An ecological and historical review of bracken (*Pteridium esculentum*) in New Zealand, and its cultural significance

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Abstract: New Zealand bracken (*Pteridium esculentum*) belongs to a group of closely related fern species of near global extent. *Pteridium* species worldwide are aggressive, highly productive, seral plants, functionally more akin to shrubs than ferns. Their deeply buried starch-rich rhizomes allow them to survive repeated fire and their efficient nutrient uptake permits exploitation of a wide range of soils. They are limited by cool annual temperatures, frost, wind, and shallow, poorly drained and acidic soils. Bracken stands accumulate large amounts of inflammable dead fronds and deep litter and often persist by facilitating fire that removes woody competitors. Bracken was present but not abundant in New Zealand before the arrival of humans. Occasional fire or other disturbances created transient opportunities for it. Rhyolitic volcanic eruptions led to short-lived expansions of bracken, and it briefly became dominant over ash-affected areas of the central North Island after the large AD 186 Taupo Tephra eruption. Andesitic eruptions had limited effects. Bracken became one of the most abundant plants in the country after the arrival of Maori in the 13th century, when massive deforestation affected most of the lowland landscape. The bracken-dominated vegetation that formed in most places immediately after burning gave way with time to fire-maintained mosaics in which bracken dominated on deeper soils and under moist, mild climates. Although Maori relied on bracken rhizome starch as a major element of their diet, food-quality rhizomes were obtained only on deep, moderately fertile soils. The dominance of bracken over very large areas was mainly a result of burning to create open landscapes for access and ease of travel. Bracken remained a troublesome weed through the European pastoral period and well into the 20th century. Bracken has a problematical role in conservation as it can form a persistent, fire-prone, low-diversity cover in drier regions. However, it is an indigenous plant that is effective in preventing erosion and, in wetter areas, it will easily suppress exotic grasses and facilitate regeneration to forest. It should be considered an essential component of landscapes conserved for their historical significance to Maori.

Keywords: bracken; *Pteridium esculentum*; history; fire; Maori; deforestation; palynology; settlement.

Introduction

Bracken (*Pteridium esculentum*) is ubiquitous throughout the lowland and montane areas of New Zealand. It is a characteristic plant of fire-affected landscapes, and provides one of the few abundant wild sources of carbohydrate. It therefore was of immense importance during the Maori settlement of New Zealand. As a persistent and aggressive weed, it is still an important plant in the current landscape. Bracken produces abundant, distinctive, well-dispersed spores that preserve well in sediments. As much of the post-human ecological history of New Zealand centres on the consequences of fire and deforestation, and as bracken was of central importance in the pre-European Maori economy, it is a key taxon in studies of the recent past. A concerted pollen analytical effort over the last 20 years directed towards understanding the timing and effects of Maori settlement has resulted in a large number of pollen diagrams from sites throughout New Zealand. Nearly all of these document forest clearance and the rise of bracken, thus providing abundant raw material for an ecological history.

In this review we will first summarise the New Zealand and selected international literature concerning the ecological role of *Pteridium*. While *Pteridium* spp. have the life-cycle and anatomical characteristics of a fern, a number of morphological, physiological and ecological attributes set them apart. The global economic importance of *Pteridium* arising from it being one the most widespread weeds, its toxicity to stock, and potential to influence human health through production of carcinogens, has resulted in an extensive scientific literature. Results from the numerous studies

of *Pteridium* made throughout the world will be used where they seem applicable to the genus in general rather than one species in particular. We will then interpret the ecological history of bracken in this country, with particular attention to its role during Maori settlement.

All *Pteridium* taxa closely resemble one another morphologically, physiologically and ecologically, and *Pteridium* has until recently been regarded as a monotypic genus consisting of two subspecies and several varieties (Tyron, 1941). However, the Australasian variety (*Pteridium aquilinum* var. *esculentum*) is now recognised as the species *P. esculentum* (Brownsey, 1989). Recent molecular and morphological studies suggest that nearly all varieties of *Pteridium* should be recognised at the species level, and *P. esculentum* has been shown to be most closely related to *P. arachnoideum* of central and southern South America (Thomson 2000). We will use *Pteridium* rather than "bracken" for the genus; *P. esculentum* we will refer to as "bracken"; and all other varieties and species will be referred to by their scientific names. Unless otherwise stated, figures are given as means ± SE.

Ecology

Biogeography

Pteridium probably evolved in tropical or subtropical environments, but is now found throughout the world with the exception of arctic, alpine and desert regions and the southern tip of South America (Page, 1976). *Pteridium* spp. are plants of high-light habitats and are suppressed by even moderate shade (Marrs, 2000). They are characteristic of deep, friable soils and mild, moist climates, and are most common in recently burnt areas, early successions, forest margins and openings within forest or woodland. They also often occur under open pine and deciduous angiosperm canopies in northern forests and in sclerophyll *Eucalyptus* forest in Australia (O'Brien, 1963; Page, 1976). Their preferred environmental space everywhere coincides with that of forest or woodland.

Pteridium esculentum occurs in Australia, New Caledonia, New Zealand, Fiji and Tonga, but apparently not on other eastern Pacific islands (Brownsey, 1989). Genetically and morphologically New Zealand populations align closely with those from Australia (Thomson, 2000), and almost certainly have been derived from the Australian mainland; repeated trans-Tasman dispersal may have kept them genetically linked. Bracken occurs throughout the New Zealand archipelago, from the Kermadec Islands in the north to the Antipodes Islands in the far south. The extreme limits probably do not represent its prehuman range as in both groups of

islands bracken has a limited distribution and is closely associated with human disturbance (Sykes, 1977; Godley, 1989). On the three main islands, bracken occurs throughout from coastal to subalpine regions (Brownsey and Smith-Dodsworth, 1989).

Morphology and physiology

Pteridium species have stout underground rhizomes up to 20 mm in diameter that bear fibrous roots, store carbohydrate reserves and from which singly spaced fronds arise. *P. esculentum* and *P. arachnoideum* are distinguished from other *Pteridium* spp. in having a dense mat of petiolar roots originating at the base of the stipe. The rhizomes form two intergrading classes (O'Brien, 1963): those with long internodes (long shoots) that store most of the carbohydrate and are responsible for most of the extension growth; and those with short internodes (short shoots) that branch laterally from the main axis and bear most of the fronds. The long shoots are often deeply buried (>0.5 m depth) and can extend several metres out from the nearest fronds (O'Brien, 1963; Knowles, 1970). The fronds arise singly, and grow through the surface layers of the soil as an unexpanded, tightly furled projection called a crosier. The frond has a stout, erect, woody stipe and a harsh, coriaceous lamina that bears 10 or more opposite pairs of primary pinnae, which in turn are further divided into secondary and tertiary pinnae (O'Brien, 1963), the ultimate segments being *c.* 3 mm wide. Twisting and arching of the pinnae creates a three-dimensional, shrub-like structure, well adapted to full light. Sun and shade fronds differ markedly, the shade lamina segments tending to be flat and broad, whereas the sun lamina are rolled, narrow and arched. *P. esculentum* seems to be better suited to full-light, droughty conditions than other *Pteridium* species, having narrower and more rolled pinnulets and a more dissected frond structure (Thomson, 2000). Bracken is highly plastic (Brownsey and Smith-Dodsworth, 1989). Fronds are often stunted and no more than 20 cm high on poor soils and in exposed, cold sites; on better soils under warm, moist climatic regimes, self-supporting stands tend to average 1–2 m tall, with some fronds up to 2.5 m. At forest margins, or where tree saplings have invaded bracken stands, dependent fronds grow almost as a liana through the tree or shrub canopy to heights of 3–6 m (Atkinson, 1923; Druce, 1957), or exceptionally 9 m (Bray, 1991).

Bracken is thus closer in its functional morphology to a shrub or liana than a fern and a stand may be ecologically equivalent to a shrubland. In the New Zealand weed control literature it is often classified as a "scrub weed" (e.g. Chavasse and Davenhill, 1973) because its ecological character aligns it for control purposes with woody weeds such as gorse (*Ulex europaeus*).

