Genetic diversity in tussock hawkweed (*Hieracium lepidulum*) and use of allele frequencies for identifying patterns of spread

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ABSTRACT

Collections of *Hieracium lepidulum* (tussock hawkweed), an adventive weed that threatens alpine and other habitats, were made from three sites in the Central Otago region and two from the Canterbury region, South Island, New Zealand. Each population was found to differ genetically from all the other populations, and there was a positive correlation between genetic distance and geographic distance among populations. This indicates that there is a low level of gene flow among populations, signifying that, although reproducing predominantly by asexual seed (so that seedlings are an exact genetic copy of the mother), there is some sexual reproduction and mutation. Because no new alleles were found in any of the populations, and because different alleles were fixed in each population, the pattern of spread has probably been by gene flow from one or a few founder populations, and subsequent sexual reproduction and genetic drift within the new 'founder' populations. As each population is genetically distinct, gene flow has been mainly by seed, rather than pollen. In Otago, the pattern was one of 'isolation by distance'; the original populations were probably from the lower slopes of the Pisa Range and spread by seed transported by wind or other means. In Canterbury, a large genetic distance separated the two sites analysed, which suggested they had arisen from different source populations. Grazing to prevent seed-set appears effective in preventing the spread of tussock hawkweed, but it is likely that biocontrol with a host-specific agent, such as a rust fungus, is less likely to be effective than is possible with a truly clonal population.

Keywords: *Hieracium lepidulum*, tussock hawkweed, adventive weed, Otago, Canterbury, gene flow, asexual seed, wind dispersal, weed control.

1. Introduction

Tussock hawkweed, *Hieracium lepidulum* (Stenstroem) Omang (Asteraceae), is a triploid, diplosporous apomict (Gadella 1972). This means that theoretically, all its seed is clonal, an exact genetic copy of the mother plant.

Since the 1990s *H. lepidulum* has been recognised as an invasive weed in New Zealand, and is unprecedented in the diversity of habitats it colonises, including waste ground, *Nothofagus* forest, pine forest, and subalpine and alpine grassland (Connor 1992; Duncan et al. 1997; Wiser et al. 1998). It is the first adventive weed to seriously threaten New Zealand alpine habitats, currently forming dense meadows at altitudes of 775 m and thriving at altitudes up to 1700 m (pers. obs.).

New Zealand populations of *H. lepidulum* have presumably spread from relatively few founder populations; seed probably arrived as contamination of imported European grass seed during the late 1800s. Its subsequent invasion of diverse habitats is therefore surprising, given that the main mechanism for the creation of genotypic variation in obligate apomicts is generally considered to be mutation.

There were two main aims to this study: First, we wanted to establish levels of genetic and genotypic diversity within and between New Zealand populations of *H. lepidulum,* providing information to underpin any strategy behind future biocontrol programmes (Burdon & Marshall 1981). Our second aim was to understand patterns of hawkweed spread by determining whether any such diversity was due to genotype sorting of original founder populations, sexual reproduction, mutation or a combination of two or more of the above. We used Inter Simple Sequence Repeat (ISSR) technology, flow cytometry, and character compatibility analysis to answer these questions. We chose to use ISSRs because they have already been shown to generate sufficient markers to easily identify genotypic diversity (Zietkiewicz et al. 1994; Chapman et al. 2000). The incorporation of strategies to minimise the effects of dominance (for a review see Sales et al. 2001) allow the estimation of F_{ST} values from dominant markers that are concordant with co-dominant allozyme markers (Aagaard et al. 1998; Jenczewski 1999). The cladistic approach of character compatibility analysis is the most appropriate analysis presently available to distinguish between recombination and mutation in clonal polyploids (Mes 1998).

2. Methods

2.1 FIELD OBSERVATIONS AND SAMPLING

Records of hawkweed density were made from each of 15 sites in the South Island. Sites included transects at 300–1700 m on the Pisa Range, 440–775 m in the Rob Roy Valley, Mt Aspiring National Park, and 500–1300 m at Broken River in the Craigieburn ski area. More site details are presented in Table 1.

Collections of *H. lepidulum* were made from five of these sites, three from the central Otago region and two from the Canterbury region (Fig. 1).

The sites were chosen to include well established, large populations and smaller, apparently founding populations. They included a range of altitudes and a range of habitats (alpine grassland to *Nothofagus* forest). The Pisa (1700 m) and Lochar Burn (390 m) sites could be considered metapopulations, lying at each end of a 3 km transect which followed a boundary fence from the top to the lower slopes of the Pisa Range

TABLE 1.   SITE DETAILS OF THE 15 *Hieracium lepidulum* POPULATIONS STUDIED.

