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A review of *Leptospermum scoparium* (Myrtaceae) in New Zealand

J. M. C. STEPHENS
P. C. MOLAN
B. D. CLARKSON
Department of Biological Sciences
University of Waikato
Private Bag 3105
Hamilton, New Zealand
jms6@waikato.ac.nz

Abstract Information about *Leptospermum scoparium* (Myrtaceae), the most widespread and important New Zealand indigenous shrub species, is reviewed. *L. scoparium* is a variable species, requiring more study of the genetically based differences between New Zealand populations and the affinity of these populations to Australian populations and other closely allied Australian species. Improved understanding of the species' variation will assist both its conservation roles and economic uses, and the need to sustain genetically distinct varieties is emphasised. Ecologically, the species has a dominant role in infertile and poorly drained environments, and a wider occurrence as a seral shrub species in successions to forest where it may be regarded as a woody weed of pasture or a useful species for erosion control, carbon sesquestration, and vegetation restoration. The main economic products derived from the species are ornamental shrubs, essential oils, and honey. The species' development as an ornamental plant and further definition of the pharmacologically active components are recommended as priority areas for research.

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INTRODUCTION

Information about *Leptospermum scoparium* is spread throughout much literature. *L. scoparium* is the most widespread and important indigenous shrub species in New Zealand, and has probably undergone the most varied development as an economic plant in the indigenous flora. Bibliographies compiled by Orwin (1974) and Williams (1981) provide background material to this review. Whilst all material that refers to *L. scoparium* in passing has not been included, each section draws upon the principal publications. Chemical control aspects are not included.

The taxonomy, morphology, distribution, habitats and plant communities, and other biological associations in which it occurs are considered here, along with its historic and current uses as a source of essential oils and honey, and for ornamental shrub development. The majority of early research considered the ecological position of *L. scoparium*, either as a dominant species where environmental stress is extreme, or as a seral species in disturbed habitats where the species was recognised as a significant weed of recently cleared forest for pasture development. Recognition of the genetic and phenotypic variation exhibited by the species led to studies isolating various components of this diversity, ranging from morphological to chemotaxonomic treatments. Commercial development as an ornamental shrub and the identification of medicinal essential oil and honey components have motivated most of the recent research, and a collation of this material is warranted.

We consider it timely to review the biology of *L. scoparium* as a basis for further economic development of the species and conservation of genetic variation.

BIOLOGY AND ECOLOGY

Taxonomy, morphology, anatomy, cytology

Leptospermum scoparium J.R. et G.Forst. (manuka, kahikatoa, tea tree, red tea tree) is a member of the Myrtaceae. This family contains at least 133 genera and more than 3800 species, and has evolutionary centres in Australia, Southeast Asia, and Central and temperate South America. Myrtaceae are characterised by a half-inferior to inferior ovary, usually numerous stamens, entire leaves containing oil glands, internal phloem, and vestured pits on the xylem vessels (Wilson et al. 2001).

Until recently Myrtaceae was divided into two subfamilies, the capsular Leptospermoideae and the fleshy-fruited Myrtoideae. An extensive review of the Myrtaceae inflorescence structure confirmed this division; the Leptospermoideae contained seven alliances including the *Leptospermum* alliance, which was further subdivided into the *Leptospermum* and *Calothamnus* suballiances (Briggs & Johnson 1979). However, cladistic analysis of morphological and anatomical characters concluded that the subfamilies should be discarded, as the fleshy-fruited *Acmena* alliance did not group within the Myrtoideae subfamily (Johnson & Briggs 1984). A cladistic re-evaluation of non-molecular characters confirmed a high level of homoplasy within Myrtaceae and limited support for any clade (Wilson et al. 1994).

Molecular analysis placed further doubt on the traditional taxonomic groupings. Sequences of the chloroplast *mat*K gene analysed in association with nonmolecular data revealed that the *Leptospermum* alliance was polyphyletic and, thus, an invalid taxonomic concept (Wilson et al. 2001). The sequencing of two chloroplast regions for 31 species within the *Leptospermum* suballiance revealed a monophyletic grouping of eight genera and the suballiance was considered a valid taxonomic unit (O'Brien et al. 2000). However, the same study concluded that *Leptospermum* is polyphyletic and should be divided into at least four genera: the persistent-fruit group, the East Australian non-persistent-fruit and West Australian non-persistent-fruit groups, and *Leptospermum spinescens* separated as a fourth genus. *L. scoparium* was not included in this analysis but its fruit morphology allies it to the persistent-fruit group.

Analysis of leaf anatomy of 40 species of *Leptospermum* showed that *L. scoparium* has the typical xeromorphic structure of the genus (Johnson 1980). The wood anatomy (Johnson 1984; Patel 1994) and the pollen morphology (McIntyre 1963) of *L. scoparium* also support the species genus classification.

A comprehensive taxonomic revision of the genus *Leptospermum* listed 79 species (Thompson 1989), which has been increased to 83 with later additions (Dawson 1997a). *L. scoparium* is one of 13 species included in the *Leptospermum myrtifolium* subgroup, the defining characteristics of which are deciduous sepals and persistent strongly wooded fruit-valves (Thompson 1989). The Australian species within this sub-group are extremely difficult to define; *L. continentale* and *L. rotundifolium* were recently elevated by Thompson (1989) from *L. scoparium* varieties to species rank. The species *L. juniperinum* and *L. squarrosum* have both been recorded as varieties of *L. scoparium* (Thompson 1989), and the endemic Tasmanian *L. scoparium* var. *eximium* could be considered to warrant species status, displaying lignotuber development which is not found in New Zealand's *L. scoparium* (Bond et al. 2004).

Initially three species of *Leptospermum* were recorded as endemic to New Zealand; the widespread *Leptospermum scoparium* and *L. ericoides*, and *L. sinclairii* restricted to Great Barrier Island (Allan 1961). Revision of *Leptospermum* led to the transfer of *L. ericoides* to *Kunzea* as *K. ericoides* (A.Rich.) J.Thompson (Thompson 1983). *L. sinclairii* was included in synonomy to this species, and a new name combination of *K. sinclairii* (Kirk) W.Harris was later published without supporting material (Connor & Edgar 1987). Accordingly, *L. scoparium* is now considered to be the only indigenous member of *Leptospermum* in New Zealand. The species is not endemic to New Zealand as indicated by Allan (1961), as it also occurs naturally in mainland Australia from the southern coast of New South Wales to western Victoria and is widespread in Tasmania (Thompson 1989).

