

Variation of inherent seed capsule splitting in populations of *Leptospermum scoparium* (Myrtaceae) in New Zealand

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Abstract Variation in the splitting of seed capsules was observed for 61 populations of *Leptospermum scoparium* from a wide latitudinal range in New Zealand raised from two sowings and grown in uniform environments. Variation ranged from populations for which capsules of all shrubs had split and shed seed within a year of their formation to those for which all shrubs had serotinous capsules that remained intact and retained seed for a longer period. There was a significant latitudinal gradient in this variation with northern populations being strongly serotinous. The variation of capsule splitting was independent of the time taken from sowing to the first flowering of plants. These results are discussed with regard to the ecological adaptation of *L. scoparium* to various habitat disturbance factors. It is concluded that the variation observed is consistent with the opinion that the New Zealand flora generally lacks fire adaptation but, since human settlement, rapid selection of fire-adapted genotypes of *L. scoparium* has occurred in populations that are seral in secondary succession to forest.

Keywords *Leptospermum scoparium*; manuka; capsule splitting; serotiny; flowering phenology; essential oil; fire adaptation; vegetation disturbance; New Zealand

INTRODUCTION

Leptospermum scoparium, commonly known as manuka or tea-tree, is a shrub occurring widely throughout lowland to subalpine areas and in many habitats in New Zealand. Allan (1961) considered the species to be endemic to New Zealand, but it is also regarded as a native species of Tasmania, New South Wales, and Victoria, Australia (Curtis & Morris 1975; Thompson 1989). Allan (1961) commented about the difficulty in classifying its multitudinous forms, and referred to Cockayne's (1919) interest in the variation within the species. Yin et al. (1984) showed patterns in variation of leaf size and shape measured from herbarium specimens collected from much of its range in New Zealand that were correlated with geographical and environmental factors. As an extension to this herbarium study, Yin et al. (1984) also revealed ecotypic differentiation in the species by cultivating 17 populations raised from seed collected from a wide latitudinal range under uniform garden conditions.

In defining two infrageneric groups in *Leptospermum* Thompson (1989) distinguished species that have small, quickly shed fruit lacking woody valves from those that have woody-valved fruit, a capsule, that remain attached for several years. *Leptospermum scoparium* falls into the second group, and within that in a subgroup of species with much woodier fruit. The capsule is loculicidal with a valve at the top of each loculus. Separation of these valves allows the release of seed.

Thompson (1989) considered that the woody character may allow recovery from fire, but qualified this by saying that most of the species in the subgroup occupy habitats in cool climates that are not particularly fire prone. In comparing their ecology in Otago, Burrell (1965) gave particular emphasis to the observation that *Kunzea ericoides*, kanuka, shed all its seed each autumn whereas *L. scoparium* retained its seed for several years unless the woody fruits were induced to open by drought or fire.

In the course of observations on the flowering patterns of populations of *L. scoparium*, and

K. ericoides (Harris 1996), it was noticed that within *L. scoparium* there were plants that separated their capsule valves and shed seed within a year of their formation, and plants that retained seed in unsplit capsules for longer periods. Consequently, records were kept of this variation in capsule splitting. The interpopulation variation recorded is related to the populations' geographical origin, the time they took from sowing to first flowering, and their leaf shape as a character previously shown to be a useful index of morphological variation of *L. scoparium* (Yin et al. 1984). The adaptive significance of this variation is considered in relation to the history of disturbance to the vegetation of New Zealand.

MATERIALS AND METHODS

Seed sources

Shrubs were raised from seed and observations on their growth and development were made at Lincoln, Canterbury, New Zealand (43°38'S, 172°29'E, 11 m a.s.l.). The seed was obtained mainly in response to a request made to staff of Botany Division DSIR (now part of Landcare Research) to collect seed from wild populations of *L. scoparium* in the course of fieldwork throughout New Zealand in late 1982 and 1983. The detail of site information provided with each seed sample varied and a summary of this is provided in Table 1. The populations are numbered 1 to 61 in order of their latitude of origin from north to south. Where latitude was not determined at the point of collection it was approximated from the locality information provided.

Cultivation of seedlings and experimental layout

Seed was sown and seedlings raised in two lots as indicated in Table 1 in an unheated glasshouse under natural daylength. The first sowing, made on 12 September 1983, included 51 populations of New Zealand *L. scoparium*. Germination from this sowing was even with the first emergence of seedlings for all populations occurring from 25 to 27 September 1983 and the appearance of the first leaves from 11 to 14 October 1983. Seedlings were pricked out into potting soil in peat jiffy pots on 18 October 1983 and grown in the glasshouse until they were planted in the field on 16 January 1984.

The second sowing of 10 more populations on 24 November 1983 filled a gap in the distributional range of samples in the central North Island. Details of the germination and development of seedlings

from this sowing were not kept. Seedlings from this sowing were pricked into jiffy pots on 11 January 1984 and planted in the field on 1 June 1984.

There were 24 seedlings raised for each population. They were placed in the glasshouse and in the field to be grown under uniform environmental conditions in a randomised block design with six replicates. Within replicates each population was represented by four plants grown together in a row. In the glasshouse pots were placed together, and in the field the seedlings were planted at 1-m spacing.

Leaf shape index

While in the glasshouse a series of measurements were made on the seedlings. Because of the different sowing dates and the timing of the measurements, the dimensions of the seedlings from the two sowing dates are not directly comparable. However, an index of leaf shape, derived as the ratio of the length and greatest width (mm) of the lamina of one leaf selected from the largest leaves per seedling, was not significantly altered by the different conditions of the two sowings. Consequently, this leaf-lamina-shape index is included in the examination of the variation patterns of the populations.