SITE	ALT., m	AGE OF POPULATION AND DENSITY	HABITAT
Rob Roy	1530	Invading front; plants sparsely scattered.	Steep NW-facing slope. *Chinochloa, Celmisia, Hebe*. Mainly confined to rock crevasses.
	1102	Scattered but common.	*Helichrysum, Gaultheria, Chionochloa, Celmisia, Muhlenbeckia*.
	775	Dense, > 15 years.	Mountain beech forest edge, *H. lepidulum* 'meadow'.
	440	Dense, > 15 years.	Mountain beech forest.
Mt Aspiring Road	330	Common. Herbarium specimen 1950.	Roadside below cliffs, 200 m before Turn-off to Diamond Lake.
Treble Cone Ski Field	1556	Scattered.	Confined to roadside, above Hut TT20 on Main St. Oversown with ryegrass/clover, looks as if introduced with grass/clover mix.
	935	Locally common.	Confined to roadside, hairpin above Hopper. Oversown with ryegrass/clover.
Criffel Range	975	Dense where ungrazed, sparse over fence, grazed.	*Chionochloa* grassland,
Pisa Range	1700	Invading front; common in sheltered areas, sparsely scattered on windswept plateau.	Plateau of Pisa Range, sheltered from wind in the escarpment lip.
	1600	Sparse.	
	1535	Sparse, common.	
	1489	Dense.	Lochar Burn side of fence. Grazed *Chionochloa*, sorrel, *Celmisia*.
	757	Dense on Pisa side, sparse on Lochar Burn side, > 15 years.	Tussock/oversown grassland.
	595	Dense in the underscrub, dwindling to nil at 620 m.	Pasture with matagouri on, and brier rose above track edge.
Lochar Burn	390	At least 15 years old. Dense mat.	Oversown pasture/*H. lepidulum* grassland.
Broken River	500–1300	Recorded in the vicinity as 'rare' 1962.* Common. Herbarium specimens from 1946.	Confined to near the edge of *Nothofagus* forest, all along track to ski hut from road end.
Mt Fyffe	1250–1440	At least 20 years old.† Scattered clumps.	Roadside and sub-alpine grassland, just below summit.

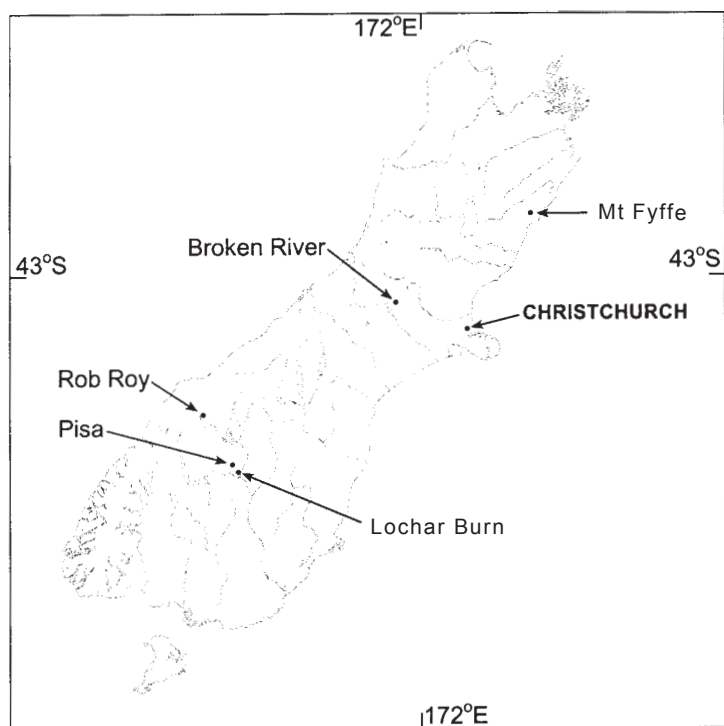* Connor (1992) † M. Morresy (pers. obs.)

Figure 1. Location of the *Hieracium lepidulum* populations used: Rob Roy, Pisa, and Lochar Burn (Otago); Broken River and Mt Fyffe (Canterbury).