The time of arrival of *L. scoparium* in New Zealand is uncertain. *Leptospermum* pollen has been dated to the Paleocene (Fleming 1975), though the representatives in the upper Cretaceous and older Tertiary beds should be interpreted to represent type pollen and not individual species (Couper 1953, 1960). Thompson (1989) suggested that *Leptospermum* may have originated in the dry Miocene conditions in Australia and that *L. scoparium* dispersal to New Zealand occurred relatively recently, as the species is not a primitive *Leptospermum* and cannot have been present earlier in New Zealand. Wardle (1991) recorded *L. scoparium* as the only New Zealand species to release seed overwhelmingly in concert after fire, a serotinous feature common in the

Australian flora. Further evidence for the recent evolution of the genus *Leptospermum* is provided by incomplete sterility barriers and the number of putative hybrids in Australia (Thompson 1989). Nevertheless only three Australian species are tetraploid, indicating that polyploidy has not been a major influence at the evolutionary centre of the genus (Dawson 1990). A number of defined *Leptospermum* hybrids exist (Harris 2000), and one wild flowering intergenic hybrid has been reported, *Kunzea sinclairii* × *L. scoparium* (Harris et al. 1992). Intergenic hybrids have also been produced from controlled crosses, but neither the *Kunzea sinclairii* × *L. scoparium* nor the *Kunzea* aff. *ericoides* × *L. scoparium* hybrids had flowered after five years (de Lange & Murray 2004).

The following description is drawn from those given by Allan (1961) and Thompson (1989). *L. scoparium* is a variable shrub or small tree usually about 2 m tall but occasionally reaching 4 m or more, and dwarfed in exposed situations. Bark is close and firm, with young stems bearing a silky pubescence but soon becoming glabrous. Leaves are highly variable both in size and shape, 7–20 × 2–6 mm, ranging from broadly elliptical to lanceolate, coriaceous with incurved margins, rigid, acuminate pungent apex, petiole, young leaves glabrous. Flowers are white or rarely pink or red, axillary or occasionally terminal on branchlets, usually solitary and sessile, 8–12 mm diam., flowering Oct–Feb. Hypanthium is usually glabrous with a distinct pedicel, expanded upper and broadly turbinate. Sepals are deciduous, oblong to broadly deltoid. Petals are 5 × 4–7 mm suborbicular and slightly clawed. Stamens occur in bunches of 5–7(–9), 2.5–3.5 mm long. Style is inset with a large stigma, often reduced or absent. Ovary is 5-locular, each ovary containing about 100 ovules. Fruits are woody persistent 5-valved capsules 6–9 mm diam., distinctly exserted beyond receptacle rim. Mature seeds are 2–3.5 mm long, irregularly narrowly linear-cuneiform or sigmoid, curved, striate.

Leptospermum scoparium is an andromonoecious species; however, the variation in percentage of perfect flowers is mostly environmentally produced (Primack & Lloyd 1980). Overall control of flowering is determined by temperature and day-length. *L. scoparium* flowering is initially activated by a long-day flowering cue, although bud development is restrained by cool temperatures throughout winter leading to spring flowering when the temperature restraint is lifted (Zieslin & Gottesman 1986).

Throughout New Zealand *L. scoparium* is normally diploid with 22 chromosomes (Dawson 1987, 1990), but two triploid and one tetraploid cultivars have been described (Dawson 1990) and wild aneuploids have been recorded (P. de Lange pers. comm.).

Intraspecific variation

Cockayne (1919, p. 73) wrote "*Leptospermum scoparium* … presents a diversity of forms which are seemingly impossible to classify. Some, it is true, are distinct races, but most are probably unfixed hybrids between races not yet defined by the plant-classifier". This statement fairly represents the variability displayed by this species. In attempts to classify the species several wild varieties have been described in New Zealand. Cheeseman (1925) agreed with Cockayne (1919) and listed one species, disputing the earlier classification of four varieties by Hooker (1867). Allan (1961) described two varieties, mentioned a further four, and suggested that the forms may either result from habitat-modification or be genetically determined. The uncertainty regarding the cause of *L. scoparium* variability is reinforced in the genus revision (Thompson 1989). Webb et al. (1988) discussed two varieties of *L. scoparium*, var. *incanum* and var. *linifolium*, and also listed the naturalised Australian species *L. laevigatum* as occurring in New Zealand.

Leptospermum scoparium var. *scoparium* was listed by Allan (1961) to represent the species description and is considered widespread. *L. scoparium* var. *incanum* (Cheeseman 1925; Allan 1961; Webb et al. 1988) has lanceolate-linear leaves c. 8 mm long, rose-tinted petals, and is common especially in the far north of the North Auckland Botanical District. *L. scoparium* var. *prostratum* (Allan 1961) has a prostrate growth form and characteristically appears on mountains. *L. scoparium* var. *myrtifolium* (Allan 1961) has smaller more ovate recurved leaves and is widespread. *L. scoparium* var. *parvum* (Allan 1961) is recorded from the Wellington District, and is a small shrub with very small flowers and hairy leathery foliage. *L. scoparium* var. *linifolium* (Allan 1961) has linear-lanceolate leaves and is also recorded as widespread. Webb et al. (1988) placed *L. scoparium* var. *incanum* and *L. scoparium* var. *linifolium* together.

Variable morphological characteristics in *L. scoparium* in New Zealand have been examined. Yin et al. (1984) studied variation of *L. scoparium* using leaf material from 182 herbarium specimens covering most of the natural range of the species, a common garden experiment, and a field analysis of natural populations. The herbarium specimens revealed significant correlations of leaf morphology with latitude, distance from coast, and annual and winter temperatures. Their common garden experiment established that leaf dimensions and plant morphology had a significant genotypic basis (Yin et al. 1984). Measurement of seven morphological characteristics of the populations grown in common conditions by Yin et al. (1984) also revealed considerable within-population genetic variability (Wilson et al. 1991). Genotypic variation has also been shown for growth form (Harris 1994), leaf variation (Harris 2002), tolerance of soil acidity (Berninger 1992), soil fertility response (Lyon et al. 1971), root anatomy (Cook et al. 1980), and freezing resistance (Greer et al. 1991; Decourtye & Harris 1992). Genotypic variance within a population in growth habit, leaf size, leaf density, and stem and foliage colour were revealed when a population was grown under common conditions by Porter et al. (1998). The flowering times within a population, among adjacent populations and geographically widely separated populations, and between seasons are highly variable (Primack 1980). This variability also has a genetic component; both age at first flowering and period of flowering differed in a common garden experiment (Yin et al. 1984).