Comparative measures made on bracken and *Blechnum discolor,* a common understorey ground fern, demonstrate the great physiological difference between bracken and more typical ferns (Hollinger, 1987). The bracken stand studied grew under a *Pinus radiata* plantation in a light environment with 21% of mean incident solar radiation, compared with a mean of 4.1% for *Blechnum discolor* in a nearby beech forest understorey. The bracken light compensation point was 11.6 ± 1.5 µmol photons m^{-2} s^{-1}, compared with 7.3 ± 0.6 for *B. discolor*. Photosynthetically active photon flux density for 90% of the maximum photosynthetic rate was 335 ± 38 µmol photons m^{-2} s^{-1} in bracken, compared with 170 ± 14 for *B. discolor*.

Unusually for a fern, *Pteridium* has a degree of stomatal control (Pitman, 1989), although much less than that of overstorey trees and it has only a sluggish response to humidity changes (Hollinger, 1987). However, despite its preference for open habitats, bracken is not particularly tolerant of heat stress (limit 47.5 ℃; Bannister and Smith, 1983). Its lignified stipe and rachis, and stiff lamina help it resist the effects of desiccation and its mucilaginous rhizomes (*c*. 90% water) provide a large water reservoir (Smith, 1986). Bracken is thus tolerant of relatively dry soils and intermittent drought and persists to the edge of the semiarid zone in Australia (Cartledge and Carnahan, 1971). *Pteridium* is not tolerant of saturated, acid soils (Birnie *et al*., 2000) and bracken rarely grows in wet sites in New Zealand (Wardle, 1991). Persistent wind stunts fronds (Druce, 1957) and bracken on the northern offshore islands of New Zealand is markedly less tolerant of salt-laden winds than competing seral species such as *Kunzea ericoides*, *Leptospermum scoparium*, *Phormium* spp. and *Metrosideros excelsa* (Atkinson, 2004). Mature bracken fronds are not particularly frost-sensitive and can resist a frost of –6.1℃ without damage (Bannister, 2003). In contrast, the young *P. aquilinum* frond is sensitive to frost (Watt, 1955), and Knowles (1970) recorded damage and death of fronds of young bracken in a montane central North Island site and attributed it to repeated frosting.

Bracken is highly efficient at absorbing and storing phosphorus and magnesium even when these elements are deficient in the soil, and fertiliser application increases storage of nutrients in the rhizomes, suggesting it competes strongly for soil nutrients (Evans *et al.*, 1990). The rhizomes of *P. aquilinum* have been reported to be efficient at mobilising phosphate from inorganic sources (Mitchell, 1973). As with most ferns in New Zealand, bracken is host to a range of mycorrhizal fungi that assist with nutrient uptake and its growth is stimulated by infection (Cooper, 1976). Bracken frond lamina have only moderate nitrogen contents (0.88–1.0%; Birrell *et al.,* 1971; Evans *et al*., 1990). However, maximum rates of photosynthesis at saturating irradiance (9.78 ± 1.18 µmol CO_2 m^{-2} s^{-1}) were equivalent to 80% of the maximum for *Pinus radiata* sun foliage at the same site (Hollinger, 1987) and close to the highest recorded for a fern (Hunt *et al.*, 2002). Moreover, its photosynthetic rate is only a little less than that of its seral competitors *Leptospermum scoparium* and *Kunzea ericoides* (10.8 µmol CO_2 m^{-2} s^{-1}; Whitehead *et al*., 2004).

High rates of nutrient acquisition and photosynthesis result in biomass accumulation that is unusually large for a fern. A well-established bracken stand in Nelson had up to 1.6 kg m^{-2} dry weight of live fronds and 7.1 kg m^{-2} dry weight of rhizomes and roots (Bray, 1991). Data from a New Zealand-wide survey of 23 lowland bracken stands gave an average of 2.92 ± 1.46 kg m^{-2} (range 0.91–5.19 kg m^{-2}) dry weight of live rhizomes (D. Whitehead, Landcare Research, Lincoln, N.Z. unpubl. data). The starch component of the *Pteridium* storage rhizome is high (10–30% of dry weight; Williams and Foley, 1976; Al-Jaff *et al*., 1982) and ensures it can survive repeated destruction of the fronds and continue growth.

Few insects use ferns as a primary food source (Hendrix, 1980; Weintraub and Scoble, 2004). Moreover, *Pteridium* fronds are defended by high levels of phenols and tannins and by the presence of a variety of genotoxins, including illudanes (Alonso-Amelot *et al*., 2001). However, the diversity of arthropods feeding on *Pteridium,* while varying considerably, is somewhat large for a fern (Lawton, 1976; 1982). Only a restricted arthropod fauna feeds on bracken in New Zealand (Winterbourn, 1987), although a bracken site near Sydney, Australia, had a rich arthropod fauna (Shuter and Westoby, 1992). Shuter and Westoby (1992) considered that this global variation in bracken arthropod faunas was a consequence of differences in regional faunal composition, but that there was also a stochastic aspect to speciation of herbivorous arthropods in a given region.

Pteridium fronds and spores possess a wide array of toxic chemicals. *Pteridium* has been recorded as causing a number of human diseases through inhalation or digestion of the spores or consumption of shoots (Wilson *et al*., 1998). In Japan and Brazil a close association has been shown between bracken consumption and cancers of the upper alimentary tract (Alonso-Amelot and Avendano, 2002). Poisoning of stock (cattle, sheep, horses and pigs) feeding on bracken has been reported widely in New Zealand (Connor, 1977). Cyanogenesis (an antiherbivore reaction to tissue chewing) in bracken is variable within and between clones, and varies with age, the younger fronds and crosiers being more toxic. New Zealand clones had the highest level of cyanogenetic activity in a sampling of 141 Australasian populations (Low and

Thomson, 1990) and this may be one reason why few arthropods feed on them.

Allelopathic inhibition of seedling growth by leachate from *Pteridium* fronds has been reported widely (Gliessman, 1976; Taylor and Thomson, 1998) but its importance is debatable (e.g. Horsley, 1977; Dolling, 1996). Partridge (1990), on the basis of extensive field observations, doubted that it was a significant ecological factor in New Zealand.

Dead or dying fronds in mature bracken stands may form *c*. 50% of frond density, and litter can represent *c*. 60% of the aboveground biomass (Bray, 1991). Large amounts of readily leached components are lost during the first few months that a dead *Pteridium* frond has contact with the ground. However, estimates of the time taken for 95% of biomass to be lost from petioles buried in litter range from 11 to 23 years. These very slow rates of breakdown have been attributed to the low nitrogen content of the petioles (Frankland, 1976), although high concentrations of phenols and tannins may also contribute. Typically deep, but variable (10–300 mm) litter layers form under dense bracken stands (Evans *et al*., 1990; Partridge, 1990), and a raw, peaty humus develops above the mineral soil. The light, insulating nature of *Pteridium* litter keeps the ground from freezing under hard frosts, and prevents water loss in summer (Frankland, 1976).

Dry, dead *Pteridium* is a light, quick-burning fuel that poses a high fire risk (Rymer, 1976). Green fronds of bracken are resistant to ignition (McGlone, *pers. obs*.) and fire is probably carried through a stand by the dead fronds and thick, dry litter layer. New Zealand has few fire-adapted species (*Coriaria arborea, Cordyline australis, Discaria toumatou, Leptospermum scoparium, Kunzea ericoides, Sophora microphylla* are the main ones) and no fire adapted canopy trees, a probable consequence of low fire frequency in the prehuman situation (Ogden *et al*., 1998). Bracken is in effect a pyrophytic "shrub" pre-adapted to high fire frequency, and its abundance after human arrival may be due partly to lack of a large suite of fire-adapted competitors.

Life cycle

As with all ferns, bracken relies on wind dispersal of microscopic haploid spores and an independent prothallial phase for sexual reproduction. More than a billion spores can be produced by a single frond (*P. arachnoideum*; Alonso-Amelot *et al*., 2001) and they are capable of retaining their viability for at least several years (Conway, 1949). The spores have a near limitless dispersal range as the occurrence of bracken in one small patch on the remote Antipodes Island in the southern ocean, and on the Kermadec Islands to the north of New Zealand, demonstrates. Bracken spore shedding in the field has been observed in New Zealand

in late summer and autumn (March–May) (Knowles, 1970) and airborne pollen and spore surveys indicate spore production begins in December–February, depending on site, and ends in April (Licitis, 1953). *Pteridium* spores germinate readily on a variety of artificial media, even in the dark, but need light and temperatures above 4.5ºC for continuing growth of the gametophyte (Conway, 1949).

