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Plants at the Cretaceous-Tertiary Boundary [and Discussion]

R. A. Spicer and N. J. Shackleton

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Plants at the Cretaceous–Tertiary boundary

BY R. A. SPICER†
Life Sciences Department, Goldsmiths' College, Creek Road, London SE8 3BU, U.K.

Environmental selection determines to a large extent the morphology and anatomy of individual plants, and the composition and structure of vegetation. The intimate relation between vascular land plants, climate and substrate produces an abundant fossil record with a strong inherent signal reflecting, in particular, air temperatures, precipitation and evaporation, light régime and seasonality. Studies of palynomorphs, cuticles and plant megafossils in detailed sedimentological and stratigraphic context across the Cretaceous–Tertiary (K–T) boundary in North America, suggest sudden and traumatic vegetational disturbance, profound and long-lasting climatic change, and survivorship patterns that are palaeogeographically heterogeneous and possibly related to the ability of taxa to enter dormancy. Some of these changes are reflected in palaeosols. Major vegetational changes are also apparent in Europe, and Asia, although the precise timing of these events is less clear. The record, as presently interpreted, is one of ecological catastrophe, some selective extinction of broad-leaved evergreen species, and long-term vegetational restructing, expressed most strongly at middle and lower latitudes in the Northern Hemisphere.

1. INTRODUCTION

The terrestrial vascular plant fossil record exhibits several characteristics that allow it to be used to elucidate past environmental change at fine scales of geographical and stratigraphic resolution. The spatial fixity of the sporophyte plant body, its intimate association and modification of substrates (palaeosols), interaction and direct exposure to the atmosphere, interception and utilization of light, and its morphological/anatomical record of growth patterns mediated by temperature and water availability result in a rich legacy of potential plant fossils that give a record of environmental conditions through time. Furthermore, many adaptations to maximize vegetative productivity, and in part therefore fitness, have evolved several times and are not taxonomically restricted. Thus the palaeobotanist interested in assessing environmental change is largely freed from the constraints of precise phylogenetic or taxonomic determinations (Spicer 1989*a*; Knoll & Niklas 1987). This is a particularly significant consideration because of the fact that much of the historically published palaeobotanical database on systematics contains high levels of investigator bias (Boulter *et al.* 1988).

As with any palaeontological record the primary database provided by the living organisms is modified considerably by the processes of fossilization. Understanding taphonomic biases is vital to any accurate account of ecological trauma, disruption of the physical environment, or extinctions. Many plant parts have a high preservation potential either because of their inherent resistance to decay (e.g. lignin and sporopollenin), or their production in large numbers (e.g. leaves), or both (e.g. pollen). Under certain circumstances even the most ephemeral elements of the life cycle may be preserved (Brack-Hanes 1978; Rothwell 1977).

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† Present address: Department of Earth Sciences, Oxford University, Parks Road, Oxford OX1 3PR, U.K.

Although the palaeobotanical record is a rich one it is also bedevilled by two factors that together serve to frustrate assessments of extinction rates. The first is that vascular land plants are very rarely preserved whole. Throughout the lifetime of most plants an indeterminate number of individual organs are shed, some of which enter depositional environments and become mixed with organs from other individuals and taxa. The difficulties of whole plant reconstruction that arise from such fragmentary preservation are compounded by mozaic evolution (see, for example, Sporne 1980; Knoll & Niklas 1987; Boulter *et al.* 1988) in which plant organs evolve to some extent independent of each other. For example, leaves are exposed to different selective pressures than reproductive organs, wood or rooting structures. Thus in angiosperms, for example, one sees intricate evolution of floral form in relation to reproductive pressures (including co-evolution with biotic pollinators), whereas leaf or wood evolutionary rates tend to reflect competition for growth requirements or changes in the physical environment. As a result, extinction rates, or rates of evolutionary radiation, based on one or more separate plant organs are a very poor reflection of what is happening to the coherent biological entities we call whole plants (cf. Lidgard & Crane 1988; Cleal 1988).

The above factors determine to a large extent the contextual framework within which any discussion of vegetational change at the Cretaceous–Tertiary (K–T) boundary must take place. A requirement not unique to the plant record is for accurate high resolution stratigraphy within complete sections using non-biological markers (to avoid circularity) spanning the K–T boundary. Unfortunately, sites where these requirements are met are mostly in the western United States and Canada, which introduces a strong geographical bias. However, less well-constrained evidence from other areas suggests this may indeed be where terrestrial K–T boundary phenomena are expressed most strongly.

2. Late Cretaceous vegetation and climate

Studies of vegetational changes at the K–T boundary have to be viewed in the context of the vegetational structure and dynamics, and climate, of the late Cretaceous. The late Cretaceous was a time of some climatic change and gradual vegetational restructuring, as the angiosperms underwent geographical and ecological diversification. It is now well established that from a late early Cretaceous low latitude cradle the angiosperms spread polewards (Axelrod 1959; Hickey & Doyle 1977) reaching 75° N by the end of the Albian (Scott & Smiley 1979; Spicer & Parrish 1986) and high southern latitudes about the same time (Douglas & Williams, 1982). Ecological diversification apparently proceeded at a slower pace. Concomitant with the rise of angiosperms (whose origin, as far as is known, was unconnected with extinctions or ecological disruption) there was a gradual decline (apparently because of competition with the angiosperms) in major Mesozoic groups such as the Bennetitales, Cycadales and conifers such as the Cheirolepidiaceae.

Using North American data, late Cretaceous vegetational and climatic change may be divided into two phases: (1) Aptian – early Cenomanian, (2) middle Cenomanian – Maastrichtian (Upchurch & Wolfe 1987). The Aptian – early Cenomanian saw the early diversification in which most foliage physiognomic types first appear, multistratal forests have a restricted distribution in time and space, and although angiosperms may dominate megafossil assemblages in certain (notably riparian) facies the palynoflora is always dominated (more than 60%) by spores and pollen from ferns, sphenophytes and gymnosperms (Upchurch &

Wolfe 1987). Early Cenomanian megafloras are diverse and widespread and the discrepancy between pollen and leaf abundances may be due to high palynomorph productivity by pteridosperms and gymnosperms, the 'preference' of gymnosperms for well-drained soils where preservation potential of megafossils is low, and the poor preservation potential of the pollen of Laurales (Muller 1981), a group that, based on megafloral evidence (Upchurch & Dilcher 1984) formed a significant component of the angiosperm flora (Upchurch & Wolfe 1987).

From the middle Cenomanian to the late Maastrichtian leaf and vegetational physiognomic types stabilize in relation to environmental parameters. At low (less than 30°) and middle (30–65°) palaeolatitudes angiosperms become the most abundant component of regional palynofloras.

