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S. Saggar · P.D. McIntosh · C.B. Hedley · H. Knicker

Changes in soil microbial biomass, metabolic quotient, and organic matter turnover under *Hieracium* (*H. pilosella* L.)

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Abstract In New Zealand *Hieracium* is an opportunistic plant that invades high country sites more or less depleted of indigenous vegetation. To understand the invasive nature of this weed we assessed the changes in soil C, N and P, soil microbial biomass C, N and P contents, microbial C:N and C:P ratios, the metabolic quotient, and turnover of organic matter in soils beneath *Hieracium* and its adjacent herbfield resulting from the depletion of tussock vegetation. The amounts of soil organic C and total N were higher under *Hieracium* by 25 and 11%, respectively, compared to soil under herbfield. This change reflects an improvement in both the quantity and quality of organic matter input to mineral soil under *Hieracium*, with higher percentage organic C and a lower C:N ratio. The microbial biomass C, N and P contents were also higher under *Hieracium*. The amount of C respired during the 34-week incubation indicated differences in the nature of soil organic matter under *Hieracium*, the unvegetated "halo" zone surrounding *Hieracium* patches, and herbfield (depleted tussock grassland). Decomposition of organic matter in these zones showed that the *Hieracium* soil had the greatest rate of CO_2 respired, and the halo soil had the lowest. We relate the enhanced organic C turnover to the invasive nature of *Hieracium*. Net N mineralization was significantly lower from the *Hieracium* soil (57 mg N g^{-1} soil N) than from herbfield and halo soils (74 and 71 mg N g^{-1} soil N, respectively), confirming that the nature of organic N in *Hieracium* soil is different from adjoining halo and herbfield soils. It seems plausible that specific compounds such as polyphenols and lignins released by *Hieracium* are not only responsible for increased organic N, but also control the form and amount of N released during organic matter transformations. We conclude that the key to the success of *Hieracium* in the N-deficient South Island high country of New Zealand lies in its ability to control and sequester N supply through modifying the soil organic matter cycle.

Key words Tussock grassland · High country · Microbial biomass · Organic C and N turnover · *Hieracium* invasion

S. Sagger (✉) · C.B. Hedley
Landcare Research, Private Bag 11052, Palmerston North, New Zealand
e-mail: saggars@Landcare.cri.nz, Tel: +64-6-3567154
Fax: +64-6-3559230

P.D. McIntosh[1]
Landcare Research, Private Bag 1930, Dunedin, New Zealand

H. Knicker
Lehrstuhl für Bodenkunde, Technische Universität München, D-85350 Freising-Weihenstephan, Germany

[1] *Present address:*
Forest Practices Board, 30 Patrick St, Hobart, Tasmania

Introduction

The invasion and continuing dominance of *Hieracium* (*H. pilosella* L.), a mat-forming, stoloniferous flatweed with an extensive underground root mass, in high country tussock grasslands of New Zealand is a serious problem, and a major threat to the ecological and economic sustainability of South Island high country pastoralism. Makepeace et al. (1985) observed that fescue tussock (*Festuca novae-zelandiae*) growing in areas of dense *Hieracium* contained low N and P. Treskonova (1991) related *Hieracium* invasion to "degradation" of tussock grasslands, but with little reference to soil properties. There is no doubt, however, that low tussock cover (*Chionochloa*, *Festuca* and *Poa* sp.) is broadly correlated with *Hieracium* dominance (Hunter et al. 1992). Recent research has shown that soils beneath *Hieracium* patches are more acid and contain more organic C and nutrients than soils under surrounding vegetation (McIntosh and Allen 1993; McIntosh et al. 1995; Boswell and Espie 1998). It appears that *Hieracium* is able to modify soils to its own advantage, and McIntosh et al. (1995) suggested the ability of *Hiera-*

cium to take up N from soils which it was invading was the reason for its success. The consequences of the observed soil changes can be predicted only if the dynamics of and functional mechanisms in soils under *Hieracium* and adjacent herbfield (depleted tussock grassland) are better understood.