At each site, ten individuals were dug up and transplanted to the glasshouse at Canterbury for flow cytometry, and leaves from each of 20 other individuals were collected and dried in silica gel for DNA analysis. Plants collected were always at least 2 m apart, to reduce the chances of sampling ramets from the same vegetative clone. Voucher specimens from each site are held in the University of Canterbury herbarium.

2.2   FLOW CYTOMETRY

Relative DNA content was determined for each live plant because a variation in DNA content of 3.7% or more (the contribution of a single chromosome to the genome) among individuals would demonstrate aneuploidy (Pfosser et al. 1995). Aneuploidy, or different ploidy levels within a population, is a good indicator of sexual reproduction. For flow cytometry, isolation of nuclei from leaf tissue followed the method of Galbraith et al. (1983) with some modifications. Punched disks of fresh leaf tissue (24 mm²) were placed with the reference in a plastic petri dish. A few drops of commercial nuclei isolation buffer, UV CyStain precise T solution A (100 mL deionised water, 2.1 g citric acid, 0.5 g Tween 20) (Partec GmbH, Münster, Germany) was added, and the tissue chopped finely with a stainless steel razor blade. After approximately 90 seconds the sample was filtered through a 30 mm filter, and 2.0 mL Partec Cystain Precise T solution B (100 mL deionised water, 7.9 g dibasic sodium phosphate, 0.5 ml DAPI stock (4.55 mg 4′,6′-diamidino-2-phenylindole, 10 mL

deionised water)) was added. Samples were then analysed for DNA content after at least 90 seconds of staining. For this, the Partec PA-II Particle Analysing System (PAS) was employed, using filter combinations of UG 1, TK420, TK590, and GG435 and a mercury arc lamp (HBO 100 W/2). Our standard was a *Hieracium lepidulum* from Rob Roy.

2.3 INTER SIMPLE SEQUENCE REPEATS

Fresh leaf tissue was used for total genomic DNA isolation; 0.10–0.15 g were crushed in a mortar containing crushed glass and 500 mL isolation buffer (200 mM Tris-HCl (pH 8.0), 250 mM NaCl, 25 mM EDTA, 0.5% sodium dodecyl sulphate (SDS) and 10 mM β-mercapthoethanol). The mixture was transferred to a 1.5 mL microfuge tube and incubated at 65^0C for 1 hour, then centrifuged at 12 000 rev/min for 5 minutes. The resulting supernatant was transferred to a clean microfuge tube and washed twice with chloroform:iso-amyl alcohol (24:1 v/v). At each wash, the mixture was centrifuged for 5 minutes at 10 000 rev/ min. The aqueous phase was transferred to a clean microfuge tube to which 300 μL cold isopropanol was added. The mixture was incubated at -20^0C for 20 minutes for DNA precipitation. The DNA was pelleted by centrifuging at 12 000 rev/min for 5 minutes, washed with 70% ethanol, spun at 10 000 rev/min for 3 minutes, air-dried for 3 minutes and re-suspended in 50 μL TE (Tris acetate; 10 mM Tris-HCl (pH 8.0), 1 mM EDTA). The ISSR primers were supplied from the University of British Columbia Biotechnology Laboratory as primer set 9. They were amplified by the modified PCR procedure of Williams et al. (1990). Ten ISSR primers were screened over 20 samples. PCR was performed in a 25 μL reaction mixture per sample (1 × Taq polymerase PCR buffer, 400 μM dNTPs, 6 mM magnesium chloride, 0.2 μM primer, 2.5 Units of Taq DNA polymerase (Roche), and 100 ng genomic DNA). The amplification was done in a PTC-200 Thermal Cycler (MJ Research). Initial denaturation was for 4 minutes at 94^0C, followed by 40 cycles of 9 seconds at 94^0C, 30 seconds at 48^0C, one minute at 72^0C, and a final extension of 4 minutes at 72^0C. The PCR products were separated electrophoretically on 2% agarose gels in 1 × TAE buffer and stained with ethidium bromide. The presence or absence of bands was scored under UV illumination. Six primers (Table 2) were selected that gave clear and consistent banding patterns for the analysis of the complete sample set.

From this, bands were scored on their reproducibility and consistency to determine the ISSR phenotype for each individual sampled. Only bands that were clear and reproducible were included in the analysis.

2.4 DATA ANALYSIS

The interpretation of allele (ISSR fragment) frequency data of dominant markers must be approached with caution, because statistical methods are based on assumptions of Hardy-Weinberg equilibrium (Lynch & Milligan 1994). Here we used the phenetic Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992), based on the analysis of pair-wise genetic distances (Excoffier et al.