Not much is known about *Pteridium* spore germination and gametophyte growth in the field, and establishment from spores has been claimed to be rare (Page, 1976). However, genetic analysis has shown most *Pteridium* populations consist of a large number of distinctive clones established via spores (Dyer, 1989). Isozyme analysis of bracken stands in the USA and UK indicated individual genotypes could extend laterally up to 400 m, although most were much smaller (Sheffield *et al*., 1989). Field observations show establishment from spores is common in New Zealand (Knowles, 1970).

Observations of bracken after fire on the central Mamaku Range (Knowles, 1970) give an insight into the colonisation process. Two small (1–2 ha) montane (*c*. 600 m altitude) forest blocks were burnt in January and February 1968. By June of that year, many sporophytes established from spores dispersed from nearby stands, but were largely destroyed by frost (extreme minimum –8.6ºC) and rain in the following winter. In August 1968, a fresh cohort of sporophytes appeared, either from over-wintering spores or slow-growing gametophytes. By early summer, on open, warm, well-drained slopes, sporophytes were abundant and 5–30 cm in diameter, and by March 1969 new fronds were emerging 60 cm away from the parent plants. By the end of summer most fronds on warm sites were 23–30 cm tall, and some were up to 60 cm with rhizomes up to 56 cm long. On shaded, damp sites, growth was slow, and sporophytes spindly and small (<2.5 cm diameter). An average bracken plant, excavated in spring of 1969, had fronds averaging 46 cm in length and a rhizome spread of 1.3 m. By January 1970, bracken was the sole dominant on favoured sites. However, competition from hardwood saplings, exotic grasses and broadleaved weeds, and bryophytes suppressed or limited bracken establishment on many sites. Knowles (1970) characterised the main factors responsible for bracken success as sheltered macrosites (especially north-facing), undulating and irregular topography providing sheltered microsites, presence of stumps, logs and slash, and well-drained soil.

Frond buds appear on the rhizome in spring and summer in mature bracken stands but do not begin to elongate rapidly until autumn and winter. Early winter subterranean growth may be an adaptation to dry summer conditions (O'Brien, 1963). Emergence of the crosiers varies temporally according to site and season

but generally begins in late October to early November and continues through to May (Clarke, 1960; Wasmuth, 1973). By early February, fronds are fully expanded but still soft; foliage is not hardened until March (Wasmuth, 1973). The crosiers are vigorous and sufficiently rigid to force their way through tough, dry clay (Crookes and Dobbie, 1963) and were recorded as emerging after having been buried by up to 60 cm of airfall volcanic ash (Nicholls, 1963). The fronds generally overwinter and may survive for two seasons (Bray 1991) but in colder sites they are frosted and die back. In most temperate Northern Hemisphere locations *Pteridium* fronds die back over winter (Watt, 1976), a consequence of the cold conditions rather than a lesser frost resistance than that of bracken in New Zealand.

Communities and succession

Bracken occurs in successional or open habitats, particularly after fire, and is widespread on sand dunes, shingle beaches, short tussock grasslands, and regenerating shrubland (Cockayne, 1928; Wardle, 1991). It is commonly associated with *Leptospermum scoparium*, *Kunzea ericoides*, *Discaria toumatou*, *Coriaria arborea* and *C. sarmentosa*, all of which have the ability to survive fire or reseed rapidly afterwards. Because of its tolerance of fire, bracken became an important weed of managed grasslands and forest plantations, especially in wet, hill country (Cockayne, 1916). It remains an important weed, infesting nearly 3% of agricultural land below 1220 m in the South Island (Bascand and Jowett, 1981), and plays a prominent role in the grassland/*Leptospermum*/fern associations that cover nearly 9% of New Zealand (Newsome, 1987). Its stands are often remarkably free of other plants, and woody plants regenerate only where taller vegetation provides shade, or where animal tracks or other disturbance has thinned or removed the litter layer (Wardle, 1991). Druce (1957) demonstrated the strong influence of microsite on bracken dominance in the Wellington region, with moist, sheltered sites favouring dense, tall bracken stands and drier, exposed sites with shallow soils having stunted, scattered fronds only.

A 6-year study of bracken at 100 sites in Canterbury and Westland (Partridge, 1990, 1992), showed succession to forest only where there were nearby seed sources, wet climates and poor competition from bracken. Wet climates favoured succession by permitting survival of woody seedlings over summer. In the dry Canterbury region, succession through to forest occurred mainly in moist gullies with little regeneration on other bracken dominated sites. In the wetter Westland region, forest regeneration took place everywhere except for the drier ridges. Experimental removal of litter and fronds showed that the presence of a bracken litter layer tended to restrict the rate of recruitment of woody seedlings, but did not prevent regeneration. Removal of bracken fronds usually made no difference to seedling size, number, or recruitment to sapling stage. Remarkably little change occurred in the stands over the six years of the study. Slow rates of change were also found in an earlier study of succession on the Canterbury Port Hills where some bracken stands resisted invasion by exotic, woody, small trees and shrubs for over 20 years (Williams, 1983). Nevertheless, in same region (Banks Peninsula) but under wet climates, bracken can greatly enhance regeneration of scrub and forest through suppressing exotic sward-forming grasses (Wilson, 1994).

History

Bracken as a fossil

Bracken macrofossils are not recorded in New Zealand except from pre-European archaeological sites, and bracken starch grains have been noted in a dog coprolite from a prehistoric Maori village (Horrocks, 2004). The fossil history of bracken therefore depends almost entirely on its spore record[1]. The spores are small (*c.* 30 ìm diameter) and distinctive (Large and Braggins, 1991) and disperse over long distances. For instance, they can contribute 3% to the pollen and spore rain as far south as Macquarie Island (Salas, 1983). Bracken spores have been reported as being under-represented in the contemporary pollen and spore rain relative to the bracken cover in surrounding vegetation (Dodson, 1976; Macphail and McQueen, 1983), but this is not our view. In densely forested regions, bracken spores form an insignificant proportion of the pollen and spore rain (Pocknall, 1982; McGlone and Wilson, 1996), but on forested mountains adjacent to areas with significant bracken cover, bracken spore percentages reach up to 10% (McGlone, 1982; Bussell, 1988; Horrocks and Ogden, 1994). In areas with bracken present locally, but not dominant, values are variable but commonly reach levels of 20%, and adjacent to a bracken stand, at least 60% (Elliot, 1999; Wilmshurst and McGlone, 2005 a). Bracken spores are durable in soils, and therefore form fossil spore banks that may be eroded and reworked into swamps and lakes (Wilmshurst *et al.*, 1999; Wilmshurst and McGlone, 2005 b.). High levels of corroded bracken spores in swamp and lake profiles can thus distort the

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[1] Frequencies of bracken spores are calculated as a percentage of a pollen sum of dryland vascular plants excluding ferns other than bracken.

interpretation of contemporary vegetation.

Pre-settlement occurrence

The macrofossil record of *Pteridium* extends back at least to the Oligocene (Page, 1976). Bracken spores are recorded from the New Zealand Oligocene (Mildenhall, 1980), but little is known of its Tertiary history. It is highly likely that *P. esculentum* is of recent origin in New Zealand given the close morphological similarity and genetic relationships of individuals throughout its wide range (Brownsey, 1989; Thomson, 2000). Long-lived, wind-dispersed spores have probably ensured continuing genetic interchange with populations in Australia and elsewhere.

A survey of *c.* 60 full glacial (25 000–15 000 ^{14}C yrs BP) pollen and spore sites, recorded no bracken spores (McGlone, *unpubl.*), despite the abundance of eroding soils and open landscapes during that time,

suggesting the cold, dry glacial climates suppressed bracken. Bracken spores are recorded only sporadically from peat and lake deposits during interglacial, forested periods including the present postglacial. Occurrences of <1% of the pollen and spore rain are typical and are consistent with recent pollen and spore spectra from heavily forested areas where bracken is present but scarce. As bracken spores occasionally make up >5% of the pollen and spores in interglacial sites, levels typical of those when there are nearby bracken stands, we can infer there has been continuous presence of bracken in New Zealand for at least several hundred thousand years.

