Corroded pollen and spores as indicators of changing lake sediment sources and catchment disturbance

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Abstract

Pollen and spores with resistant exines are preferentially preserved in soils, and during periods of soil erosion they can become incorporated into lake sediments. As a result, the contemporary vegetation may be poorly represented by the palynomorphs in the lake sediments because of the reworked component of inwashed pollen and spores. We record the proportion of palynomorphs with corroded exines in sediment cores from four lakes in the eastern North Island of New Zealand to document changing sources of palynomorphs over the last \sim 2000 years. During this period, the catchments experienced major vegetation disturbances, both natural (from volcanism and fire) and anthropogenic including deforestation ca. 600 years ago, and the European conversion of fern-scrubland to pasture in the 19th century. Corroded palynomorphs are more abundant in inwashed sediments than authigenic sediments. Catchment soil disturbance was minor during the forested period, and characterised by small, inwashed, sediment pulses after storms, and a relatively low percentage of corroded palynomorphs. Although initial Maori forest clearance by fire led to a temporary increase in erosion in one lake catchment, rapid replacement of forest by a dense bracken fern cover helped to minimise soil erosion and reworking of palynomorphs in this period. European pastoralists replaced the bracken fern with shallow-rooted pasture grasses about 150 years ago. In erosion prone lake catchments, this led to a rapid increase of inwashed eroded soils and littoral sediments, and their component of resistant palynomorphs, reaching the lake sediments. As a result, the palynological records from these catchments during the European period are distorted by reworking. By contrast, over the same period, the palynological record from a lake with no inflowing streams and stable catchment soils more faithfully represented the contemporary vegetation cover. Exine corrosion has been used to help identify periods of reworking in the lake sediments and to allow for a correction of distortion caused by reworking.

Introduction

Lakes with inflowing waterways and surrounded by steep slopes may receive a large proportion of their sediments from allochthonous sources, mainly inwashed soils and riverbank sediments. Soils can be mobilised during high rainfall events, and transported to the lake basins where they become incorporated into lake sediments, a process which may be accelerated by disturbance or human impacts in the catchment. Prolonged storage of pollen and spores (palynomorphs) in soils exposes their exines to chemical oxidation and biological degradation (Havinga 1964). Although

the cytoplasm of pollen and spores (palynomorphs) deteriorates rapidly in such conditions, the extremely resistant outer walls (exines) which are made up of inert sporopollenin, often survive but become corroded or pitted (Havinga 1964, 1984; Cushing 1967; Lowe 1982). In contrast, contemporaneous palynomorphs deposited aerially on the lake surface and incorporated into authigenic lake sediments, subsequently undergo little or no exine deterioration. Because of the high levels of chemical and biological activity in soils, the more resistant pollen and spore types become over-represented in them. As a result, soil palynomorph spectra may eventually consist mostly of resistant pollen and spores that have accumulated over a long period of time. When such soils are reworked into lake sediments, the pollen and spore contribution of the contemporary vegetation is not accurately represented e.g., Wilmshurst et al. (1999). Mixed-aged pollen and spores in lake sediments also make it difficult to obtain accurate accelerator mass spectrometry (AMS) radiocarbon dates, from both bulk lake sediments, and palynomorph concentrates.

Fern spores often form an important component of the total palynomorph spectra. However, their representation and interpretation are complicated by their generally superior ability, relative to angiosperms and gymnosperms, to resist decay, which can often make them the most persistent palynomorphs. This is clearly demonstrated by palynological results from estuarine and deep-sea cores where fern spores often dominate the palynomorph count, occasionally to the near exclusion of angiosperms (Wilmshurst et al. 1999; McGlone 2002; Swales et al. 2002). Abundance of fern spores in sediments is therefore not necessarily a reliable indicator of actual fern abundance. Fern spore records, and in particular those of bracken (Pteridium esculentum (G. Forst.) Cockayne) and tree ferns (Dicksonia spp. and Cyathea spp.), are widely used in New Zealand and elsewhere in the Pacific to help pinpoint natural vegetation disturbance after fire or volcanism e.g., Wilmshurst et al. (1997) and the beginning of human occupation and the course of landscape modification (McGlone 1983a; Kirch 1997; Parks 1997; Newnham et al. 1998; McGlone and Wilmshurst 1999).