First flowering and capsule splitting

Flowering of shrubs from the first sowing first occurred in October 1984 and from then its progress was recorded weekly. In the course of these observations it was noticed that splitting of capsules varied amongst shrubs. Regular weekly observation on the flowering of shrubs raised from the second sowing did not commence until spring 1986. No shrubs of the second sowing flowered in the flowering season starting in spring 1984 and a record was made on 19 February 1986 of which plants had flowered in the season starting spring 1985. Thus, when capsule splitting was scored for the first sowing on 29 July 1986, capsules present on plants had been formed during two flowering seasons. When plants of the second sowing were scored on 18 August 1986 capsules present were from only the 1985/1986 flowering season.

Capsule splitting, i.e., separation of the valves at the top of each loculus of the capsule to release seed, was scored on the following scale from an assessment of all the capsules on a shrub without reference to their age: 0, no capsules split; 1, some split; 2, more than half split; 3, most split. Capsules present on dead branches were disregarded.

Two character indices were determined from these scores. The first was the percentage of plants

Table 1 Locations, latitudes, and site information for New Zealand *Leptospermum scoparium* populations. So., (1) sown 12 Sep 1983, (2) sown 24 Nov 1983; Fl.%, percentage of plants in population that flowered in 1984/85; Sp.%, percentage of plants in population with split capsules; P.m., population means of the score of the extent of capsule splitting; L/R, mean population seedling leaf lamina length-to-width ratio.

Population number, location, land district	Latitude °S	Site information	So.	Fl.%	Sp.%	P.m.	L/R
1 Motutangi Swamp, Houhora, North Auckland	34°53'	Swampy gumland	1	42.8	0.0	0.00	3.23
2 Karikari Peninsula, North Auckland	34°55'	Dense manuka scrub on peat soil over old sand	1	31.6	5.3	0.05	3.21
3 Pink Slip, Ahipara, North Auckland	35°10'	Gumland	1	73.7	10.5	0.11	2.97
4 Lake Waipareheka, Ngawha, North Auckland	35°24'	On lake margin	1	42.8	28.6	0.29	3.23
5 Dargaville to Kaikohe road, North Auckland	35°40'	Bush margin near road	1	39.1	60.9	0.52	3.14
6 Mt Hobson, Great Barrier I., North Auckland	36°11'	Gumland association with <i>Kunzea sinclairii</i> , 400 m a.s.l.	1	25.0	8.3	0.08	—
7 Sunnybrook Scenic Reserve, Wellsford, North Auckland	36°20'	—	1	66.7	29.2	0.29	3.51
8 Okahukara Peninsula, Kaipara Harbour, North Auckland	36°21'	On roadside with kanuka	1	27.3	59.1	0.64	2.92
9 Cape Colville, Coromandel Peninsula, South Auckland	36°28'	Roadside with kanuka	1	17.4	50.0	0.63	3.02
10 Albany Scenic Reserve, North Auckland	36°43'	—	1	40.9	31.8	0.32	3.09
11 Karakatuwhero Beach, East Cape, Gisborne	37°36'	Isolated stand on sand flats near beach	1	16.7	29.2	0.41	4.60
12 Mt Maunganui, South Auckland	37°38'	Coastal scrub on summit	1	31.8	36.4	0.36	3.49
13 Waikawa Point, East Cape, Gisborne	37°41'	Windswept hillside exposed to salt spray	1	45.4	61.9	0.76	2.96
14 Mamaku Plateau, South Auckland	38°06'	Roadside stand	1	66.6	9.5	0.21	2.82
15 Kuirau Park, Rotorua, South Auckland	38°08'	Poor soil over pumice on edge of a geothermal pool with <i>K. ericoides</i>	1	25.0	60.0	0.80	3.11
16 Travel Lodge Motel, Rotorua, South Auckland	38°09'	Thermal area on sandy pumice soil with <i>K. ericoides</i> and <i>Cyathodes fasciculata</i>	1	78.2	30.4	0.43	2.47
17 Waipa Valley, Rotorua, South Auckland	38°12'	Wet, flat basin	1	91.7	25.0	0.33	2.62
18 Mt Tarawera, South Auckland	38°14'	—	1	100.0	45.8	0.58	2.58
19 Mt Tarawera, South Auckland	38°14'	Isolated plant on top of mountain	1	57.1	33.3	0.48	2.71
20 Rainbow Mountain, Rotorua, South Auckland	38°19'	Geothermal area growing with <i>K. ericoides</i> var. <i>microflorum</i>	1	63.6	63.6	0.77	2.41
21 Papatu Scenic Reserve, Matawai, Gisborne	38°21'	Roadbank	2	—	22.7	0.27	3.63
22 Matawai to Traffords Hill road, Gisborne	38°23'	Young plants on roadside	1	37.5	75.0	1.04	3.00