Bracken and volcanically induced successions

Although andesitic eruptions (mainly from the Taranaki and Tongariro volcanic centres in the Central North Island) can cause significant forest destruction, they tend not to lead to a primary succession dominated by bracken (McGlone and Topping, 1977; McGlone *et al.*, 1988; Lees and Neall, 1993), perhaps because away from the immediate surrounds of the eruption centre, the tephra falls cold and deposition is often small in scale and intermittent over several years. In contrast, rhyolitic eruptions, which are usually large in scale and associated with extremely hot, gas-charged ground flows (ignimbrites) as well as air-fall tephra, can give rise to bracken-dominated primary successions. The rhyolitic Taupo Tephra eruption (*c.* 1850 BP or AD 186) was the largest New Zealand eruption in the last 26 000 years, and covered 20 000 km^2 with pyroclastic flows (Fig. 1; Wilson and Walker, 1985). Forest was almost completely incinerated within the ignimbrite zone, and the physical and chemical effects of the widespread tephra fall disrupted forest canopies beyond the ignimbrite limits (Wilmshurst and McGlone, 1996). Vast floods of tephric alluvium flowed down rivers with headwaters in the central North Island, creating new terraces. Destruction of forest, provision of sterile soil surfaces and log-and-stump ground shelter provided optimal conditions for bracken sporelings. The timing of the eruption in late autumn (Clarkson *et al.*, 1988) was also ideal for bracken establishment as the fronds of surviving stands would have been fully mature and the moist conditions of autumn and early winter ideal for gametophyte development.

After the eruption there was an increase in fire which may have resulted from a major increase in fuel load through the tephra-induced death of many of trees in eastern and central North Island (Wilmshurst and McGlone, 1996). Sites directly affected by the ignimbrite flow all had a brief period during which bracken was dominant along with *Coriaria*, grasses, and a range of seral shrubs. Beyond the ignimbrite zone where the tephra was all airfall, the bracken
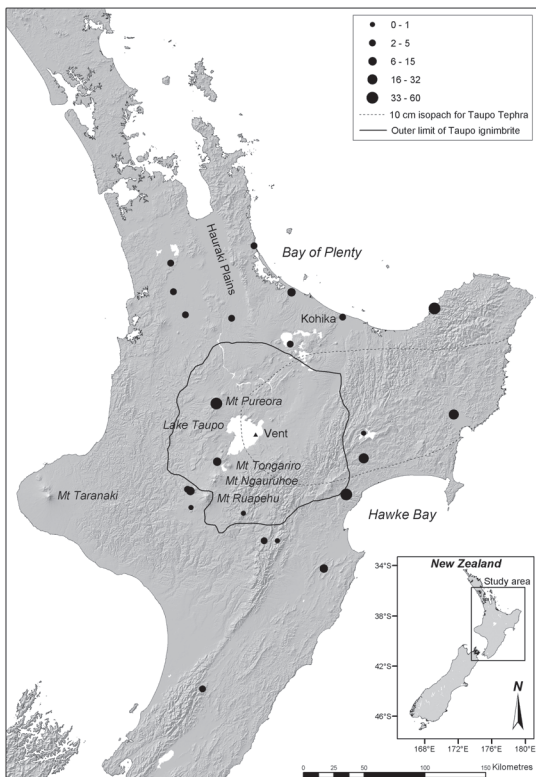

Figure 1. Distribution of central North Island palynological sites in which there is a macroscopic layer of the AD 186 Taupo Tephra (circles). Circle area is equivalent to the highest bracken spore percentages immediately following emplacement of the pumice.

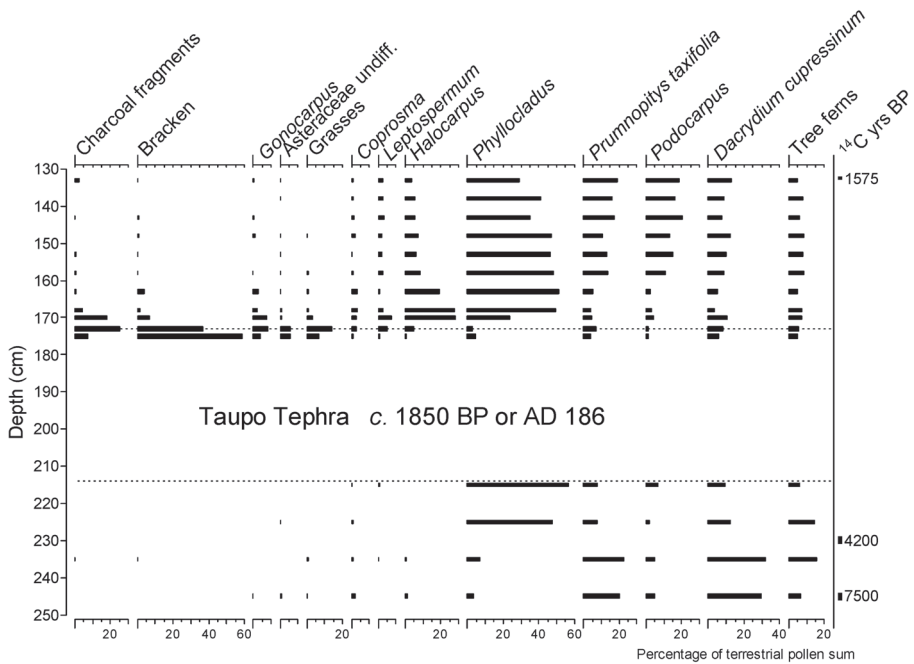**Figure 2.** Pollen diagram, Ongarue mire, Mt Pureora. This montane peat bog, 30 km from the Taupo eruption vent, was over-ridden by the Taupo ignimbrite and records the immediate and rapid recovery of the forest vegetation through bracken-led succession. Note the abrupt peak of bracken in the redeposited upper layers of the ignimbrite showing that it dominated the first vegetation to establish on the new surface.
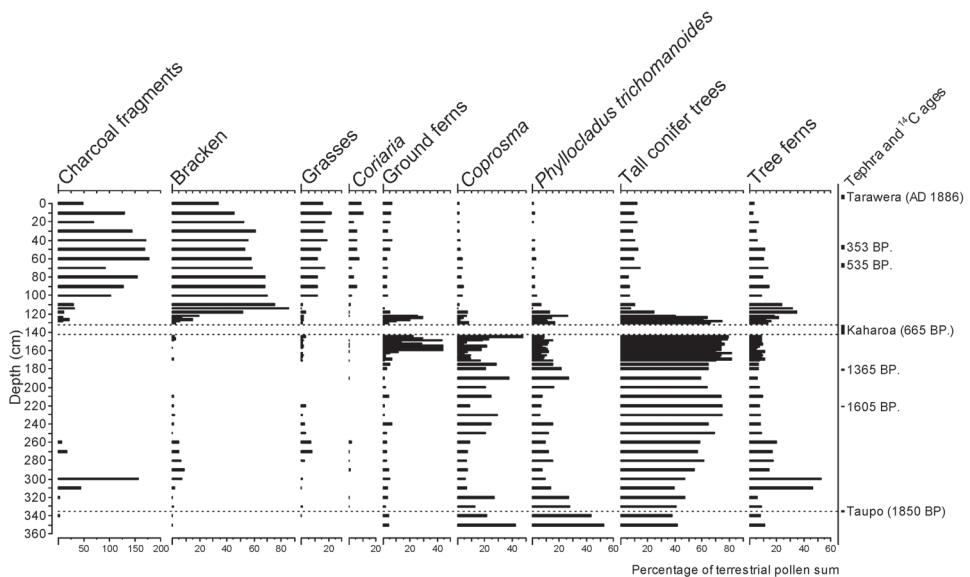

Figure 3. Pollen diagram, Kohika, coastal Bay of Plenty (McGlone and Jones, 2004). The deposition of the Kaharoa Tephra did not immediately affect the forest; the bracken rise and charcoal influx appears to have been an independent result of subsequent Maori burning. Note the earlier surge of bracken and charcoal following disruption of the catchment by the Taupo Tephra eruption, and inwash of sediment to the site.

response was more patchy, but the area affected extended from the Hauraki Plains in the north (Newnham *et al*., 1995) to southern Hawke's Bay (McGlone, 2002) (Fig. 1). Bracken colonisation must have commenced immediately after the eruption, as bracken spores are abundant within the unconsolidated tephric sediments that were inwashed after emplacement of the ignimbrite (Fig. 2; Wilmshurst and McGlone, 1996; Horrocks and Ogden, 1998a). Tall forest re-established rapidly on most sites, and within 200 years the central North Island was essentially reforested (Wilmshurst and McGlone, 1996).