Bracken is of particular importance as it is used as a major chronological and stratigraphical marker for human settlement in palaeoecological

records (McGlone and Wilmshurst 1999). Maori settlers arrived in New Zealand from eastern Polynesia in the 13th century and cleared a large proportion of forest cover by fire, particularly in the drier, eastern areas (McGlone 1983a). Bracken was a vigorous invader following fire, and repeated fires maintained its dominance on the landscape for hundreds of years until the start of European agriculture and forestry in the 19th century (McGlone 1983a; McGlone and Wilmshurst 1999). However, in many New Zealand pollen diagrams, bracken spores still dominate recent palynomorph spectra, even though this fern became relatively uncommon with agricultural improvements. A better understanding of depositional and preservation processes is necessary, therefore, to accurately interpret the fossil record.

This study examines the preservation status and representation of fossil pollen grains, as well as bracken and tree fern spores in sediment cores from three lakes with erosion-prone catchments and one with a stable catchment in the North Island of New Zealand. Detailed fossil palynomorph analyses have been published from two of the longest cores (Wilmshurst 1997; Wilmshurst et al. 1997) and these document episodes of natural forest disturbance (primarily fire and several volcanic eruptions) and anthropogenic vegetation change over the last \sim 2000 years. Preservation of pollen, bracken and tree fern spores from these sediment cores are quantitatively analysed to establish: (1) if there is a difference between palynomorph preservation in authigenic and allogenic lake sediments; (2) whether pollen and spore preservation has changed over time under different regimes of vegetation and soil stability; and (3) whether contemporaneous and secondary sources of pollen and spores to lake sediments can be identified. Information about pollen and spore preservation, sources and their transport routes to lake sediments will allow real disturbance-induced vegetation changes to be recognised and separated from spurious signals of disturbance caused by contamination of the fossil palynomorph record with inwashed palynomorphs.

Study sites

The study sites are located about 35 km apart in the Tutira and Putere districts of Hawke's Bay, in the eastern North Island of New Zealand (Figure 1). Cores were taken from two lakes in the Tutira catchment (39 $^{\circ}$ 22' S, 176 $^{\circ}$ 90' E): lakes Tutira (core LT16) and Waikopiro (core LW8), and two from the Putere catchment $(38°57′ S,$ $177°02'$ E): lakes Rotonuiaha (core RNUI3) and Rotongaio (RNGA3) (Figure 1). Detailed pollen, tephra and charcoal analyses covering the last \sim 2000 years have been published for each of the longest records from Tutira (LT16) and Putere (RNUI3) (Eden and Froggatt 1996; Wilmshurst 1997; Wilmshurst et al. 1997). The two shorter cores (LW8 and RNGA3) have vegetation histories that overlap with the more recent zones in the longer cores. Lake Tutira (surface area 1.8 km^2 , max. depth 38 m) receives its main inflow from the Papakiri stream at the northern end of the lake (Figure 1). Lake Wakopiro (surface area 0.11 km^2 , max. depth 14 m) has no permanent inflowing streams but often receives overflow from Lake Tutira. Lake Rotonuiaha (surface area

 0.44 km^2 , max. depth 29 m) receives inflow from three streams, including one that drains lake Rotoroa to the east. Sediments in these three cores contain many inwashed, graded sediment beds (or erosion pulses). These become increasingly abundant towards the present, particularly in the last \sim 150 years when the catchments were converted to pasture and became more erosion prone (Wilmshurst 1997). By contrast, Lake Rotongaio (surface area 0.94 km^2 , max. depth 5 m), the shallowest of the four study lakes, has no direct inflow, but is fed by seepage and is surrounded by dense swamp communities. Lake Rotongaio therefore makes an ideal comparison with the other three lakes as it receives little allogenic sediment.