TABLE 2. SUMMARY OF ISSR BANDS SCORED.

PRIMER	PRIMER SEQUENCE	NO. OF BANDS PER PRIMER	NO. OF POLY-MORPHIC BANDS
UBC900	5$'$-ACTTCCCCACAGGTTAACACA-3$'$	7	7
UBC895	5$'$-AGAGTTGGTAGCTCTTGATC-3$'$	7	5
UBC866	5$'$-(CTC)^6-3$'$	7	7
UBC845	5$'$-CTCTCTCTCTCTCTCTRG-3$'$	7	7
UBC822	5$'$-TCTCTCTCTCTCTCTCA-3$'$	7	7
UBC810	5$'$-GAGAGAGAGAGAGAGATG-3$'$	6	3

1992), to estimate variance components for the ISSR phenotypes. Variation was partitioned among individuals/within populations, among populations/within regions, and among regions. The resulting coefficients of subdivision, Φ_{ST}, Φ_{SC}, Φ_{CT} are analogous to Wright's (1965) F_{ST} statistics, but they differ in their assumptions of heterozygosity. Φ_{ST} was also calculated for among-site variance among each pair of Otago sites and the two Canterbury sites. Significance values were assigned to variance components on the basis of a set of null distributions generated by a permutation process which draws 1000 individual samples from the raw matrix and randomly assigns individuals to one of the six populations (Excoffier et al. 1992). AMOVA is now routinely used in the analysis of RAPD and ISSR data (Huff et al. 1998; Bartish et al. 1999; Kimball et al. 2001).

Multivariate cluster analysis and Principal Coordinate Analysis (PCO), using the program MVSP version 3.1 (Kovach Computing Services Pentraeth, UK 1998), were used to visualise the data. A UPMGA dendrogram, based on the Nei & Li (1979) similarity matrix was used to illustrate the relationships among all the 89 individuals from each of the five sites. The Nei & Li (1979) measure of genetic distance is an appropriate one for ISSR data, as only shared presence of bands is used to calculate similarity. Spatial representation of relative similarities among individuals was provided by the PCO.

A Mantel test was carried out to determine if there was a significant correlation between genetic distance (Nei & Li 1979) and geographic distance (km), using the program 'Tools for Population Genetic Analyses' (TFPGA) (Miller 1997). We did not seek to estimate values of gene flow, because Slatkin's (1985) estimate assumes that populations are at an equilibrium for migration and drift, and that there has been sufficient time for mutation to have generated new alleles in populations.

In order to determine if intra-population genotypic variation was due to mutation within a single clone or the result of recombination (Brookfield 1992) we used the cladistic approach of character compatibility analysis (Mes 1998). This technique is suitable for the analysis of dominant molecular data in polyploids because allelic interpretation is not necessary. Because a clone is characterised by the accumulation of mutations unique to this clone, and because these mutations can be arranged in a strictly hierarchial manner, compatibility analysis can be used to define inter-nested groups of individuals (Mes 1998). Recombination will lead to incompatibility of individuals, because

it allows for all four pairwise combinations of two unordered binary characters (Meacham 1994), i.e. ISSR fragments in this study. Such incompatible character state occurrences can be used as an indication of both recombination (the number of genotypes removed from a data set to produce compatibility) and mutation (the number of compatible genotypes), when summed over the whole data matrix (Mes 1998; van der Hulst et al. 2000). We used the program Phylogenetic Inference by Compatibility Analysis (PICA) version 4.0 (Wilkinson 2001) for our analysis.

3. Results and discussion

3.1 CONFIRMATION OF APOMIXIS

All of the ten individuals from each of the five populations spontaneously set seed in the glasshouse. All of the 15 emasculated capitula (three from each population) produced over 95% filled seed.

3.2 DNA CONTENT

All ten individuals from each of four sites Pisa, Lochar Burn, Rob Roy and Mt Fyffe had DNA contents that were between 1 and 1.2 times the amount of DNA of the standard Rob Roy plant, which indicated that they were all the same ploidy level, which is triploid in *H. lepidulum* (Tutin et al. 1976). Broken River was not sampled for genome size because the plants were destroyed before analysis because of insect infections.

3.3 GENETIC DIVERSITY

The six ISSR primers produced a total of 41 clear and reproducible bands, 36 (88%) of which were polymorphic (Table 2).