According to Upchurch & Wolfe (1987) low–middle northern latitude (30–45°) vegetation was predominantly evergreen megathermal, and the resulting leaf assemblages are characteristically thick-textured and predominantly entire-margined (greater than 70%). Low leaf size in both fine and coarse-grained facies, few species with either drip tips or probable vine habit, and the prevalence of leaves with emarginate apices suggest sub-humid conditions, whereas small diaspore size (Tiffney 1984) is both consistent with sub-humid conditions and indicative of open-canopy structure.

In the Santonian (Coniacian?) palms first appear in megathermal environments, but by the Campanian they were common in mesothermal situations (Bell 1957; Daghlian 1981; Hickey 1984).

The absence of growth rings in fossil wood from low–middle latitudes (Creber & Chaloner 1985; Wolfe & Upchurch 1987) suggests minimal seasonality in the climate. Angiosperm woods from trunks up to 1 m in diameter exhibit large quantities of parenchyma with vessels of large diameter, often solitary, occurring at low frequency (Wheeler *et al.* 1987; Wolfe & Upchurch 1987); features that today are typical of tropical woods. Abundant parenchyma and wide solitary vessels are unusual in present-day sub-humid environments that tend to be highly seasonal. The lack of good modern analogues for this kind of environment makes interpretation of the wood anatomy problematical, particularly because of the physiognomic signal of the leaves. Wolfe & Upchurch (1987) suggest the closest living analogue might be tropical evergreen vegetation on sandy soils, where low nutrient status limits leaf size, and they suggest that abundant parenchyma and solitary vessels may be adaptive under conditions of low seasonal variation in precipitation, with no period of drought.

At high–middle latitudes (45–65° N) angiosperm dominance in the palynofloras is reached between the Turonian and Campanian (D. J. Nichols, unpublished data cited by Upchurch & Wolfe (1987)). By the Santonian the megafossil record is also dominated by angiosperms in terms of species and specimen abundance, at least locally. Physiognomic analysis of leaves suggests mesothermal evergreen vegetation in which 45–65% of species are entire-margined (= 13–20 °C mean annual temperature), but the rarity of drip tips suggests that rainforest was absent. Leaf size is greater than in the lower latitude assemblages, suggesting more humid conditions.

At 45° N early Maastrichtian angiosperm and gymnosperm woods have virtually no growth rings whereas those from the Maastrichtian of central Alberta (65° N) exhibit well-defined rings with a high ratio of late wood to early wood (Ramanujam & Stewart 1969), suggesting growth was limited later in the growing season because of shortened day length, drier conditions or lower temperatures.

At high northern palaeolatitudes there is a rich fossil record (Hollick 1930; Smiley 1966, 1969*a*, *b*; Spicer & Parrish 1986; Spicer 1987; Spicer *et al.* 1987) documenting the existence of a vegetational physiognomic type now extinct: the Polar Broadleaved Deciduous Forest (Wolfe 1985). This forest type is characterized by deciduous conifers plus numerous platanoid, hammamelid and trochodendroid, thin-textured deciduous angiosperm leaves exhibiting a large range of leaf sizes. Entire-margined forms rarely constitute more than 30% of the assemblages. In spite of moderately high angiosperm leaf diversity (Spicer & Parrish 1986; Spicer 1987) in the Cenomanian, the regional vegetation was dominated by large deciduous conifers, together with a variety of ginkgophytes. Ferns, sphenophytes (e.g. *Equisetites*), and deciduous cycads also occurred in some abundance. Leaf and vegetational physiognomic analysis, together with studies of comparative diversity and wood anatomy from northern Alaskan floras, suggest mean annual sea-level temperatures at 75° N were in the order of 10 °C, possibly rising to 13 °C in the Coniacian, before declining by the Maastrichtian to 5–6 °C at 85° N (Parrish & Spicer 1988). By the crude application of the present-day average adiabatic lapse rate of 6 °C per 1000 m these temperatures suggest mean annual temperatures of 0 °C (and therefore the possibility of permanent ice) above 1700 m at 75° N in the Cenomanian and above 1000 m at 85° N in the Maastrichtian (Spicer 1989*b*).

Sedimentological evidence, together with an abundance of coals, leaf characteristics, and wood relatively free of false rings, suggest water was not limiting to plant growth at high latitudes in the Cenomanian. However, an increase in fossil charcoal may indicate a degree of drying in the Campanian and Maastrichtian (Spicer & Parrish 1987).

3. VEGETATIONAL CHANGES AT THE K–T BOUNDARY

(*a*) *The palynological record*

It is now well established that in many parts of the world the boundary between the latest Cretaceous and earliest Tertiary beds is marked by a boundary clay associated with anomalously high iridium concentrations (see, for example, Alvarez *et al.* 1984), shocked quartz grains (see Izett & Bohor 1986) and, occasionally, mineral spherules (see Bohor *et al.* (1987)).

The most widely recognized plant–fossil boundary indicator is a sudden and severe attenuation in abundance and diversity of pollen grains typical of the Cretaceous at or near a boundary clay. This is followed by a sudden rise in spore abundance in the immediate post boundary sediments. Subsequent to this so called 'fern spike' the proportion of spores gradually declines as pollen increases once more in abundance and diversity, but this time with characteristic Palaeocene forms (see Tschudy & Tschudy (1986) and references therein). So pronounced is this pattern that it was recognized in the Western Interior of the United States long before the bolide impact scenario (Alvarez *et al.* 1980) was proposed (see, for example, Leffingwell 1971; Tschudy 1971). So consistent is the palynological signal that it is sometimes used to define the boundary in the absence of corroborating data such as anomalously high iridium levels and shocked quartz (Tschudy 1973): a situation that introduces a certain circularity.

Detailed studies of complete non-marine boundary sections ranging from New Mexico to Saskatchewan show that although the general pattern of palynological change is broadly consistent, the pollen taxa that are affected and the timing of 'originations' and 'extinctions' with respect to the boundary varies geographically (Tschudy & Tschudy 1986; Sweet & Braman 1988). The likelihood of palynomorph reworking across the boundary is minimized in complete coal-bearing boundary sections and thus temporal resolution of changes in the spore assemblages is generally high.

In the northern region of the Western Interior key pollen species such as *Aquilapollenites* spp. (except *A. spinulosus*) and *Proteacidites* are confined to the Cretaceous, with other taxa (*Gunnera microreticulata*, *Liliacidites altimurus*, *Liliacidites complexus* and *Cranwellia striata*) also disappearing at the boundary. Some species (*Wodehouseia spinata*, *Tricolpites parvistriatus* and *Arecipites columellus*) suffered a dramatic decline at the boundary, whereas others (*Kurtzipites trispissatus*, *Triporopollenites plektosus*, *Ulmipollenites* spp. and *Alnipollenites* spp.) appear to pass relatively unaffected into the Tertiary (Leffingwell 1971). In the southern region, the Raton Basin, the only northern region pollen type to occur in Cretaceous rocks and then disappear at the boundary is *Proteacidites* spp. Typical southern region taxa to disappear are '*Tilia*' *wodehousei*, *Trisectoris* and *Trichopeltinites* (probably a fungal thallus). *Trichopeltinites* reappears in the Eocene of the Mississippi Embayment (G. R. Upchurch, Jr, personal communication 1988) and may be an indicator of warm conditions. Taxa common to both the uppermost Cretaceous and continuing into the basal Tertiary include: *Gunnera microreticulata*, *Fraxinopollenites variabilis*, *Liliacidites complexus*, *Thomsonipollis magnificus*, *Tricolpites anguloluminosus*, *Pandaniidites radicus*, *Arecipites columellus* and *Salixipollenites* sp.