The lake catchments are typical of the soft-rock hill country in Hawke's Bay, which consists of highly erodible sandstone and siltstone interbedded with limestone and conglomerates of Pliocene and early Pleistocene age, mantled with

Figure 1. Map showing the Hawke's Bay district of New Zealand (a), with the relative locations, lake catchment areas, and coring locations of the Tutira (b) and Putere (c) study areas.

tephra from the 1850 BP Taupo eruption (Page et al. 1994). Both districts have warm, dry summers and moderate winter temperatures with a mean annual temperature of ca. $12.5\,^{\circ}\text{C}$ and a mean annual rainfall of ca.1400 mm/yr at Tutira, and ca. 2000 mm/yr at Putere (Thompson 1987). Rainfall variability is high in both locations, and severe storms of extratropical origin occasionally pass over the area causing major flooding, landslide erosion and siltation. Current land-use is dominated by livestock production. At Tutira, permanent pasture covers about 90% of the catchment. The remaining land supports swamp, and small pockets of Leptospermum scrub and regenerating podocarp-hardwood forest. In the Putere catchments, ca. 75% of the land area is under permanent pasture, the remainder being covered by bracken and scrub (Kunzea ericoides (A. Rich.) Joy Thomps. and Leptospermum scoparium J.R. Forst and G. Forst.).

Methods

Sediment cores

Sediment cores were taken from the deepest part of each lake basin using an air-assisted Mackereth piston corer (Mackereth 1958). The coring sites were located away from inflowing rivers or streams to avoid direct fluvial inwash. Erosion pulses were identified in the sediment cores as coarse allogenic catchment material that visibly graded upwards from sand to silt, then to fine clay. Erosion pulses indicate a discrete episode of soil erosion in the lake catchment after a high intensity rainstorm (Dearing 1991; Page et al. 1994). The thickest single erosion pulse unit (116 cm) was found in the upper sediments of core LW8 and was related to an erosion event following a storm in 1938 (Page et al. 1994). The erosion pulse sediment (mostly inorganic) is defined here as allogenic, and nonerosion pulse sediment as authigenic. Erosion pulses were easily distinguished from the often textureless, organic-rich, authigenic lake sediments, although the latter also contained finegrained inorganic sediments washed in during normal low-intensity rainfall events. Sediment cores were subsampled (0.5 cm^3) at 10 cm or 15 cm intervals, and at closer intervals of 0.5 to 1 cm above tephra deposits, for pollen and spore

analysis (Wilmshurst 1997; Wilmshurst et al. 1997).

Fossil pollen and spore analysis

Pollen and spore analysis followed standard procedures (Moore et al.1991), and charcoal was quantified during pollen analysis using the point count technique (Clark 1982). Palynomorph counts were expressed as relative percentages of a palynomorph sum including all terrestrial pollen grains and bracken spores. Fern spores other than bracken were excluded from the sum because of their tendency to be abundantly produced but poorly dispersed, which results in their erratic representation (Pocknall 1980). Tree fern spores are excluded from the sum as they are often highly over-represented in the fossil record due to reworking (Wilmshurst et al. 1999; McGlone 2002; Swales et al. 2002).

Differential pollen and spore preservation

After palynomorphs were counted, the occurrence of exine 'corrosion' was then recorded for all pollen grains, bracken spores and tree fern spores (number as close to 100 as possible for each palynomorph group). The preservation category 'corroded' (based on Cushing 1967) best described the type of palynomorph deterioration seen in the Tutira and Putere cores. Pollen and spores were categorised as 'corroded' if any part of the ektexine (outermost layer of exine) was etched or pitted (Figure 2). Corrosion may affect only part of the exine. Severe corrosion may result in most of the ektexine being eaten away, leaving only remnants upon the surface of the intact endexine (inner layer of exine). This creates the impression of a 'ghost' grain or spore, most commonly seen in the more resistant fern spores. Initially, we attempted a more complex corrosion scale to quantify the degree of exine corrosion, but it was difficult to apply consistently and provided no more information than a simple corrosion/no corrosion category. Two other categories of deterioration, 'degraded' and 'crumpled', commonly recorded in other works (e.g., Cushing 1967; Birks 1970; Tolonen 1980; Hall 1981; Lowe 1982;

Figure 2. Examples of (a) patchy exine corrosion of a *Dacrydium cupressinum* pollen grain (longest dimension 50 μ m), (b) corroded exine of a Cyathea dealbata type tree fern spore (longest dimension 55 μ m) and by comparison (c) an intact, well-preserved Pteridium esculentum spore (longest dimension 30 μ m) (all photomicrographs taken at 400 \times magnification).

Havinga 1984) were rarely seen in the palynomorphs from the Tutira and Putere cores.