The ability of the species to respond phenotypically to different environments was shown when Burrell (1965) transplanted seedlings of *L. scoparium* from Central Otago to Dunedin, where they immediately produced larger leaves but remained typical of the ecotype. Another example of the species' phenotypic plasticity was provided by Gaynor (1979), who showed that branching height in the field was correlated with soil depth.

Burrell (1965) noted that *L. scoparium* in Central Otago retained intact capsules until opening was induced by either drought or fire, and later studies have shown that the rate of capsule splitting differs between populations. Genetic control of capsule splitting was confirmed in a common garden experiment, and it was hypothesised that the difference between New Zealand populations had arisen from rapid selection by regular fire disturbance since the arrival of people (Harris 2002). However, a South Island field study showed that population differences of capsule splitting related to a much longer history of fire exposure in the regions displaying serotiny (Bond et al. 2004).

Distribution, habitats, and plant associations

Although the time of arrival of *L. scoparium* in New Zealand is uncertain, current opinion suggests a relatively recent dispersal from Australia (Thompson 1989). The distribution within New Zealand would have been restricted until the land clearance associated with human settlement vastly increased the area of low-nutrient environments to which the species was adapted in Australia (Thompson 1989).

Leptospermum scoparium has two main ecological roles in New Zealand vegetation: permanent dominance of extreme environments or as a seral species (Burrows 1973; Wardle 1991). Permanent dominance occurs on sites that are unfavourable for the development of climax forest as they are too wet, dry, cold, exposed, infertile, or unstable. The seral role is on disturbed sites, where *L. scoparium* is an early woody species in the succession to forest. This role has been greatly extended by human disturbance (Molloy 1975; Wardle 1991).

Five vegetation communities, the Northland gumlands, Waikato wetlands, East Coast regenerative seral scrub, North Island Volcanic Plateau heathlands, and Westland pakihi swamps, which contain *L. scoparium* as a major component and occupy large areas, are considered in detail. The common woody dicotyledonous members of these *L. scoparium*-dominated communities are listed in Table 1.

Soils too wet and infertile for the establishment of climax forest are widespread throughout New Zealand, ranging from gumland in Northland to mire in Southland, upon all of which *L. scoparium* dominates (Burrows et al. 1979). The Northland gumlands are typically leached infertile clays with perched water tables and sand podzols sustaining *L. scoparium* heathland (Esler & Rumball 1975; Beever 1988; Enright 1989; Wardle 1991). Whilst much of this land has been cleared and drained for farmland, significant remnants remain. The 16 000 year old Ahipara plateau (Wardle 1991) and the Ngarura swamp in the Waipoua forest (Burns & Leathwick 1996) are examples of self-maintaining *L. scoparium* heathland in this region. Studies of the far north (Enright 1989), Waipoua Forest heathlands (Burns & Leathwick 1996), and heath near Kaikohe (Esler & Rumball 1975) listed 10 woody dicotyledonous species in two or more reports. Two of these 10 species are invasive introductions, *Hakea sericea* and *Ulex europaeus*; the remaining eight form the endemic community in this environment (Table 1).

Waikato oligotrophic lowland mires exhibit a range of infertility yet all support permanent *L. scoparium* populations (Burrows et al. 1979; Wardle 1991). A comparison of three of these Waikato environments, the extreme Kopuatai bog (Irving et al. 1984), the intermediary Moanatuatua bog (Burrows et al. 1979; Clarkson 1997), and the relatively

Table 1 Principal associated woody dicotyledonous species in five *Leptospermum scoparium*-dominated environments. Northland gumland: ^{1}Enright 1989; ^{2}Burns & Leathwick 1996; ^{3}Esler & Rumball 1975; ^{4}Burrows et al. 1979; Waikato wetland: ^{5}Irving et al. 1984; ^{6}Burrows et al. 1979; ^{7}Clarkson 1997; East Coast seral shrub: ^{8}Clarkson et al. 1986; ^{9}Regnier et al. 1988; ^{10}Clarkson & Clarkson 1991; ^{11}Whaley et al. 2001; Volcanic Plateau heathland: ^{12}Rogers & Leathwick 1994; ^{13}Atkinson 1981; ^{14}McQueen 1961; ^{15}Leathwick 1987; ^{16}Clarkson 1984; Westland pakihi: ^{17}Rigg 1962; ^{18}Burrows et al. 1979; ^{19}Mark & Smith 1975; ^{20}Norton 1989.

Northland gumland	Waikato wetland	East Coast seral scrub	Volcanic Plateau heathland	Westland pakihi
Dracophyllum lessonianum ^{1,2,3,4}	*Epacris pauciflora* ^{5,6,7}	*Coprosma rhamnoides* ^{8,10}	*Dracophyllum longifolium* ^{12,13}	**Dracophyllum* spp. ^{17,18,19,20}
Epacris pauciflora ^{1,2,3,4}		*Coprosma robusta* ^{8,9,11}	*Dracophyllum subulatum* ^{12,13,14,16}	*Epacris pauciflora* ^{17,18}
Leucopogon fasiculatus ^{1,2,3,4}	*Erica lusitanica* ^{5}	*Coriaria arborea* ^{8,9,11}	*Kunzea ericoides* ^{12,13,16}	*Metrosideros umbellata* ^{18,19}
Myrsine australis ^{1,2}	*Salix cinerea* ^{5,7}	*Cyathodes juniperina* ^{10,11}	*Leucopogon fasiculatus* ^{13,15,16}	*Weinmannia racemosa* ^{18,19,20}
Pimelea prostrata ^{1,3}		*Hebe stricta* ^{8,11}		
Pomaderris kumeraho ^{1,3,4}		*Kunzea ericoides* ^{8,9,10,11}	*Calluna vulgaris* ^{13}	*Ulex europaeus* ^{17}
Pomaderris phylicifolia ^{1,3}		*Pittosporum ralphii* ^{9,11}	*Erica lusitanica* ^{14,15}	
Weinmannia silvicola ^{2,3}		*Pittosporum tenufolium* ^{8,9,10}		
		Pseudopanax arboreus ^{8,9}		
Hakea sericea ^{1,3,4}		*Weinmannia racemosa* ^{8,11}		
Ulex europaeus ^{1,3}				
		Ulex europaeus ^{8}		

**Dracophyllum* spp. represents *D. longifolium* and *D. palustre* which are possibly the same taxon (Allan 1961, p. 533).

more fertile Whangamarino fen (Clarkson 1997), reveals five other woody dicotyledons present with *L. scoparium*. Of these, the endemic species *Epacris pauciflora* was noted in every report and the introduced *Salix cinerea* in two. *Erica lusitanica* occurred only at Kopuatai, but was included because of its invasive abilities (Table 1).

