gymnosperms</i>	cone-bearing plants; ancestral to angiosperms
<i>malic acid</i>	HOOC-CH ₂ -COH ₂ -COOH
<i>monocotyledons</i>	angiosperms having a single seed leaf
NADP-me	nicotinamide adenine dinucleotide phosphate; co-factor to malic enzyme
NAD-me	nicotinamide adenine dinucleotide; co-factor to malic enzyme
<i>nicotinamide</i>	a pyridine base C ₆ H ₆ N ₂ O
<i>oxaloacetate</i>	HOOC-CH ₂ -CO-COOH
<i>oxygenase</i>	enzyme that catalyzes addition of molecular oxygen to an organic compound
PGA	photochemical assimilation of CO ₂
PCR	photochemical reduction of CO ₂
PEP	phosphoenolpyruvate
PEP-CK	phosphoenolpyruvate carboxykinase: an enzyme that fixes CO ₂ as malic or aspartic acid in C ₄ photosynthesis
PGA	phosphoglyceric acid (see definition)
<i>phosphoenolpyruvate</i>	3-carbon molecule; HOOC-CO(PO ₃ H ₂)-CH ₂
<i>phosphoglyceric acid (PGA)</i>	a three carbon organic acid that is the first stable product of photosynthesis in the Calvin cycle; HOOC-CH ₂ O-CH ₂ O-PO ₃ H ₂
<i>quantum yield</i>	photosynthetic light-use efficiency
<i>Rubisco</i>	an enzyme that catalyzes reduction of CO ₂ in photosynthesis, or O ₂ assimilation in photorespiration. ribulose-1,5-biphosphate (RuBP carboxylase). H ₂ O ₃ P-CH ₂ O-CO-CH ₂ O-CH ₂ O-CH ₂ O-PO ₃ H ₂

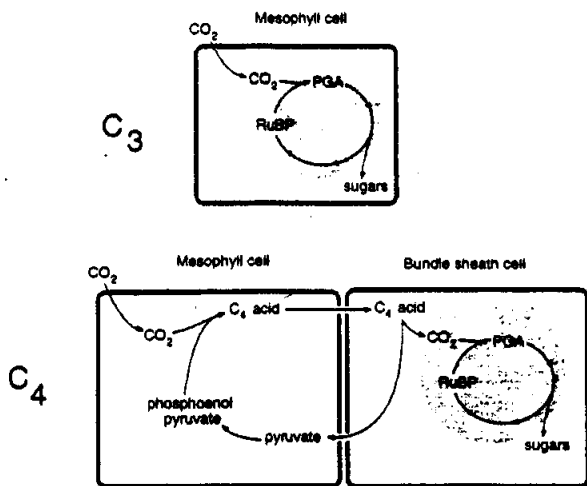


FIGURE 2.—Comparison of C_3 and C_4 cycles.

carboxylase reaction; this process is called photorespiration. In spite of the high selectivity for the carboxylase activity, the oxygenase activity becomes significant at high O_2/CO_2 ratios (i.e., above about 400). In addition the oxygenase activity increases at a faster rate than does the carboxylase with increasing temperature (Jordan and Ogren, 1984). The result of these factors is that C_3 plants become starved for CO_2 at low atmospheric CO_2 (< 400 ppm) and at high growing temperatures. C_4 photosynthesis gets around the problem of oxygenase activity by increasing the internal CO_2 concentration at the site of Rubisco carboxylation as discussed above. Figure 4 shows the crossover between C_3 and C_4 grasses with respect to temperature and atmospheric CO_2 -based relative quantum yields (light use efficiency) of C_3 and C_4 plants (Ehleringer et al., 1997; Collatz et al., 1998).

Atmospheric CO_2 presently (AD 2000) is about 365 ppm. However, bubbles trapped in glacial ice show that the Glacial and Interglacial periods of the Pleistocene had CO_2 concentrations of about 200 and 300 ppm, respectively. At either of these levels, C_3 plants are starved for CO_2 . CO_2 starvation of C_3 plants is characteristic on Earth for at least the last one million years, and probably much longer (see discussion below).

WHERE IS C_4 PHOTOSYNTHESIS FOUND?

C_4 photosynthesis is only found in angiosperms. It is very important in monocotyledons (henceforth monocots) but is uncommon in dicotyledons (henceforth dicots). It is found in a total of 18 plant families (Table 2) — 15 families of dicots and 3 families of monocots. In general, plants using this photosynthetic pathway are found in regions that are warm during the growing season. C_4 photosynthesis in dicots also is associated with soil salinity.

C_4 photosynthesis in monocots.—Only in the grasses (Poaceae) and sedges (Cyperaceae) do C_4 plants make up a dominant or sub-dominant fraction of the global biomass or the globally averaged primary productivity. C_4 grasses comprise approximately half of the 10,000 grasses species (see Table 2 and 3).

The modern distribution of C_4 grasses is determined primarily by rainfall distribution and temperature during the growing season (Teeri and Stowe, 1976). Grasses make up important components of ecosystems where rainfall is approximately equal to potential evapotranspiration; this includes the tropical savannas, temperate to boreal steppes, alpine

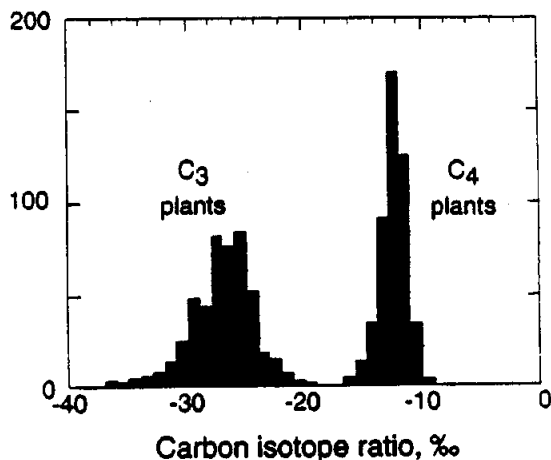


FIGURE 3.—Histograms showing the isotopic composition of C_3 and C_4 plants.

meadows, and many semi-arid deserts in the tropics to temperate zones. In truly arid climate regions where potential evapotranspiration exceeds available moisture, grasses make up a subordinate component of the biomass. On a global basis, C₄ grasses dominate when growing season temperatures exceed about 22° C (see compilation in Ehleringer et al., 1997). Figure 5 shows that C₄ grasses are important components of tropical to temperate grasslands and savannas, but that they become an insignificant part of the biomass at high latitudes. The fraction of C₄ grass species in continental environments is highest at low latitudes, and diminishes at higher latitudes (Fig. 6).

There are slight variations in C₄ photosynthesis that are of interest in paleoenvironmental reconstructions. In particular, the sub-pathways NADP-me, NAD-me, and PEP-ck, have slightly different CO₂ fixation reactions from the atmosphere (Kanai and Edwards, 1999). In addition, these pathways have two important isotopic groupings that are related to moisture stress. Dengler and Nelson (1999) recognize eight different structural types, four of which concern us here: "classical" NADP-me, Aristidoid NADP-me, "classical" NAD-me, and "classical" PEP-ck. (The other four have are subsets of the above mentioned "classical" forms.) These have different quantum yields (Ehleringer et al., 1997), stable isotope compositions, and distribution patterns. The "classic" NADP-me subpathway is found in mesic environments and has a slightly higher δ¹³C value than other C₄ grasses (Vogel et al., 1978; Hattersley, 1982, 1992; Cerling and Harris, 1999). In contrast, Aristidoid NADP-me, NAD-me, and PEP-ck grasses are found in more xeric environments, and are about 1‰ depleted in ¹³C compared to the more mesic adapted "classical" NADP-me grasses.

C₃/C₄ abundances can vary by season. In the Sonoran Desert of the southwestern USA, C₄ grasses dominant during the summer monsoonal season, but C₃ grasses dominant in the winter (Ehleringer, 1978). Ode et al. (1980) documented that C₃ grasses dominate the northern Great Plains in the spring and are replaced by C₄ grasses as the summer waxes, reaching a peak in July.

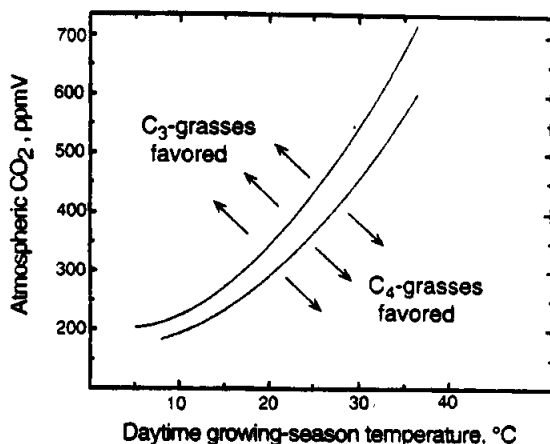


FIGURE 4.—Crossover between C₃ and C₄ plants based on relative quantum yields (see Cerling et al., 1997; Ehleringer et al., 1997).

C₄ photosynthesis in dicots.—C₄ photosynthesis in dicots is much less common than in monocots, but it is found in 15 different plant families of dicots (Table 2, also see Sage et al., 1999a). The Chenopodiaceae is the dominant dicot family exhibiting C₄ photosynthesis, making up more than half of the currently recognized C₄ dicot genera. C₄ dicots generally are found in regions of high soil salinity. In most regions C₄ dicots make up a small fraction of the biomass, although it can be very important locally. P'yunkov (1997) has found that C₄ dicots make up most of the primary productivity in portions of southern Siberia. Ehleringer et al. (1997) showed that C₄ dicots have a much lower quantum yield than most other groups of plants, and that they become at a competitive advantage to C₃ photosynthesis only when atmospheric CO₂ falls to concentrations as low as 200 ppm. This has important implications for the development of C₄ photosynthesis in dicots because CO₂ concentrations as low as 200 ppm have not been maintained for periods longer than about 50,000 years or so, based on the known interglacial - glacial oscillations of CO₂ between about 300 and 200 ppm, respectively.

Distributions of C₃ and C₄ grasses in the savanna and steppe ecosystems

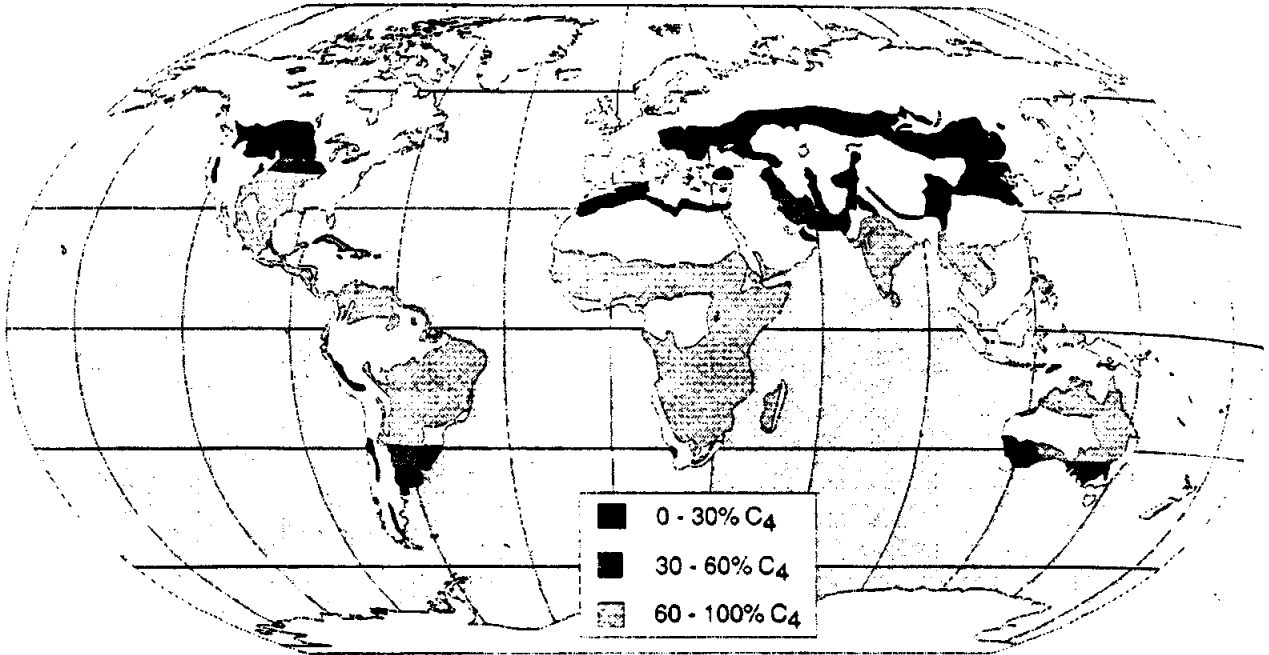


FIGURE 5.—Distribution of C₃ and C₄ grasses in savanna and steppe ecosystems.