Above the boundary clay there are usually a few millimetres of organic-rich rock generally devoid of palynomorphs. Sapropel and fusain are often, but not always, found in this layer suggesting rotting or burnt vegetation or both. This 'barren zone' is (usually) overlain by several centimetres of carbonaceous mudstone or coal which yields abundant fern spores and very few pollen grains. This spore-rich horizon is interpreted as representing the first Tertiary vegetation and indicates an abrupt and profound post-boundary vegetational change in that region. Angiosperm pollen typically undergoes a slow recovery in abundance until about 10–15 cm above the boundary it again predominates (Tschudy & Tschudy 1986). In some instances aberrant grains occur several metres above the boundary suggesting, perhaps, prolonged periods of stress (Fleming 1988).

Careful work by Hotton (1988) at six boundary sites in Montana reveals palynological changes consistent with traumatic ecological disturbance and at least local extinctions. Before the boundary within the Hell Creek Formation (Cretaceous) there is little change in overall diversity, or in the diversity and abundance of 'doomed' species. However, within any given section, major palynological changes occur at a single horizon just above an iridium anomaly. These changes consist of 21–46% of Hell Creek species disappearing or becoming extremely rare, and 18% undergo significant decline. Overall there are three to six times as many rare forms in the Hell Creek than the subsequent Tullock (Palaeocene) Formation. Immediately above the boundary there is typically a coal yielding unusually high percentages of *Cyathidites* fern spores and few other species. Spores, however, tend to be abundant in most Tullock coals. Hotton (1988) considers that 30–40% of the species losses might be attributable to post-boundary facies changes. Although partial recovery takes place within 10–30 cm of the boundary Hell Creek levels of diversity are never achieved within the Tullock.

The range of 21–46% 'extinctions' noted by Hotton in a restricted geographical area exceeds that exhibited across the latitudinal range from the Raton Basin (Tschudy & Tschudy (1986) imply greater than 25%) to Saskatchewan (30%) (Nichols *et al.* 1986) and, although some differences may be due to Hotton's figure including all taxa whereas the other reflects only angiosperm losses, no clear latitudinal trend is demonstrated.

Sweet & Braman (1988) note a different sequence of events in western Canada between palaeolatitudes 60 and 75° N. Differences in assemblage composition can be related to differences in depositional environment and latitudinal shifts in the angiosperm flora in response to climatic differences. Despite this background heterogeneity Sweet & Braman identified four sequential palynofloral changes across the boundary (marked by a geochemical anomaly and shocked quartz). These include an extinction event 5–10 m below the boundary extinctions, a miospore–gymnosperm assemblage beginning 5–10 cm above the boundary within which newly introduced species occur together with Maastrichtian relicts, and a last reduction of diversity approximately coincident with the first occurrences of *Wodehousia fimbriata* approximately 3–15 m above the boundary. Sweet & Braman (1988) consider these phenomena difficult to explain as the result of a single bolide impact and suggest the causes for biotic change are, as yet, undetermined.

At very high northern palaeolatitudes Frederiksen *et al.* (1988) observe a variety of angiosperm pollen forms representing understorey or disturbed-site herbs and shrubs that were probably insect pollinated. Although the latest Maastrichtian and the boundary itself is not apparent early Palaeocene palynofloras have a distinctly different angiosperm flora, reduced in diversity and predominantly representing anemophilous taxa. Megafossil evidence (Spicer & Parrish 1989) supports the interpretation of Frederiksen *et al.* (1988) that the Cretaceous–Tertiary transition on the North Slope of Alaska saw a change from a predominantly conifer-dominated vegetation to one rich in wind-pollinated angiosperm trees. The lack of an intact section raises the possibility that these changes could be the result of long-term climatic fluctuations.

Tschudy & Tschudy (1986) note that all the extinctions they observed were only regional, in that elsewhere in North America all the Cretaceous pollen types continue through into the Tertiary. What Tschudy & Tschudy did not determine, however, was the extent of reworking present in the other North American records. In the case of *Aquilapollenites*, however, there is a genuine continuation into the Tertiary in Japan (Saito *et al.* 1986).

Whether or not the extinctions were regional or global, the North American plant microfossil record demonstrates four types of biotic change at the K–T boundary. In addition to the abrupt loss of certain taxa, as typified by *Proteacidites* spp., some taxa, such as *Wodehouseia*, seem to undergo a pseudoextinction at the 'species' level. In the northern Western Interior the Cretaceous form *W. spinata* is replaced above the boundary by its presumed descendant *W. fimbriata*. *Kurtzipites trispissatus* typifies a third type of boundary change in which a pollen type appears in the Maastrichtian, reaches its zenith at the boundary and subsequently becomes a significant element in the 'recovery' pollen flora. Other species of *Kurtzipites* exhibit this pattern but all become extinct by the middle of the Palaeocene. The fourth type of biotic change is represented by a large group of pollen types that was little affected by the K–T boundary event. Many Cretaceous forms pass into the Palaeocene and some survived to the Eocene or younger. Where ecological trauma is well documented new Palaeocene forms are slow to appear and previously rare Cretaceous forms adopt a new ecologically dominant role in early Palaeocene vegetation (Nichols & Fleming 1988).

Evidence that the terminal Cretaceous non-marine ecological trauma was experienced outside North America comes from a marine boundary sequence at Hokkaido, Japan (Saito *et al.* 1986). Here, pollen and spores of land plants exhibit an immediate post-boundary increase in the proportion of fern spores to pollen, but this is followed by an increase in pine pollen. Saito *et al.* (1986) interpret this as indicating that pine was an early colonizer of the devastated landscape. Although pine can behave as a 'weed' (e.g. *Pinus pinaster* in South Africa (Carlquist 1975, p. 96)) conifers with long life cycles are not well suited to this role unless there is a major deterioration of the climate. Bisaccate pine pollen grains are produced in large numbers and are particularly suited to long distance transport into marine environments. It is likely then that the abundance of pine in the recovery vegetation, relative to other taxa, is exaggerated in this instance.

The El Kef section, Tunisia, preserves Maastrichtian pollen from the palm-rich province of Africa – South America together with pollen of the *Normapolles* type (see Batten (1981) for a review of these forms) characteristic of Europe and eastern North America. In the transition to the Tertiary, palynological diversity declined and only pollen typical of the European source to the north occurs in the Palaeocene sediments (Méon 1988).