Leptospermum scoparium is prevalent on infertile leached Westland pakihi soils, and a number of widespread communities have been studied in Westland in the northern area (Rigg 1962; Burrows et al. 1979; Norton 1989), the central area (Burrows et al. 1979), and the southern reaches (Mark & Smith 1975). The communities differ according to latitude yet a common theme is found. One woody dicotyledonous species was always recorded with *L. scoparium* in the northern area, five species in the southern study bordering with forest, and in central Westland the reported species were the same as those found in both the other areas. Thus, a typical vegetation community of Westland pakihi contains only 4 of the 19 endemic species found in association with *L. scoparium*, and the exceptionally invasive *Ulex europaeus* was included despite being recorded on better-drained ridges in one report (Table 1). However, *L. scoparium* dominance may be replaced by larger forest species in the pakihi areas provided fire is infrequent and the environment is not exceptionally infertile (Williams et al. 1990).

In south Westland (Wardle 1974) and Fiordland (Wardle et al. 1973) lowland swamps are prime habitats, and montane raised mires in Fiordland (Burrows & Dobson 1972; Mark et al. 1979) and Otago (Johnson et al. 1977) also carry *L. scoparium*. Following fire in a Southland bog, *L. scoparium* dominated the environment rapidly (Johnson 2001). In association with swamp-like environments *L. scoparium* dominates lake shorelines around the southern lakes where it survives temporary submergence (Johnson 1972; Mark et al. 1977; Robertson et al. 1991). In these conditions the species differentiates specialised aeration tissue, aerenchyma, in submerged roots allowing long-term dominance in waterlogged environments (Cook et al. 1980).

Areas too high and cold for the establishment of climax forest occur in both main islands (Wardle 1991). *L. scoparium* occurs above the tree line (Wardle 1963; Gibbs 1966) and on upland peat and gley soils of both main islands (Burrows et al. 1979), and is frequent on inhospitable sites at low and high altitude in south Westland (Burrows 1964; Wardle 1977) and Southland (Burrows 1964; Burrows et al. 1979), and in montane scrubland on Stewart Island

(Wells & Mark 1966). However, at high altitude in Otago growth is limited to warmer microclimates (Wilson et al. 1989). Comparison of the five studies of montane flora in the central North Island, the Rangipo Depression (Rogers & Leathwick 1994) and the volcanic slopes of Mt Tongariro (Atkinson 1981) at high altitude, and at lower altitude the widespread ignimbrite pumice plain near Tokoroa (McQueen 1961), the Waipapa Ecological Area (Leathwick 1987), and Pureora mountain mires (Clarkson 1984), demonstrates greater diversity as forest species return to more hospitable environments. Four endemic woody dicotyledonous species are noted as common throughout the region, and the invasive heathers *Calluna vulgaris* and *Erica lusitanica* were recorded at the higher and lower sites, respectively (Table 1).

In coastal environments throughout New Zealand *L. scoparium* and *K. ericoides* are found on areas too exposed for forest (Morton & Miller 1968; Molloy 1975). *L. scoparium* occurs on sites as diverse as the edge of mangrove swamps in the Auckland region (Wardle 1991), the Cape Reinga district in the far north (Wheeler 1963), Farewell Spit in Nelson (Burrows 1973), and the coastal cliff zones around southern Wairarapa and Wellington (Burrows 1973).

Areas too infertile for the establishment of forest overlap with the above categories, as the environments are the same. Oligotrophic mires and swamps, extreme coastal and altitudinal sites, and heavily leached soils have all been discussed. *L. scoparium* is also present in other situations: the geothermic heated environments of the central North Island (Wells & Whitton 1966; Given 1980), edaphically dry pumice in the central North Island (Elder 1962), and as a consistent understorey on poor gleyed soils in forested areas (Burrows 1973). *L. scoparium* is also tolerant of South Island ultramafic soils (Lyon et al. 1971; Lee et al. 1975, 1983; Lee 1992).

Natural unstable environments also lend themselves to colonisation by *L. scoparium*. Landslides in Fiordland forests are rapidly covered by *L. scoparium* in a seral role (Mark et al. 1964). *L. scoparium* establishes on braided river beds (Burrows 1973) and unconsolidated coastal deposits where it is a woody pioneer (Wardle 1991).

Soils too dry for climax forest vegetation present a more complicated picture. Typically these areas occur in the eastern rain shadow of the New Zealand mountain ranges (Wardle 1991). *L. scoparium* occurs as a dominant species in relatively higher rainfall areas of these regions, but becomes uncommon in dryer situations where *Kunzea ericoides* dominates (Wardle 1971, 1991). In Otago where yearly rainfall is less than 650 mm, *K. ericoides* is more common, interspersed with *L. scoparium* on boggy land (Burrell 1965). Self perpetuation of *K. ericoides*/*L. scoparium* scrub occurs where broadleaf forest establishment is either prevented (Wardle 2001) or retarded by site conditions (Dobson 1979).

In contrast to the permanent *L. scoparium* populations, seral communities also exist and form a significant proportion of the species' modern range. *L. scoparium* is found in moist forested regions forming similarly aged stands in a nursery role for climax vegetation following fire or other disturbance (Burrows 1973; Payton et al. 1984) where it may persist for more than a century (Mark et al. 1989). The species also establishes easily in open undergrazed pasture (Grant 1967), and its presence in this situation indicates unsustainable clearance of forest or scrub to establish pasture (Bascand 1973). *L. scoparium* may be the initial woody pioneer on moderately fertile well-drained soil due to prodigious seed set and rapid germination and growth (Mohan et al. 1984a,b). The species has an overriding germination response to full light spectra coupled with an inhibition by far-red wavelengths typical of pioneer species on disturbed sites (Herron et al. 2000; McKay et al. 2002). *L. scoparium* seed does not exhibit dormancy, and the unshed seed in capsules is probably the main reservoir of seed as the soil seed bank is non-persistent (Mohan et al. 1984a). Accordingly, *L. scoparium* scrub regeneration and re-establishment, which has been a feature of New Zealand hill farming, can be avoided with suitable land management such as the fertilisation and retention of a heavy sward (Levy 1970). Communities of *L. scoparium* are not permanent in regions where the rainfall is adequate to allow the establishment of climax broadleaved forest (Esler & Astridge 1974; Wardle 1991), and replacement by *K. ericoides* and subsequent establishment of forest has been recorded in Canterbury and Otago (Burrows 1961; Molloy & Ives 1972; Dobson 1979; Allen et al. 1992), Kapiti Island (Esler 1967), and the Hauraki Gulf islands (Atkinson 1954; Bellingham 1955; Esler 1978). The East Coast region of the North Island provides an example of these communities where large areas of coastal and lowland hillsides are covered with dense seral scrub, established since forest clearance for pasture development. Three types of *L. scoparium* scrub were described in the Motu Ecological District by Clarkson et al. (1986): *L. scoparium*, *L. scoparium*/*Coprosma* spp./*Hebe* spp., and *L. scoparium*/*Kunzea ericoides* scrub. Generally the same situation exists around the East Cape (Regnier et al. 1988; Clarkson & Clarkson 1991; Whaley et al. 2001). Ten endemic woody dicotyledons were recorded in two or more studies (Table 1). Most of these species are associated with regenerating forest expected in a seral *L. scoparium* environment. Whilst *Ulex europaeus* was only recorded in one study, distribution is widespread and this species is accordingly included.