Table 1 *Continued*

Population number, location, land district	Latitude °S	Site information	So.	Fl.%	Sp.%	P.m.	L/R
23 Puatai Road, East Cape, Gisborne	38°31'	Roadside stand	1	39.1	43.5	0.56	4.49
24 Waitahanui, east of Lake Taupo, South Auckland	38°48'	On pumice in scrub with broom and <i>Dracophyllum</i>	2	–	21.7	0.30	2.33
25 National Park on road from Tokaanu, Wellington	39°20'	On bush margin at roadside	2	–	43.5	0.56	3.40
26 Desert Road summit, Wellington	39°20'	Small shrubs near roadside	2	–	81.9	1.45	2.67
27 Moawhango, Wellington	39°35'	Trees to 5 m tall on steep bank above river terrace	2	–	70.0	1.60	2.96
28 Rangitikei River, Utiku, Wellington	39°45'	Trees to 5 m tall and smaller shrubs on slopes above sandstone bluffs	2	–	100.0	2.63	3.06
29 Waituna West, Wellington	40°03'	Shrubs 2–4 m tall, regenerating at roadsides	2	–	78.3	1.09	3.23
30 Ballantrae, South Ruahine Range, Wellington	40°17'	Regenerating scrub in pasture	1	4.2	66.7	1.17	3.21
31 Manawatu Gorge, Wellington	40°19'	Small regenerating shrubs on road bank	2	–	67.0	1.29	3.45
32 Otaki Gorge Road, Wellington	40°50'	Occasional shrubs on hillsides	2	–	94.7	2.16	2.79
33 Akatarawa, Wellington	41°05'	Along stream margins	1	12.5	85.7	1.52	2.84
34 Rimutaka Road summit, Wellington	41°07'	W-facing aspect, shrubs tending prostrate	1	87.5	45.8	0.83	2.84
35 Karaka Point, Picton, Marlborough	41°15'	Dense stand on exposed peninsula	1	52.1	69.6	1.00	2.83
36 Pelorus Bridge, Marlborough	41°18'	On swampy terrace	2	–	95.2	2.05	3.98
37 Muritai Scenic Reserve, Clifford Bay, Marlborough	41°41'	Shrubs to 3 m tall on sandy loess soil slope	1	0.0	88.2	1.71	2.36
38 Martins Quarry, Westport, Nelson	41°45'	Mixed gorse and manuka	1	87.5	65.2	0.96	2.64
39 Waima River, Marlborough	41°53'	Regenerating shrubs, 1 m tall, on floodplain near river outlet at coast	1	12.5	95.8	2.08	2.31
40 Charleston, Nelson	41°54'	Regenerating scrub at edge of old mining dam	1	56.5	65.2	1.13	2.71
41 Okiwi Bay, Marlborough	42°13'	Mixed manuka-kanuka at margins of hillside bush	1	4.8	100.0	2.80	2.16
42 Parapara Stream, Puhipuhi River, Kaikoura, Marlborough	42°15'	Regenerating stand after fire, NW side of ridge along stream, c. 400 m	1	0.0	95.7	2.00	2.36
43 Grahams Terraces, Nelson Creek, Westland	42°24'	On pakihi	1	34.8	100.0	2.17	2.26
44 Whalesback, Canterbury	42°28'	Shrubs to 4 m tall in grassland, mainly in gullies	1	50.0	91.7	1.58	2.07

Table 1 *Continued*

Population number, location, land district	Latitude °S	Site information	So.	Fl.%	Sp.%	P.m.	L/R
45 Jacks Pass, Hanmer, Canterbury	42°29'	Mixed regenerating manuka and kanuka on grassy hillsides, shrubs 1–2 m tall	1	69.6	95.8	1.74	2.18
46 Lottery River, Canterbury	42°37'	Mixed manuka and kanuka on slopes above river, shrubs 1–2 m tall	1	58.3	95.9	1.58	2.31
47 Stinking Stream, Hanmer, Canterbury	42°41'	Common scrub plant on flats and terraces	1	91.7	79.2	1.38	2.34
48 Craigieburn Forest Park, Canterbury	43°06'	Regenerating shrubs 1–2 m tall, at edge of beech forest and on open grassy hill faces	1	66.6	100.0	2.88	2.27
49 Viewhill, Canterbury	43°18'	On hillside in scrub/beech forest mostly on perimeters of wet areas	1	91.7	91.7	1.25	2.58
50 Eyrewell Scenic Reserve, Canterbury	43°23'	Uncommon, mainly occurring as single plants in dense kanuka	1	95.5	72.7	1.00	2.65
51 Birchview, Rockwood Range, Canterbury	43°30'	Common on well-drained flats and on hillsides	1	100.0	45.5	0.73	2.63
52 Peel Forest Park, Canterbury	43°55'	Shrubs 1 m tall, in scrub-tussock association	1	91.6	58.3	0.79	2.95
53 Peel Forest Park, Canterbury	43°55'	Bushy shrubs up to 2.5 m tall in upper levels of forest and in regenerating scrub and bush	1	41.7	25.0	0.25	2.63
54 Lake Ohau, Canterbury	44°14'	Dense manuka stand at edge of lake, tall slender trees to 5 m tall	1	41.7	35.0	0.50	2.76
55 Herbert Forest Waianakarua, Otago	45°16'	Mixed manuka and kanuka in reverted grassland	1	62.5	78.3	1.09	2.50
56 Waianakarua, Otago	45°16'	—	1	54.1	87.5	1.58	2.31
57 Lake Te Anau, Southland	45°20'	Manuka scrubland, growing over bracken on moraine	1	95.6	87.0	1.70	2.22
58 Lawrence to Waipori road, Otago	45°53'	Shrubs 0.5–2 m tall, on rolling hill schist country, 450 m	1	75.0	65.2	0.83	2.50
59 Blue Mountains, Otago	45°53'	Shrubs 1–2 m tall in mixed scrub-tussock on flat ridge crest at 600 m at upper limit of manuka	1	79.1	62.5	1.04	2.78
60 Dicks Hill, Otago Peninsula, Otago	45°53'	Shrubs 1–1.5 m tall, in manuka-dominant scrubland on grassy hillside with limestone outcrops	1	41.7	75.0	1.25	2.63
61 Bluff Hill, Southland	46°36'	Coastal scrub	1	95.4	72.7	1.45	2.38