Rawat *et al.* (1988) report on pollen zonations that encompass the K–T boundary in the Krishna–Godavari basin, India, and although independent stratigraphic resolution is coarse, some palynofloral turnover has been used to position the boundary. This suggests some vegetational change may be present. Even if, however, independent evidence subsequently shows the boundary is correctly positioned, the degree of vegetational disruption would appear to be milder than that experienced in North America.

No unweathered K–T boundary outcrops are known from Australia (Hannah & Partridge 1988) but well data may indicate some palynological changes (Baird 1988). There appears to be an early Palaeocene diversity decreased within the genus *Proteacidites*, but coarse sampling renders any conclusions regarding actual vegetational change highly speculative.

In New Zealand, K–T palynological changes are considerably less dramatic than those of the mid Cretaceous, the Palaeocene–Eocene boundary, or the end of the Eocene (Raine 1988). Sequences in coal measures indicate little modification of the podocarp-dominated vegetation across the K–T boundary which is marked palynologically by the extinction and appearance of mostly angiosperm taxa.

The K–T boundary record on Seymour Island, Antarctic Peninsula, is similar to that of New Zealand in that there is no evidence for an abrupt change in the podocarp vegetation, despite evidence for reworking of Cretaceous pollen into Tertiary sediments (Askin 1988*a*, *b*). Podocarp pollen is prevalent throughout succession, together with diversifying angiosperm pollen assemblages. Cryptogam spores are low in diversity and abundance. Gradual long-term turnover in the palynofloras is consistent with coeval changes in regional palaeogeography and climates. Latest Cretaceous angiosperm pollen is diverse but highly provincial; a pattern also seen at high northern latitudes (Frederiksen *et al.* 1988; T. A. Ager, personal communication 1986).

(*b*) *Leaf megafossil studies*

Because of their limited potential for transport and reworking, a more spatially and temporally constrained picture of terminal Cretaceous plant disturbance is emerging from the study of plant megafossils and dispersed cuticles. Hickey (1981), working on assemblages from Wyoming and Montana, reported extinctions comparable in intensity to those of the Palaeocene–Eocene boundary, although in northeastern Asia extinctions may have been slightly more severe (Krassilov 1983). These studies suffered, however, by being done at a somewhat coarse stratigraphic resolution.

Wolfe & Upchurch (1986, 1987) have studied in detail leaf and cuticle assemblages at a large number of Western Interior (U.S.A.) boundary sites that display a continuous sedimentary sequence from the Cretaceous to the Tertiary. Instead of concerning themselves with the taxonomic problems inherent in studies of leaves of this age, Wolfe & Upchurch studied environmental and vegetational changes using foliar physiognomy.

Based on 15 sections in the Raton Basin that can be related to the iridium anomaly Wolfe & Upchurch (1987) recognize five vegetational–floristic phases that serve as a general comparison model for sections elsewhere.

Phase 1 (Lancian age – latest Cretaceous) is characterized by broadleaved evergreen vegetation with high diversity. Leaves tend to be small in size with thick hairy cuticles and very few have drip tips. This type of foliar physiognomy indicates a sub-humid (dry) vegetation which persists up to the boundary clay. Evergreen conifers were also present.

Phase 2 (immediately above the boundary) consists entirely of leaves and rhizomes of a fern (morphologically similar to extant *Stenochleana*) and cuticles typical of herbs.

Phase 3 (extending up to 2 m above the boundary) is typified by a depauperate flora of large leaves with drip tips and thick smooth cuticles. Overall, the leaves suggest early successional vegetation in an environment of high precipitation.

Phase 4 (lasted throughout the next 200 m of section) is characterized by an increasing (but still low) leaf diversity. Physiognomically a warm humid environment is indicated.

Phase 5 (throughout the next 150 m of section) indicates low diversity megathermal rainforest.

Wolfe & Upchurch (1986, 1987) suggest that the megafossil pattern of floristic change at the K–T boundary is indicative of an ecological trauma followed by a steady recovery, over perhaps 1.5 Ma, that mimics normal seral succession. The immediate post-boundary vegetation is fern-dominated like modern rainforest vegetation that is devastated by volcanic eruption (Spicer *et al.* 1985), but that is not to say that the K–T boundary trauma was volcanic in origin. It is also evident that although the long-term thermal régime appears to have been little affected, there was a significant increase in humidity (probably precipitation) that lasted well into the Palaeocene. This pattern of increased precipitation is not confined to the Raton Basin and is seen elsewhere in North America.

Leaf data from 66 collections at 8 geographical locations ranging from the Mississippi Embayment to Alberta also show a major shift in vegetational patterns at the boundary. The latest Cretaceous vegetation at palaeolatitudes less than 65° N appears to have been evergreen-rich. However, the post-boundary recovery vegetation was essentially deciduous, even at low middle palaeolatitudes. In the Raton Basin 75% of leaf taxa become at least locally extinct at the boundary, and extinction rates both in the Raton and Denver Basins are highest in the evergreen taxa. In central Alberta only 24% of leaf taxa became extinct, although the gymnosperms were strongly affected. In general, extinction was most pronounced in megathermal and mesothermal broadleaved evergreen vegetation and lowest in broadleaved deciduous vegetation. Deciduous elements had the lowest extinction rates in all types of vegetation, whereas in mesothermal vegetation (between palaeolatitudes 45 and 65° N) evergreen elements were particularly hard hit. Similarly, among conifers, evergreen species became extinct whereas deciduous species survived. The latest Cretaceous mesothermal broadleaved evergreen forests of high–middle latitudes of North America were succeeded by dominantly broadleaved deciduous forests in the earliest Palaeocene. Maastrichtian evergreen elements were replaced by taxa from the more northerly polar broadleaved deciduous forests.

Johnson & Hickey (1988) and Johnson (1988), working in Montana and North Dakota, have developed a biostratigraphy using 798 leaf species at 62 localities spanning 110 m of the latest Cretaceous Hell Creek Formation and the overlying 100 m thick earliest Palaeocene Ludlow member of Fort Union. At Mamarth (southwest North Dakota) 7498 specimens have been used to define three biozones in the 'Lancian Stage' of the Hell Creek and one in the Ludlow Member. The boundary, above the basal lignite of Fort Union Formation, is marked by a weak iridium anomaly and constrained by palynology, magnetostratigraphy, vertebrate biostratigraphy, sedimentary facies and lithology (Johnson 1988). The boundary is preceded by considerable floral turnover in latest Cretaceous, including immigration from the south of typically Raton forms near the base of the magnetostratigraphic unit Chron 29R (approximately 40000 years before the end of the Cretaceous), followed by a diverse basal Palaeocene megaflora. The warming implied by the northward migration of taxa is matched by an increase in the proportion of entire-margined leaves, and an increase in leaf size suggests an increased precipitation: evaporation ratio (K. R. Johnson, personal communication 1988). However there is no evidence for a fern spike. Johnson & Hickey suggest that floristic change was due to long-term environmental processes with only a portion due to traumatic disturbance.