Unshaded portions of the continental areas represent regions where grasses are sub-dominant or of low significance in the local ecosystem.

WHEN DID C₄ ECOSYSTEMS BECOME IMPORTANT?

The oldest documented C₄ plants (Tidwell and Nambudiri, 1989), based on their having both Kranz anatomy and their tissues having a $\delta^{13}\text{C}$ of about -12‰, are fossil grasses from Miocene deposits in California that have an estimated age of 12.5 million years (Cerling, 1999). Although other earlier plants have been postulated as using the C₄ photosynthetic pathway, their identification is based on similarity of phytoliths (Dugas and Retallack, 1993) rather than on anatomy or a diagnostic carbon isotope ratio.

Two methods are of particular use in reconstructing the fraction of C₄ biomass in ecosystems: paleosols and fossil tooth enamel. Cerling (1984) showed that soils preserve the carbon isotope ratio of ecosystems and, therefore, fossil soils have been used to reconstruct the fraction of C₄ biomass in fossil ecosystems.

However, many terrestrial deposits do not have carbonate bearing paleosols that meet the criteria for ecosystem reconstruction. Fossil soils must be leached of detrital carbonate, and pedogenic carbonate must be precipitated in the unsaturated zone where mass transfer is controlled by gas diffusion. In certain sequences, fossil soils have recorded the transition from C₃ to C₄ ecosystems (Quade et al., 1989). Because tooth enamel is enriched in ¹³C by 14‰ compared to diet (Fig. 7) and because mammals have selective diets, fossil tooth enamel can serve as a useful proxy to determine when C₄ plants became a significant fraction of the biomass.

Figure 8 shows that equids in Africa, Asia, and North America all changed from a virtually pure C₃ diet to one with a significant C₄ component between 8 and 6.5 Ma. Equids previously have been interpreted to having adapted to a grazing habit in the early Miocene in North America when their teeth became greatly elongated, or hypsodont

CERLING—THE C₄ WORLD

TABLE 2.—Families and genera containing identified C₄ species. Taken from Sage et al. (1999a) which has a more complete list than is given here. Note: some of these genera also exhibit C₃ photosynthesis (see Sage et al., 1999a).

FAMILY	GENERA
Dicotyledoneae	
Acanthaceae	<i>Blepharis</i>
Aizoaceae	<i>Cypselea, Gesekia, Sesuvium, Trianthema, Zaleya</i>
Amaranthaceae	<i>Amaranthus, Froelichia, Gomphrena</i> and others
Asteraceae	<i>Chrysanthellum, Glossocardia, Isostigma, Pectis</i> and others
Boraninaceae	<i>Heleotropium</i>
Capparidaceae	<i>Cleome</i>
Caryophyllaceae	<i>Polycarpaea</i>
Chenopodiaceae	<i>Atriplex, Climacoptera, Salsola, Suaeda</i> and many others
Euphorbiaceae	<i>Euphorbia</i> (also CAM)
Molluginaceae	<i>Glinus, Mollugo</i>
Nyctaginaceae	<i>Allionia, Boerhavia, Okenia</i>
Polygonaceae	<i>Calligonum</i>
Portulacaceae	<i>Anacampseros, Portulaca</i> (also CAM)
Scrophulariaceae	<i>Anticharis</i>
Zygophyllaceae	<i>Kallstroemia, Tribulus, Zygophyllum</i>
Monocotyledoneae	
Cyperaceae	<i>Bulbostylus, Cyperus, Eleocharis, Fimbristylus, Kyllinga, Mariscus, Pycneus,</i> and many others
Hydrocharitaceae	<i>Hydrilla</i>
Poaceae	<i>Andropogon, Aristida, Arundinella, Axonopus, Bothriochloa, Bouteloua, Brachyachne, Cenchrus, Chloris, Chrysopogon, Cymbopogon, Danthoniopsis, Digitalia, Dimeria, Echinochloa, Enneapogon, Eragrostis, Eriachne, Eulalia, Garnotia, Hyparrhenia, Ischamum, Leptochloa, Loudetia, Mesosetum, Miscanthus, Muhlenburgia, Panicum</i> (also C ₃), <i>Paspalum, Pennisetum, Saccharum, Setaria, Sorghum, Spartina, Sporobolus, Stipagrostis, Themeda, Triodia, Urochloa, Zea</i> and many others

(MacFadden, 1992). Equids expanded from North America into the Old World at about 10.5 million years ago, although they did not reach South America until about 2.5 million years ago. Therefore, equids apparently were pre-adapted to the diet of C₄ grasses in widespread parts of the world and, therefore, exploited C₄-grasses as the C₄-biomass increased in the late Miocene to early Pliocene. The resulting new global vegetation

pattern, where C₄ biomass makes up a significant fraction of global biomass, can be considered as the "C₄-world." Various estimates of net primary productivity (NPP) suggest that C₄ photosynthesis makes up about 25% of the global NPP of plants (Collatz et al., 1998). Because virtually all of this is confined within intermediate to low latitudes, the C₄ contribution to NPP at low latitudes is considerably higher than 30%.

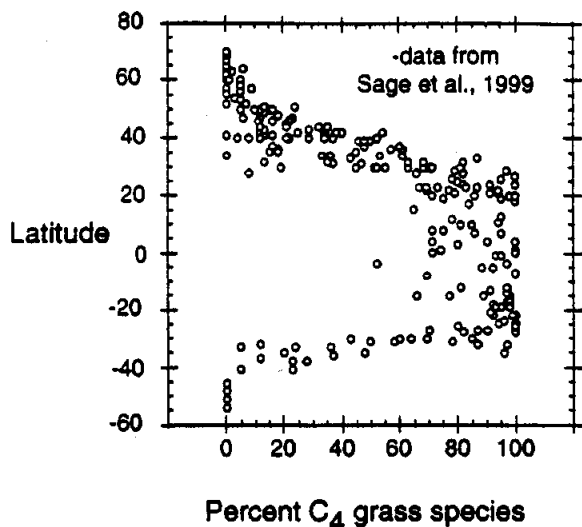


FIGURE 6.—Percentage of C_4 grass species in continental regions (compiled from data in Sage et al., 1999b).

The late Miocene transition into the “ C_4 -world” took considerable time during which global NPP changed to having a significant C_4 component (Fig. 9). Paleosols in Pakistan record that the changeover from a C_3 -dominated (>90% C_3 plants) ecosystem to a C_4 dominated ecosystem (>75% (?) C_4 plants) was rapid on a geological time scale, but was gradual from the local perspective. Equids first record a suggestion of C_4 diet at 8 million years ago, while the paleosol evidence hints at significant C_4 biomass at about 7.5 million years ago. Equids with a C_4 -dominated diet (>75% C_4) are present at about 6.5 million years, although the average paleosol values do not indicate C_4 predominance (>75%) until somewhat later. Seasonal changes in vegetation and diet across the C_3/C_4 transition in the Siwaliks are presently being studied.

A global forcing function must have been responsible for the near-coincident expansion of C_4 biomass in Asia, Africa, North America, and South America. Cerling et al. (1997) and Ehleringer et al. (1997) suggested that the abrupt increase in C_4 biomass was likely due to a decline in atmospheric CO_2 during the Neogene which was triggered when the atmospheric $CO_2:O_2$ ratio

declined below about 1:400. For the modern atmospheric value of 21% oxygen, this corresponds to a threshold of about 500 ppm. As it is very unlikely that atmospheric O_2 levels can change enough to significantly affect the $CO_2:O_2$ ratio, the key for C_3/C_4 competition most likely is controlled by CO_2 changes in the atmosphere. However, estimates of paleo- CO_2 concentrations, based on alkenones and carbonates in marine sediments, indicates low levels (between ca. 200 and 400 ppm) of atmospheric CO_2 for the last 25 million years (Pagani et al., 1999a, b). It has been proposed that global aridity was the trigger for C_4 expansion (Pagani et al., 1999a, b). This seems unlikely considering that C_4 grasslands are found primarily in regions where mean annual rainfall is between about 400 to 1000 mm/year, conditions which are dry, but by no means arid.

How to confuse CO_2 stress with aridity.—Most paleoenvironmental interpretations are based on analogies linked to modern plant distributions that have as important controls

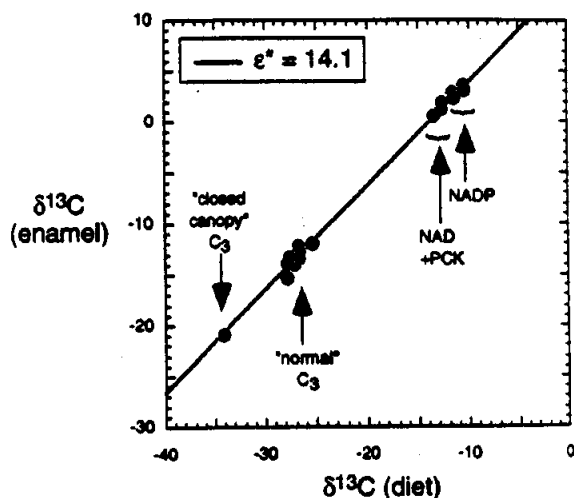


FIGURE 7.—Relationship between the $\delta^{13}C$ of diet and that of tooth enamel for large ungulates shows that the isotope enrichment between diet and tooth enamel is 14.1‰; based on data of Cerling and Harris (1999).

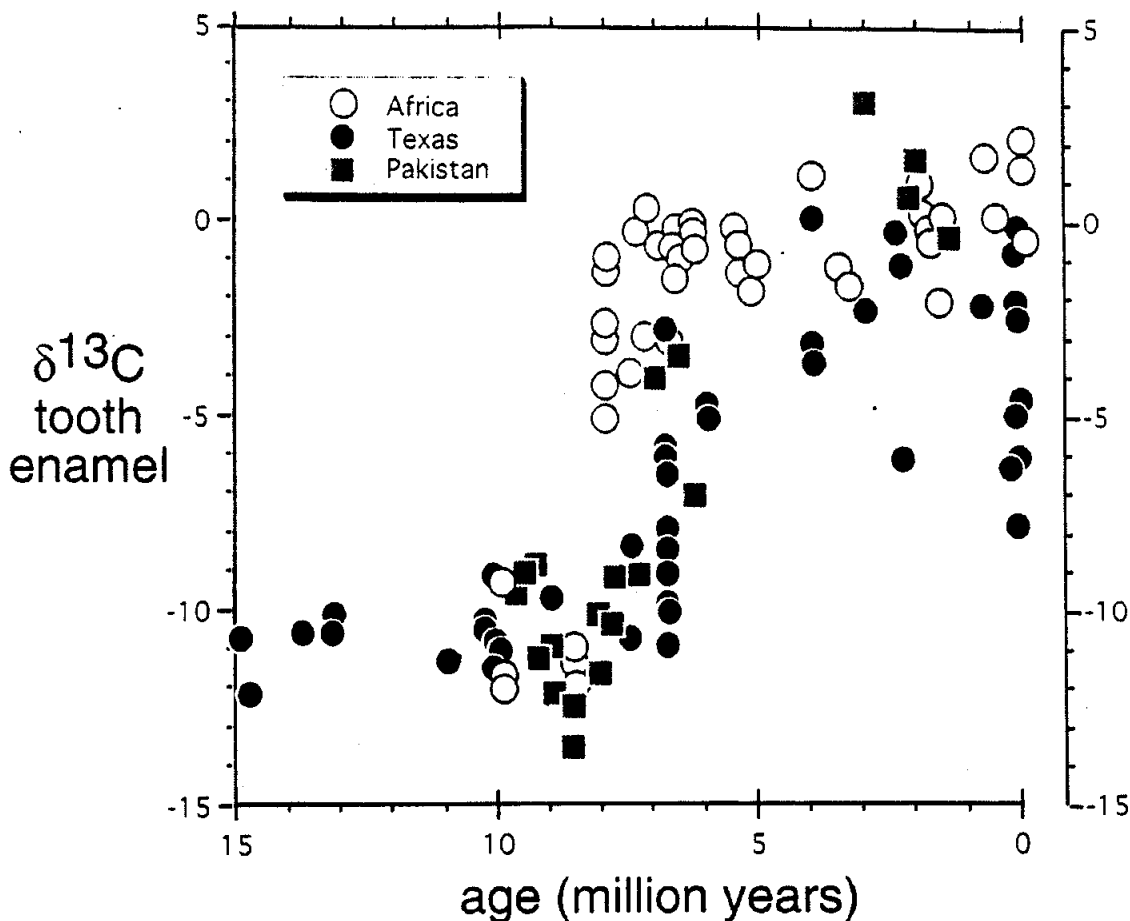


FIGURE 8.— $\delta^{13}\text{C}$ values for equids from North America (Texas), Pakistan (Siwaliks), and East Africa. All show an increase in $\delta^{13}\text{C}$ between about 8 and 6 million years ago, indicating a widespread increase in the global biomass of C₄ plants.