Results

Fossil pollen and spore records

The following is a summary of the changes documented in the pollen diagrams from lakes Tutira (LT16) and Rotonuiaha (RNUI3) (Wilmshurst 1997; Wilmshurst et al. 1997), and Waikopiro and Rotongaio (Figure 3a–d). The pollen diagrams are all divided into three distinct vegetation zones, based on the inferred dominant vegetation cover i.e., forest, bracken or pasture. These 'zones' of dominant vegetation cover are summarised below:

Forest zone (ca. $2000 - 600$ ¹⁴C BP): Tall multistoried, evergreen lowland podocarp-hardwood forest covered the catchments (Wilmshurst et al. 1997; McGlone 2002). Short-lived forest disturbances (lightning-strike fires and volcanism) occurred within this period, and are marked by temporary declines in forest taxa, with corresponding increases in seral taxa, most notably bracken spores. Both minor fire episodes and major forest disturbance following the 1850 BP Taupo eruption (Wilmshurst and McGlone 1996) were characterised by short-term forest collapse with corresponding increases of bracken, grasses and other seral taxa, followed by a recovery back to a closed canopy forest within ca. 200 years.

Bracken zone (ca. 600 BP–1870 AD): Early-Maori fires began in the region ca. 600 BP and rapidly removed forest from the catchments, as indicated by a massive reduction in pollen from tall forest taxa, and a concurrent long-term

increase in bracken spores and pollen from shrubland taxa that replaced the forest (Wilmshurst 1997). Deforestation is associated with a major erosion episode only in the Lake Tutira core (Figure 3a).

Pasture zone (1870 AD to present): This zone represents the start of the European settlement period and is marked by the first appearance of exotic pollen types, the reduction of the lowland podocarp-hardwood forest to remnants, and the clearance of bracken fern and shrubland for permanent pasture. However, bracken spores remain high (up to 80%) in this zone.

Cores from lakes Tutira (LT16) and Rotonuiaha (RNUI3) record all three zones, whereas Lake Rotongaio (RNGA3) records only the Pasture, Bracken and upper part of the Forest zones, and Lake Waikopiro (LW8) only the Pasture and upper part of the Bracken zones.

Erosion pulses

The positions of the erosion pulses in cores LT16, RNUI3 and LW8 are given in the lithology columns of Figure 3. Erosion pulses were not present in core RNGA3. Erosion pulse sediment in each core is presented as a percentage of the total sediment depth in each of the three designated zones from the pollen diagrams, i.e., Pasture, Bracken and Forest (Figure 4). The sediments in the Pasture zones of all cores (except RNGA3) contained more erosion pulse sediment than in any other zone, with highest proportions in LT16 and LW8 at 70%. There is a trend in each core for an increasing proportion of erosion pulse sediment towards the present.

Differential preservation of palynomorphs in authigenic and allogenic sediments

The total percentage of corroded palynomorphs found in authigenic and allogenic sediments of cores LT16, RNUI3, LW8 and RNGA3 are presented in Figure 5a. In each core there are more corroded palynomorphs in allogenic than authigenic sediments. The percentage of corroded bracken spores, pollen grains and tree fern spores

Figure 3. Summary percentage pollen diagrams for cores from lakes (a) Tutira (LT16), (b) Rotonuiaha (RNUI3), (c) Waikopiro (LW8) and (d) Rotongaio (RNGA3) showing three vegetation zones (Forest, Bracken and Pasture zones- derived from dominant vegetation type). Diagrams also show in the lithology column, the position of erosion pulse sediments in each core and volcanic tephra layers (from Wilmshurst et al. 1997): including Kaharoa Tepha (Ka, ca. 665 \pm 15¹⁴C yrs BP), Ruapehu Tephra (Tufa Trig Formation member 5 (Tf5), ca. 750¹⁴C yrs BP) and Taupo Tephra (ca. 1850¹⁴C yrs BP).

Figure 3. Continued

Figure 4. Erosion pulse sediment as a percentage of sediment in the three vegetation zones (Forest, Bracken, Pasture) of cores from lakes Tutira (LT16), Rotonuiaha (RNUI3) and Waikopiro (LW8).

in authigenic and allogenic sediments is presented in Figure 5b. All palynomorph groups show more corrosion in the allogenic sediments than in the authigenic sediments. Bracken spores are the least corroded of all palynomorphs in both types of sediment. Tree fern spores in the authigenic sediments are more corroded than pollen and bracken spores. The increasing order of corrosion for all palynomorphs in the authigenic sediments of the cores is, RNGA3 \rightarrow RNUI3 \rightarrow LT16 \rightarrow LW8. This order correlates with increasing amounts of allogenic sediment in these cores.