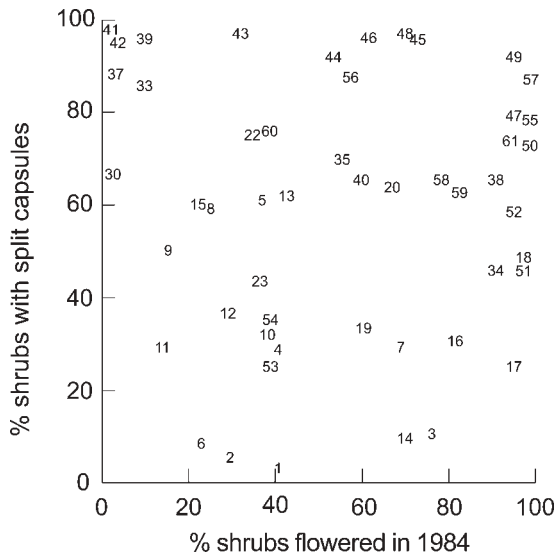


Fig. 1 Relationship between the percentage of shrubs in each of 51 *Leptospermum scoparium* populations sown on 12 Sep 1983 that flowered in the 1984 flowering season and the percentage of the shrubs with split capsules in 29 Jul 1986.

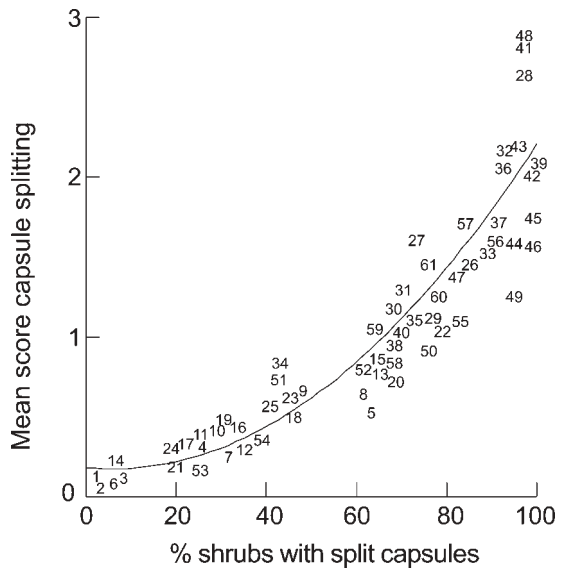


Fig. 2 Relationship between the percentage of shrubs with split capsules in each of 61 populations of *Leptospermum scoparium* and the population mean of the score of capsule splitting.

in a population with split capsules. The second was the mean of the score of the plants in each population, which provides further discrimination of the extent to which populations split capsules and shed seed early.

To examine if the age of capsules present on a shrub influenced the score for capsule splitting of populations of the first sowing, the percentage of shrubs that flowered for the first time in the season starting spring 1984 was determined. Most flowering commenced in October and November, but some plants flowered outside these months. Thus, shrubs indicated as first flowering in 1984 included any that flowered before 30 June 1985.

Statistical analyses

Relationships between the population means for capsule splitting, earliness of flowering, seedling leaf shape, and the latitude of origin of the populations were examined by correlation, regression, and graphical analysis using procedures provided by the SYSTAT 7.0 statistical package.

RESULTS

The indices for earliness of flowering of populations of the first sowing, percentage of shrubs in the populations with split capsules, the population means for the capsule splitting scores, and the lamina length-to-width ratio are presented in Table 1.

For populations of the first sowing, variation of both the percentage of split capsules ($r = 0.050$ for 49 d.f., n.s.) and the mean capsule splitting score (Fig. 1, $r = -0.128$ for 49 d.f., n.s.) was independent of the earliness of flowering percentage. This indicates that the capsule splitting observations from the two sowings can be directly related. It also indicates that the populations have a wide range of combinations of the rate of seed production on shrubs and the rate seed is dispersed from shrubs (Fig. 1). Of specific interest are the four coastal Marlborough populations (37, 39, 41, 42) and the Akatarawa population (33) that share the combination of being slow in coming to flower but being quick to shed seed.