No private bands were recorded from any of the populations. The number of polymorphic bands varied between 24 at Mt Fyffe and 13 at Broken River (Table 3).

TABLE 3. SUMMARY OF BAND CHARACTERS FOR ALL FIVE SITES.

SITE	ROB ROY	PISA	LOCHAR BURN	BROKEN RIVER	MT FYFFE	ALL
Total no. of bands	39	40	39	39	41	41
No. fixed	18	21	20	26	17	5
No. variable	21	19	19	13	24	36
No. unique	0	0	0	0	0	0
% variable	57	47	49	33	59	88

Cluster analysis (Fig. 2) on all five populations revealed one main cluster with 75% similarity to a small cluster comprising only individuals from Mt Fyffe. Furthermore individuals within each population were clustered, so that except for a few exceptions (Fig. 2) each population had its own node.

Three Lochar Burn individuals fall within the predominantly Pisa cluster, and a Mt Fyffe individual is closely related to individuals from Broken River.

Most individuals differed in their ISSR phenotype, which we refer to as genotype in the rest of this paper. Every individual sampled from the invading front below the Rob Roy glacier was genotypically unique. Only two individuals shared the same genotype from the Pisa population and similarly only a single shared genotype was recorded from each of the Lochar Burn and Mt Fyffe populations. The plants from Broken River comprised sixteen unique genotypes and two shared ones (Fig. 2).

Patterns of genetic similarities among genotypes in all of the five populations were similar, with most genotypes being 90% or more similar, although at Rob Roy several genotytpes were 89–87% similar.

Ordination analysis complemented the cluster analysis by providing spatial representation of relative similarities among individuals (Fig. 3). The two-dimensional PCO plot clearly differentiates the Otago and Canterbury sites, and, with one exception, the Broken River and Mt Fyffe sites.

Individuals from the three Otago sites, clustering towards the left of the PCO plot, are less distinct, with individuals from the Pisa population scattered between the Lochar Burn and Rob Roy population clusters. Axis 1 explained 22.8% of the variation, and Axis 2, 12.6%.

The apparent patterns revealed by clustering and ordination analysis were analysed by AMOVA (Table 4), which showed that almost half of the total ISSR variation (46%) could be explained by variation within populations, 31% by variation among the populations within regions and 22.8% among regions (Otago v. Canterbury). Φ_{ST}, analogous to Wright's (1965) F_{ST} statistic = 0.54 ($p < 0.001$), which is indicative of high levels of genetic structuring and low levels of gene flow.

The results of the Mantel test to determine if there was a significant correlation between genetic distance (Nei 1972) and geographic distance (km) over the five sites was significant ($r = 0.97$).