Where forest on steep slopes has been cleared for pasture establishment the land is often prone to erosion. The value of *L. scoparium* as protective scrub is now recognised, as it provides rapid (Smale et al. 1997) and excellent protection from shallow landslides (Watson & O'Loughlin 1985), and the presence of mature stands assists erosion control (Bergin et al. 1995). *L. scoparium* foliage can intercept a significant amount of rainfall (Burke 1981), as much as 40–50% in a storm event (Aldridge & Jackson 1968). Together with soil binding by roots this rainfall interruption is effective in erosion control. Carbon accumulation by *L. scoparium* is rapid and similar to that of plantation forestry (Scott et al. 2000).

The variety of environments in which *L. scoparium* occurs indicates the species' wide ecological amplitude, and a large population of any one endemic woody dicotyledonous species is not found in association with *L. scoparium* throughout its entire range. *Epacris pauciflora* and *Dracophyllum* spp. are common on the infertile lowlands, the seral shrub community contains a selection of early successional forest species, and the montane environments carry a mixture of *Dracophyllum* spp. and hardier forest species.

The same situation is seen with the introduced shrubs. *Ulex europaeus*, *Cytisus scoparius*, and *Teline monspessulana* are widespread throughout New Zealand, particularly in scrubland on low fertility hill country, yet these species do not inhabit poorly drained environments in appreciable numbers (Roy et al. 1998). *Hakea sericea* and *H. salicifolia* are both common in wet lowland environments as far south as northern Westland (Roy et al. 1998), but neither is found on the East Coast. The introduced Ericaceae species remain locally distributed apart from *Erica lusitanica*, which is now widespread on low-fertility wet soils throughout New Zealand (Roy et al. 1998).

A number of direct plant associations also occur with *L. scoparium*. The rare non-green orchid *Gastrodia minor* shares mycorrhizae with *L. scoparium* along with other plant species and is distributed throughout New Zealand (Wardle 1991). *L. scoparium* acts as a host for the widely distributed large-leafed mistletoe *Ileostylus micranthus* (Molloy 1975), but *I. micranthus* exhibits low host specificity and is most frequently found in association with *Coprosma* spp. (Patel 1991). The widespread parasitic dwarf leafless mistletoe *Korthalsella salicornioides* attaches preferentially to *Leptospermum* and *Kunzea* (Stevenson 1934), but is also found with other endemic species and has been recorded in association with introduced *Erica* spp. (Bannister 1989).

INSECT ASSOCIATIONS

Insect associations may be divided into two sections: the species involved in the pollination of *L. scoparium* and the insect pests.

Pollination

Much of New Zealand's insect-pollinated flora has inconspicuously coloured flowers, which has been historically attributed to the lack of specific insect associations (Godley 1979; Lloyd 1985; Wardle 1991). The small white flowers of *L. scoparium* are classified as open-access with a dish/bowl shape and, typical of this type, are visited by a range of insect pollinators (Newstrom & Robertson 2005). Heine (1937) recorded representatives from the orders Coleoptera and Diptera. A detailed study of montane *L. scoparium* visitors revealed a range of insects arriving in a structured pattern (Primack 1978). Open flowers were visited by large tachinid and calliphorid flies at dawn, followed by a great variety of small Diptera with increasing temperature. In fine weather indigenous Hymenoptera visited flowers from mid morning. The bees and flies ended visits in the late afternoon, and in the early evening in settled weather moths (Pyralidae, Geometridae, Noctuidae) and craneflies (Tipulidae) were recorded. Nocturnal moth visits have been noted (Newstrom & Robertson 2005). The introduced honey-bee (*Apis mellifera*) also collects both pollen and nectar (Butz Huryn 1995). These observations confirm the non-specific pollinators associated with *L. scoparium.*

Insect pests

The principal insect pests associated with *L. scoparium* in New Zealand are the scale insects, order Homoptera. Of the 17 species listed by Hoy (1961), most are distributed throughout New Zealand at low levels of infestation. The three most commonly found species are the endemic *Coelostomidia wai-*

roensis and introduced *Eriococcus orariensis* and *E. leptospermi*. The condition commonly described as manuka blight is associated with infestation by the introduced insect species and the development of a covering of sooty mould on the resultant honeydew.

Coelostomidia wairoensis is distributed throughout the North Island and the northern and eastern South Island and is associated with *Capnodium elegans*, one of the fungi that produce the visually diagnostic sooty mould on the stems of infested plants. *C. wairoensis* has not been reported to kill *L. scoparium* (Hoy 1961). *Eriococcus orariensis*, also associated with *Capnodium* spp., is common throughout New Zealand but absent in wetter regions and the sub-alpine belt (Wardle 1991). *E. orariensis* was introduced involuntarily from Australia in the mid 20th century, where it does not cause widespread death of the principal host species *Leptospermum juniperinum* in the southern and eastern areas of the mainland or *L. scoparium* in Tasmania. Once introduced into New Zealand it was deliberately spread and brought about a rapid eradication of large areas of *L. scoparium*. The removal of plant nutrients by the scale insect weakens the plants so that they are unable to survive environmental stress, and reduced photosynthetic efficiency may result from the covering of foliage by the sooty mould (Hoy 1961). The virulence of *E. orariensis* has been significantly reduced by the subsequent spread of the entomogenous fungus *Myriangium thwaitesii*, and the revival of *L. scoparium* has been as spectacular as the initial decline (Hoy 1961). However, there is no record of resistant forms of *L. scoparium* in the literature. This disease complex does not affect the extensive cultivar plantings in the British Isles, as the primary pest *Eriococcus orariensis* has not been introduced (Dawson 1997b). *Eriococcus leptospermi*, often found together with *E. orariensis* throughout New Zealand, inhabits the bark surface towards the stem tips. Heavy infestation does not lead to plant death and *E. leptospermi* appears to be immune to *M. thwaitessi* (Hoy 1961).