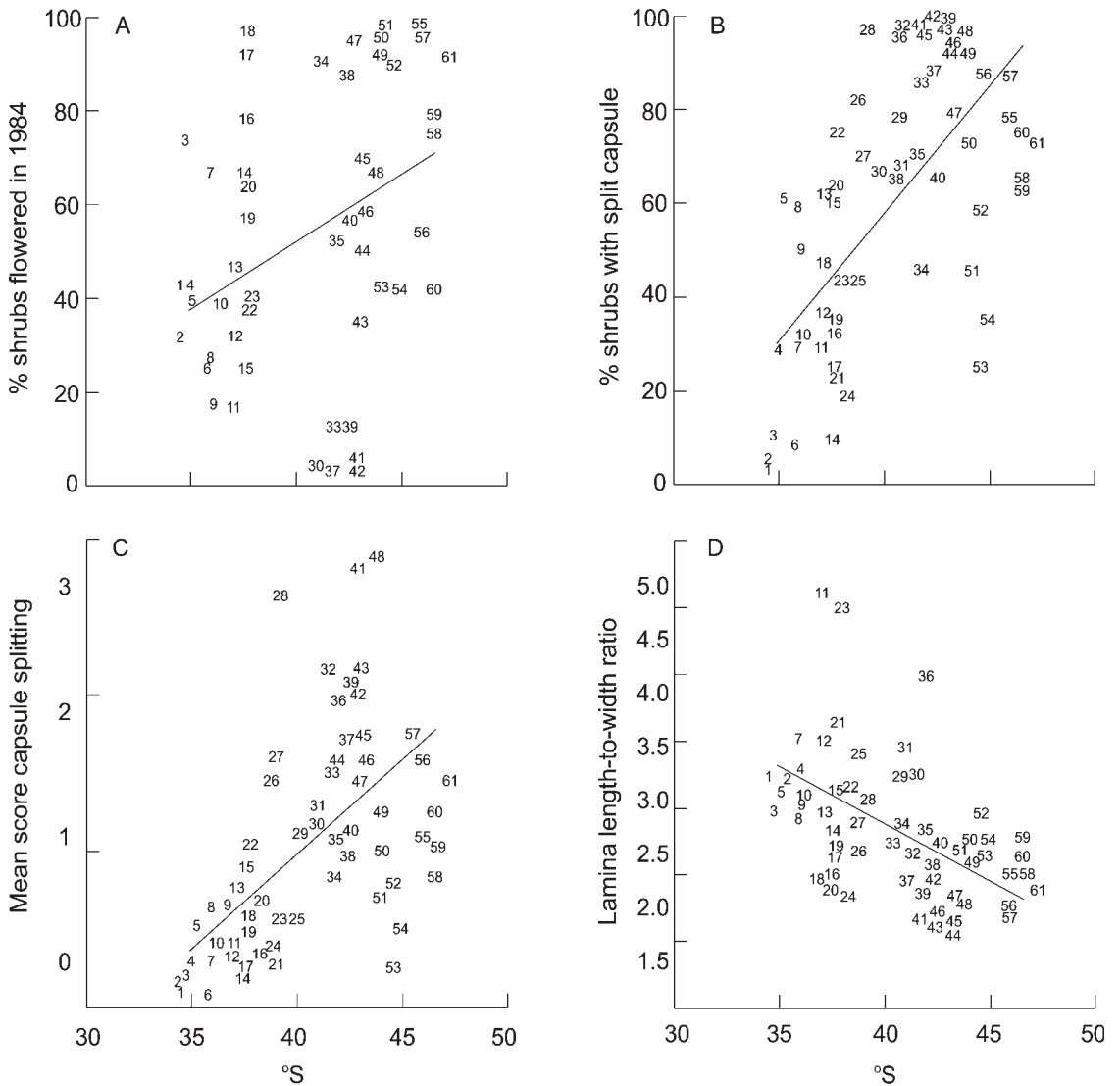


Fig. 3 Relationships between flowering, capsule splitting and lamina shape characteristics of 61 populations of *Leptospermum scoparium* and their latitude of origin in New Zealand. **A**, % of shrubs that flowered in the 1984 flowering season; **B**, % of shrubs with split capsules in 1986; **C**, mean of the score of capsule splitting in 1986; **D**, leaf lamina length-to-width ratio of seedlings.

As shown by the curvilinear relationship ($P < 0.001$, Fig. 2), populations that had a high percentage of plants with split capsules also scored higher for the degree of splitting of the capsules on plants within those populations. This was especially the case for three populations, 28 (Rangitikei River), 41 (Okiwi Bay), and 48 (Craigieburn), from widely separated locations. The three northernmost populations (1, 2, 3) together with populations 6

(Mt Hobson) and 14 (Mamaku Plateau) had the strongest expression of retaining seed in unsplit capsules.

There was a trend for first flowering to be earlier with increasing latitude ($P < 0.01$, Fig. 3A). Although populations from similar latitudes vary widely in this flowering phenology character, there were no significant outliers from the regression. Note that the exclusion of the 10 populations from the

second sowing leaves a gap of populations in the area of latitudes 38° to 40°, which could be misinterpreted as groupings of northern and southern populations. However, as noted for Fig. 1, populations 33, 37, 39, 41, 42, and also population 30 (Ballantrae), show up as a geographical group that are slow to flower.

Southern populations have a stronger tendency to split capsules than northern populations ($P < 0.001$, Fig. 3B). None of the populations lies significantly outside this trend. The relationship emphasises the geographical proximity of the five populations (1, 2, 3, 6, 14) that show the strongest retention of seed in unsplit capsules. The mean score for capsule splitting shows a similar relationship to latitude ($P < 0.001$, Fig. 3C) to that for the percentage split capsules (Fig. 3B). Although no populations are significantly outside the regression, populations 28, 41, and 48 emerge as a group for which their constituent shrubs show especially strong expression of capsule splitting.

Seedling lamina were significantly broader the further south the origin of the population ($P < 0.001$, Fig. 3D). Three populations, 11 (Karakatuwhero), 23 (Puatai Road), and 36 (Pelorus Bridge), were outside this trend as they had lamina distinctly narrower than all the other populations, and their removal from the regression markedly strengthened its significance. Regressions between the capsule splitting indices and lamina shape were both significant ($P < 0.001$) indicating that capsule splitting was greater for populations with broader lamina. However, inclusion of latitude and lamina shape together as independent factors in multiple regressions to predict capsule splitting reduced the lamina shape effect to non-significance.