Small rhyolitic eruptions tend to create bracken successions close to the vent only, as for instance in the case of the Rotoma Tephra in the Bay of Plenty (McGlone, 1983a). The tephra deposition from the medium-sized Kaharoa Tephra eruption (665 ± 15 BP; wiggle-match age, AD 1314 ± 12; Hogg *et al.*, 2003) was largely confined to the Bay of Plenty northwards. Its presence was closely associated with an upsurge of bracken at many sites, but in some cases the bracken rise had begun before the eruption. Maori settlement was just beginning at that time and, although the eruption may have contributed to the loss of forests by making them more vulnerable to fire, the fires that destroyed them seem to have been anthropogenic (Fig. 3; Newnham *et al.*, 1998; McGlone and Jones, 2004).

The eruption of Mount Tarawera (Bay of Plenty) in AD 1886 dispersed thick tephra and mud over a partly cleared landscape. Bracken recovered well after the eruption in areas where it was growing already, crosiers pushing up through tephra up to 60 cm deep. However, bracken seems to have had a limited role in primary successions on the mountain itself, as on offshore islands after recent volcanic eruptions (Clarkson, 1990).

Bracken and prehuman fire

Fire was of rather limited extent and frequency in prehuman New Zealand (Ogden *et al*., 1998) and, even when charcoal fragments are abundant in profiles, bracken spores are few. For instance, charcoal has been recorded frequently in full glacial sequences in Northland but percentages of bracken spores has been low (e.g. Newnham, 1992). During the Holocene, charcoal fragments were uncommon, but charcoal with small associated amounts of bracken spores has been recorded at a few sites (McGlone *et al.*, 1984; McGlone and Moar, 1998; Newnham *et al.*, 1995; Wilmshurst *et al.*, 1999). Substantial (>10%) prehuman bracken spore representation has been recorded only at one site, Lake Tutira in northern Hawke's Bay (Wilmshurst *et al.*, 1997). Unlike many other regions of the world, fires were too small and too infrequent to foster significant bracken stands.

Human settlement and spread of bracken

No New Zealand archaeological site has been radiocarbon dated as being older than the 13th century (Anderson, 1991) and Maori genetic structure is consistent with arrival at around that time (Penny *et al*., 2002). Nevertheless, human presence perhaps as early as the 1st century has been postulated on the basis of a possible early introduction of *Rattus exulans* (Holdaway, 1996, 1999) and landscape disturbance in the late Holocene (Sutton, 1987). The rat evidence has been contested on the basis of the late appearance of dated rat-gnawed seed cases (Wilmshurst and Higham, 2004) and technical problems associated with dating small bones (Anderson, 2000). As regards landscape disturbance as evidence for human settlement, it is impossible to distinguish the effects of storms, flooding, lightning fires and earthquakes from disturbances that might be attributed to human activities, in the absence of archaeological evidence. We therefore adhere to the "short chronology" (McGlone and Wilmshurst, 1999a) in which New Zealand was settled by a substantial
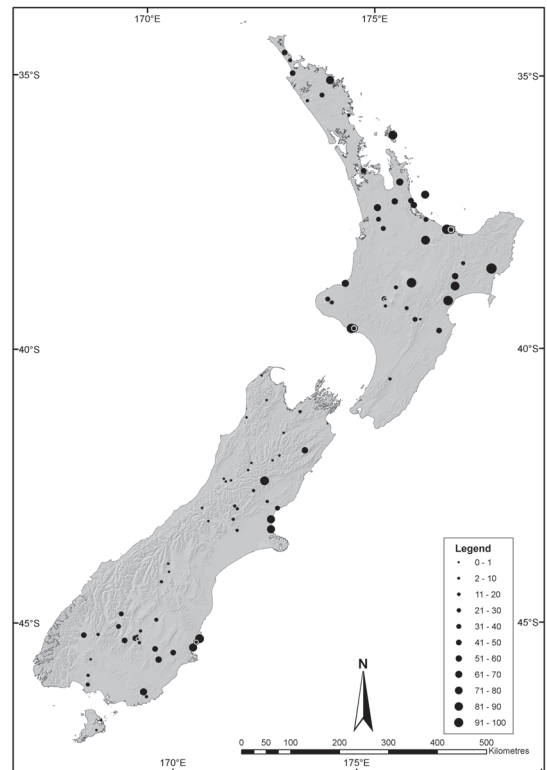

Figure 4. Maximum bracken spore percentage (based on terrestrial pollen sum including bracken) recorded in the Maori post-deforestation phase, from 97 selected published and unpublished pollen and spore profiles.
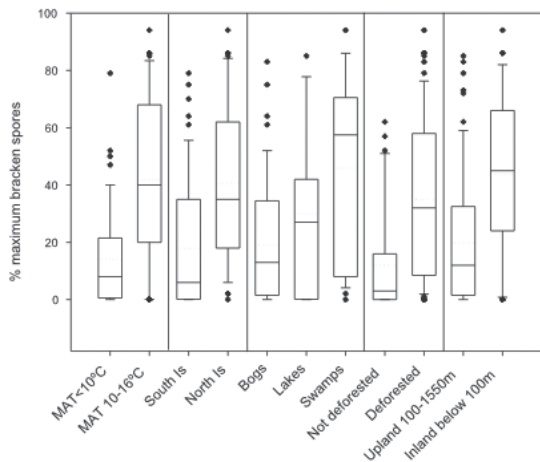
Figure 5. Box plots of maximum bracken spore percentage recorded in the Maori post-deforestation phase from 97 selected published and unpublished pollen and spore profiles grouped in relation to: mean annual temperature (MAT), location (North Island or South Island location); site type (bog, lake or swamp); nature of surrounding landscape (whether largely forested or not); altitudinal range (lowland: <100 m; upland: 100–1500 m). Box encloses 75–25 percentiles; the solid horizontal line represents the median value, the dotted line the mean. Dots represent outlier values.

Table 1. Pearson correlations (*r*) between maximum percentage of bracken spores (arcsine square-root transformed) and continuous environmental variables derived from LENZ layers (Leathwick *et al.*, 2002).

Variable	*r*	df	*P*
Longitude	0.502	78	<0.0001
Latitude	0.342	78	0.0019
Elevation (m)	-0.400	79	0.0002
Mean annual temperature	0.474	79	<0.0001
Mean annual solar radiation	0.346	79	0.0016
Mean annual rainfall	-0.298	79	0.0069
Potential evapotranspiration	-0.376	77	0.0006
Soil water deficit	0.262	79	0.0183
Vapour pressure deficit (October)	0.466	79	<0.0001

number (*c.* 200) of East Polynesian people early in the 13th century.

Many pollen diagrams record forest clearance as indicated by a sustained decline of forest and rise of pollen and spores of seral plants together with a large influx of charcoal (McGlone, 1983b, 1989). However, radiocarbon dates cannot be used in isolation to provide precise calendar ages for events during initial settlement. The radiocarbon calibration curve at around the 13th century does not permit unique assignment of dates, and compounds the unavoidable problems of obtaining accurate radiocarbon dates from disturbed landscapes and erratically growing deposits (McGlone and Wilmshurst, 1999a). In the northern North Island the Kaharoa Tephra (*c.* AD 1314) provides an unambiguous marker (Newnham *et al.*, 1998), but a single horizon can only set limits, not date precisely. The most that can be said at present is that onset of New Zealand-wide forest destruction began somewhere between AD 1200 and 1400 (McGlone and Wilmshurst, 1999a).

There are now >150 pollen-analysed sediment profiles of Holocene age from New Zealand. We have selected 97 of these that detail the Maori settlement period and for each site we have taken the highest recorded percentage for bracken as an indicator of its maximum dominance (Fig. 4). We also recorded bracken abundance immediately before the European era. The statistical relationship between bracken abundance and geographical and climatic factors is presented in Table 1 and Fig. 5.