Percentage corroded palynomorphs within the Forest, Bracken and Pasture zones of each core are presented in Figure 6. There is a general trend for the pollen and spores to be more corroded in the Pasture zones than in the Bracken or Forest zones. In the Bracken and Forest zones of all cores, bracken spores are the least corroded of the palynomorph groups.

Discussion

There is a higher proportion of corroded pollen, bracken and tree fern spores in allogenic erosion pulse sediment than in other lake sediment (Figure 5a–b) because the palynomorphs are derived from inwashed catchment soils remobilised into the lake during high-rainfall erosion events.

The process of corrosion must therefore occur some time after the pollen and spores are initially released from the source vegetation, either during the time they are in catchment soils and/or in the process of being transported to the lake by water.

Sources and transport of tree fern spores

Tree ferns produce vast numbers of relatively heavy spores but they tend to be poorly dispersed. As a result, most of these spores fall close to the source plants, and are under-represented at more distant sites (Macphail and McQueen 1983). However, tree fern spores can become over-represented in soils and, through reworking, in lake sediments. Tree fern spores are extremely resistant to deterioration because of their high sporopollenin content and thick walls. Experimental evidence indicates that while the exines of thickwalled spores can become corroded, they are not often completely destroyed (Havinga 1984). Greater resistance and preferential preservation may explain the apparent paradox of tree fern spores being highly corroded compared with pollen and bracken spores in this study (Figure 5b). These factors also explain why tree fern spores are both over-represented and highly corroded in the Pasture zones (Figures 3 and 6), where the percentage of allogenic erosion pulse sediment is

Figure 5. (a) Boxplots of percentage corroded palynomorphs (combined data) recorded in the authigenic and allogenic erosion pulse sediments of cores from lakes Tutira (LT16), Rotonuiaha (RNUI3), Waikopiro (LW8) and Rotongaio (RNGA3). (b) Boxplots of percentage corroded bracken spores, pollen grains and tree fern spores (combined from all cores) recorded in authigenic and allogenic erosion pulse sediments. Box plots graph data as a box representing statistical values. The lower boundary of the box indicates the 25th percentile, the straight line within the box marks the median, the dotted line the mean, and the upper boundary indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Black dots represent outlying points. At least three points were required to compute the 25th and 75th percentiles, five points to compute the 10th percentile, and six points to compute the 5th, 90th, and 95th percentiles. A set of points is not drawn if a percentile point cannot be computed (SigmaPlot: SYSTAT Software Inc. 2002).

greatest. Over-representation of tree ferns attributed to water-transported eroded catchment soils or riverbank sediments has been recorded in other lake sediment palynomorph profiles in New Zealand (Pocknall 1980; McGlone 1983b; Wilmshurst et al. 1999).

When the Tutira and Putere catchments were under a dense cover of forest, tree ferns were abundant in the forest understorey and in shady river gulleys, and the soils were far less vulnerable to erosion (Wilmshurst 1997; Wilmshurst et al. 1997). During this time, soils were probably the

major source of the corroded tree fern spores in lake sediments. However, in the Bracken zones, and more specifically the Pasture zones, where erosion pulse sediment increased as a proportion of the sediment type, eroded riverbank and littoral sediments were likely to have provided the main source of corroded tree fern spores rather than soils. Palynomorph analysis of surface soil samples from the Tutira and Putere catchments (Wilmshurst and McGlone, 2005) revealed a surprisingly low abundance of tree fern spores (5%) when compared with the surface lake sediments (up to 20%) and relatively low levels of corrosion (10% in soils, 50% in the surface lake sediments). Thus, tree fern spores in the surface lake sediments were probably derived from sources other than surface soils, such as regolith and riverbank sediments. As biological activity is generally higher in riverbank sediments than in topsoils (Havinga 1984), pollen and spores stored within such sediments may decay more rapidly than in the soils. Experimental studies of palynomorph preservation in river clay soils have shown pollen deterioration was so rapid that more than half the pollen grains were lost to corrosion within the first two years, after which decay occurred at a slower rate and reduced some pollen types to trace amounts (Havinga 1984). In contrast Lycopodium spores were found to remain well preserved throughout the duration of the experiment, demonstrating the robust nature of thick-walled spores compared with most types of pollen grains.