temperature, precipitation, and atmospheric CO₂. The factors interpreted as "aridity" have effects parallel to that caused by CO₂ stress. Under high water stress conditions, plants close their stomata to conserve water; however, this also restricts CO₂ uptake and places C₃ plants at a disadvantage. Therefore, interpretations of "aridity" based on changing plant distributions through time must be tempered by considerations of CO₂ starvation as well. Major changes in flora towards "arid-adapted" plants can result from either water- or CO₂-stress.

WHAT ARE THE CONSEQUENCES OF C₄ PHOTOSYNTHESIS TO MAMMALIAN PHYSIOLOGY?

Important extinctions and periods of faunal turnover are related to the transition to the "C₄-world." Figure 10 shows that the most important faunal turnover events in North America and Pakistan occurred during the transition from C₃- to C₄-dominated ecosystems.

The leaf structure of C₃ and C₄ plants, as depicted in Figure 1, shows that there are

TABLE 3.—Grass tribes, their photosynthetic pathways, and notes on their distribution. Adapted from Sage et al. (1999a), Chapman and Peat (1992), and Chapman (1996).

SUBFAMILY NOTES ON DISTRIBUTION AND ON TRIBES

Arundinoideae

cosmopolitan; mostly C₃, but with some C₄ genera. Includes the reeds (e.g., *Phragmites*). No cereal grasses.

Exclusive C₃: Amthipogoneae, Arunineae, Cyperochloaeae, Micrairieae, Spartochloaeae, Steyermarkochloaeae

Exclusive C₄: Aristideae (*Aristida*, *Stipagrostis*), Eriachneae (*Eriachne*, *Pheidochloa*)

Danthonieae: All C₃ except *Centropodia*

Bambusoideae

low latitude, forested, wet; exclusively C₃. Includes rice (*Oryzae* and *Zizania*)

Anomochloaeae, Brachyelytreae, Bambuseae, Centrotheceae, Diarrheneae, Ehrharteae, Guaduelleae, Olyreae, Oryzae, Phaenospermateae, Phareae, Phyllorhachideae, Puelieae, Strptochaeteae, Streptohyneae

Chloridoideae

low latitude, dry climates. all C₄ except *Eragrostis waller* i. Cereals include millet (*Eleusine coracana*) and tef (*Eragrostis tef*)

Aeluropodeae, Chlorideae, Cynodonteae, Eragrosteeae, Jouveae, Lappanineae, Orcuttieae, Pappophoreae, Peltureae, Perotideae, Pommereulleae, Spartineae, Sporoboleae, Trageae, Triodieae, Unioleae

Panicoideae

tropical to warm temperate. Cereals include millet (*Echinochloa curs-galli*, *Panicum miliaceum*, *Pennisetum glaucum*, *Setaria italica*), tonio (*Digitaria iburua*), sorghum (*Sorghum bicolor*), and maize (*Zea may*). Also sugar cane (*Saccharum officinaru*)

Exclusive C₃: Isachneae

Exclusive C₄: Andropogoneae, Maydeae

C₃ and C₄: Arundinelleae, Neurachneae, Paniceae

Poodieae

cool temperate to polar, or alpine. exclusively C₃. Includes the cereals: oats (*Avena*), barley (*Hordeum*), wheat (*Triticum*), rye (*Secale cereale*)

Aveneae, Brachypodieae, Bromaeae, Meliceae, Poeae, Seslerieae, Triticeae

Stipoideae

temperate to cold and arid; exclusively C₃

Ampelodesmeae, Anisopogoneae, Lygeae, Nadeae, Stipeae

$$\text{Faunal change index} = \frac{(N_F + N_L)}{N_{GR} \Delta T}$$

N_F = number of First Appearances
 N_L = number of Last Appearances
 N_{GR} = Genetic Richness (# of genera)
 ΔT = time (Million Years)
 ΔT 's chosen to be of similar duration
 $N_F, N, N_{GR}, \Delta T$ from Pakistan: Barry et al (1995)
 N. America: Janis (1998)

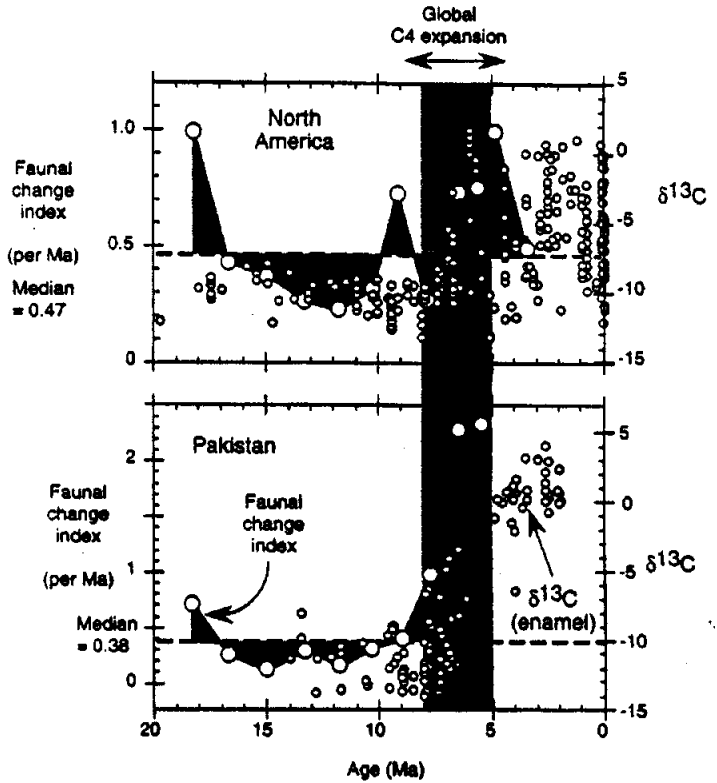


FIGURE 9.—Schematic diagram showing relative temporal changes in the net primary productivity (NPP) of C₃-dicots and gymnosperms, C₃-monocots, and C₄-monocots. For simplicity and because they make up a small fraction of NPP, C₄-dicots and CAM plants are not included in this consideration.

important anatomical differences that could be of major importance to the differences in their relative digestibilities. Nutrients available to herbivores are concentrated near the sites of carboxylation, in the mesophyll cells for C₃ plants and in the bundle sheath cells for C₄ plants. The distribution of these cells explains why C₃ plants have a higher nitrogen content than analogous C₄ plants: the N-rich cells where carboxylation takes place are “diluted” by N-poor cells. Figure 11 shows that C/N ratios for C₃ dicots are lower than that for C₃ grasses, which in turn is lower than that for C₄ grasses. The extra machinery of C₄ photosynthesis comes at a cost of lower nutrient quality. In addition, the sites of N-rich cells in C₄ plants are located inside the thicker protective bundle sheath. Therefore, the protein is less

available. Thus, C₄ plants have a lower nutrient quality and availability than do C₃ plants.

SUMMARY

In this review we have tried to answer a number of questions about the reasons for the distribution of C₄ plants in space and time. C₄ plants have a CO₂ concentration mechanism that gives them a competitive advantage over C₃ plants in times of low atmospheric CO₂ concentration and high temperature. Because of temperature dependence, they are found mainly in tropical through the warm-temperate ecosystems. C₄ plants are found only in angiosperms where they are dispersed across 15 families of dicots and three families of monocots. Only in the grasses do they make up a significant

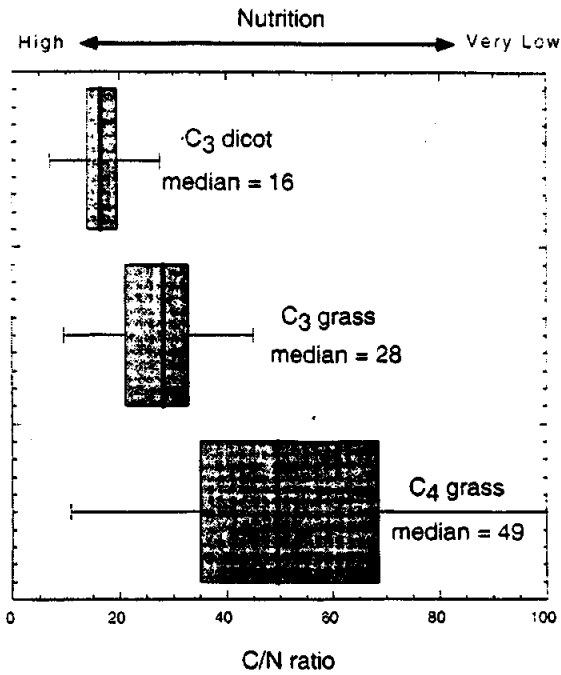


FIGURE 10.— $\delta^{13}\text{C}$ values for ungulates in Pakistan and equids in North America compared with faunal turnover with time.

fraction of the global biomass. Therefore, C_4 plants are the dominant part of semi-desert, savanna, and grassland ecosystems between about 0 and 40 degrees latitude.

Although C_4 plants have been in existence for at least 12 million years, it is only in the last ca. 7 million years that they made up a significant fraction of global primary production. A global expansion of C_4 biomass occurred between about 8 and 5 million years ago, and has been recognized in North America, South America, Asia, and Africa in this interval. Since this C_4 -expansion, the global ecology has been a " C_4 -world" that differs in many respects from any previous ecosystem. Because of biochemical differences in C_4 photosynthesis compared to C_3 photosynthesis, C_4 plants are more difficult to digest and have lower protein contents than do C_3 plants. These factors may have been important in the subsequent evolution of mammals, including humankind.

ACKNOWLEDGEMENTS

We thank F. H. Brown for comments on the manuscript.

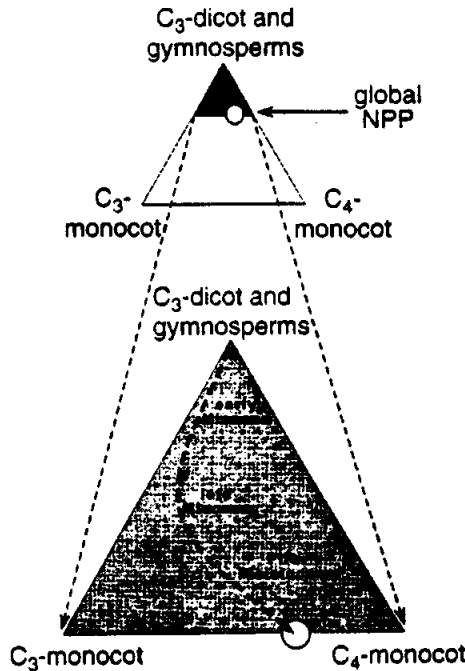


FIGURE 11.—C/N ratios of C_3 dicots, C_3 grasses, and C_4 grasses.