DISCUSSION

Genotypic variation of capsule splitting

It is emphasised that the genotypic variation of capsule splitting shown by populations of *L. scoparium* within the species' range in New Zealand was observed by chance. Had a study been specifically designed to investigate the adaptive significance of capsule splitting, sampling would have been directed to cover other ecological variables in addition to the latitudinal gradient that has a dominating influence on the results. Further, observations on capsule splitting would have been more intensive and continued over a time sequence, and would have included observations on capsule splitting in the wild populations from which seed was obtained.

As seed collection was largely voluntary there was no control over the number of shrubs that were sampled for seed at a given wild site. Andrew Purdie and I sampled from several shrubs for the sites where we collected seed, but for one site (population 19, Mt Tarawera) it is recorded that there was one isolated plant. Thus, the number of parent shrubs sampled at a site may have influenced the mean characteristics of the progeny raised for that population. Countering this possible effect is the observation that *L. scoparium* readily outcrosses to several other *Leptospermum* species, but plants can also self (Harris 1995, 2000).

Even if the number of shrubs sampled per site has influenced progeny means, this possibility does not invalidate the highly significant trends of variation associated with the long latitudinal range of New Zealand. Further, it does not invalidate comparisons between broad groupings of populations with reference to the disturbance characteristics of their sites. However, caution would need to be exercised in comparing differences between closely located populations, especially if more localised influences on variation of capsule splitting were invoked.

Serotiny and fire ecology

The variation in capsule splitting in *L. scoparium* can be compared with variation in the percentage of *Pinus contorta* (lodgepole pine) trees bearing serotinous cones, i.e., those held closed by a resin that is sensitive to and opens in response to high temperatures generated by fire, in different populations of the species' range in the Rocky Mountains, North America. Populations growing in areas prone to a high frequency of fire have a higher percentage of serotinous cones than populations from areas where fire is less frequent (Lotan 1975). However, most stands have trees with serotinous and open cones, which is interpreted as allowing the species to regenerate after both low- and high-intensity fires.

From the commonly held opinion that *L. scoparium* is a fire-adapted species (Burrell 1965; Basher et al. 1990; Ogden et al. 1998) it could be concluded that the variation of capsule splitting shown by the *L. scoparium* populations indicates adaptation to the frequency of fire at their wild sites. However, particularly because it is generally regarded that the native vegetation of New Zealand lacks fire adaptation (Ogden et al. 1998), it is appropriate to consider other vegetation disturbance factors that could drive selection for the capsule-splitting variation.

Environmental and inherent induction of capsule splitting

Environmental factors that induce the splitting of capsules need to be distinguished from inherent characters that determine whether shrubs open their capsules to shed seed irrespective of environmental stimuli. Clearly fire induces capsules to split and shed seed, and at the same time provides open ground on which seed can germinate and establish in the absence of intense competition from other plants. Burrell (1965) found that seed from capsules opening within an hour of the passage of a fire germinated as well as seed from unharmed shrubs. However, seed removed from capsules and subjected to 100°C air temperature for 5 minutes decayed.

Burrell (1965) also observed that other environmental shocks, such as transplanting, drought, or unusual cold, caused capsules to split and shed seed. Root disturbance caused by other influences, such as soil slipping or wind dislodgment of shrubs, would have a similar effect to transplanting. Although Baylis (1959) reported that the unignified capsules on shrubs of *L. scoparium* without foliage damage were induced to shed their seed prematurely by an episode of cold that damaged *Nothofagus menziesii* (silver beech) on Maungatua near Dunedin, it seems more likely he observed inherent capsule splitting in the local population of *L. scoparium*. The uniform garden conditions at Lincoln were less stressful than those that prevail in many of the wild sites of the populations. The possibility of cold-stress-induced capsule splitting at Lincoln is further contradicted by the observation that capsule splitting was more prevalent in populations from southern (Fig. 3B,C) and also montane habitats, most notably population 48 (Craigieburn). Observations of *L. scoparium* shrubs in the Craigieburn region show that most of their capsules are split by May, within 6 months of their formation.

Inherent seed release for habitats with frequent low-level vegetation disturbance

Regular, steady release of seed can be envisaged as adaptation to habitats where there is frequent, low level, patchy disturbance to vegetation, providing niches suitable for seed germination and seedling establishment. There were four populations in which all shrubs had split capsules (Table 1) and three of these had particularly strong expression of early seed release (Fig. 3C). It is possible to suggest disturbance factors that could favour an ecological strategy of regular seed release. For population 28 (Rangitikei River) the situation, on slopes above sandstone

bluffs, indicates regular erosion to provide bare substrate suitable for colonisation by *L. scoparium*. Similarly, at the site of population 48 (Craigieburn), slope-related erosion and frost riving continuously provide patches of bare substrate. Population 41 (Okiwi Bay) from wind-shorn vegetation had a proportion of distinctive low stature shrubs in the population raised from seed (Harris 1994). Damage to vegetation by wind and salt spray may regularly provide gaps for seedling establishment at this site.

Population 43 (Grahams Terraces) is from an area of pakihi. Pakihi are characterised by severely leached soil with perched water tables, are usually dominated by *L. scoparium*, and most have derived from burning of areas of forest and tree-heath since human occupation. However, Wardle (1991) considered that areas of “natural pakihi” exist as climax vegetation on soils too intractable to support closed scrub or forest. In this situation *L. scoparium* would not be subjected to exclusion by light competition as succession progresses, and steady release of seed would be sufficient to sustain its plant population in pakihi. Pakihi habitat is also of interest in consideration of the antiquity of *L. scoparium* in the flora of New Zealand.