All sites displayed considerable matrix incompatibility; total matrix incompatibility and its reduction upon successive deletion of genotypes for each site is presented in Fig. 4. Although this type of analysis does not allow a precise estimation of the frequency of recombination (Mes 1998), the fact that 9–14 genotypes in all populations except Mt Fyffe had to be removed in order to gain compatibility is indicative of substantial recombination. The relatively few genotypes deleted from Mt Fyffe probably reflect its small sample size (van der Hulst et al. 2000).
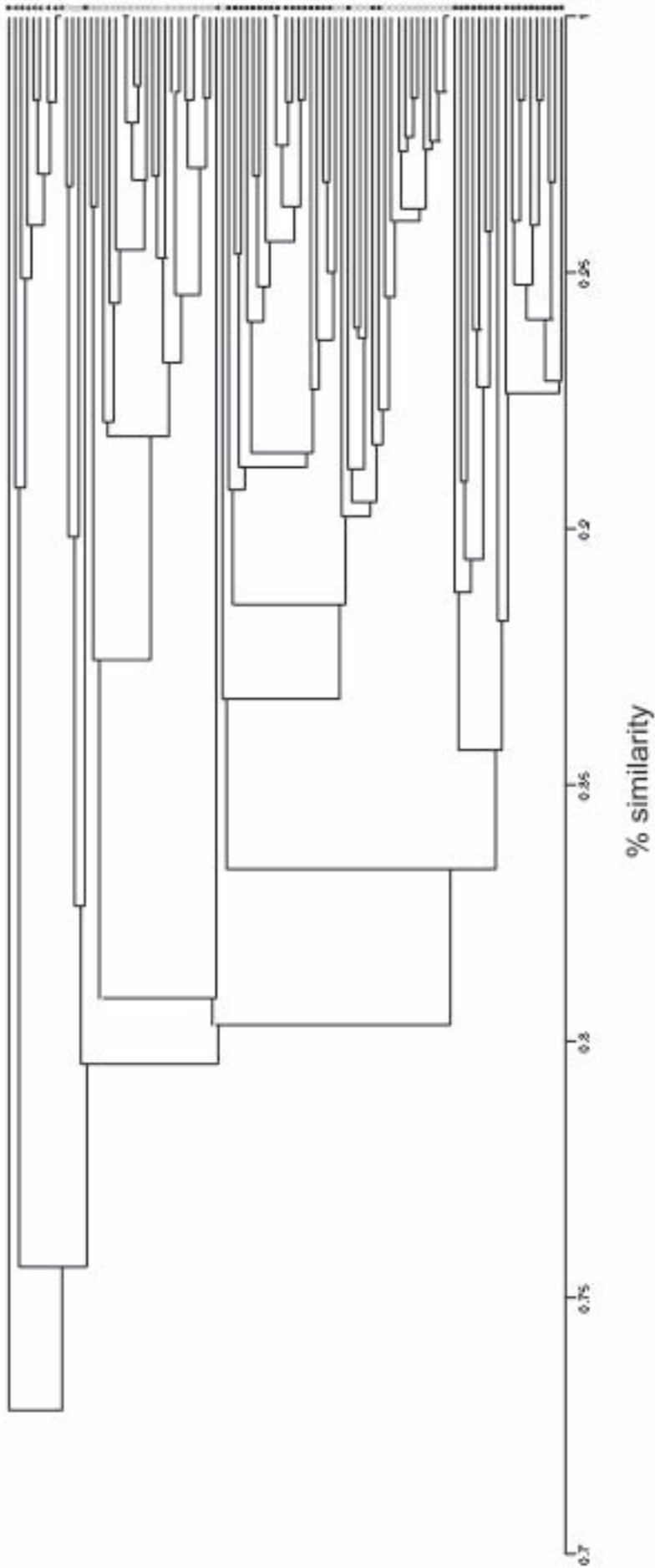
Figure 2. UPGMA dendrogram depicting patterns of genetic similarity by 41 ISSR fragments and 89 individuals of *Hieracium lepidulum* from the five populations included in this study.
■ Rob Roy, ▢ Pisa, ■ Lochar Burn, ◢ Mt Fyffe, ▢ Broken River.

% similarity

Figure 3. Principal coordinates plot of 41 ISSR fragments depicting patterns of relatedness and genetic variation among 89 individuals from 5 populations of *Hieracium lepidulum*: ■ Rob Roy, ▢ Pisa, ■ Lochar Burn, ▲ Mt Fyffe, ▢ Broken River.
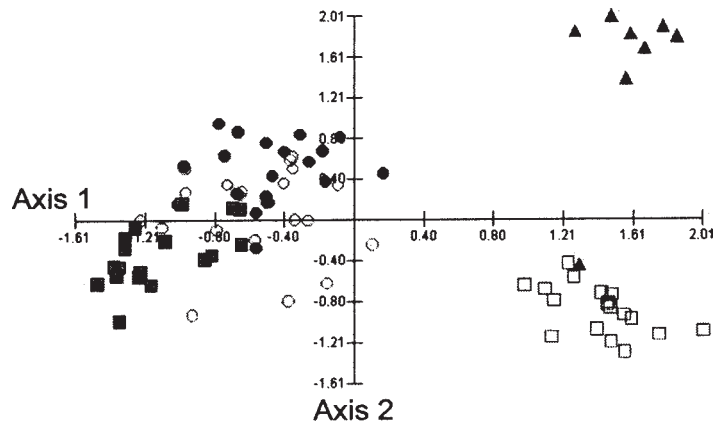

TABLE 4. NESTED ANALYSIS OF MOLECULAR VARIANCE (AMOVA) FOR 89 INDIVIDUALS OF *Hieracium lepidulum* USING 41 ISSR FRAGMENTS.

The total data set contains individuals from five sites and two regions: Rob Roy, Pisa, and Lochar Burn (Otago); Broken River and Mt Fyffe (Canterbury). Statistics include sums of the squared deviations (SSDs), mean squared deviations (MSDs), variance component estimates, the percentage of the total variance (% Total) contributed by each component, Φ statistics, and the probability, *p*, of obtaining a more extreme component estimate by chance alone (estimated from 1000 sampling realisations).