Reworked littoral sediments may also have acted as a source of corroded tree fern spores. Tree fern spores are larger and heavier than most pollen grains and may only be transported a short distance from river flat and river gully sources, causing them to concentrate in the coarse littoral sediments. Experimental work on the differential transport of pollen and spores has shown that palynomorph size, and possibly specific gravity, control the rate of settling, with the larger types settling first (Holmes 1990). Coarse sandy bed

Figure 6. Boxplots of percentage corroded pollen grains, bracken spores and tree fern spores within each vegetation zone of cores from lakes Tutira (LT16), Rotonuiaha (RNUI3), Waikopiro (LW8) and Rotongaio (RNGA3). There are no data for the Forest and Bracken zones of LW8. Box plots graph data as a box representing statistical values described in the caption Figure 6. Bo
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materials, over which the water current flows, were also found to increase the deposition rates of palynomorphs. The robust nature of tree fern spores and their resistance to deterioration in such environments may also encourage their concentration in littoral sediments relative to pollen grains. This may explain why the core from Lake Rotongaio (RNGA3) had relatively high percentages of corroded tree fern spores (Figure 6) despite the sediments containing no inwashed erosion pulses. The littoral sediments may contribute relatively larger amounts of corroded pollen and spores to Lake Rotongaio than to the other lakes in this study, because its small size, gently sloping catchment and shallow water depth (5 m) make it more susceptible to wind turbulence, lowered water tables and drying of littoral sediments.

Bracken spore preservation and representation

Bracken spores preserved in the Forest and Bracken zones of all cores are less corroded than in the Pasture zones of all cores (Figure 6). This suggests the corroded spores were derived from different sources under different catchment regimes. Although the same pattern occurs with the corroded pollen and tree fern spore data, the difference is more pronounced for bracken spores.

The predominantly well-preserved bracken spores recorded in the Forest and Bracken zones (Figure 6) were probably derived from a contemporaneous bracken cover in the catchments generated by natural and anthropogenic disturbance events respectively (Wilmshurst et al. 1997). These generally well-preserved spores would have been transported shortly after their release to the lakes mostly through surface runoff and stream transport, and to a lesser extent by aerial dispersal. Peck (1973) showed that contemporary bracken spores can be almost entirely water transported to a lake basin. Cushing (1964) suggested that, when contemporaneous pollen grains reach the lake sediments by water transport, they are characteristically highly corroded. However, this does not seem to apply to the bracken spores because of their relatively greater resistance to deterioration compared with most types of pollen. The outer perine of the bracken spore probably offers some protection during transport and against decay, and may explain why these otherwise thin-exined spores are apparently more resistant and on average show less corrosion than many pollen types in both authigenic and allogenic sediments (Figure 5b).

Bracken is over-represented in the Pasture zones, the frequency of bracken spores remaining high despite the fact that European settlers cleared bracken from the catchments before the 1900s (Guthrie-Smith 1969). The proportion of corroded bracken spores also increases in the Pasture zones, and is positively correlated with increased amounts of eroded inwashed sediment in the European period (Figures 4 and 6). Corroded bracken spores in the Pasture zones are therefore mostly derived from a secondary source, most likely with inwashed catchment soils that contain a reservoir of old corroded bracken spores that have accumulated over the preceding 600 years following deforestation. Different palynomorph spectra found in surface moss cushions (representing aerial fallout), soils (containing preferentially preserved, and mostly robust palynomorphs) and surface lake sediments (mixture of sources, but more similar to the soils) from the Lake Tutira catchment support this suggestion (Wilmshurst and McGlone, in press). Whereas topsoils contained $40 - 70\%$ bracken spores, and up to 76% of these spores were corroded, moss cushions contained <5% bracken spores all of which were well-preserved.

The over-representation of bracken in the Pasture zones reduces confidence in the interpretation of the bracken spore curves. We tested if reworked corroded spores are distorting the accurate representation of contemporaneous sources of bracken. The proportion of corroded bracken spores recorded in the Tutira and Putere cores was subtracted from the original bracken spore count, and this new 'corrected' value recalculated as a percentage of the terrestrial palynomorph sum (Figure 7).