When the Maori settlement pattern stabilised, an average of 36% of the pollen and spore rain in areas largely without forest consisted of bracken spores, and in forested tracts the average was 18%. Even remote mountainous sites in the North Island recorded 2–10%. About one-quarter of the sites, mainly in northern and coastal districts, had maximum values >50%. There is a bias according to site: bracken spores in bogs made up an average of 20.2 ± 4.1%; in lakes, 32.2 ± 7.1%; in swamps, 45.4 ± 5.3%. Site type significantly affected bracken spore content (GLM $F_{2,78} = 4.79$, $P = 0.0109$) and bogs and swamps were significantly different in this respect ($P = 0.0004$; Tukey posthoc comparison test). Swamps and lakes sampled in this study tended to be at lower altitudes than bogs, and all have a propensity to over-represent spores through reworking from soils in the catchment (Wilmshurst and McGlone, 2005 b). All climatic and geographical variables had a significant correlation with maximum bracken spore percentages, but a forward-selection-procedure multiple regression model for prediction of highest bracken spore percentages selected only mean annual temperature (MAT) and vapour pressure deficit (VPD) as significant factors (arcsin √% bracken = $-0.51 + 0.05$MAT $+ 1.39$ VPD; $R^2 = 0.31$; $P < 0.0001$). Four factors were probably important in explaining

these relationships: bracken growth is favoured by warm sites; fires are easier to light and spread more rapidly in the presence of warm, dry air; succession to forest is significantly delayed in dry, cold climates; and human population density was higher in warm areas. On the other hand, colder, drier climates favoured the spread of grassland and hence the relatively low bracken spore percentages in the South Island.

Early fires (pre-600 yrs BP) have been recorded in pollen diagrams from Northland to Southland but no region can be identified as the first to be affected. The simplest explanation is that exploration and settlement were more or less simultaneous throughout (McGlone *et al*., 1994). Nevertheless, some areas were deforested at a relatively late date. The central Taranaki coast, a well-populated area at European contact, was not cleared until after 450 BP (or *c.* AD 1400; McGlone *et al*., 1988), and the north Taranaki coast not until the 17th century (Wilmshurst *et al*., 2004). Likewise, some inland sites in the South Island (Te Anau: Wilmshurst *et al*., 2002; Hope River: Cowan and McGlone, 1991) did not experience major fires until the 15th and 16th centuries. In Taranaki (and other wet west coast localities), a superhumid, mild climate may have limited the ability to set fires, and in the wetter

inland areas of the South Island, high rainfall and the prevalence of dense *Nothofagus* forest may have inhibited fire.

At most fire-affected sites there was a steep, incremental increase in the percentages of bracken spores matched by an increase in microscopic charcoal particles (Fig. 3, 6). Although uncertain sedimentation rates preclude any precise estimate, at most sites the rise of bracken to its maximum values must have taken more than 10 years and in most cases between 50 and 100 years. As bracken was capable of occupying large areas devastated by volcanic eruptions within a few years, and modern observations show recently burnt sites can become bracken-dominated in the course of an autumn, a single large fire should have resulted in an abrupt increase in the percentage of bracken spores. The incremental increase of bracken spores seen at most deforestation sites must therefore be related to repeated fires.

Present-day New Zealand forests generally are not easy to burn as their complex structure and dense understoreys on rugged terrain in high-rainfall areas mitigate against fire spreading easily. *Nothofagus* in particular is fire-resistant because of the high mineral content of the leaves and wood (Wardle, 1984), and in
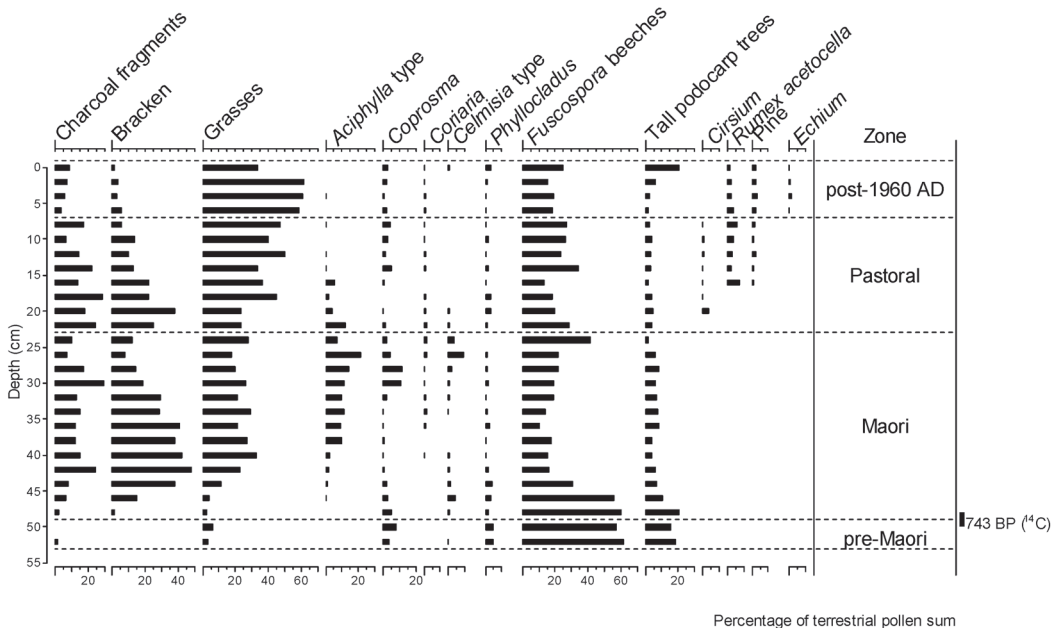

Figure 6. Pollen diagram, Winterton Bog, northeastern South Island (McGlone and Basher, 1995). This site is just above the regional treeline on the flanks of the Inland Kaikoura Range. Bracken declines after an early post-deforestation peak in face of increasing grass and *Aciphylla*, and further declines immediately before European pastoralism in response to increasing scrub. Early European burning resulted in a brief resurgence of bracken, but then its replacement with grassland.

some areas patches have survived in the face of 100 years of European fire (Wilson, 1994). *Agathis australis* forest has burnt relatively freely in both pre-European and European-settlement times and complex conifer-angiosperm forest is probably of moderate vulnerability (Ogden *et al.*, 1998). Pollen evidence from some northern North Island sites that remained largely in conifer-angiosperm forest indicates that repeated small-scale burning may have been maintained for many hundreds of years (Byrami *et al.*, 2002; Ogden *et al.*, 2003). Maori burning in the mid-19th century was characterised by small, incomplete burns that provided extensive forest edge, dead and dying fuel, and pockets of highly inflammable vegetation in the form of bracken, *Coriaria*, and *Leptospermum* shrubland (Walsh, 1896). As a burnt area increases in size, the seed rain from angiosperm competitors is dramatically reduced. The crucial difference between Maori-induced fire and natural fire with respect to bracken abundance may be that the Maori regime, characterised by systematic, repeated burning, ultimately created large areas where bracken was freed from significant competition. Under a natural fire regime, small, irregular burns repeated at long intervals did not permit this ecological release.

Other ferns, and in particular the rhizomatous *Paesia scabulera* and *Histiopteris incisa*, are strong competitors with bracken under certain conditions. *Paesia* and *Histiopteris* establish in similar situations to those of bracken after fire, i.e. in the shelter of burnt logs and stumps, *Paesia* favouring drier, more open sites, and *Histiopteris* moister, cooler, less well-lit situations (Atkinson, 1923; Clarke 1960). However, both are inferior competitors to bracken in open sites: *Paesia* is much shorter in stature, not reaching much over 1 m, whereas *Histiopteris*, which attains a height of 2 m, is more mesic in its ecology, and cannot compete on open, drier sites. After European-era forest and shrubland fires in wet inland Taranaki, *Paesia* and *Histiopteris* would often dominate first, but later be overtopped by bracken (Levy, 1923). Bracken, moreover, has a decisive advantage over *Paesia* and *Histiopteris* in repeat burns, as the latter have shallow surface rhizomes that are easily damaged by fire in contrast to the bracken rhizomes, which are deeply buried and insulated by litter. Ground ferns rarely are important during deforestation phase pollen diagrams, although there are sites where spores of *Paesia* (Elliot *et al.*, 1998), *Histiopteris* (Horrocks and Ogden, 1998b), or of the *Blechum capense* type (Cowan and McGlone, 1991; Ogden *et al.*, 2003) were common. These are invariably swamp sites, suggesting their burnt margins supported fern-brakes of these species where bracken was excluded because of its intolerance of saturated soils. The very dominance of bracken across the landscape during the period of Maori fire suggests that it easily outcompeted other ferns on well-drained,

open sites, ceding ground only in damp, shaded or poorly drained sites.