The general pattern of increased precipitation is supported by sedimentological evidence. Coal is more abundant in the Palaeocene than the Cretaceous and leaching of calcareous palaeosols in Montana (see Retallack *et al.* 1987) has been attributed to a change from a sub-humid to wet climate, and possibly a period of 'acid rain', following the boundary event.

The expansion of range of broadleaved deciduous forests that occurred in the Palaeocene gave rise to an increase in genetic diversity. This is seen most strongly in the Juglandaceae but overall a threefold increase in dicot families represented in the polar broadleaved deciduous forest occurs during the Palaeocene (Wolfe 1987). Even today the mesic northern hemisphere deciduous forests are diverse compared with Southern Hemisphere forests growing under similar conditions, but even these are much reduced in comparison with those of the late Palaeocene and Eocene (Wolfe 1987). The increase in diversity occurred after the inoculation of mid-latitude vegetation by northern taxa that had a lower latitude origin earlier in the Cretaceous. At present, there is no evidence of major clades (for example families or orders) originating at high latitudes (Spicer *et al.* 1987).

The ability of some plants to enter dormancy appears to have conferred a major advantage at the K–T boundary and this would be consistent with a short duration cold–dark excursion, during which evergreen taxa were adversely affected, before a new stable 'wet' climate régime was established. Such an interpretation clearly favours the possible existence of a 'boundary event winter'.

The reduced extinction rates at low latitudes (less than 45° N) probably reflects the limited magnitude of the low temperature excursion: in tropical régimes freezing sufficient for mass kill of the megathermal vegetation may not have been experienced. Southern Hemisphere vegetation was much less severely affected at the K–T boundary and even today is evergreen-rich compared with the Northern Hemisphere (Wolfe 1987). Evergreen refugia in mesothermal vegetation must have been few because of the prolonged regional effect and the successful influx and persistence of deciduous elements. A viable deciduous-rich ecosystem was established before megathermal evergreens could evolve into mesothermal vegetation. However, increased Palaeocene precipitation in megathermal régimes may have been a critical factor in the origin of angiosperm-dominated paratropical and tropical rainforest. The increase in precipitation may also have played a role in the extinction of some taxa but it would not have brought about the overall pattern of an increase in deciduousness.

Despite the apparent devastation of the northern mid-latitude vegetation 'standing crop' at the time of the boundary event, and attendant ecological and environmental trauma, most plant lineages, including many evergreens, were able to pass through the boundary and evolve in new directions in the changed post-boundary conditions. The key to this success of plants, even under severe environmental stress, undoubtedly lies in their ability to enter dormancy, either in a mature state (deciduousness or dying back to a perennating organ such as a rhizome) or in seed form. The exposure of buried seeds during increased post-boundary erosion of a denuded landscape would have quickly re-established most lineages. Most vertebrate animals, on the other hand, are poorly equipped to survive prolonged adverse conditions and at the very least populations would have been decimated.

If we assume that the events at the K–T boundary were the result of a 'boundary-event winter' the effects on the vegetation might be expected to be strongly dependent on the duration, intensity and timing of the event, and, in the case of the bolide scenario, the location of the impact site. Tinus & Roddy (1988) suggest that if the impact occurred during spring growth and the effects produced no fatal chill, defoliation might affect deciduous plants more strongly than evergreens because not only would an entire year's crop of leaves be lost but so would the stored food reserves invested in the lost leaf crop. All plants would be relatively safe so long as they remained dormant but subsequent bud break would render all plants susceptible to darkness, temperature fluctuations and/or atmospheric pollutants. If the effects were prolonged slow starvation might kill the trees. If the event occurred late in late summer evergreens might be expected to suffer more because deciduous plants would already be prepared for their normal period of dormancy. In view of the fact that respiration increases with temperature the effects of prolonged darkness might be expected to be more severe at lower latitudes, notwithstanding a cooling induced by loss of insolation. A consequence of these predictions is that any global-scale event would be expected to display a degree of symmetry between Northern and Southern Hemispheres.

Unfortunately, these predictions are difficult to reconcile with the observed global patterns of vegetational change and local extinctions. Although clearly at mid-northern latitudes broadleaved evergreens are selectively eliminated, lower latitude evergreens and those in the Southern Hemisphere are not. Although very incomplete, data from the Southern Hemisphere reveal very minor vegetational changes. This suggests the putative dust cloud must have had a relatively localized effect in the Northern Hemisphere, was probably not 'global', and thus was likely to have been of short duration. The selective evergreen losses are a little easier to explain if a cooling of the Northern Hemisphere took place that was of sufficient intensity to chill broadleaved evergreens fatally only in the northern parts of their range. However, such a freeze would be unlikely to kill soil-buried seeds (from which the evergreens could recover) unless it were very severe. Such an implied severity might be expected to have adversely affected local and more northerly deciduous plants to a far greater extent than is evident from the fossil record.

Many boundary sections yield an abundance of fusain or other evidence of post-boundary fire (Tschudy & Tschudy 1986; Saito *et al.* 1986; Wolbach *et al.* 1985) and the suggestion has been made that wildfires were started as the result of the presumed bolide impact (Wolbach *et al.* 1988). Such a scenario is difficult to envisage, however, because at the time of the impact most vegetation would have been living and with a high moisture content. It is more likely that numerous wildfires started in post-event dead vegetation as the result of frequent lightning strikes produced in a destabilized atmosphere. In a post-event world the recently killed and relatively desiccated forests would have provided ample fuel and would have been easily ignited.

These fires probably had little effect on land-plant extinction because the distribution of fusain in the late Cretaceous fossil record suggests that wildfires were common and probably were an integral element in shaping late Cretaceous vegetation. The lack of fusain (which has a very high preservation potential) at all the intact terrestrial boundary sites, and the apparently minor vegetational disturbance in the Southern Hemisphere, argues strongly against a simultaneous global conflagration (cf. Wolbach *et al.* 1988).

4. Conclusions

Even under the most traumatic of environmental changes plant life shows a remarkable capacity for survival and, as far as can be ascertained, true (that is permanent global loss of the gene line) extinctions of major groups due to catastrophic events are few. When true plant extinctions have occurred they appear to be the result of interplant competition or the loss of specific environments to which a particular group or groups have become irreversibly specialized. Extinctions tend to follow innovation (Knoll 1984; Boulter *et al.* 1988).