At the other extreme are the five populations for which more than 90% of the shrubs had no split capsules. All these were northern; the site information for three (populations 1, Motutangi Swamp; 3, Pink Slip, Ahipara; 6, Mt Hobson) and probably another (population 2, Karikari Peninsula) indicates gumland habitat, and the fifth (population 14, Mamaku Plateau) is from a volcanically derived landscape. Wardle (1991) defined gumlands as wet heathlands occupying former kauri (*Agathis australis*) lands and indicated that pakihi is similar except that the herbaceous phase is longer before dominance of *L. scoparium*. Fire destruction of kauri forest induced most of the once extensive areas of gumland in North Auckland. However, Wardle (1991) indicated that some smaller areas of gumland may have been “natural” being derived by similar processes to those forming natural pakihi. The most extensive remaining area of gumland not converted to pasture is on the Ahipara Plateau. Wardle (1991) emphasised that after the frequent fires on this area *L. scoparium* regenerates prolifically and grows 10–20 cm per year in stands dense enough to exclude further establishment of seedlings. Therefore, shrubs that retained seed in their capsule would have a strong selective advantage through the opportunity of massive establishment of their progeny with the next episode of fire.

Even for *L. scoparium* populations that have strong retention of seed in capsules, continual seed fall will occur especially as plants age and vascular connections to the capsules break down causing them to dry and split. This happens when branchlets bearing capsules die from a variety of causes including shading, breakage by wind or animals, manuka blight, and drought. Probably these causes determined the seasonal pattern of seedfall observed by Mohan et al. (1984a) in a 30–35-year-old *L. scoparium* stand in the Waitakere Ranges near Auckland. From the latitudinal variation of capsule splitting (Fig. 3C) it is likely that this stand had a high proportion of genotypes with seed-retaining capsules. Although they did not directly measure the quantity of seed retained in the seed capsules, Mohan et al. (1984b) inferred from their germination studies that the major “seed bank” of this stand was in the unshed capsules. Populations that inherently split capsules and shed seed within a year of their formation are likely to have a marked peak of seed fall in autumn.

Natural fires as a selection pressure

It is necessary to consider if the frequency of natural fires could have driven the selection to the predominance of non-splitting capsules in northern *L. scoparium* populations before the arrival of humans in New Zealand. In reference to this question there is the contrast between the freely capsule-splitting population 43 (Grahams Terraces) on pakihi (and also possibly population 36, Pelorus Bridge), and the gumland populations' retention of seed in unsplit capsule, even though these sites have habitat characteristics in common. Ogden et al. (1998) provided a map showing the probability of natural fires in New Zealand. This shows that the five northern seed-retaining populations (1, 2, 3, 6, and 14) are from areas of higher fire risk than the pakihi populations (43, 36). Further, three northern populations (5 (Dargaville), 8 (Okahukara), 9 (Cape Colville)) with intermediate capsule splitting characteristics (Fig. 3B) are from lower-fire-risk areas of North Auckland and the Coromandel Peninsula.

However, populations from the south-eastern North Island and eastern South Island, which have the highest risk of natural fire, have a higher frequency of capsule splitting than the five seed-retaining northern populations. Radiocarbon dates from the eastern South Island (Ogden et al. 1998) indicate that the fire interval was about 200 years in the period 10 000 to 3000 BP, decreased to about 50 years in the period 3000 to 1000 BP, and fell to 7–14 years

in the last millennium coincident with the presence of people in New Zealand. For forest regions of the North Island Ogden et al. (1998) estimated that the fire interval in any one locality before the arrival of people could have been as long as one or two millennia. Fires ignited by volcanism in the central North Island were estimated to occur at intervals of 300–600 years. It is suggested that selection for seed retention in capsules as an adaptation to fire would have little momentum in the fire intervals prevailing before human settlement. Slow, steady release of seed would be favoured in habitats where levels of disturbance by factors other than fire provided patches of ground on which *L. scoparium* establish. The species would have been excluded by forests that covered most of New Zealand, but could have persisted in refugia such as natural pakihi and gumland.

Human-lit fires as a selection pressure

It is suggested that the geographical pattern of seed capsule splitting shown (Fig. 3 B,C) has been significantly determined by selection pressures induced by human-lit fires. Burrell (1965) considered that *L. scoparium* plants were probably several years old before they flowered. That may be true in many wild situations where plant growth conditions are limiting, but in the garden situation at Lincoln most shrubs flowered and set viable seed the year after they were sown. Consequently, even if the period of occupation of New Zealand by a sizeable population of Maori is only 1000 years, there could have been hundreds of cycles of natural selection on populations of *L. scoparium* initiated by burning to regenerate areas of bracken (*Pteridium esculentum*) for production of aruhe (fern root), the staple food supply of Maori. Bracken was burnt every 3–5 years, otherwise the areas on which it grew returned to scrubland and, eventually, forest (Best 1942). Also, clearing of land by Maori for cultivation, of which the main crop was kumara (*Ipomoea batatas*), relied principally on fire. Abandonment of areas used for the production of aruhe and kumara would have allowed establishment of *L. scoparium*. Further, fire would have spread beyond the areas manipulated for food production to provide more area for *L. scoparium* establishment. Maori activities of these kinds were most intensive in the north of New Zealand (Best 1925) and it is suggested that this is a key influence on the north-to-south variation of capsule splitting. The extensive use of fire to clear forest and scrub for pasture that came with European settlement of New Zealand (Levy 1951) would have continued

selection for the fire-adaptive character of serotinous capsules.