Over much of the North Island the bracken dominance established during the early Maori deforestation phase was maintained up until the European pastoral and forestry era, with only a slight to moderate decline (e.g. Fig. 3). However, in other areas, the high levels of bracken dominance achieved early on were not maintained, especially in the eastern South Island (Fig. 6; McGlone, 2001). Of sites with significant bracken spore representation (maximum >5%) during the Maori era, more South Island than North Island sites had a subsequent decline of ≥50% in bracken abundance (37% versus 16%; $\chi^2 = 3.897$, df = 1, $P < 0.05$). Perhaps the simplest explanation for this bracken decline is a reduction in burning by Maori, and therefore regrowth of shrubland or forest. At some sites where microscopic charcoal levels have been quantified, charcoal influx slowed at the time that bracken declined (see McGlone, 2001 for examples). On the other hand, burning continued in most areas and the first European observers recorded widespread landscape firing (Bidwill, 1841; Walsh, 1896; McGlone, 1983b). Both early observations and pollen records indicate that in the absence of bracken, grasses, *Aciphylla* spp., *Coriaria* spp. and *Leptospermum*, *Kunzea*, and *Discaria toumatou*, all dependent on or encouraged by fire, dominated the vegetation over vast areas (Buchanan, 1868; Cockayne, 1928; McGlone, 2001). Therefore, in most areas where the early dominance of bracken was not sustained, bracken was supplanted by other fire-tolerant species and thus a reduction in fire *per se* cannot be the reason for its decline.

We suggest that the initial overextension of bracken abundance, even when prolonged by repeated fire, could not last. Competitor species have propagules orders of magnitude heavier than bracken spores and therefore dispersed more slowly. When they eventually spread into bracken-dominated areas, they competitively supplanted bracken on sites where conditions suited it less well. As we have seen, although bracken has some degree of stomatal control, deep moisture-retaining rhizomes, and reasonable frost resistance, it is stunted by wind, and many tussock grasses and shrubs are hardier and more drought-resistant. Bracken cannot occupy frosty flats (Wardle, 1991; Rogers, 1994) and is replaced by *Phormium*, scrub or tussocks on exposed ridges (Druce, 1957; Elder, 1962). Consequently, bracken has a minimal presence in cool, drought-prone districts of the inland, southeastern South Island (Bascand and Jowett, 1981; Newsome, 1987).

Decline of bracken may also have been promoted by soil changes that followed clearance and repeated firing. The cleared soils after a forest fire are ideal for

bracken as they are sterile yet contain abundant, readily available nutrients, thus providing a secure environment for its vulnerable gametophytes. On the other hand, repeated burning depletes nutrient levels, and Bidwill (1841, p. 68) noted how repeated fire gradually reduced the height of bracken stands on pumice soils from 3 m to 15 cm, at which point short tussock invaded. Forest also appears to have kept soils relatively dry through evapotranspiration, canopy interception and re-evaporation in many places (Pearce and Rowe, 1979). Forest clearance therefore tends to be associated with the eventual development of poorly drained acid soils in cooler districts (McGlone and Wilmshurst, 1999b). However, *Pteridium* is not competitive on shallow, acid soils, where stunted shrubs or grasses have an advantage, or on wet, peaty soils where *Phormium*, sedges, rushes and tussock grasses dominate.

Bracken and erosion

Deforestation during the Maori era led to pulses of increased erosion in soft-rock hill country immediately after burning (McGlone, 1989; McSaveney and Whitehouse, 1989), although long-term erosion rates did not change markedly (e.g. Swales *et al*., 2002). A detailed history of erosion in the soft-rock Tutira catchment (Wilmshurst, 1997; Wilmshurst *et al*., 1997; Eden and Page, 1998) showed that, although sedimentation increased after Maori deforestation, bracken cover was nearly as effective as forest in preventing erosion. After subsequent conversion of the catchment from bracken to pasture-grass, sedimentation rates increased by a factor of five. The effectiveness of bracken in preventing erosion in the face of repeated fire lies in its maintenance of a live network of deeply buried, fibrous rhizomes and protection of the soil surface by deep litter and densely matted roots.

Maori use and management of bracken

Given the absence of *Pteridium* in the East Polynesian homeland of the Maori (Leach, 2003), its importance as a food item in 18th and early 19th century Maori diets raises questions about the circumstances under which it was adopted, the chronology of its use, and the means by which Maori enhanced its availability.

Unquestionably, bracken rhizome (aruhe) had become a staple for many Maori communities by the 18th century, although early European explorers sometimes misjudged its role, describing it as a seasonal stop-gap while sweet potato crops were growing, or as rations for people under stress of warfare, or as a miserable substitute for starchy crops in regions unsuited to Maori gardening (Leach, 2001). In fact it was the preferred choice for the many groups whose seasonal fishing and fowling activities, and dispersed gardens, required regular movement within their tribal territories. Fern root was light when dried, and provided it was kept dry, lasted months, or even years (Colenso, 1880), compared with the heavy and bulky tubers of sweet potato or corms of taro, both of which were difficult to store and transport. Fern root continued to be used by Maori travellers until the mid-19th century when wheat flour became widely available (Leach, 2001).

Drying usually immediately followed the digging; the rhizomes were stacked in the shade where the wind could blow through them and left for 2 weeks before being stored (Colenso, 1880). Rhizomes of various species of *Pteridium* were prepared in much the same way elsewhere in the world [e.g. Canary Is (Sparrman, 1953); temperate Australia (Backhouse, 1843; Gott, 1982); western USA (Norton, 1979)]. When the fern root was needed for consumption, Maori prepared a small fire in which the rhizomes, broken into 20 cm lengths, were briefly "roasted" or heated through, after being dipped in water (presumably to prevent charring). The fern root sections were then transferred one at a time to an anvil (usually a flat, water-worn stone) and beaten with a wooden mallet or small club to separate the starch from the fibre. Occasionally, a bone or stone beater was employed, or a fortuitously shaped lump of wood, but properly made wooden tools with handles were preferred for the long periods of beating involved in preparing a meal for several people. Each section of root was beaten singly, then doubled over and rebeaten. When softened, they were thrown to the diners who, after chewing, spat out the remaining fibre wad into a personal basket (Leach and Purdue, 2003). By the 18th century Maori had developed several distinctive forms of wooden fern-root beater for this operation. On special occasions, cooked fern root might be soaked in water in a wooden bowl to extract its starch, or soaked in *Coriaria* spp. (tutu) fruit juice to give it a sweeter flavour. Colenso (1880) wrote that in spring the crosiers were eaten fresh. If this was a common practice, and it is not described by other commentators, there was a potentially serious risk to the consumers from the compound ptaquiloside, a potent carcinogen that occurs unpredictably in bracken fronds and crosiers in some stands throughout New Zealand (Rasmussen *et al.*, *in press*).

The conditions under which the rhizome grew greatly affected its size and the proportion of fibre to starch, and hence the nutritional value. Dried Australian *Pteridium* has been reported to contain 47.6 g carbohydrate, 2.0 g protein, 1.0 g fat and 46.6 g fibre per 100 g (Hodgson and Wahlqvist, 1993). Bracken growing under sub-optimal conditions would have contained a much greater quantity of fibre. Shortland (1851, p. 201) observed: "It must not be supposed, as some have believed, that the fern root, wherever it

grows, is fit for food. On the contrary, it is only that found in rich loose soils, which contains fecula in sufficient quantity for this purpose." Even in the favourable location on the south bank of the Waitaki River where his Maori guides dug fern root for the next leg of their journey north, he noted "a great deal of discrimination was used in selecting the best roots, which were discoverable by their being crisp enough to break easily when bent" (Shortland, 1851, p. 201). The best roots were considered to be those from loose rich soil on which the bracken stands had been left undisturbed for several years (Colenso, 1880). Thomson (1859, p. 154) stated: "three-year-old plants furnish the best fern root, and such is an inch in circumference. The deeper the root is found in the ground, the richer it is." The height to which the fronds grew was often taken as an indicator of the quantity of starch likely to be obtained from the rhizome (Yate, 1835; Wade, 1842).