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OUT OF THE GARDEN AND INTO THE COOLER? A QUATERNARY PERSPECTIVE ON DEEP-TIME PALEOECOLOGY

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MOST OF WHAT WE KNOW about ecology inevitably comes from Late Quaternary ecosystems, particularly those of the past few decades. 20th Century ecosystems are the only ones for which we have direct observational and experimental studies. We can obtain detailed records of ecological dynamics at decade- to century-scales over the past few centuries using historical, permanent-plot, demographic, and paleoecological techniques, but only for a select few ecosystems. Radiocarbon-dated fossil assemblages provide records of ecological changes over the past 25,000 years. Because ^{14}C -dating allows independent dating of the assemblages with precision of 50-500 years, detailed spatiotemporal patterns of change can be outlined, but these are limited to certain kinds of organisms and to regions with a high density of fossil sites. When we go beyond the radiocarbon barrier 30-40,000 years ago, the density of datable terrestrial assemblages decreases sharply, and our views of past ecosystems become murkier.

Biologists, both neo- and paleo-, are confronted with a fundamental dilemma. The contemporary biota and ecosystems of the planet are historical products, so to understand them fully we must examine evolutionary and environmental history across a range of timescales (10^0 - 10^9 yr). At the same time, the fossil record provides only limited and fragmentary glimpses of this history, so we must draw from our understanding of modern organisms and ecosystems to interpret that record. However, as we increase the timespan under consideration, we also increase the range of environmental variability, the likelihood of novel environmental and biotic combinations, and the evolutionary distance between past and modern biota.

A "powers-of-ten" temporal analysis illustrates the problem. At the time of this writing (May 2000),

we are in the second year of a La Niña climatic event, characterized by relatively wet winter/spring conditions in the Pacific Northwest and dry conditions in the Southwest. The wildfires currently raging in Arizona and New Mexico are predictable outcomes of this atmospheric circulation pattern. Ten years ago, we were in the first few months of a strong five-year El Niño, in which precipitation patterns were reversed between the two regions. Geographic distributions of sedentary species have not changed in the elapsed decade, but other ecological patterns—regional patterns of productivity, distributions of certain migratory species, population size and recruitment history of many species, regional fire occurrences—have differed, many related to this ENSO (El Niño-Southern Oscillation) variation. We have learned much about ecological effects of ENSO during the past decade, so we can now go back to explain ecological patterns and events recorded in 1990 with considerable confidence.

For the year 1900, we have a more limited instrumental network of environmental conditions, but sufficient to know that 1900 was in the middle of a moderate multi-year El Niño event, which was superimposed on a late 19th Century warming trend in many areas as we emerged from the multi-century "Little Ice Age." We depend upon non-instrumental records (historical documents, tree-rings, etc.) to work out details of the latter. Overall, environmental conditions were similar to the present, and historical records, photographs, field observations, and records from herbaria and museums indicate that, although the landscape has changed considerably owing to direct and indirect effects of human activities, ecosystems not dramatically altered by human impacts are similar to those of 1900. We can apply ecological knowledge gained in the past century to explain

phenomena recorded in 1900, as well as those recorded in natural archives such as tree-rings and sediments.

Although 1000 A.D. is well beyond the reach of instrumental records, we can still infer the environment of many regions from historical documents and temporally precise natural archives (tree-rings, ice cores, varved sediments), and archives with poorer precision provide more general information. Paleocological data indicate that, although the climate of some regions differed modestly from today, geographic distributions of most species have not changed much, and species assemblages in the fossil record are recognizable on the modern landscape. Once again, application of current ecological knowledge is straightforward. Although differing frequencies and magnitudes of environmental variability (e.g., ENSO, drought cycles) affected some ecological processes (e.g., fire, recruitment, mortality), we can study those influences based on what we know of the present and more recent past.

Going back to 10,000 years ago takes us beyond recorded history, so we are limited to proxy evidence for environment and biota. The planet was in an unfamiliar climatic regime, with Northern Hemisphere atmospheric circulation strongly influenced by the presence of the remnant Laurentide Ice Sheet covering much of Canada. Furthermore, orbital parameters were very different from today. For example, summer insolation in the Northern Hemisphere was higher, while winter insolation was lower. Paleoclimate inferences from proxy data are less precise than for more recent intervals, but are consistent with predicted effects of the altered orbital forcing and the ice sheet. ENSO variation appears to have been dampened relative to the past few millennia. The biotic record indicates substantial geographic displacements of species ranges relative to today, and many regions were occupied by vegetation and faunal assemblages that have no modern counterpart. We can still apply our ecological knowledge of the individual species to interpretation of the record, but the uncertainties are substantial, especially where the environment and/or communities are unlike any existing at the present.

The next step, 100,000 years ago, places us in the early phases of the last glacial period. We can infer much about the prevailing environment from proxy records, but temporal precision is coarse for many records. Ice-core records indicate that atmospheric CO₂ concentrations were <80% of pre-industrial levels. The Earth was in an interstadial period, during which continental ice sheets were in a temporary retreat phase. Pollen and macrofossil records indicate that, although the plant taxa were modern, plant associations in many parts of the world were unlike any found today. Records of terrestrial fauna, although less well-dated, show similar patterns for the period, as well as many now-extinct vertebrate species and genera.

Skipping into the Tertiary (10,000,000 years ago), we enter a substantially altered world, with different continental positions, minimal ice sheets, and unique patterns of atmospheric and ocean circulation. Temporal precision of records is reduced, so we run a greater risk of comparing proxies or assemblages that differ by 10³-10⁶ years in age. Many modern genera can be identified from the fossil record, but often on continents where they no longer exist, and usually consisting of different species. Some of those species have modern descendants, but other species, as well as many genera and a few families, represent now-extinct lineages. Taphonomic knowledge, as well as ecological knowledge of the taxa and growth forms in the record, aid in interpretation, but we are forced to fill in substantial detail with our imaginations.

The pre-Quaternary world is obviously peculiar to our modern eyes. For that matter, any world dating before the Late Holocene is peculiar — many of the current vegetational, biogeographic, and climatic patterns of Earth developed only within the past 3000 years. If the biological and environmental configurations at any point in time are unique, can lessons drawn from the single period we know well (*viz.*, the Late Quaternary) be applied to another (say, the Late Miocene)? Addressing this question requires something on the order of a series of workshops and a comprehensive research program, rather than a single short paper. I will offer some perspectives as a Quaternary ecologist, and outline some discussion points, in

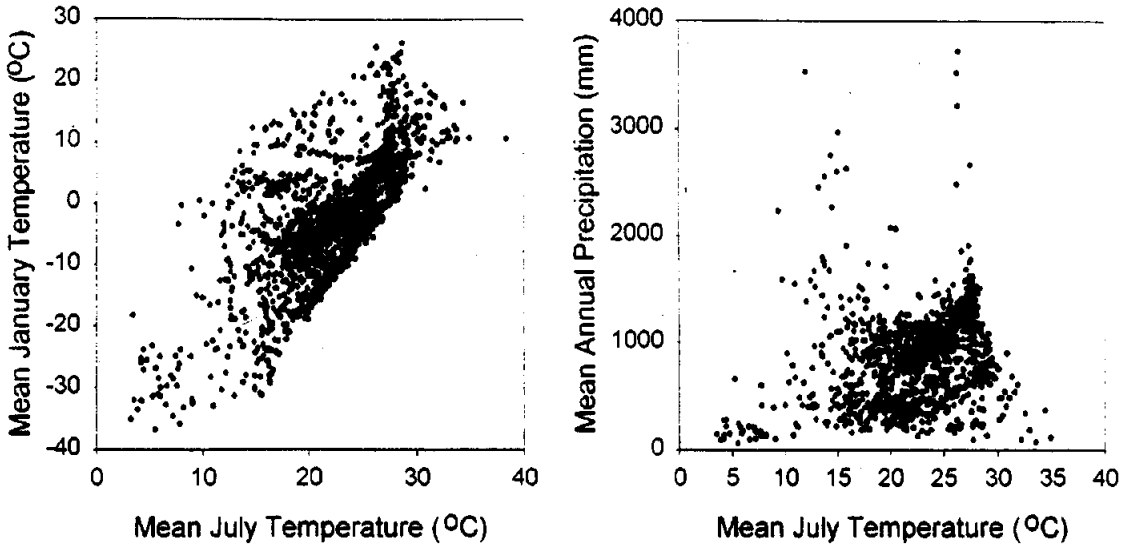


FIGURE 1.— Realized environmental space for the late 20th Century (1951-1980) in North America for three climatic variables, represented by the point clouds in the diagrams. The points represent 3364 climate stations in Canada, Alaska, continental United States, and Mexico (Vose et al., 1992). Note the large portions of “empty” environmental space (i.e., areas unrepresented by points). Some of those empty areas are physically impossible. Others are unrepresented in North America, but occur on some other continents today. Others have been represented in North America within the past 25,000 years (see Figure 2), but are absent from the continent (and in many cases the globe) now. Note that these graphs are two-dimensional representations of a three-dimensional space, and hence mask the full extent of “empty” environmental space. The three-dimensional space defined by these variables is a mere slice of an n -dimensional hyperspace.

hope of fostering dialogue between Quaternary ecology and deep-time paleobiology.

INDIVIDUALISM: CHANCE OR NECESSITY?

It is certainly no secret among paleobiologists that Quaternary ecologists, particularly those studying terrestrial biota, have reached consensus that species responded individually to the dramatic environmental changes of the past 25,000 years. Species that co-occur widely today had different centers of distribution during the Last Glacial Maximum, and migrated at different rates and in different directions during the Holocene (Davis, 1976, 1981; FAUNMAP, 1996). Many

modern species associations can be traced back only 3000 to 9000 years (Webb, 1987, 1988; Huntley, 1990a, 1990b; Overpeck et al., 1992). Vegetational zonation patterns along elevational gradients have changed substantially during the Holocene (Thompson, 1988; Betancourt et al., 1990; Jackson and Whitehead, 1991; Spear et al., 1994). Species assemblages unlike any found today are documented widely in the early Holocene and late-glacial (West, 1964; Graham, 1986; Jacobson et al., 1987; Overpeck et al., 1992; FAUNMAP, 1996).

The mechanisms underlying these dynamics are less widely understood or agreed upon. The individualistic patterns have been viewed as stochastic manifestations, arising from the vagaries

of "refugium" location, random dispersal and colonization events, and geographic barriers (Davis, 1976, 1981, 1983; Birks, 1989). I held this view until the mid-1980s, as did many other Quaternary ecologists; some adhere to it today. The stochastic view was inspired by Gleason's (1926) hypothetical examples in which random colonization events gave rise to multiple, stable associations in identical environments. It also fit well with Egler's (1954) "initial floristic composition" hypothesis for secondary succession, and with increasing attention in the 1970s and 1980s to stochasticity, incumbency, and non-equilibrium as important attributes of community structure (e.g., Sale, 1977; Connell, 1978; Sousa, 1979; Simberloff, 1980; Wiens, 1984).

An alternative, environmentally deterministic interpretation of Quaternary ecological dynamics developed in the 1970s (Webb, 1981; Prentice, 1983; Webb et al, 1983), and was articulated in a series of papers associated with COHMAP (Cooperative Holocene Mapping Project) (Webb, 1986, 1987, 1988; Huntley, 1988, 1990a, 1990b). Some form of this view is probably held by most Quaternary ecologists today. My own epiphany came in part from recognition (based on the COHMAP effort) that spatially correlated climate variables can change independently in time while remaining correlated in space (Jackson and Whitehead, 1991). It was then a simple matter to plug that observation into ecological niche theory and explore the consequences (Jackson and Overpeck, 2000).