SOURCE OF VARIATION	DF	SSD	MSD	VARIANCE COMPONENT	% TOTAL	Φ STATS	P-VALUE
Among regions (Otago and Canterbury)	2	96.8	96.8	1.48	22.77	Φ_{CT} 0.23	< 0.001
Among sites/within regions	3	115.0	38.3	2.02	31.09	Φ_{SC} 0.40	< 0.001
Among individuals/within populations	84	252.3	3.0	3.00	46.14	Φ_{ST} 0.54	< 0.001
Among sites in Otago							
Pisa/Lochar Burn	39	131.1	24.7	1.10	28.12	Φ_{ST} 0.28	< 0.001
Pisa /Rob Roy	39	165.6	37.6	1.71	33.72	Φ_{ST} 0.34	< 0.001
Lochar Burn/Rob Roy	39	165.0	47.6	2.23	41.90	Φ_{ST} 0.42	< 0.001
Among sites in Canterbury							
Broken River/Mt Fyffe	28	118.2	45.8	3.42	56.42	Φ_{ST} 0.56	< 0.001

Figure 4. Reduction of matrix incompatibility upon successive deletion of ISSR genotypes in each of the five populations of *H. lepidulum* included in this study: ■ Rob Roy, ▢ Pisa, ■ Lochar Burn, ▲ Mt Fyffe, ▢ Broken River. The number of genotypes that needed to be deleted to eliminate incompatibility are given by the point of intersection of the *x* axis.
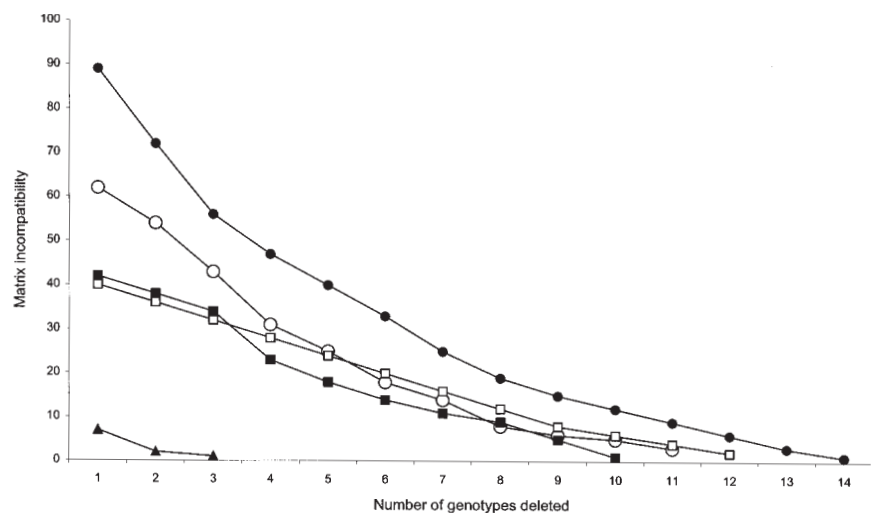
4. Conclusions

4.1 GENETIC DIVERSITY

All five populations of *H. lepidulum* included in this study had high levels of genetic and genotypic diversity. Most individuals in all the populations were unique.

Evidence from compatibility analysis demonstrated that this variation has arisen by a combination of both low levels of sexual reproduction and mutation. Clearly, although *H. lepidulum* is called an 'obligate' apomict, this is not strictly true. The significance of this is that the populations will be able to evolve resistance to host-specific control agents or herbicides.

Each population was different genetically from all the other populations, and there was a positive correlation between genetic distance and geographic distance among populations. This indicates that there is not very much gene flow between populations, although the possibility of gene flow increases the closer the populations are to each other.

New populations most probably become established from seed, transported by wind or other means, rather than from pollen. The significance of this is that, if a resistant gene evolves in one population, it is much less likely to spread to other populations than it would in an outcrossing species.

4.2 ALLELE FREQUENCIES

All New Zealand populations of tussock hawkweed are likely to carry reduced genetic variation, compared with native European populations. In this study the Lochar Burn population was the largest and most established New Zealand population, having been present for at least 15 years and now covering many hectares of oversown tussock grassland. The Pisa population, higher up the Pisa Range, is more recent, and has probably been founded from wind-borne seed from lower slopes. Its difference in allele frequencies from Lochar Burn can best be explained as a consequence of founder effect and drift. Alternatively, or in addition, selection may be acting to differentiate the populations because the Pisa site suffers a more extreme environment than the lower slopes of the Lochar Burn site.