Soils over much of New Zealand are shallow and acid (Meurk, 1995). Therefore, although bracken was abundant throughout the North Island, and in coastal districts and wetter, milder sites in the inland ranges in the South Island, areas suitable for intensive rhizome harvesting were much more restricted. The areas now suitable for intensive horticulture (e.g. central Hawke's Bay; lowland Bay of Plenty) probably approximate those most productive of bracken rhizomes in pre-European times, i.e. "low-lying rich alluvial grounds" (Colenso, 1880). Bracken appears not to have been managed as a horticultural crop as it was not planted into prepared ground. Firing of stands to reduce woody competition and rejuvenate the underground rhizome network would appear to be the only management technique used. According to Colenso (1880, p. 21), burning off the bracken fern patches "in the proper season, in August, improved them", perhaps by increasing the light available to the next season's new foliage. Ecological observations support the Maori rationale for burning bracken stands every 3–5 years (Best, 1925, 1942). At a hill site in Wellington, five fires over 30 years were sufficient to arrest the invasion of bracken stands by beech-hardwood forest (Druce, 1957), and succession to forest from bracken in the absence of fire was well advanced after 15 years (Croker, 1953).

The correct time for digging was given by Thomson (1859) as November, and by Markham (1963) as the spring months following a late winter burning. Firing the tangled fronds of previous years' growth would also have aided the digging by removing impediments to the efficient use of the long digging stick, and by revealing the crosiers as they emerged in early summer. The thickness of these "fiddleheads" may have been a useful guide to the quality of the subterranean rhizomes. How often an individual bracken patch could be dug

for rhizomes is not known. Detailed monitoring of a bracken stand in Nelson showed that above-ground biomass had recovered fully four years after release from grazing that had kept plants at a very low density. Below-ground (96% rhizome) biomass was slower to increase, and had reached only $c.$ 25% of its maximum (achieved after 20 years) by year four (Bray, 1991).

As *Pteridium* does not occur in the east Pacific homelands, the discovery that it produced rhizomes with edible starch took place in New Zealand, although it must have been prompted by familiarity with the preparation of roots of other ferns found on tropical islands and used as emergency foods or by groups living or travelling in interior valleys (Leach, 1986). We suggest, therefore, that the discovery of the food potential of bracken rhizome would have followed shortly after settlement of New Zealand. *Dicranopteris linearis*, the false staghorn fern of East Polynesia, is referred to as *anuhe* in several parts of tropical East Polynesia (Leach, 2003), a name from which the Maori term for bracken, *aruhe*, is undoubtedly derived. Anuhe is light demanding and quickly covers hillsides following repeated fires and the appreciation by early Maori of its ecological similarity with bracken is probably the basis for the near-identical name as there is no sound evidence that the roots of *Dicranopteris* were used as food.

Although bracken fields in milder districts on deep alluvial or colluvial soils along rivers or on lower hill slopes must have produced significant amounts of starch, it seems unlikely that the massive extent of bracken at the time of European settlement could be accounted for by its importance as a food staple. Areas with few inhabitants (e.g. Kaingaroa Plateau and the Southern Lakes) had extensive bracken cover, but little of it can have produced rhizomes of food quality. Moreover, throughout most of the country no particular effort was needed to encourage bracken. During the 19th and early 20th centuries, bracken proliferated after forest clearance and maintained itself on land where it was already common, despite the best efforts of farmers to suppress it. Bracken remained a serious weed that invaded pasture and suppressed plantation trees (Levy, 1923; Guthrie-Smith, 1969; Chavasse and Davenhill, 1973) until the advent of efficient systemic filicides in the second half of the 20th century (Clarke, 1960).

The history of other western and eastern Pacific islands, the homelands of the Maori, is closely associated with fire, and the widespread clearance of vegetation (Athens, 1997). While New Zealand forests yielded a number of animal and vegetable foods, primarily birds and forest fruits (Best, 1942), their contribution was dwarfed by that obtained from marine and freshwater fisheries, gardens, and bracken fields. There seems little doubt that the favoured Polynesian

landscape was generally open, with forest present in patches, or restricted to steeper, wetter terrain. Maori had a population density intermediate between that of the intensely horticultural communities of the tropical and subtropical Pacific and those of hunter-gatherer societies such as that of Australia (McGlone *et al*., 1994). Lack of a year-round, cultivated, carbohydrate staple ensured a reliance on hunted and gathered foods, and thus utilisation of the whole landscape. The need to travel long distances for trade or seasonal food-gathering put a premium on open, easily navigable terrain. This need is exemplified by Colenso's (1844) account of his overland "excursion" in the North Island in 1841–1842. Although the fern-brakes they travelled through "abounded with their dreaded subtile yellow dust", his Maori guides preferred this to dense forest, "vociferating loudly their being privileged to see a 'koraha maori' (indigenous fern-land, open country) again" after travelling several days through Urewera forests (Colenso, 1844, p. 49). There can be few other explanations for the clearance and persistent re-firing of vast areas of the South Island and central districts of the North Island that had only transient human occupation (McGlone, 2001). Therefore, while bracken was undoubtledly used as a supplementary food where suitable stands occurred within these deforested inland districts, there is no need to hypothesise that maintenance of such stands was the primary reason for burning.

The abandonment by Maori of the inland seasonal food-gathering round with the beginning of European settlement and the associated provision of new food sources, and population decline through disease and conflict, is reflected in some pollen profiles, which show a decline in charcoal and bracken, and a resurgence of shrubland (e.g. Fig. 6). In general, bracken percentages drop during the European farming period with the spread of improved pastures, but in inland areas of the South Island where management was largely by burning, there is often a secondary bracken peak following the introduction of stock (e.g. Fig. 6).

Bracken in the contemporary landscape

Bracken is one of a small group of indigenous plants (including among others *Coriaria* spp., *Discaria toumatou*, *Leptospermum scoparium*, and *Ozothamnus leptophyllus*) that were, or continue to be, important economic weeds of agricultural and forestry land. The ambiguous status of these species as indigenous plants and also weeds should not be problematic. Nearly all indigenous weeds in New Zealand were pre-adapted to the new ecological landscapes created by settlers by virtue of their possession of one or more fire-related features such as underground storage organs, resprout ability, seed banks, serotiny, and good propagule dispersal. As we have shown with bracken, settler

activity massively expanded the area over which they were common. It is therefore no cause for alarm if these indigenous weeds are reduced in range and abundance, as they are highly unlikely to become threatened in any serious way. However, that is not to say that they should be treated solely as weeds.

If we consider the original ecological status of bracken as a fugitive plant of disturbed ground, and possibly permanently present only on unstable substrates such as unconsolidated sand dunes, its main contemporary role is as successional cover. Because bracken will often appear spontaneously after fire, thereby reducing the abundance of exotic woody weeds and rapidly invades abandoned pasture if nearby, suppressing sward-forming exotic grassland, it promotes indigenous forest regeneration. It is also effective at preventing soil erosion because of its network of tough rhizomes. However, on the debit side, a low-diversity, fire-prone bracken cover that is neutral or inhibitory as regards forest regeneration may form in dry regions and thus will last for many years, if not indefinitely. While such vegetation cover has the merit of being indigenous, it is anomalous from the point of view of the prehuman state and also has low biotic diversity. The utility of bracken from an indigenous reafforestation point of view is therefore very much site-dependent, and it would be appropriate in some conservation situations to consider it as a weed.

Unlike other indigenous plants such as *Phormium* spp. and *Podocarpus totara* used by the pre-European Maori, bracken has little direct use by Maori today. However, we should remember that bracken was a characteristic and economically indispensable plant of the pre-European Maori landscape. Its relatively low stature, persistence, soil-binding ability, inexpensive management, and high cultural significance should be seen as assets in areas reserved for their historical value. Therefore, bracken should be encouraged as an authentic and practical vegetation cover for many historic sites.

Acknowledgements

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