QUASI-DETERMINISTIC INDIVIDUALISM: A CONCEPTUAL MODEL OF THE WAY THE QUATERNARY WORLD WORKS

Individualistic responses of species to environmental changes of the Late Quaternary can be explained as quasi-deterministic phenomena by a simple conceptual model, outlined in detail by Jackson and Overpeck (2000). This model represents an expansion of classical niche theory

(Hutchinson, 1978) to accommodate current knowledge of the nature of environmental change. Here I present the model as a set of axioms, corollaries, and deductions (theorems) about environment, niche, and community.

Axiom 1: The environment experienced by an organism is multivariate, and can be described as an n-dimensional hyperspace.—This seemingly self-evident statement needs elaboration to be fully appreciated. "Climate," often treated as a single if amorphous variable, or reduced to "temperature," is a combination of many variables that individually and interactively influence the establishment, growth, and reproduction of organisms. For a terrestrial plant, a partial list of relevant temperature-related variables might include maximum summer temperature, minimum winter temperature, mean growing-season temperature, duration of winter days with temperature below a damage threshold, frequency of years with temperatures suitable for seed germination during the appropriate season, frequency of years or successive years with summer temperatures above a carbon-gain threshold, number of consecutive days with temperatures above a damage threshold, frequency of years with subfreezing temperatures in late spring or early fall, and frequency of days with early-morning temperatures below a low-temperature photoinhibition threshold. Some of these variables interact with moisture-related variables, often in compensatory fashion (e.g., higher temperatures can be tolerated if water supply is abundant).

Climate responses of plants are often described in terms of climatic averages, but most plants are sensitive to intra- and interannual variability in climate. Perennial plants respond to interannual climatic variation by varying net primary production and carbon allocation. This, of course, is why we can derive annually resolved records of variation in temperature- and moisture-related variables from tree-ring widths. This variation is also manifested in carbon storage, reproductive effort, and defense against herbivores and pathogens. Most species are capable of surviving average conditions at sites where they do not occur,

infrequent episodes (e.g., early or late frost outbreaks, droughts) prevent population establishment or persistence.

Population maintenance requires successful reproduction, and seed germination, seedling survival, and recruitment into reproductive age-classes are often sensitive to different conditions than are adult growth or reproduction. For many plant species, seed germination and seedling growth during the first few years depend upon particular seasonal conditions that are essentially unperceived by adults of the same species. For example, seedlings with shallow root systems are more sensitive to short-term growing-season drought than mature trees with better-developed root systems. In woody vegetation, this sensitivity is manifested in irregularity of recruitment events for individual species—recruitment is often episodic rather than uniformly distributed among years. Some of this variation is attributable to interannual variation in pollination success and seed crop (themselves determined in part by environmental variation), but much comes from interannual and interdecadal variation in germination and survival related to climatic variation. In non-woody plant communities, relative abundance of species often varies on annual to decadal timescales in response to climate variation.

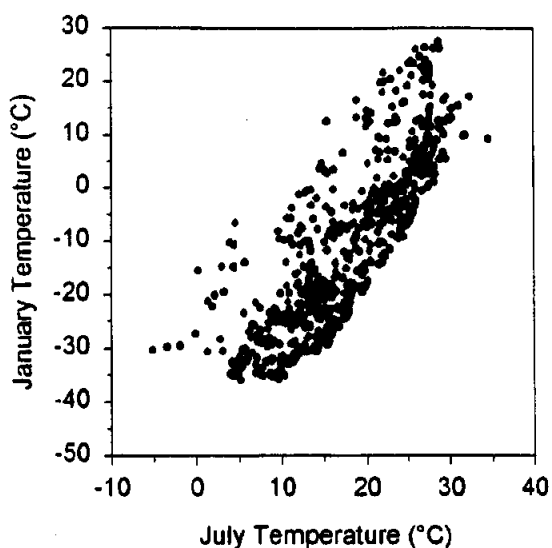
Axiom 2: The environmental space that actually occurs on Earth is a subset of the total potential environmental space (Fig. 1).—This observation has not been well-discussed in the niche literature. Not all possible combinations of variables can occur on the surface of Earth at a particular time; some portion of the environmental hypercube will be empty (i.e., devoid of points corresponding to locations on Earth; Fig. 1). Some combinations of variables are physically impossible on the planetary surface (e.g., extreme low temperatures and high precipitation). Some variables have a higher magnitude of change in time than in space (e.g., although atmospheric CO₂ concentration decreases with increasing elevation, there are no points on Earth's surface sufficiently high to have CO₂ concentration approaching that of the Last Glacial Maximum). And the surface of

the planet is finite and spatially heterogeneous, so not all combinations of bedrock or soil chemistry and climate are possible. The particular combinations of environmental variables that occur at any given time can be defined as the *realized environmental space* (Fig. 1).

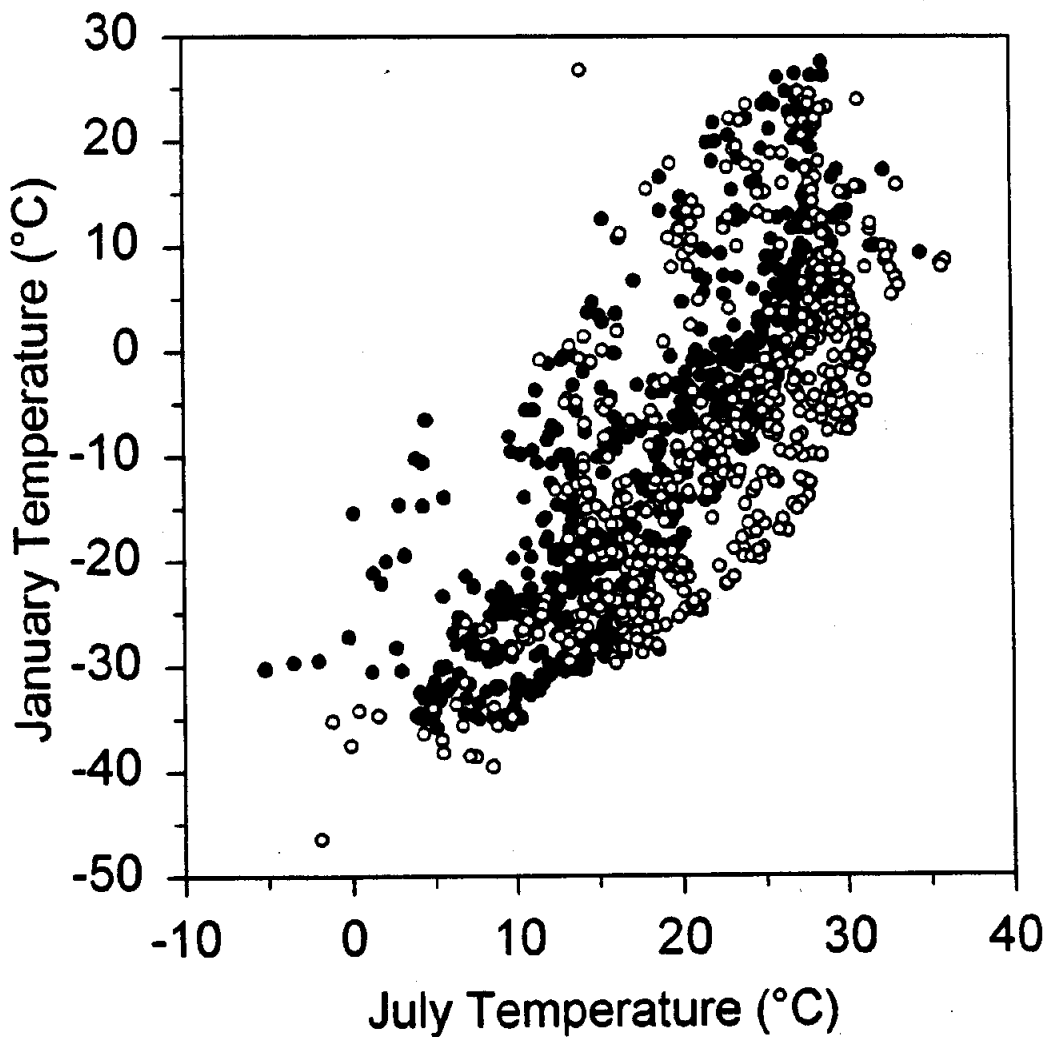
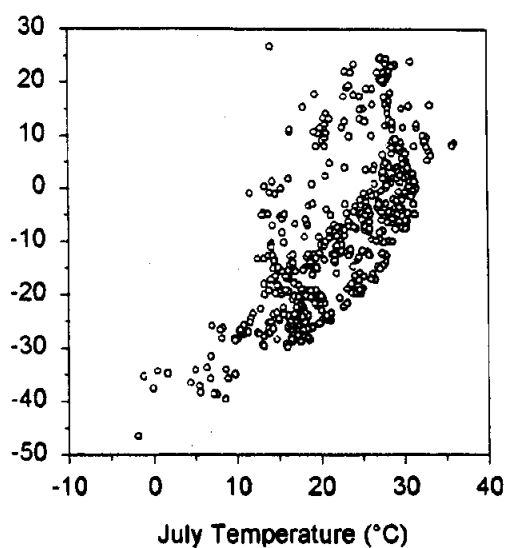
Axiom 3: The shape and position of realized environmental space change in time (Fig. 2).—Environmental change can lead to new configurations of the realized environmental space. Many climatic variables are correlated in space (e.g., summer and winter temperature along latitudinal and elevational gradients, temperature and precipitation along elevational gradients). The variables, however, can change in different directions through time, while still being spatially correlated. For example, between 14,000 and 6000 yr B.P., Northern Hemisphere summer insolation, at mid-latitudes was as much as 9% higher than today, while winter insolation was as much as 15% lower, owing to changes in Earth's orbital parameters (Berger, 1978; Berger and Loutre, 1991). This anomaly, in turn, led to greater seasonal contrast (i.e., warmer summers together with cooler winters) in many regions during that period, and other factors (ice sheets, ocean circulation, etc.) led to additional changes. These and other kinds of environmental changes result in fundamental changes in the shape and position of the realized environmental space (Fig. 2).

The dramatic effects of orbital changes, ice-sheet effects, and atmospheric trace gases (CO₂, methane) on climate change at multimillennial timescales are well-documented (e.g., Wright et al., 1993; Webb, 1998). Much recent attention in paleoclimatology has focused on higher-frequency temporal dynamics (decades to millennia). Variation in seasonal and geographic distribution of precipitation is of particular ecological interest. Variation in El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), linked to quasicyclic shifts in sea-surface temperatures respectively in the tropical Pacific and North Pacific, result in subcontinental shifts in distribution of winter precipitation in North America (Mantua et al., 1997; Cayan et al., 1998; Dettinger et al., 1998). The North Atlantic

Modern



Simulated (11,000 yr B.P.)



Oscillation (NAO) causes annual and decadal changes in winter temperatures and precipitation in eastern North America, Europe, and Africa (Hurrell, 1995). For especially sensitive regions (e.g., southwestern U.S., Pacific Northwest, northern plains, southeastern U.S., southern Alaska, eastern Canada), winters may alternate at annual to decadal scales between wet and dry, with different regions experiencing precipitation maxima at different times. These and similar oscillations have been linked to episodic variations in fire regimes, drought mortality, population density, and population recruitment in plants and animals (e.g., Swetnam and Betancourt, 1998; Post and Stenseth, 1998; Post et al., 1999).

The behavior of ENSO, PDO, NAO, and other oscillations over long timespans is poorly understood, but the variation is clearly not stationary (i.e., not evenly spaced fluctuations about a constant mean). These oscillations have undergone shifts in magnitude and frequency during the past century, and evidence is accumulating that larger changes have occurred during the past 25,000 years (Clement et al., 1999; Rodbell et al., 1999; Cane et al., 2000). Such shifts may underlie many observed changes in Holocene climate that are not attributable to orbital forcing in a straightforward way. A simple shift in the frequency and/or duration of one or the other phases of ENSO, for example, would lead to large, ecologically significant changes in precipitation

regimes over much of North America.