If true extinctions at the K–T boundary are few, there is clear evidence for local extinctions and 'lazarus taxa' (taxa which appear to become extinct but which later reappear). Clearly there were numerous refugia. Although this was a time of global warmth, Cretaceous high-latitude coastal vegetation was well adapted to freezing conditions and long periods without sunlight. Mid-latitude coastal vegetation rarely, if ever, experienced frosts. The higher extinction rates among thermophilous broadleaved evergreen taxa at middle northern latitudes and the survival and expansion of deciduous northern taxa suggests strongly that darkness or cold, or both, filtered Northern Hemisphere plants at the end of the Cretaceous. Responses of presumed herbaceous plants at very high northern latitudes, and trees at middle northern latitudes, are consistent with a 'boundary-event winter' in which low temperatures killed mid-latitude evergreens. Limited data from very high northern latitudes do show some vegetational change, which may be used to argue for a northern spring onset for the boundary event in that even deciduous trees and herbaceous plants would be most vulnerable at that time of year. However, until more is known of these high latitude floras our understanding of the timing of the event must remain highly speculative.

Light attenuation with perhaps no evergreen-lethal chill (standing-crop evergreens could have been killed by extended darkness alone) is perhaps less likely because this would have had no effect whatsoever on the evergreen seed bank unless the period of darkness was prolonged (much greater than 10 years). Obviously, survivorship among the deciduous plants would then also have been limited. However, the deleterious effect on the standing crop of low light levels would have been enhanced by relatively warm conditions because respiration rates would have not been depressed by cold.

Southern Hemisphere responses at mid to high latitudes, in so far as they are known, suggest little difference in susceptibility between evergreens and deciduous plants and no wholesale ecological disruption. Clearly, more data are required from Europe, Asia and low palaeolatitudes in both hemispheres, but at present the boundary event seems to have had most effect in northern mid-latitudes and western North America in particular. It is unlikely that Deccan Traps volcanism was responsible for the ecological disruption because floristic changes, although not well defined, are clearly not pronounced in India.

Johnson's (1988) observations of climatic warming, coupled with evidence of at least local increase in water availability in the very latest Cretaceous of the western high plains of the U.S.A., imply the boundary event occurred against a backdrop of changing climates. By way of comparison and contrast, Stott & Kennett (1988) note that oxygen isotope studies using foraminifera suggest that surface waters of high latitude southern oceans experienced a latest Cretaceous cooling of about 5 °C. This cooler temperature was maintained at high latitudes well into the Palaeocene, but at low latitudes temperatures recover after the boundary. Although the significance of these changes is difficult to evaluate at present, the very latest Cretaceous was a time of complex climatic variation that was apparently interrupted by the boundary event. The abrupt climatic change that accompanied the boundary event ushered in a new stable climatic régime that continued well into the Palaeocene. Under the early Palaeocene climate in northern mid-latitudes forest ecosystems evolved a new stable structure and composition. Previously rare species assumed new dominant roles and underwent evolutionary change as a consequence. It is likely that these changes, both climatic and vegetational, induced profound ecological stress in the terrestrial faunal realm, giving rise to enhanced extinction rates.

Existing scenarios are clearly inadequate to explain all the patterns of regional extinction, survivorship and ecological restructuring that took place at the end of the Cretaceous. The difference in seed versus standing crop survivorship is a particularly interesting problem with respect to the 'event winter' scenario. Detailed understanding of latest Cretaceous vegetation and climatic heterogeneity is needed before the K–T boundary events can be properly understood. Even more obscure is the evolution of early Palaeocene forests and yet it is here that we see for the first time the forest types that characterize much of the Northern Hemisphere today. A study of the post K–T boundary recovery, involving as it does evolutionary, ecological and climatic change, offers exciting future challenges.

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REFERENCES

Alvarez, L. W., Alvarez, W., Asaro, F. & Michel, H. V. 1980 Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science, Wash.* **208**, 1095–1108.

Alvarez, W., Alvarez, L. W., Asaro, F. & Michel, H. V. 1984 The end of the Cretaceous: sharp boundary or gradual transition? *Science, Wash.* **223**, 1183–1186.

Askin, R. A. 1988*a* Campanian to Paleocene spore and pollen assemblages of Seymour Island, Antarctica. In *Abstracts of the 7th International Palynological Congress, Brisbane*, p. 7.

Askin, R. A. 1988*b* The palynological record across the Cretaceous/Tertiary transition on Seymour Island, Antarctica. In *Geology and paleontology of Seymour Island, Antarctic peninsula* (*Mem. geol. Soc. Am.* **169**) (ed. R. M. Feldmann & M. O. Woodburne), pp. 155–162.

Axelrod, D. I. 1959 Poleward migation of early angiosperm flora. *Science, Wash.* **130**, 203–207.

Baird, J. G. 1988 Palynostratigraphy of the Late Cretaceous – Early Tertiary of the eastern portion of the Gippsland Basin. In *Abstracts of the 7th International Palynological Congress, Brisbane*, p. 9.

Batten, D. J. 1981 Stratigraphic, palaeogeography and evolutionary significance of late Cretaceous and early Tertiary Normapolles pollen. *Rev. Palaeobot. Palynol.* **35**, 125–137.

Bell, W. E. 1957 Flora of the Upper Cretaceous Nanaimo Group of Vancouver Island, British Columbia. *Mem. geol. Surv. Can.* **293**, 1–84.

Bohor, B. F., Triplehorn, D. M., Nichols, D. J. & Millard, H. T. Jr 1987 Dinosaurs, spherules, and the "magic" layer: a new K–T boundary clay site in Wyoming. *Geology* **15**, 896–899.

Boulter, M. C., Spicer, R. A. & Thomas, B. A. 1988 Patterns of plant extinctions from some palaeobotanical evidence. In *Extinction and survival in the fossil record* (*Spec. Vol. Syst. Ass.* **34**), pp. 1–36.

Brack-Hanes, S. D. 1978 On the megagametophytes of two lepidodendracean cones. *Bot. Gaz.* **139**, 140–146.

Carlquist, S. 1975 *Ecological strategies of xylem evolution.* (259 pages.) Berkeley: University of California Press.

Cleal, C. J. 1988 Questions of flower power. *Nature, Lond.* **331**, 344–346.

Creber, G. T. & Chaloner, W. G. 1985 Tree growth in the Mesozoic and Early Tertiary and the reconstruction of palaeoclimates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **52**, 35–60.

Daghlian, C. P. 1981 A review of the fossil record of monocotyledons. *Bot. Rev.* **47**, 517–555.

Douglas, J. G. & Williams, G. E. 1982 Southern polar forests: the early Cretaceous floras of Victoria and their palaeoclimatic significance. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **39**, 171–185.

Fleming, R. F. 1988 Palynology of the Cretaceous–Tertiary boundary in the Raton Basin: implications for development of the Tertiary flora. In *Abstracts of the 7th International Palynological Congress*, *Brisbane*, p. 50.

Frederiksen, N. O., Ager, T. A. & Edwards, L. E. 1988 Palynology of Maastrichtian and Paleocene rocks, lower Colville River region, North Slope of Alaska. *Can. J. Earth Sci.* **25**, 512–527.

Hannah, M. J. & Partridge, A. D. 1988 Cretaceous–Tertiary boundary localities in Australia. In *Abstracts of the 7th International Palynological Congress*, *Brisbane*, p. 65.