The new graphs (Figure 7) clearly illustrate the small differences between the original and corrected counts of bracken spores in the Forest zones of all cores (mean difference in Forest zone varied from 0.1 to 0.9%) where soil erosion and spore corrosion were both low. This reflects the contemporaneous origin of the bracken spores after both minor (small eruptions and fires) and substantial volcanic (Taupo eruption) eruptions and fire disturbance events affecting the catchments (Wilmshurst et al. 1997).

Figure 7. Bracken spore curves for cores from lakes Tutira (LT16), Rotonuiaha (RNUI3), Waikopiro (LW8) and Rotongaio (RNGA3). Lines represent the original bracken count as a percentage of the terrestrial pollen sum, whereas the bars represent the recalculated 'corrected' bracken spore curves (see text). Values to the right of the curves are the mean difference \pm standard deviation between the original and corrected bracken spore percentages for each zone.

At the beginning of the Bracken zones, a surge of bracken spores indicates anthropogenic deforestation by fire, and is replicated in cores from most of the drier regions of New Zealand and dated to the 13th century (Newnham et al. 1998; McGlone and Wilmshurst 1999). This bracken signal is dominated by relatively well-preserved bracken spores (Figures 6 and 7) and is contemporary with deforestation and the establishment of a bracken-dominated vegetation cover on the landscape. The mean difference between original and corrected bracken spore percentages in the Bracken zones of the cores varied from $3.0 - 9.2\%$ (although the mean difference in the Lake Waikopiro core (LW8) was higher at 21.9% but only contained the upper part of the Bracken zone).

In the Pasture zones, there is a substantial increase in the percentage of corroded bracken spores, and in the mean difference between the original and corrected bracken spore percentages compared with Bracken and Forest zones (Figure 7). Mean differences in the Pasture zones of Lake Tutira (LT16) and Waikopiro (LW8) cores were 30.0% and 32.4% respectively (Figure 7), but lower in the Putere lake cores (16.9% and 6.4%), where there was less erosion pulse sediment (Lake Rotonuiaha core RNUI3) or none (Lake Rotongaio core RNGA3) (Figure 3). The minimal erosion in the Lake Rotongaio catchment, and the

small mean difference between original and corrected bracken spore percentages emphasises the link between eroded catchment soils and reworked sources of bracken spores in the other lake cores, which contain numerous erosion pulse sediments (Figures 3 and 4). Therefore, lakes with greater soil erosion in their catchments can be expected to suffer more from reworking of preferentially preserved but corroded spores from soils.

Although bracken spores still remain higher than expected in the Pasture zones after the correction factor has been applied, compared with the low abundance of this fern in the catchment today, the corrected curves do provide an improved representation of bracken in the catchments. Similar results were obtained from a swamp peat core near Gisborne, on the east coast of the North Island, New Zealand (Wilmshurst et al. 1999), where bracken spores were identified as being contemporaneous after vegetation disturbance following the 1850 BP Taupo eruption, but increasingly more derived from inwashed soils some time after deforestation to the present.

Pollen grain preservation and derivation

Contemporary pollen rain has probably contributed the most significant proportion of the total pollen content in both the allogenic and authigenic lake sediments, because the fossil pollen records from the Tutira and Putere lake sediment cores are not as 'distorted' (i.e., contaminated with noncontemporaneous sources of pollen) as the bracken profiles are. In addition, surface lake sediment pollen spectra do not closely resemble those derived from catchment soils in the Tutira and Putere catchments (Wilmshurst and McGlone, in press). Moreover, distortion is not even apparent in the Pasture zones of LT16, LW8 and RNUI3, which contain a high proportion of inwashed erosion pulse sediment (Figure 4). If the erosion pulses contained only soil-derived pollen, then the pollen diagrams would be obviously distorted with each pulse, and they are not.

The most likely routes for pollen derived from the contemporary vegetation to reach the lake sediments is by aerial fallout or from watertransported slope-wash following settling on catchment surfaces. The well-preserved component of pollen grains in the lake sediments probably represent aerially derived pollen grains, which tend not to be corroded. Exine corrosion would have occurred during the settling period on the catchment before being transported to the lake basins by surface runoff or into rivers as inwashed contemporary pollen. The settling period may vary from several weeks to months (Havinga 1964) depending on rainfall and slope angle. Experimental work on differential pollen preservation has shown how exine corrosion can proceed rapidly after initial deposition in the catchment, with many pollen types displaying signs of corrosion within the first few years after exposure to attack (Havinga 1984). Cushing (1964) also identified this 'inwashed contemporary' pollen in lake sediments from east-central Minnesota and found the grains deposited in this way were characteristically highly corroded. In this study, inwashed contemporary pollen is probably incorporated in both the authigenic sediments as well as the erosion pulses along with smaller proportions of soil-derived pollen, and may account for the bulk of corroded pollen grains in both sediment types.