Axiom 4: Each species is characterized by a fundamental niche, which occupies some portion of the environmental hyperspace (Fig. 3a).—Individuals of a species can develop, survive, and reproduce only within a subset of the total range of environmental conditions that might occur. The fundamental niche of a species represents the particular combinations of environmental variables that allow survival and reproduction of individuals of that species, and can be envisioned as a solid occupying some portion of the total environmental space (Fig. 3a; see Jackson and Overpeck, 2000 for a fuller discussion). The fundamental niche can undergo evolutionary change owing to directional selection or to other factors (e.g., genetic drift).

Axiom 5: No two species occupy the same total fundamental niche.—In classical niche theory, this axiom derives from the competitive exclusion principle, which emphasizes resource axes of the niche. It can also be justified for environmental/habitat axes (e.g., climatic tolerances). By definition, species differ in morphology, anatomy, and physiology, so differences in environmental tolerances are inevitable. For example, subtle differences in leaf morphology can have large ecophysiological consequences (Jordan and Smith, 1993; Smith et al., 1997).

Axiom 6: The potential niche is defined as the intersection between the fundamental niche and the realized environmental space (Fig. 3a).—The

FIGURE 2 (OPPOSITE).—How realized environmental space can change through time. Black dots represent the modern realized environmental space defined by two variables (mean July and January temperature) for North America. Note similarities with Figure 1; differences are attributable to different data sets. The open circles represent simulated paleoclimate for 11ka (11,000 years Before Present), when orbital parameters, ice-sheet extent, and trace-gas concentrations were very different from today. Note that, although the point clouds overlap, the 11ka point-cloud occupies environmental space not represented in North America today. The primary difference is an increase in July temperature and decrease in January temperature at 11ka relative to today. Individual points represent random 2% subsets of values from a 25-km equal-area grid for North America. Modern data are gridded from modern climate stations (Thompson et al., 1999). The 11ka data are from NCAR CCM1 simulations (Bartlein et al., 1998). Modified from Jackson and Overpeck (2000).

potential niche is introduced as a new concept here, made necessary by the changing nature of the realized environmental space. The potential niche represents the particular portion of environmental space that individuals of a species might potentially occupy at a given time (i.e. during a particular realization of the environmental space; Fig. 3a).

Axiom 7: The realized niche defines the environmental space actually occupied by populations of a species at a given time (Fig. 3a).—The realized niche is a subset of the potential niche, and is governed by biotic interactions (interspecific competition, producer/consumer relations, mutualisms) and by dispersal and colonization processes. A species may not occupy its entire potential niche because individuals have not yet managed to disperse to all suitable sites, or because they are excluded by the presence of competitors or harmful consumers, the absence of necessary mutualists (e.g., mycorrhizae, pollinators), or other factors.

Corollary 1 (of Axioms 3, 4, and 6): The potential niche will change in size, shape, and position as the realized environmental space changes (Fig. 3b).—If the fundamental niche remains constant as the environment changes, shifts in the realized environmental space will lead to changes in the portions of overlap between the fundamental niche and the realized environmental space (Fig. 3b). Any changes in the potential niche will inevitably result in changes in the realized niche.

Corollary 2 (of Axiom 6): Individuals of different species can co-occur only where their potential niches overlap (Fig. 4).—Overlap of potential niches is a necessary but not sufficient condition for co-occurrence; sites within that area of overlap must be colonized by individuals of each species (i.e., the realized niches must also overlap).

Corollary 3 (of Axioms 3, 5, and 6): The potential niches of two or more species may overlap at certain times but not others (Fig. 4).—As the shape and position of the realized environmental space changes, it may overlap at some times with the fundamental-niche intersection of groups of species and not at other times.

Theorem 1a (from Corollary 1): Species that have relatively slow evolutionary response times

will track environmental changes by tolerance, migration, or extinction (Fig. 3b).—These species-level responses will be aggregates of similar population-level responses at individual sites. If the environment at a particular site occupied by a population of a species remains within the potential niche of that species after an environmental change, the population can potentially remain in place (tolerance), although it may change in size and have different neighbor species (competitors, consumers, etc.). If the environment at the site passes out of the potential niche as a result of environmental change, the local population is fated for extirpation. New sites, formerly outside the potential niche, may pass into the potential niche as the environment changes. Populations can be established at those sites provided individuals or propagules can disperse to them (migration) (Huntley and Webb, 1989).

Theorem 1b (from Axioms 3 and 4): Species with relatively rapid evolutionary response times will track environmental changes by adjustments in the fundamental niche.—Evolutionary adjustment in equilibrium with environmental change is possible only if the evolutionary response time is rapid relative to the rate of environmental change (Webb, 1997). Theorems 1a and 1b are not mutually exclusive; some local populations of a species may track environmental change via evolution while others undergo extinction or disperse to newly suitable sites. However, the primary modes of response for terrestrial plant species to millennial-scale changes during the late Quaternary have consisted primarily of tolerance, migration, and extinction (Webb, 1997; Jackson and Overpeck, 2000).

Theorem 2a (from Corollaries 2 and 3): Particular species associations will emerge under some environmental conditions and then vanish as the environment changes (Fig. 4).—If the magnitude of change in the shape and position of the realized environmental space is sufficiently large, then species assemblages should change. Some species associations will disappear, replaced by new ones. In the course of time, a species may co-occur with a wide array of other species, not always simultaneously. Aggregation and

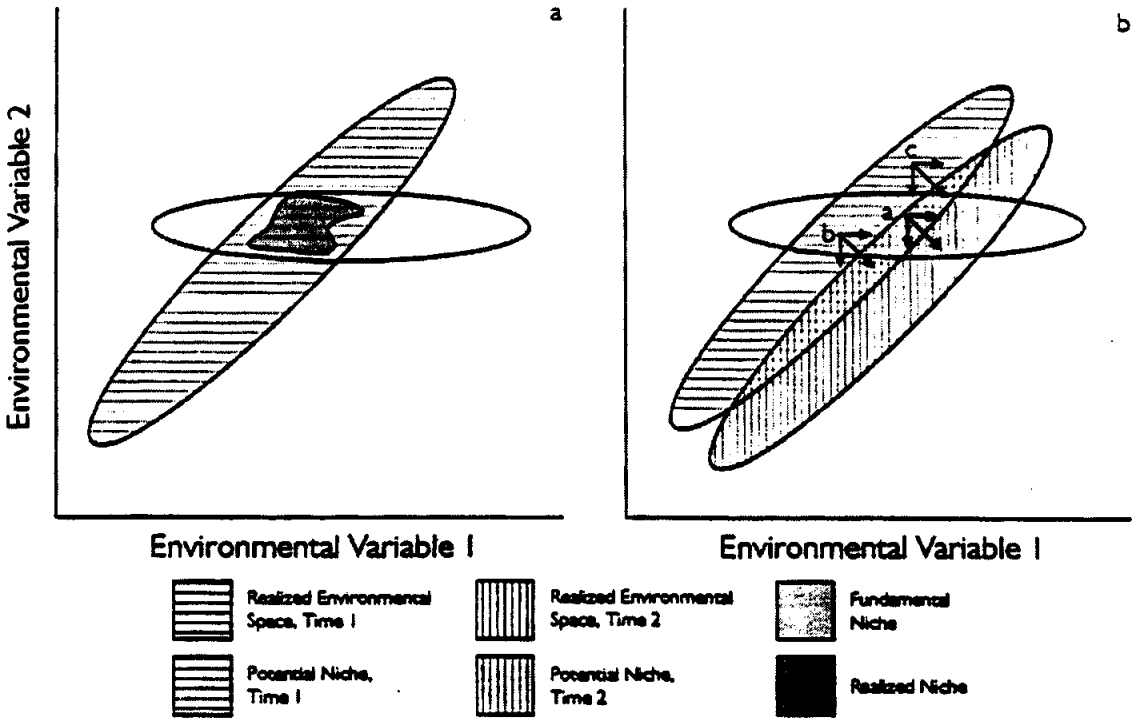


FIGURE 3.—a. Conceptual diagram of fundamental, potential, and realized niches of a species in response to two environmental variables. Note that the potential niche is the intersection between the fundamental niche and the realized environmental space, and hence changes in realized environmental space will force changes in the potential niche. The realized niche is a subset of the potential niche. b. Potential population responses to shifts in the realized environmental space. Arrow vectors represent the net environmental change at particular sites between Time 1 and Time 2. Site a remains within the potential niche of the population, so the population can persist after the environmental change. Site b passes out of the potential niche, so the population is fated for extirpation. Site c, unsuitable for the species at Time 1, passes into the potential niche at Time 2 and can be colonized by populations of the species.

disaggregation of species assemblages is a direct consequence of alternating overlap and non-overlap of realized niches. Such alternation may result from alternating overlap and non-overlap of potential niches (Fig. 4), or from biotic factors such as migration lag and interspecific interactions.

Theorem 2b (from Axioms 3 and 4): Pairs or groups of species with similar fundamental niches and rapid evolutionary response times may track environmental changes together by parallel adjustments in their respective fundamental

niches.—This theorem is in apparent conflict with Axiom 5, but could hold for groups of coevolved species that have similar environmental tolerances but diverge along resource gradients. Such species groups might occur in microhabitats (e.g., rotting logs, leaf galls, or deep ocean floors) where environmental changes are buffered. The key to such parallel responses would be the rate of evolutionary response relative to the rate and magnitude of environmental change as experienced by the organisms and populations.

WHAT'S LEFT TO CHANCE

I have designated the theory described above as quasi-deterministic. It is deterministic in that changes in the geographic distributions, habitat locations, and population sizes of species, as well as changes in community composition, are treated as predictable manifestations of environmental change. Although the theory emphasizes environmental forcing (e.g., non-overlap of potential niches is a sufficient mechanism for the failure of particular species to co-occur), it accommodates biotic and stochastic processes as well (species may also fail to co-occur because of migration lag, geographic barriers, or biotic interactions).

The deterministic underpinnings of the theory are supported by several lines of paleoecological evidence. First, plant species are capable of very rapid migration (10^2 - 10^3 m/yr); in many cases migration rates were limited by rates of climate change or ice retreat rather than by seed dispersal (Clark, 1998; Clark et al., 1998). Second, several well-documented cases of early Holocene species associations unlike any modern associations cannot be explained by migration lag (Jackson et al., 1997). Third, unique species associations were most widespread during periods in which the realized environmental space was most likely to have differed from today (Huntley, 1990a; Overpeck et al., 1992; Williams et al., 2000). Fourth, climatic change appears sufficient to explain most vegetational changes at subcontinental spatial and millennial temporal scales (Prentice et al., 1991; Williams et al., 2000). Finally, north-moving species tended to occupy low-elevation sites and then move upslope, while south-moving species colonized sites at higher elevations before moving downslope (Gaudreau, 1988; Gaudreau et al., 1989), a pattern predicted if species adjust geographic ranges in approximate equilibrium with climatic change.

Stochastic processes undoubtedly play important roles at more restricted spatial and temporal scales (e.g., secondary succession, patch dynamics, landscape mosaics), as argued by Webb (1986) and Prentice (1983, 1992). In certain cases,

they can play important roles at broader scales (centuries to millennia, regional to continental) by constraining the size of the realized niche relative to the potential niche.

Individuals of a species will not be able to occupy a suitable site unless they can disperse to it, and hence geographic barriers and ineffective dispersal may impose limitations. Large-seeded woody plants have been able to jump across barriers on the order of 10^2 km (Clark et al., 1998). However, dispersal events of greater magnitude (transoceanic, transmontane, transcontinental) were rare until the widespread human movements of the late Holocene.

Individuals of a species might be excluded from a site because enemies (competitors, consumers) arrived there first or because friends (mycorrhizae, pollinators) haven't kept up. In the case of competitors, if the new species is equally or better suited for local environments, disturbances will eventually allow entry into the local community. Similarly, if absence of mutualists is a limitation, the species need only await immigration of the missing species. Such "stochastic" limitations are unlikely to last very long. If required mutualists cannot survive in the local environment, or if competitors prevent the species from ever becoming established, or if consumers eliminate any colonizers, the realized niche of the species is certainly constrained (i.e., smaller than the potential niche), but such cases are hardly stochastic. Except for geographic barriers, stochastic factors are unlikely to influence species populations, geographic distributions, and community composition beyond restricted spatial and temporal scales. I acknowledge the occasional asteroid impact, as well as other high-magnitude rare events (intercontinental invasions, pathogen outbreaks, methane hydrate outbursts, etc.).