Hickey, L. J. 1981 Land plant evidence compatible with gradual not catastrophic change at the end of the Cretaceous. *Nature, Lond.* **292**, 529–531.

Hickey, L. J. 1984 Changes in the angiosperm flora across the Cretaceous–Tertiary boundary. In *Catastrophies in Earth history: the new uniformitarianism* (ed. W. A. Bergren & J. A. Van Couvering), pp. 279–314. Princeton University Press.

Hickey, L. J. & Doyle, J. A. 1977 Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.* **43**, 3–104.

Hollick, A. 1930 The Upper Cretaceous Floras of Alaska. *U.S. geol. Surv. prof. Pap.* **159**, 1–123.

Hotton, C. 1988 Cretaceous–Tertiary palynostratigraphy in east central Montana, U.S.A. In *Abstracts of the 7th International Palynological Congress*, *Brisbane*, p. 76.

Izett, G. A. & Bohor, B. F. 1986 Microstratigraphy of continental sedimentary rocks in the Cretaceous–Tertiary boundary interval in the Western Interior of North America. *Geol. Soc. Am. Abstr. Progr.* **18**, 644.

Johnson, K. R. 1988 High resolution megafloral biostratigraphy for the late Cretaceous and early Paleocene of N. Dakota and Montana. *Geol. Soc. Am. Abstr. Prog.* **20**, 379.

Johnson, K. R. & Hickey, L. J. 1988 Patterns of megafloral change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains. In *Abstracts – Global Catastrophies in Earth History*, *Snowbird, Utah, October 20–23 1988*, p. 87.

Knoll, A. H. 1984 Patterns of extinction in the fossil record of vascular plants. In *Extinctions* (ed. M. Nitecki), pp. 21–68. Chicago: University of Chicago Press.

Knoll, A. H. & Niklas, K. J. 1987 Adaptation, plant evolution, and the fossil record. *Rev. Palaeobotan. Palynol.* **50**, 127–149.

Krassilov, V. A. 1983 Evolution of the flora of the Cretaceous period: is a Cenophytic era necessary? (In Russian.) *Paleontol. Zh.* 93–95.

Leffingwell, H. A. 1971 Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) Formations of the Lance area, Wyoming. In *Symposium on palynology of the late Cretaceous and early Tertiary* (*Spec. Pap. geol. Soc. Am.* no. 127) (ed. R. M. Kosanke & A. T. Cross), pp. 1–64.

Lidgard, S. & Crane, P. R. 1988 Quantitative analyses of the early angiosperm radiation. *Nature, Lond.* **331**, 344–346.

Méon, H. 1988 Sporo-pollenic studies of El Kef outcrop (N.W. Tunisia), palaeogeographic implications. In *Abstracts of the 7th International Palynological Congress*, *Brisbane*, p. 109.

Muller, J. 1981 Fossil pollen records of extant angiosperms. *Bot. Rev.* **47**, 1–142.

Nichols, D. J., Jarzen, D. M., Orth, C. J. & Oliver, P. Q. 1986 Palynological and iridium anomalies at Cretaceous–Tertiary boundary, south–central Saskatchewan. *Science, Wash.* **231**, 714–717.

Nichols, D. J. & Fleming, R. F. 1988 Plant microfossil record of the terminal Cretaceous event in western United States and Canada. In *Abstracts – Global Catastrophies in Earth History*, *Snowbird, Utah, October 20–23 1988*, p. 130.

Parrish, J. T. & Spicer, R. A. 1988 North Polar Late Cretaceous temperature curve: evidence from plant fossils. *Geology* **16**, 22–25.

Raine, J. I. 1988 The Cretaceous/Cainozoic boundary in New Zealand terrestrial sequences. In *Abstracts of the 7th International Palynological Congress*, *Brisbane*, p. 137.

Ramanujam, C. G. K. & Stewart, W. N. 1969 Fossil woods of Taxodiaceae from the Edmonton formation (Upper Cretaceous) of Alberta. *Can. J. Bot.* **47**, 115–124.

Rawat, M. S., Swamy, S. N. & Juyal, N. P. 1988 Cretaceous/Tertiary boundary changes in the palynofossil assemblage of the Krishna–Godavari Basin, India. In *Abstracts of the 7th International Palynological Congress, Brisbane*, p. 138.

Retallack, G. J., Leahy, G. D. & Spoon, M. D. 1987 Evidence from paleosols for ecosystem changes across the Cretaceous/Tertiary boundary in eastern Montana. *Geology* **15**, 1090–1093.

Rothwell, G. W. 1977 Evidence for a pollen-drop mechanism in Paleozoic pteridosperms. *Science, Wash.* **198**, 1251–1252.

Saito, T., Yamanoi, T. & Kaiho, K. 1986 Devastation of the terrestrial flora at the end of the Cretaceous in the Boreal Far East. *Nature, Lond.* **323**, 253–256.

Scott, R. A. & Smiley, C. J. 1979 Some Cretaceous plant megafossils and microfossils from the Nanushuk Group, Northern Alaska, a preliminary report. *Circ. U.S. geol. Surv.* **794**, 89–112.

Smiley, C. J. 1966 Cretaceous floras of the Kuk River area, Alaska – stratigraphic and climatic interpretations. *Bull. geol. Soc. Am.* **77**, 1–14.

Smiley, C. J. 1969*a* Cretaceous floras of the Chandler–Colville region, Alaska – stratigraphy and preliminary floristics. *Bull. geol. Soc. Am.* **53**, 482–502.

Smiley, C. J. 1969*b* Floral zones and correlations of Cretaceous Kukpowruk and Corwin formations, northwestern Alaska. *Bull. Am. Ass. Petrol. Geol.* **53**, 2079–2093.

Spicer, R. A. 1989*a* Physiological characteristics of land plants in relation to environment through time. *Proc. R. Soc. Edinb.* (In the press.)

Spicer, R. A. 1989*b* Reconstructing high latitude Cretaceous vegetation and climate: Arctic and Antarctic compared. In *Antarctic paleobiology and its role in the reconstruction of Gondwana* (ed. T. N. Taylor & E. L. Taylor). Berlin: Springer-Verlag.

Spicer, R. A. 1987 The significance of the Cretaceous flora of northern Alaska for the reconstruction of the Cretaceous climate. In *Das Klima der Kreide-Zeit* (*Geol. Jb.* A **96**) (ed. E. Kemper), pp. 265–291.

Spicer, R. A., Burnham, R. J., Grant, P. R. & Glicken, H. 1985 *Pityrogramma calomelanos*, the primary, post eruption colonizer of Volcán Chichonal, Chiapas, Mexico. *Am. Fern J.* **53**, 1–5.

Spicer, R. A. & Parrish, J. T. 1986 Paleobotanical evidence for cool North Polar climates in the mid-Cretaceous (Albian–Cenomanian). *Geology* **14**, 703–706.