The proportion of corroded pollen grains increases in the Pasture zones compared with the Forest and Bracken zones, and this coincides with an increase of erosion pulse sediments in these zones caused by clearance of soil-stablising vegetation. Tolonen (1980) also found the proportion

of inwashed soils and corroded pollen reaching the lake sediments increased after forest clearance in Finland during the early Iron Age. Similarly, Bonny (1976); Pennington (1979) and Davis et al. (1984) also found more degraded pollen and spores in sediment cores from lakes that received a high percentage of pollen through stream inflow and soil wash-off relative to direct aerial deposition. However, as the majority of the corroded pollen grains do not appear to be derived from eroded soils, the increased corrosion may be explained by a shift in the most abundant type of pollen from zone to zone and their resistance to deterioration. In the Forest zone, the pollen was dominated by saccate Podocarpaceae tree taxa; in the Bracken and Pasture zones the dominant pollen types were Coriaria spp. and Poaceae, respectively.

The pollen of Podocarpaceae and Coriaria spp. have relatively thick exines and are robust, whereas the thin exines of Poaceae pollen are easily corroded. Thus, the higher incidence of corrosion in the Pasture zones may simply reflect the lower resistance of the dominant pollen type in the zone rather than an increase of inwashed and corroded soil pollen. Alternatively, greater runoff from the cleared catchments may have flushed more inwashed contemporary pollen into the lakes and less was lost to deterioration in the soils. These conclusions indicate that more detailed pollen preservation analyses that target pollen taxa of particular interest may further enhance fossil pollen interpretations.

Conclusions

This study has shown how pollen and spore preservation and routes of palynomorph transfer to lakes have changed under different catchment conditions. Under a predominantly forested catchment, pollen and spores were generally well preserved, and exine corrosion at its lowest. The most important routes of pollen and bracken spore transfer to the sediments were via aerial deposition and water transport from the catchment surfaces. As a result, the palynomorph spectra provide an accurate representation of the contemporary vegetation on the catchment at this time. After deforestation, repeated fires led to a bracken fernshrubland replacing the forest. However, the dense network of underground bracken rhizomes, and intact roots of the burnt trees remaining in the ground helped to maintain soil stability and minimise soil disturbance. During this period, pollen and spore sources and transfer routes were similar to those that were operating under forested catchments.

During the most recent phase of vegetation change in the catchments over the last \sim 150 years, when remnant forest and fern-shrubland was replaced with permanent pasture, aerially deposited contemporaneous pollen and spores contributed less to the palynomorph spectra. Markedly increased rates of soil erosion under a cover of shallow-rooted permanent pasture caused an increase in the proportion of corroded inwashed contemporaneous and reworked spores derived from eroded catchment soils and riverbank sediments. Tree fern spores and bracken spores are the most resistant palynomorphs in these reworked deposits. Increased erosion over the last \sim 150 years has remobilised these spore banks in soils and riverbank sediments and effectively distorted the fidelity of the fossil palynomorph records over this time. In particular, the bracken and tree fern spores recorded in the European period may date back as far as the previous forest period more than 600 years earlier. The palynomorph spectra from Lake Rotongaio provides an exception to this pattern; pollen and spores are relatively well preserved, and show a high fidelity to the catchment vegetation cover. This is because of its smaller, shallower catchment size, minimal soil erosion, and the absence of inflowing watercourses into the lake.

This study highlights the utility of recording preservation status of palynomorphs during routine counting. During periods when either sediments or rapid vegetation change indicate the possibility of increased catchment erosion, allowance has to be made for non-contemporaneous palynomorph influx. Reworked palynomorphs not only have the potential to distort the accuracy of the fossil record in vegetation reconstructions, but also to reduce the validity of quantitative pollen/ climate reconstructions where modern pollen training sets are used to develop transfer functions. A further consideration is that the direct AMS radiocarbon dating of pollen and spores instead of bulk sediments can decrease rather than increase

the accuracy of dates if there has been a significant influx of reworked palynomorphs.

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