PATTERNS OF THE DEEP QUATERNARY

In the previous two sections I outlined what I perceive to be the consensus view in Quaternary ecology, acknowledging that it is not accepted universally. It is based primarily on paleoecological

and paleoclimatic studies of radiocarbon time, integrated with ecological and climatic studies of the 20th Century. The past 25,000 years captures only a fraction of the Quaternary, in a period (glacial maximum through deglaciation through part of an interglacial interval) that is not even representative of most of Quaternary time (essentially a purgatory fluctuating somewhere between interglacial and maximum glacial). Unfortunately, the spatial density of paleoecological data diminishes as we go beyond the radiocarbon barrier, and our ability to date records of terrestrial biota independently and precisely also declines.

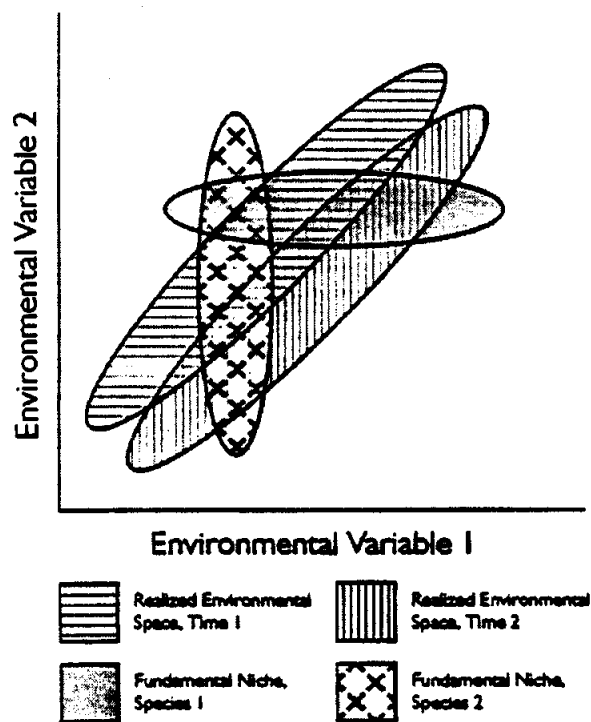


FIGURE 4.—How environmental changes can affect species associations. The potential niches of Species 1 and 2 overlap at Time 1, so they can form assemblages at sites within that portion of realized environmental space. At time 2, the potential niches are disjunct, and the two species cannot co-occur anywhere.

Several continuous pollen records span all or most of the last glacial/interglacial cycle (i.e., the past 125,000 years), and a few have associated tephra layers, which allow dating and correlation with marine-sediment and ice-core records independent of “wiggle-matching.” Lago Grande di Monticchio in southern Italy (Watts et al., 1996a, 1996b, 2000; Allen et al., 1999) provides one such record of unusually high quality, spanning the last 102,000 years. The pollen sequence shows features typical of the past 25,000 years, in this case transition from full-glacial cold steppe vegetation through late-glacial wooded steppe to Holocene temperate deciduous and mixed forests. Although the region has been occupied by deciduous forests for the past 10,000 years, composition has changed in response to climatic changes (Watts et al., 1996a; Allen et al., 1999).

The Monticchio record before 25,000 yr B.P. spans a series of alternating stadial periods, cool intervals in which continental glaciers advanced, and warmer interstadial periods of ice retreat. The pollen sequence from 75,000 to 25,000 yr B.P. consists of alternating open steppe (stadial) and wooded steppe (interstadial) (Watts et al., 1996b, 2000; Allen et al., 1999). The stadials and interstadials were not strictly cyclic. Interstadial wooded steppe was dominated in some cases by *Betula*, in others by *Abies*, and in others by Cupressaceae (probably *Juniperus*). Steppe vegetation also varied in composition from one stadial to the next.

The period from 102,000 to 75,000 yr B.P. consists of two interstadials with temperate deciduous forest, and one stadial with steppe. Pollen assemblages of the stadial period were markedly unlike the later stadials. Vegetation of the interstadials, although physiognomically similar to Holocene forests, were compositionally different, with higher abundances of *Abies* and *Fagus* pollen than recorded at any time in the Holocene (Allen et al., 1999).

Another high-quality record, from Carp Lake in central Washington, USA (Whitlock and Bartlein, 1997), appears to span the past 125,000 years. Dating beyond the radiocarbon range is tentative, consisting of a tephra layer (tentatively

dated at 100,000 yr B.P.) and two "wobble matches" with marine isotope records. The Carp Lake record shows full-glacial and late-glacial cold steppe, followed by warm steppe and then forest in the Holocene. Although vegetation before 25,000 yr B.P. was somewhere between forest and steppe (i.e., open forest or wooded steppe), floristic composition changed often and dramatically (Whitlock and Bartlein, 1997). Of the eight pollen assemblage zones before 30,000 yr B.P., no two are alike, and none are similar to either the Holocene or the last glacial maximum.

The pre-LGM vegetational changes recorded at both Monticchio and Carp Lake can be explained by climatic variation; the records are climatically consistent with insolation variations and independent paleoclimate records (Whitlock and Bartlein, 1997; Allen et al., 1999). Pollen records with similar or longer timespans show the same kinds of vegetational turnover (e.g., Hooghiemstra, 1984; Adam, 1988; Follieri et al., 1988; Grimm et al., 1993; Tzedakis, 1994; Reille et al., 1998). Quasi-cyclic patterns, in which particular pollen types alternate (e.g., Adam, 1988; Grimm et al., 1993), are typically in regions where inability to identify pollen grains below the family or genus level may mask compositional differences.

Another glimpse of "deep Quaternary" paleoecology is offered by buried sediments, particularly lake sediments, that span all or most of an interglacial period (e.g., Björck et al., 2000). Such records are scarce in North America, but many have been recorded from northern Europe. Pollen records from the last interglacial contrast with those from nearby Holocene sites, both in North America (Kapp and Gooding, 1964; King and Saunders, 1986; Schweger and Matthews, 1991) and Europe (Litt et al., 1996; Zagwijn, 1996; Reille et al., 1998; Björck et al., 2000). Taxa appeared and attained abundance maxima in different order, and many pollen assemblages of the last interglacial have no Holocene counterparts. West (1980) noted similar patterns among several different interglacials in southeast Britain. Climatic forcings (orbital parameters, trace-gas concentrations, global ice volume) varied among interglacials (Berger and Loutre, 1991; Imbrie et

al., 1992; Petit et al., 1999), and hence each interglacial period was characterized by a unique sequence of realized environments (Watts, 1988).

Quaternary interglacials are cyclic in that each is characterized by deglaciation, followed by warming to a thermal maximum in which continental ice sheets are absent from all continents except Greenland and Antarctica, followed in turn by cooling as the next glacial period approaches. These shared features of interglacial climates lead to some common patterns in vegetational sequences among interglacial periods within the same region (West, 1980; Watts, 1988). In temperate northwestern Europe, for example, interglacials commence with forests dominated by boreal and cool-temperate trees, followed by temperate forests dominated by deciduous trees, followed in turn by increases in cool-temperate and boreal conifers and deciduous trees. However, every interglacial has had an unique climatic signature, resulting in unique floristic and vegetational patterns superimposed on the cycles.

PEERING INTO THE PLIOCENE AND BEYOND

The entire Quaternary has been characterized by continual reorganization of terrestrial communities and ecosystems as the environment has changed. Marine-sediment and ice-core records indicate significant climatic changes at timescales of 10^3 - 10^5 years throughout the Quaternary and late Pliocene (e.g., Webb and Bartlein, 1992; deMenocal, 1995; Petit et al., 1999), and the available long-term pollen records show changes at these timescales (see references in previous section). If the last 25,000 years are, in fact, a "time of crisis and restructuring" (Brett et al., 1996), the same can be said for the past 2.5 million years or more.

Just as the last 25,000 years represent only a fraction of Quaternary time, the Quaternary represents a minute fraction of Phanerozoic time. The Quaternary Earth comprises an unique set of continental, orographic, eustatic, cryospheric, and hypsometric configurations, with relatively low atmospheric CO₂ concentrations (until the last century). Atmospheric and oceanic circulation

patterns are certainly different from earlier periods of Earth's history, and the nature, magnitude, and frequency of climatic changes at timescales of 10^2 - 10^5 years might be different also.

Environmental dynamics of the Quaternary appear to be typical of the Late Cenozoic. Records of $\delta^{18}\text{O}$, dust, and other proxies from Pliocene and Miocene marine sediments indicate significant climatic variation at frequencies of 10^3 - 10^5 years (Tiedemann et al., 1994; deMenocal, 1995; Miller et al., 1996; Wrenn et al., 1999), and pollen records spanning large portions of the Late Cenozoic show changes in terrestrial vegetation at similar frequencies (Barnosky, 1984; Hooghiemstra, 1984; Combourieu-Nebout, 1994; Hooghiemstra and Ran, 1994; Leopold and Liu, 1994). The Late Cenozoic, however, still represents an "icehouse" world. Is the Late Cenozoic an anomalous period of Earth history, characterized by environmental inconstancy and biotic flux?

WERE ECOSYSTEMS SENT FORTH FROM THE GARDEN?

Much recent discussion in paleobiology has centered on the reality and nature of coordinated stasis—the persistence or recurrence of particular biotic assemblages in the fossil record over timespans of 10^6 - 10^7 years (Brett et al., 1996; DiMichele and Phillips, 1996a; DiMichele et al., 1996; Ivany, 1996). Although coordinated stasis is defined as an empirical phenomenon (Brett et al., 1996), discussions frequently invoke tightly coevolved interactions among species or clades as a mechanism for assemblage recurrence or persistence. Advocates of coordinated stasis have argued that environmental and biotic patterns of the Quaternary are uncharacteristic of most of the Phanerozoic (DiMichele, 1994; Brett et al., 1996; DiMichele and Phillips, 1996b; Schopf and Ivany, 1998). By this view, Late Cenozoic cooling was accompanied by a transition from a world characterized by stable environments and/or integrated communities (The Garden), to one with fluctuating environments and individualistic biota (The Cooler). Brett et al. (1996) suggest that these kinds of regimes may have alternated during the Phanerozoic.

To what can recurrence of biotic assemblages over long time periods in the pre-Quaternary fossil

record be attributed? Bennett (1997) has summarized evidence for Milankovitch-frequency climatic variation throughout the Phanerozoic (see also Parrish, 1998). Orbital variations and interactions with ocean circulation and ENSO/NAO-type cycles should lead to changes in atmospheric circulation at timescales of 10^3 - 10^5 years, regardless of the presence of continental ice. For example, substantial variations in low-latitude monsoon strength and in ENSO-type regimes, resulting from orbital forcing in the (mostly) ice-free Holocene, are documented from paleoclimatic and modeling studies (Wright et al., 1993; Webb, 1998; Clement et al., 1999). The Late Cenozoic is probably not unusual in terms of frequency of environmental change, although the magnitude of variation in some variables (e.g., temperature) has probably changed.

Environmental variability through the Phanerozoic, however, does not require that we default to community integration as the mechanism underlying coordinated stasis. Based on how environmental space differs among habitats, and how habitats differ in the plasticity of that space, I suggest that long-term assemblage recurrence in the pre-Quaternary can be adequately explained by extrinsic mechanisms (*sensu* Ivany, 1996).

MOUNTAINS AND MANGROVES: ALL PALEOECOLOGY IS LOCAL

Each habitat (terrestrial upland, rocky intertidal, marine benthic, coastal wetland, etc.) presents an unique set of environmental gradients, resources, challenges, and constraints, which collectively comprise the environmental space relevant to biota of that habitat. The environmental space for each habitat will consist of a different suite of environmental variables, so each habitat will have a characteristic environmental space, which will change in characteristic ways. Patterns of change for communities and ecosystems should differ predictably among habitats, depending on how the realized environmental space changes, and on how the fundamental niches of species are arrayed within environmental space.