In the north, rapid closure of stands in a successional direction to forest excluding establishment of later cohorts of seedlings, combined with short fire intervals, would favour strong selection towards seed retention. In dry south-eastern regions, even with increased fire frequency, slower closure of stands and low-level disturbance steadily providing bare ground would continue to favour selection of capsule-splitting genotypes.

Fleming (1975) considered *Leptospermum* as being present in New Zealand since the Palaeocene whereas Thompson (1989) considered *L. scoparium* a relatively recent arrival by long-distance dispersal, where its establishment was limited to edaphically suited areas. Fires lit by Maori brought into existence larger areas of low-nutrient-status conditions similar to those to which the species was pre-adapted in Australia. Just how recently *L. scoparium* dispersed to New Zealand could be indicated by comparison with Australian populations of the species. Such comparison could also address whether the unsplit capsule character was a later introduction to New Zealand or was present in populations of the species before the arrival of Maori. Populations of *L. scoparium* from south-western Tasmania grown at Lincoln all had unsplit capsules, consistent with the long fire history of that region associated with Tasmanian Aborigines.

Relationships of capsule splitting with leaf morphology and essential oil chemotype

The data for variation in leaf lamina shape showing a gradient to broader lamina in southern populations (Fig. 3D) is consistent with the trend shown by Yin et al. (1984). This follows the same direction as capsule splitting, so that broad-leaved populations are more likely to have a higher proportion of capsule-splitting genotypes and vice versa. In general, the continuous nature of this variation does not support taxonomic definition of contrasting forms that could represent different episodes of long-distance dispersal from Australia. However, the three populations (11, Karakatuwhero; 23, Puatai Road; 36 Pelorus Bridge) with particularly narrow leaves for their latitude (Fig. 3D) may be distinctive enough to warrant taxonomic definition. This is supported by the information that population 11 has unusually high levels of triketone essential oil, especially leptospermone, and population 23 has higher than average contents of this oil for New Zealand populations of *L. scoparium* (Perry et al. 1997a).

More recent extensive surveys of *L. scoparium* chemotype variation undertaken by Crop & Food Research has indicated that high triketone chemotypes are restricted to two regions in New Zealand, the East Cape, and the western side of the Marlborough Sounds where population 36 (Pelorus Bridge) is located (M. Douglas pers. comm. 2001). Even if these three populations represent a taxon distinct from *L. scoparium*, their range of capsule splitting, from 29.2 to 95.2%, falls into the range of variation of the other populations.

Another aspect of essential oil variation of both *L. scoparium* and *K. ericoides* (Perry et al. 1997b) is of particular interest when considering the fire ecology of these species. Populations of *L. scoparium* from North Auckland characteristically have chemotypes with high contents of monoterpene pinenes, a characteristic shared with Australian populations of the species (Perry et al. 1997a; M. Douglas pers. comm. 2001). All New Zealand and Australian populations of *K. ericoides* assayed had high contents of α -pinene (Perry et al. 1997b). Since monoterpenes are volatile and highly flammable their high content in vegetation could foster quicker passage of fire, thereby reducing slow burning which would be more destructive of seed released from capsules. Judd (1993, 1994) demonstrated that small myrtaceous capsules provided mediocre insulation for seed from the heat of fire and were likely to be effective only where flame residence times were in the order of seconds rather than minutes. The coincidence of high monoterpene and non-splitting capsule genotypes in northern North Island *L. scoparium* populations reinforces the indication that these populations are more fire adapted than southern populations.

Rate of attainment of reproductive maturity

Harris (1996) suggested that variation in the flowering patterns of *K. ericoides* populations provides adaptation to different seral situations, with shrubs that were quick to flower and produce seed adapted to frequently disturbed habitats and those slow to flower adapted to persist longer in successions towards forest. The present study shows that *L. scoparium* reaches the maturity required to flower more quickly than *K. ericoides* and this is consistent with *L. scoparium* being a shorter-lived species, occupying shorter seres in successions to forest (Burrell 1965; Wardle 1991). The weak trend for northern populations to take longer to reach the maturity for flowering (Fig. 3A) may be because they require a greater heat sum for this and were

therefore disadvantaged compared with southern populations when grown at Lincoln, where temperatures are lower than their wild sites. The absence of correlation between the rate of reaching flowering and release of seed (Fig. 1) suggests that different combinations of these phenological characters would be favoured by the wide variety of ecological situations in which *L. scoparium* occurs. For example, the characteristic phenology of the coastal Marlborough populations (37, 39, 41, 42) could be adaptation to habitats where competition does not threaten rapid exclusion in a succession, and at the same time regularly provides disturbed patches for establishment of new shrubs.

CONCLUSIONS

While *L. scoparium* has often been given as an example of one of the few species in the New Zealand flora that has fire adaptation characteristics, this study suggests that in the period before human settlement factors other than fire dominated the direction of its natural selection. It is suggested that the species has undergone rapid natural selection towards more fire-adapted genotypes in previously forest-dominated areas of New Zealand since Maori arrived. The serendipitous finding of inherent variation of capsule splitting in *L. scoparium* points the way to further experimental investigations of the adaptive characteristics of the species. These investigations could include the flammability characteristics of different essential oil chemotypes, the heat responses of different capsule types and the seed they contain, and determination of the genetic differences between New Zealand and Australian populations of *L. scoparium*.

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