The Rob Roy population is almost certainly a founder population, or 'invading front', a consequence of wind-borne seed from the *H. lepidulum* 'meadow' lower down the Rob Roy Valley. It is very sparse, with individuals mostly confined to sheltered microsites such as holes in the ground or rocky outcrops. It has a high variance in genotypic diversity (Fig. 2), another characteristic associated with founder populations.

The high Φ_{ST} value of 0.56 for the Broken River and Mt Fyffe populations may be explained by breeding system, a combination of different source populations, and founder effect. The Broken River population is an established, large

population, with individuals having been in the area since at least the early 1960s (Connor 1992). Tussock hawkweed has been present along the Mt Fyffe track for at least 20 years (M. Morresy pers. obs.), but has not noticeably spread, and is still confined to small patches along the track edge. Compatibility analysis has shown that mutation rather than combination could explain 70% of the genotypes found at Mt Fyffe, although this could be an underestimate because of the small population size.

Drift is the most likely explanation for allelic differentiation among populations. Further investigations using genetic fitness measures, competition and common garden experiments will be useful in identifying adaptation. Genotypic variation has arisen through both recombination and mutation, which suggests that apomictic taxa are as likely to be as long-lived in evolutionary terms as outcrossing ones, especially as polyploidy has the advantage of buffering inbreeding depression.

4.3   PATTERNS OF SPREAD IN OTAGO

A combination of genetic analysis and information from herbarium specimens suggest two possible patterns of spread. One is for a few seeds to colonise new areas from a nearby site, and subsequently spread by a combination of apomixis (asexual seed production) and some residual sexual seed production (inbreeding). Alternatively, each population has arisen independently from early founder populations (going back to the 1940s), and has again spread by apomixis and inbreeding.

The fact that each population was genetically distinct, but that there was a positive correlation between geographic and genetic distance supports the first course, but probably both patterns of spread have been important.

The fact that no 'new' alleles were found in any of the populations indicates a common European source to all populations.

Hawkweed populations are thriving and spreading in Otago, unlike the case in many Canterbury sites. More research is needed to explain this, but it is worth noting that there does not seem to have been a sudden 'burst' of variation in the sites which are spreading (Otago) compared with those that are not (Mt Fyffe in Canterbury).

4.4   AREAS VULNERABLE TO HAWKWEED SPREAD

Comparing herbarium records with current distribution patterns it appears that ungrazed tussock grassland at altitudes of 300–1700 m is particularly vulnerable to tussock hawkweed spread. Landcare Research records show that it is only recently that tussock hawkweed has become invasive in sub-alpine to alpine grassland in Canterbury (Newall & Syrette pers. comm.). Our observations show that plants will thrive up to 1700 m at least, if sheltered. The understorey of beech forest, and sub-alpine scrub is also vulnerable. For example, in scrub behind Mt Percival, Hanmer Range, north Canterbury, no tussock hawkweed is

obvious in the grassland, but under cover of matagouri, flax or coprosma it is dense.

Not all areas appear to be as vulnerable, however. For example, tussock hawkweed has been present at Castle Hill Scenic Reserve and Cave Creek, Broken River since at least 1955 (herbarium specimens) and has not become invasive. Likewise at Mt Fyffe it has been present along the track for at least 20 years but, if anything, is declining in density, although, in the ranges behind Mt Fyffe, it is invasive in places (M. Morresy pers. obs.). Herbarium records indicate that it has been present in Molesworth since 1965, and is especially invasive out of sight, beneath shrubs. These observations suggest that, in some cases at least, shelter is important for establishment.

4.5 PROSPECTS FOR CONTROL

The invasion process in tussock hawkweed is still not fully understand, and records must be kept vigilantly to ensure there is an accurate description of its invasion, in order to devise the most appropriate means of control.

At present, grazing to prevent seed-set appears extremely useful and effective in preventing the spread of tussock hawkweed. It is likely that biocontrol with a host-specific agent, such as a rust fungus, will not necessarily be effective because, despite its predominantly apomictic breeding, tussock hawkweed does have some residual sexual reproduction and therefore may be able to evolve resistance to parasites. Finally, evidence from Treble Cone ski field (Table 1) suggests that tussock hawkweed seed may still be being spread inadvertently as a contaminant of grass seed.

5. Acknowledgements

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