Manuka beetles (*Pyronota* spp.) are also widespread, often found on light sandy montane soils associated with grassland on forest margins. These species appear to be non-specific feeders, often preferring grass root material to *L. scoparium* (Thomson et al. 1979), and may have a role in pollination (Heine 1937). The leaf-feeding manuka moth (*Declana floccose*) is also common, and other widespread insect pests are webworm (*Heliostibes atychioides*), the wood-boring larvae of the longhorn beetle (*Ochrocudus huttoni*) and the gall-forming mite (*Aceria manukae*) (Molloy 1975), and the introduced wood-borer (*Amasa truncates*) (Brockerhoff & Bain 2000).

FUNGAL ASSOCIATIONS

Many fungi have been noted in association with *L. scoparium*; but published records are far from comprehensive. A search of the New Zealand Fungal Herbarium database (www.landcareresearch.co.nz/research/biodiversity/fungiprog/) revealed 699 *L. scoparium*-hosted specimens. Ascomycota are represented by 15 orders comprising 71 genera and species; Basidiomycota 9 orders and 195 genera and species; Deuteromycotina by 21 Hyphomycetes and 8 Coelomycetes. Details of their ranges throughout New Zealand are not complete.

Leptospermum scoparium ectomycorrhizae and endomycorrhizae (vesicular-arbuscular) are frequent yet the number of partners is unknown, and endomycorrhizae infection appears to be more common (Moyersoen & Fittler 1999). Although Hawksworth et al. (1995) identified the order Glomales (Ascomycota) as the most common endomycorrhizal symbiont, the herbarium collection does not include any specimen from this order, probably due to the difficulties associated with classification and laboratory growth. However, Baylis (1971) successfully infected *L. scoparium* with an endomycorrhiza in laboratory conditions, and in a study of five South Island sites dominated by *Nothofagus*, *Pinus radiata*, or podocarp/broad-leaved forest, 5 of the 12 endomycorrhizal symbionts described were found in association with *L. scoparium*, whereas only 10–36% of the infections were ectomycorrhiza at four of these sites (Cooper 1976). *L. scoparium* is one of the principal ectomycorrhizal hosts in New Zealand's endemic flora, with *Kunzea ericoides* and *Nothofagus* spp. (Hall et al. 1998). *L. scoparium* ectomycorrhizal infection appears to be determined by the presence of the appropriate inoculum and alternative host plant species, particularly *Nothofagus* spp. (Moyersoen & Fitter 1999). The ectomycorrhizal species recorded in New Zealand have recently been reviewed, listing 22 Basidiomycota and 6 Ascomycota families in association with *L. scoparium* (Orlovich & Cairney 2004). The invasive basidiomycete *Amanita muscaria*, often found with *L. scoparium* (Ridley 1991), is considered able to displace the native species (Orlovich & Cairney 2004).

The principal role of *L. scoparium* mycorrhizal partners is the improvement of phosphorus uptake (Baylis 1971; Johnson 1976; Hall 1977) allowing rapid growth and exploitation of available light (Wardle 1991). The level of mycorrhizal infection correlates with available phosphorus and growth conditions (Baylis 1975; Cooper 1975; Hall 1975). The development of *L. scoparium* ectomycorrhizae may also facilitate the growth and succession of *Nothofagus* spp. seedlings (Baylis 1980).

A narrow but characteristic range of *L. scoparium* endophytic fungi was reported from a study in the Auckland province (Johnston 1998). *Phyllosticta* spp., in association with *Diploceras leptospermi* and Coelomycete, dominated natural populations, with a range of other species present in insignificant and variable proportions. The opportunist endophytes *Botryosphaeria* and *Alternaria* sp. were prominent in planted *L. scoparium* stands, indicative of a host under environmental pressure (Johnston 1998). Within natural sites neither the species diversity nor the variability of infection rate could be explained by any obvious correlation with plant age or any environmental factor (Johnston 1998). *Phyllosticta* species were specific to *L. scoparium* and not recorded on *Kunzea ericoides*, yet *D. leptospermi* was present on both species (Johnston 1998) in contradiction to an earlier report (Bagnall & Sheridan 1972). The fungal species' pathogenicity is unknown though six of the families represented grow as epiphytes and are associated with leaf wounds (Johnston 1998). *Capnodium* spp. are also associated with *L. scoparium* foliage and bark, but as a result of *Eriococcus* spp. invasion (Hoy 1961).

TRADITIONAL AND HISTORIC USES OF *LEPTOSPERMUM SCOPARIUM*

Traditional uses

Six entries for *L. scoparium* are listed in the dictionary of Maori plant names, manuka and kahikatoa being the most common (Beever 1991). Manuka is most frequently used throughout New Zealand, and kahikatoa is common in Northland. The word kahikatoa also translates as a weapon made of *L. scoparium* (Williams 1975), and the plant name may be derived from this association. An alternative suggestion is that manuka was used as a generic name for the two common seral Myrtaceae species in New Zealand, the names kahikatoa and kanuka representing *L. scoparium* and *Kunzea ericoides*, respectively (T. Roa pers. comm.). The common names of tea tree and red tea tree are explained by use of the leaves for a tea and the red colour of the wood. The Maori and common names for *K. ericoides* are manuka, kanuka, tea tree, and white tea tree, again indicating beverage use and wood colour, and often leading to understandable confusion and misidentification. Titree is an incorrect name for both species, and refers to species of *Cordyline* (Brooker et al. 1987).

Maori used *L. scoparium* for food, medicine, and timber. Pia manuka, the sugary gum found occasionally on young branches, was considered a delicacy and given to infants, or was used to alleviate coughs in adults (Crowe 1981). Brooker et al. (1987) listed a number of traditional medicinal uses. A decoction of leaves was taken, applied as a salve, directly chewed, or the vapours inhaled. The bark was used in a similar way to alleviate bronchial complaints. The tough wood was harvested for implement making, and a review of museum artefacts illustrated seven tools made from the plant's timber (Cooper & Cambie 1991).

The first recorded European use was during James Cook's voyages, when *L. scoparium* leaves were initially used as a tea substitute, and later employed as an antiscorbutic in brewing beer (Cooper & Cambie 1991). Whalers continued to rely upon *L. scoparium* as a tea substitute (Brooker et al. 1987), giving rise to tea tree as a common name, and early settlers became so attached to the concoction that the importation of Chinese tea was considered unnecessary by one author (Crowe 1981). *L. scoparium* has continued to be valued for firewood and charcoal, and is often used for smoking fish.