In an earlier section I emphasized the large

number of climate-related environmental variables relevant to upland plants, the complex ways in which atmospheric circulation influences these variables, and the dynamic nature of atmospheric circulation at timescales of 10^2 - 10^5 years. Substantial and complex changes in the configuration of the realized environmental space for terrestrial uplands at these timescales are inevitable. Terrestrial ecosystems are in a continual state of reorganization in response to environmental changes at a wide range of timescales, and have probably been so since colonization of uplands by land plants.

Biota of other habitats are influenced by different suites of environmental variables, and in some cases the configuration of the realized environmental space may not change substantially, in spite of substantial climate change (Jackson and Overpeck, 2000). For such habitats, species associations might be relatively stable over long timescales (possibly up to 10^7 years). Atmospheric changes may be dampened or simplified for some habitats (e.g., marine benthos, coral reefs). Sea level may rise and fall, and water temperature and salinity may fluctuate, but the overall structure of realized environmental space may be little altered. Environmental changes may lead to spatial shifts in species distributions, but not to wholesale reorganization of species associations or patterns along gradients (Jackson and Overpeck, 2000).

Other habitats are more exposed to the dynamics of the atmosphere, but the primary environmental gradients that structure communities may still be conserved in the face of climatic change. For example, coastal wetlands are characterized by landscape patterns and gradients that are dominated by the physics of geomorphic processes and the chemistry of salinity and oxidation/reduction. Plant species of coastal wetlands are arrayed along gradients of hydrology, salinity, substrate, and redox conditions. Climatically induced changes in sea level or river discharge may displace these gradients spatially, but will not necessarily lead to recombinations of environmental variables or reconfigurations of environmental gradients. We would see the same arrays of species along salinity, redox, and hydrological gradients.

Climatic changes might cause large-scale latitudinal displacements, which, if large enough, might lead to major alterations of realized environmental space. For instance, if tropical climates moved to another coastal configuration (e.g., from a gentle coastal plain to a rocky shore), we might expect to see some species associations diminish in extent or disappear. But a return of tropical climates to the coastal plain would restore the pre-existing environmental configuration, and the pre-existing biotic patterns, provided the elements of the original biota were still extant.

For example, wetlands of southwest Florida consist of coastal mangrove swamps and protected salt marshes, and inland freshwater marshes and wooded swamps. These ecosystem types are each characteristic of particular environments and landforms, and species are arrayed along gradients of salinity, wave or flow mechanics, water depth, redox conditions, and nutrient availability (Tomlinson 1986; Mitsch and Gosselink, 1993; Odum and McIvor, 1990). These environmental factors occur in a wide range of combinations, governed by the physics and chemistry of coastal, fluvial, and groundwater processes. The realized environmental space and the environmental complex-gradients (*sensu* Whittaker 1967) controlling vegetation patterns are likely to be conserved under different climatic regimes (Fig. 5a).

Rhizophora is the most salt-tolerant and wave-tolerant species of these wetlands. Accordingly, regardless of climatic conditions, it will always occupy the seaward side of the spatial gradient, with *Avicennia* and then *Conocarpus* occurring landward as salinity, wave mechanics, and inundation frequency decrease. Inland or upriver, beyond saltwater and spray influence, *Taxodium* occupies the core of frequently inundated surfaces, with other trees (pines, palms, oaks) in the less frequently inundated margins.

Mangrove species are intolerant of extended subfreezing temperatures. Hence, winter cooling would lead to southward contraction of mangroves and associated species, while winter warming would allow northward expansion. In both cases, the biotic patterns along hydrological and chemical gradients would be conserved. Changes in other variables

(precipitation, growing-season temperatures) would likely have little direct effect on the species arrays, although the gradients might move laterally owing to changes in riverine and estuarine hydrology. Spatial patterns and species associations in subtropical wetlands are likely to persist in the face of a broad array of climatic changes.

In contrast, biotic patterns along an elevational gradient are dominated by atmospheric variables.

Temperature decreases and precipitation increases with increasing elevation, regardless of climatic regime. However, the *rates* of temperature and precipitation change along the slope depend on atmospheric circulation patterns. The mountains of western North America have a diverse array of vegetational zonation patterns, which result in large part from the diverse array of climatic complex-gradients in the region. As an example, the Front

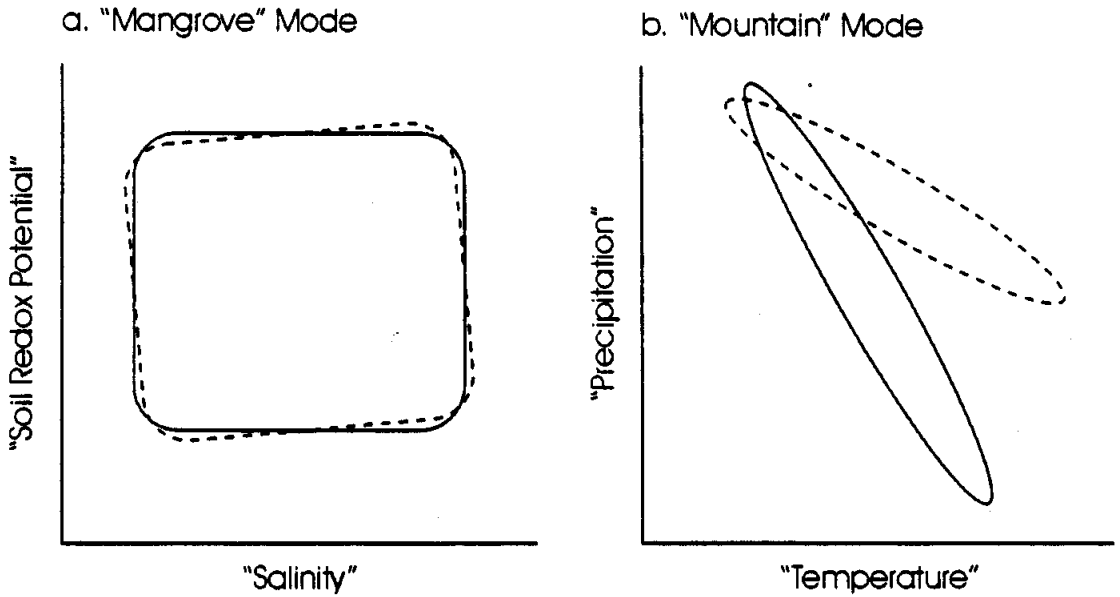


FIGURE 5.— Models of the realized environmental space for two contrasting habitats. a. A series of multiple measurements of salinity and redox potential at coastal/inland wetland complexes along the Atlantic Coast from the Keys to Cape Cod would yield repeating patterns - the shape of the environmental space defined by the two variables would change little, in spite of substantial climatic differences among sites. These variables, important in structuring wetland communities, are controlled by local physical, chemical, and hydrological processes. Such habitats ("mangrove" mode) might be expected to maintain community patterns along coastal-inland gradients under a relatively wide range of climatic regimes. b. A series of multiple measurements of temperature and precipitation along mountain slopes through part of the American West would yield a diversity of patterns. All would share an inverse relationship between the variables, but slope and origin of the relationships would differ between (and within) individual mountain ranges. In this example, the solid ellipse might represent environmental space along the western slope of the summer-dry Front Ranges, while the dashed ellipse represents the summer-wet eastern slope of these ranges. These variables, important in structuring upland communities along elevational gradients, are controlled by atmospheric circulation at local, regional, and continental scales. Such habitats ("mountain" mode) might be expected to show different community patterns along elevational gradients depending on the particular climatic regime.

Ranges of Colorado and Wyoming face the Great Plains, and their east slopes receive abundant precipitation from Gulf of Mexico sources in spring and summer. In contrast, the western slopes of these ranges tend to be summer-dry because the Gulf moisture is blocked by the mountains. Thus, the slope of the relationship between summer precipitation and temperature is steeper on the west slopes than the east (e.g., Fig. 5b). Although vegetational zonation patterns on the uppermost slopes are similar regardless of aspect, downslope the vegetational zonation of the east and west sides of the ranges becomes very different (Knight, 1994).

The contrast between east and west slopes of the Front Ranges represents a spatial manifestation of current atmospheric circulation patterns. This spatial contrast is analogous to the kinds of temporal changes in atmospheric circulation that mountains experience. For example, a weakening of the circulation pattern responsible for advection of Gulf moisture into the Great Plains would steepen the precipitation/temperature gradient along the east slopes of the Front Ranges. In general, as atmospheric circulation patterns change, new combinations of temperature and precipitation will appear along elevational gradients. Vegetational zonation and species associations along mountain slopes are likely to be ephemeral.

The environmental space relevant to organisms of upland habitats, whether arrayed primarily along elevational, geographic, or edaphic gradients, changes in the "mountain" mode described above (Fig. 5b; see also Figs. 2 and 3). That of certain other habitats, including low-latitude coastal wetlands and coral reefs, may change in a "mangrove" mode (Fig. 5a).

BRIDGING QUATERNARY AND DEEP-TIME PALEOBIOLOGY

I offer this paper to stir up some dialogue between Quaternary and deep-time paleoecologists. I freely admit my individualistic bias—as a plant ecologist working with both modern and Late Quaternary systems, I find it difficult to imagine the world working any other way.

Paleobiologists are correct to point out that the Quaternary offers only an incomplete glimpse of the full array of environmental, ecological, and evolutionary dynamics that have shaped our world. Through much of the 1970s and 1980s, Quaternary paleoecologists argued, with eventual success (Davis, 1994), that in focusing on dynamics of years to decades, ecologists were missing fundamentally important context, patterns, and mechanisms. Thus, Quaternary scientists can appreciate that much can be learned by bridging between the Quaternary and earlier time periods. I conclude by listing a few areas of potentially fruitful crossover inquiry:

Comparative environmental studies.—What are the primary environmental variables that structure communities and ecosystems in specific habitats? Are the same variables likely to have been important throughout the Phanerozoic?

Environmental plasticity.—To what extent does the shape of the realized environmental space of a particular habitat change at different timescales? Does the realized environmental space ever return to preexisting configurations?

Regime shifts in time.—The Late Cenozoic is certainly characterized by climates and climate dynamics that were absent at earlier times or restricted mainly to mid- to high latitudes. What is the full range of modes of environmental variation in the Phanerozoic? Are some habitats more likely to buffer environmental variation at timescales up to 10^7 years than others? At what timescales do the peaks of environmental variance occur for specific kinds of habitats? Do some habitats have more spectral peaks between 10^1 - 10^7 years than others?

Attribution of causes.—Is a "mangrove model" (or other extrinsic mechanism) sufficient to explain particular cases of long-term stasis? Is invocation of community integration necessary to account for observed patterns? On which hypothesis should the greater burden of proof be placed? How can strong tests be devised to discriminate between these hypotheses in deep time?

Comparative taphonomy.—What is highlighted and what is hidden by different kinds of data? This has been the object of much discussion within

paleobiology, but taphonomic dialogue must be part of any Quaternary/pre-Quaternary comparison.

Comparative data analysis.—How are conclusions influenced by how data are measured and analyzed (e.g., Rahel, 1990; Webb, 1993)? Are taxonomic units comparable among time periods and taxonomic groups?

Deep phylogeny.—If we reduced Quaternary taxa to higher-level categories, would we perceive something akin to coordinated stasis through glacial/interglacial cycles? Phylads differ in their sensitivity to different environmental factors, and in their ability to find adaptive solutions to particular problems posed by the environment. What kinds of long- and short-term patterns might emerge in phylad arrays along gradients (e.g., DiMichele and Phillips, 1996a)?

Inadvertent icehouse preparations.—Pre-Quaternary biota provided the raw material for the ecosystems of the icehouse world. Why did certain groups disappear during or after the icehouse transition and not others? What kinds

of pre-Quaternary traits might have been “pre-adaptive” for the icehouse world?

Reciprocal studies.—The particular kinds of records selected for study by Quaternary paleoecologists frequently differ from those of deep paleoecology. To ensure fair comparisons between different time periods, we should apply Quaternary-like methods to Quaternary-like sediments in deeper time, and deep-time methods to deep-time-style records in the Quaternary. What model systems can be identified for various time periods?

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