Spicer, R. A. & Parrish, J. T. 1987 Plant megafossils, vertebrate remains, and paleoclimate of the Kogosukruk Tongue (late Cretaceous), North Slope, Alaska. In *Geologic studies in Alaska by the United States Geological Survey during 1986* (*Circ. U.S. geol. Surv.* **933**) (ed. T. D. Hamilton & J. P. Galloway), pp. 47–48.

Spicer, R. A. & Parrish, J. T. 1989 Late Cretaceous–early Tertiary palaeoclimates of northern high latitudes: a quantitative view. *J. geol. Soc.* (In the press.)

Spicer, R. A., Wolfe, J. A. & Nichols, D. J. 1987 Alaskan Cretaceous–Tertiary floras and Arctic origins. *Paleobiology* **13**, 73–83.

Sporne, K. R. 1980 A re-investigation of character correlations among dicotyledons. *New Phytol.* **85**, 419–449.

Stott, L. D. & Kennet, J. P. 1988 Cretaceous/Tertiary boundary in the Antarctic: climatic cooling precedes biotic crisis. *Geol. Soc. Am. Abstr. Prog.* **20**, 251.

Sweet, A. R. & Braman, D. R. 1988 Floral Changes within the interval containing the Cretaceous–Tertiary boundary in western Canada: a stratigraphic, palaeogeographic and palaeoenvironmental perspective. In *Abstracts of the 7th International Palynological Congress, Brisbane*, p. 161.

Tiffney, B. H. 1984 Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. *Ann. Mo. bot. Gdn* **71**, 551–576.

Tinus, R. W. & Roddy, D. J. 1988 Effects of global atmospheric perturbations on forest ecosystems: predictions of seasonal and cumulative effects. In *Abstracts – Global Catastrophies in Earth History, Snowbird, Utah, October 20–23 1988*, p. 196.

Tschudy, R. H. 1971 Palynology of the Cretaceous–Tertiary boundary in the northern Rocky Mountains and Mississippi Embayment regions. *Spec. Pap. geol. Soc. Am.* no. 127, 65–111.

Tschudy, R. H. 1973 The Gasbuggy Core – a palynological appraisal in Cretaceous and Tertiary rocks of the southern Colorado Plateau. In *Memoir: Durango, Colorado* (ed. J. E. Fasset), pp. 131–143. Colorado: Four Corners Geological Society.

Tschudy, R. H. & Tschudy, B. D. 1986 Extinction and survival of plant life following the Cretaceous–Tertiary boundary event, Western Interior, North America. *Geology* **14**, 667–670.

Upchurch, G. R. Jr & Dilcher, D. L. 1984 A magnoliid leaf flora from the mid Cretaceous Dakota Formation of Nebraska. *Am. J. Bot.* **71**, 119.

Upchurch G. R. Jr & Wolfe, J. A. 1987 Mid Cretaceous to early Tertiary vegetation and climate: evidence from fossil leaves and woods. In *The origin of angiosperms and their biological consequences* (ed. E. M. Friis, W. G. Chaloner & P. R. Crane). Cambridge University Press.

Wheeler, E., Lee, M. R. & Matten, L. C. 1987 Dicotyledonous woods from the Upper Cretaceous of southern Illinois. *Bot. J. Linn. Soc.* **95**, 77–100.

Wolbach, W. S., Lewis, R. S. & Anders, E. 1985 Cretaceous extinctions: evidence for wildfires and search for meteoric material. *Science, Wash.* **230**, 167–170.

Wolbach, W. S., Gilmour, I., Anders, E., Orth, C. J. & Brooks, R. R. 1988 Global fire at the Cretaceous–Tertiary boundary. *Nature, Lond.* **334**, 665–669.

Wolfe, J. A. 1985 Distribution of major vegetational types during the Tertiary. *Monogr. Am. geophys. Un. Geophys.* **32**, 357–375.

Wolfe, J. A. 1987 Late Cretaceous – Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology* **13**, 215–226.

Wolfe, J. A. & Upchurch, G. R. Jr 1986 Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary. *Nature, Lond.* **324**, 148–152.

Wolfe, J. A. & Upchurch, G. R. Jr 1987 Leaf assemblages across the Cretaceous–Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proc. natn. Acad. Sci. U.S.A.* **84**, 5096–5100.

Discussion

N. J. Shackleton, F.R.S. (*Sub-Department of Quaternary Research, University of Cambridge, U.K.*). If current understanding of oceanic events at the K–T boundary is correct, atmospheric CO_2 must have risen rapidly by about a factor of two or three as a consequence of the drastic reduction in the biological pumping of carbon from surface to deep ocean. Obviously this would have affected global climate, but I wonder whether the direct effect of this rise in CO_2 on plant water use efficiency might bias Dr Spicer's inference from plant leaf shapes of changing precipitation across the boundary?

R. A. Spicer. Changes in atmospheric CO_2 levels are known to affect stomatal action, and thereby water relations, in several species of modern plants but the extent to which this occurs varies from species to species (see, for example, Bazzaz 1980; Moore 1983). This, in turn, alters competitiveness and, by extrapolation, the composition of vegetation (Jarvis & McNaughton 1986). Unfortunately, far too little is known about this phenomenon and its retrodictive value for the Cretaceous or Palaeocene world for us to quantify its possible effect in biasing estimates of precipitation:evaporation ratios. Intuitively, sudden (say less than 1 Ma) changes in atmospheric CO_2 to the extent of doubling or quadrupling present atmospheric levels are unlikely to induce sufficient selection of the genome to bring about wholesale changes in leaf morphology at the species level. To generate the extent of changes in assemblage composition that are observed would require rapid simultaneous evolution of species. Nevertheless, the possibility that the proportions of taxa might change is a real one but here the magnitude of the effect is unlikely to alter significantly the conclusion that precipitation increased.

Fortunately, one does not have to rely solely on data from individual plant specimens. It has long been recognized that the onset of coal deposition in the Western Interior of the U.S.A. is approximately coincident with the K–T boundary (Brown 1962) which, together with an increase in the abundance and size of river channels, also suggests more humid conditions in the Palaeocene than the Maastrichtian. The more parsimonious explanation of the biotic and abiotic changes across the boundary is that the precipitation:evaporation ratio increased, but this does not exclude changes in CO_2 levels.

References

Bazzaz, F. A. 1980 Consequence of elevated CO_2 concentrations for plant photosynthesis, growth and competition. In *Abstracts of the 5th International Congress on Photosynthesis, September 7–13. Halkidiki, Greece.*

Brown, R. W. 1962 Paleocene flora of the Rocky Mountains and Great Plains. *U.S. geol. Surv. prof. Pap.* no. 375. (119 pages.)

Jarvis, P. G. & McNaughton, K. G. 1986 Stomatal control of transpiration: scaling up from leaf to region. *Adv. ecol. Res.* **15**, 1–49.

Moore, P. D. 1983 Plants and the palaeoatmosphere. *J. geol. Soc. Lond.* **140**, 13–25.