Ornamental use

Leptospermum is a genus of ornamental worthiness, and has been cultivated since its introduction to Europe. The greatest numbers of cultivars have been bred from *L. scoparium*. Approximately 150 named cultivars have been derived from *L. scoparium*, whilst the balance of the genus is represented by about 20–30 cultivars (Dawson 1997a).

Material collected during James Cook's first voyage of discovery included both *L. scoparium* and *K. ericoides*, both of which were incorrectly assigned to the genus *Philadelphus* in the unpublished Primitae Florae Novae Zelandiae, prepared by Solander (Harris 2001). Three species were listed as growing at Kew Gardens by 1789, and prior to this four species of greenhouse *Philadelphus* were offered to the public in the late 1770s (Cooper & Cambie 1991). The specimens were subsequently reclassified correctly as either *L. scoparium* or *K. ericoides* (Harris 2001). *L. scoparium* was first described in 1776 from material collected from Dusky Sound, Fiordland, by J. R. & G. Forster during Cook's second voyage. By 1896 *L. scoparium* was acclimatised in Cornwall and described as a favourite conservatory plant (Cooper & Cambie 1991).

The discovery and use of rare wild variants has enhanced the range of *L. scoparium* cultivars available. Outstanding single white- or pink-flowered specimens have been identified in the wild, and a number of double white- or pink-flowered plants discovered and propagated throughout the 20th century. A red-flowered plant was found in the wild twice, leading to the release of another set of cultivars. Wild prostrate forms have also been used (Dawson 1997a).

These unusual wild plants have been developed by deliberate hybridisation, and Lammerts (1945) pioneered controlled breeding in California. Subsequent horticulturists have increased the range of *L. scoparium* cultivars, notably E. F. Jenkins and Sons (Victoria, Australia), J. Hobbs (Auckland, New Zealand), Duncan and Davies (New Plymouth, New Zealand), and G. Hutchins (Essex, England) (Dawson 1997b). This development allowed Dawson (1997b) to list 23 outstanding named *L. scoparium* cultivars. More recently, Harris (2000) recorded the development of four named inter-specific cultivars, all having *L. scoparium* as one parent and one of the Australian species *L. rupestre*, *L. spectabile*, or *L. polygalifolium* as the other, and a *L. rotundifolium* × *L. scoparium* hybrid has been bred (Bicknell 1995).

Studies have also been completed to improve the horticultural qualities of *L. scoparium*. Pot plants have been developed (Bicknell 1985), cut flower life (Bicknell 1995) and flowering cue (Zieslin & Gottesman 1986) investigated, frost hardiness considered (Greer et al. 1991; Decourtye & Harris 1992), and tolerance to soil acidity studied (Berninger 1992). Nonetheless, one of the greatest drawbacks of cultivated *L. scoparium* in New Zealand is manuka blight, and a cultivar resistant to the scale insect pest has not yet been developed.

Leptospermum scoparium has been extensively planted in the milder areas of the British Isles as a semi-hardy garden plant and is described as ubiquitous in Ireland gardens (Cooper & Cambie 1991). Despite the extent of garden planting in the British Isles naturalisation is only reported at Tresco Abby, Isles of Scilly, where groves of self-sown seedlings are found (Bean 1973). It is probable that naturalisation has occurred in the milder areas of England and Ireland but has not been reported. The species has also naturalised in Hawai‘i, where escapes from garden plantings have colonised disturbed wet forest areas and become a significant weed (Wagner et al. 1990).

Essential oils

Essential oils distilled from the leaves of *L. scoparium* have received considerable commercial attention during the last decade. The New Zealand Phytochemical Register – Part III (Cambie 1976) lists earlier research that identified these oils.

An analysis of 16 commercial samples of *L. scoparium* essential oil revealed 100 components, of which 51 were identified and made up about 95% of the content. The oils fell into three major sections, triketones approximately 20%, sesquiterpene hydrocarbons 60–70%, and monoterpene hydrocarbons about 5% (Christoph et al. 1999), in contrast to about 75% monoterpene hydrocarbon α-pinene present in *Kunzea ericoides* (Perry et al. 1997a).

A review of the essential oils of New Zealand suggested that *L. scoparium* oils would differ between and within natural populations (Douglas et al. 1994), and this was confirmed by the variation of the component essential oils of natural populations of *L. scoparium* grown in a common garden experiment (Perry et al. 1997b). Two plants from each population were sampled: the East Cape population contained a high triketone level, high levels of α-pinene and β-pinene monoterpene hydrocarbons were found in Northland populations, and the balance of populations contained a complex mix of sesquiterpene and oxygenated sesquiterpene hydrocarbons. Australian *L. scoparium* samples grown in the same common environment had a higher monoterpene level than the New Zealand populations. The *L. scoparium* chemotypes reported matched the morphological types to some degree (Perry et al. 1997b).

Porter & Wilkins (1998) showed a similar pattern to those reported by Perry et al. (1997b), describing four groups of oil profiles found in wild populations: triketone-rich in the East Cape; monoterpene-, linalool-, and eudesmol-rich in Nelson; monoterpene- and pinene-rich in Canterbury; and triketone-, linalool-, and eudesmol-deficient in the rest of New Zealand. The average composition of *L. scoparium* essential oil was defined as ≤3% monoterpenes, ≥60% sesquiterpenes, and ≤30% oxygenated sesquiterpenes and triketones.

A detailed field study of New Zealand *L. scoparium* populations confirmed the presence of *L.*

scoparium chemotypes: monoterpene-enriched areas in Northland and the West Coast, triketone-enriched in East Cape and Marlborough, and sesquiterpene-rich oils throughout the rest of the country. Eleven chemotypes were recognised by the division of the major oil types referred to above and subdivision of the sesquiterpenes and oxysesquiterpenes (Douglas et al. 2004). The triketone-enriched oils have been found to carry the greatest antibacterial activity (Christoph et al. 2000), and are marketed as Manex™.

A chemotaxonomic analysis of *Leptospermum* has been completed. In dealing with species allied to *L. scoparium*, Brophy et al. (1999) showed that Australian *L. scoparium* populations in Victoria and Tasmania had different essential oil profiles from the New Zealand populations; in particular, triketones were not found. The persistent woody-fruited group of *Leptospermum* established by Thompson (1989) was not amended, and in general the *L. scoparium* essential oils did not differ in comparison with this group; however, the authors concluded that *L. scoparium* is a variable taxon that may require division (Brophy et al. 1999).

Nevertheless, within-population variation of essential oil content was shown in a study of *L. scoparium* grown in a common garden experiment from seed collected from five wild plants within a 5 m^2 area (Porter et al. 1998). The oil profiles of both young and mature plants differed within and between seasons, and the principal component responsible for most variation differed between plants whenever sampled. The morphology of the plants also differed markedly. The need for extensive sampling over a period of more than one growing season to produce reliable essential oil profile data for chemotaxonomic or variety selection was acknowledged.

Manuka honey

Cockayne (1916) recognised *L. scoparium* as a major source of superfluous honey produced by the introduced honeybee, reflecting the abundance of the plant and the surplus nectar production. Butz Huryn (1995) reviewed the literature in detail. *L. scoparium* honey has a distinctive flavour, colour, and consistency and until recently was used solely for culinary purposes.

A number of studies analysing the antibacterial activities of New Zealand honeys have been completed. Whilst many honey types contained significant levels of antibacterial activity due to enzyme-produced hydrogen peroxide, only *L. scoparium* (manuka) honey often contained a relatively high level of non-peroxide activity (Molan et al. 1988; Allen et al. 1991). The non-peroxide antibacterial activity was considered linked to the floral source (Molan & Russell 1988). However, *L. scoparium* honey samples have demonstrated a considerable range of potency of non-peroxide antibacterial activity. A typical agar diffusion assay study reporting a mean antibacterial activity of 18.6 units, equivalent to the activity of 18.6% w/v phenol, for 19 *L. scoparium* honey samples, with a standard deviation of 8 units (Allen et al. 1991). The variability was initially attributed to sample misidentification or processing differences (Allen et al. 1991), and later to a regional difference in phytochemical composition or concentration (Molan 1995). The non-peroxide antibacterial activity of *L. scoparium* honey was named the Unique Manuka Factor (UMF®), leading to the development of a range of medical products from *L. scoparium* honey containing high levels of UMF®.

Attempts to identify the active component responsible for the non-peroxide antibacterial activity present in *L. scoparium* honey have continued unsuccessfully. Two approaches have been investigated: seeking correlation between the antibacterial activity and the trace organic substances to determine the honey's floral source identified by GC-MS, and the identification of the fraction responsible for the non-peroxide activity. Identification of the components of *L. scoparium* honey confirmed that the constituents are different from those found in the antibacterial *L. scoparium* essential oil (Tan et al. 1988); the triketones found responsible for the antibacterial activity of the essential oil (Christoph et al. 2000) are not found in the honey. The identified phytochemical components of *L. scoparium* honey are similar regionally throughout New Zealand, accordingly not accounting for the non-peroxide variability (Tan et al. 1989; Wilkins et al. 1993; Weston et al. 2000). However, the phytochemical components of New Zealand *L. scoparium* honey differ from those of the Australian *L. polygalifolium* honey that also exhibits a non-peroxide antibacterial effect (Yao et al. 2003).

Extraction of potentially active organic fractions (Russell et al. 1990) was followed by the isolation of the phenolic components (Weston et al. 1999), oligosaccharides (Weston & Brocklebank 1999), and antibacterial bee peptides (Weston et al. 2000). These components were found to account for little of the non-peroxide activity, and Weston (2000) suggested that the non-peroxide antibacterial effect was an additional peroxide effect and that the assay developed to remove peroxide from honey (Molan & Russell 1988) was consistently failing.

However, the residual hydrogen peroxide in *L. scoparium* honey has been shown not to account for the non-peroxide antibacterial activity by chemical manipulation (Snow & Manley-Harris 2004). Furthermore, a difference in the mode of action of dissimilar honeys has been indicated in studies that determine the minimum inhibitory concentrations for control of wound-infecting bacterial species (Willix et al. 1992). Methicillin-resistant *Staphylococcus aureus* responded to the same concentrations of *L. scoparium* honey and a honey with activity due to hydrogen peroxide, yet vancomycin-resistant *Enterococcos faecium* required approximately double the concentration of the latter honey to be inhibited compared with the *L. scoparium* honey (Cooper et al. 2002). Additionally, the peroxide antibacterial activity of honey is not effective against all bacterial species. *Heliobacter pylori* was inhibited by a 5% solution of *L. scoparium* honey but was not inhibited by a 40% solution of a honey with activity due to hydrogen peroxide, whereas both honeys were equally effective against *Staphylococcus aureus* (Al Somal et al. 1994). These observations indicate that an as yet unknown agent other than hydrogen peroxide significantly contributes to the antibacterial activity of *L. scoparium* honey.

CONCLUSIONS

Leptospermum scoparium is tolerant of infertile environments, thriving in a wide range of marginal and disturbed environments. The seral habitat in New Zealand has been greatly extended by human vegetation disturbance, and due to its invasive nature, the species has been regarded as an agricultural woody weed. Recent studies have altered the perception of *L. scoparium*. The species' role in erosion control, carbon sequestration, and vegetation restoration by succession, along with the commercial value of the essential oils, honey, and ornamental varieties, make further examination of the species necessary and timely.

The taxonomic status of the species needs to be thoroughly clarified in New Zealand and Australia. In all probability *L. scoparium* is an undefined species aggregate in New Zealand (P. de Lange pers. comm.) The relationship of *L. scoparium* populations within New Zealand, populations within Australia, between New Zealand and Australian populations, and the closely related Australian species, should be investigated. The Australian tea tree *Melaleuca alternifolia* (Myrtaceae), which is used for essential oil production, has received just such a comprehensive treatment (Rossetto et al. 1999; Lee et al. 2002). Conventional techniques such as uniform environment studies and essential oil profiles, with modern molecular genetic studies, should be included in such a study.

The increased seral range of *L. scoparium* has most likely allowed gene flow between previously isolated populations in New Zealand. The genetic properties of unique populations, for example, the dwarf population identified on the Kaikoura coast (Harris 1994), may be lost due to interbreeding. The need to sustain genetic integrity of New Zealand species has been recognised (Simpson 1992; Atkinson 1994), and *L. scoparium* is certainly another example of a species exhibiting a combination of phenotypic and genotypic variation throughout its natural range.

A revised systematic treatment of *L. scoparium* would resolve many questions surrounding the species. The regional differences of essential oils profiles and honey non-peroxide antibacterial activity may relate to genetic differences between populations, but this awaits experimental confirmation. Horticultural cultivar development may be enhanced, particularly the search for a plant resistant to manuka blight. Agronomic development of the species as a crop plant providing an abundant and reliable source of the pharmacologically active essential oils and honey could be pursued. The conservation and, where necessary, the repopulation of genetically unique varieties could be actively promoted to ensure the survival of the entire genetic spectrum of this interesting and valuable species.

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