In previous studies neither soil microbial biomass nor organic matter dynamics was studied. There is considerable evidence that microbial biomass C, N and P measurements could be used to evaluate the influence of land-use change on soils (Yeates et al. 1997; Yeates and Saggar 1998) and how organic matter turnover controls the fluxes of nutrients. Microbial biomass measurements combined with soil respiration (metabolic quotient, qCO_2) have frequently been used as an index of soil development or degradation (Insam and Domsch 1988; Insam et al. 1989) and to assess the quality of organic matter input (Anderson and Domsch 1990, 1993).

Because *Hieracium* invasion occurs in tussock grasslands more or less depleted of their original cover of tussock species (*Chionochloa*, *Festuca* and *Poa* sp.), and its growth causes profound changes in the chemical soil properties, it is relevant to study its effects on changes in microbial biomass and organic C turnover. Information on changes in microbial biomass, qCO_2 and organic C turnover may help understanding of the processes that aid the invasion of this and other weeds, and discourage grass species growth and persistence.

Our aim in the present study was to determine the pattern of change in microbial biomass C, N and P and metabolic quotient in the different soil zones (Fig. 1) caused by *Hieracium* invasion of depleted tussock grasslands. A second aim was to examine the decomposition of organic matter in these zones to determine the impact of invasion on organic matter turnover. This information could also be utilized to determine whether progressive *Hieracium* invasion was correlated with the "quality" of organic matter inputs.

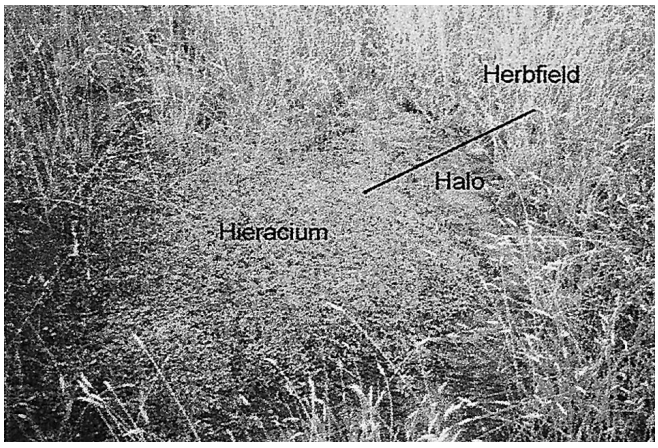

Fig. 1 *Hieracium pilosella* L. invading tussock grassland showing the characteristic patch form, the halo with little or no vegetation, and surrounding herbfield (depleted tussock grassland mixed herbfield and annual grasses)

Materials and methods

Soil, sampling and analysis

The site used by McIntosh and Allen (1993) and McIntosh et al. (1995) for this study was on Glencairn Station (NZMS 260 H39 827490), near Twizel, South Island, New Zealand. The site is at 440 m altitude, receives 500–600 mm precipitation, has a northerly aspect and a 15° slope. Soils at the site are developed on thin loess of greywacke origin over bouldery fan alluvium derived from greywacke of the Benmore Range. The soils are classified in the NZ Soil Classification (Hewitt 1992) as Immature Pallic Soils and in Soil Taxonomy (USDA 1994) as Typic Ustochrepts. The soils are S-deficient but natural levels of available P are moderate (Olsen-P = 11; site G4, McIntosh et al. 1985). The sites have never been fertilized.

Since 1978 the site has been grazed at an estimated stocking rate of 0.6 SU ha^{-1} (SU = Stock Unit; one stock unit consumes approximately 550 kg DM (Dry matter) ha^{-1} and is equivalent to 35 kg liveweight lamb or 50–60 kg liveweight ewe). No *Hieracium* was noted in 1978 but since that time *Hieracium* has established in numerous patches. At the time of sampling *Hieracium* patches typically had 0.5–1.2 m diameter and almost 100% *Hieracium* cover with no other plant species present. Patches were surrounded by an approximately 15-cm wide "halo" of almost bare ground (Fig. 1). Some patches larger than about 1.5 m diameter had senescent centres. According to McIntosh et al. (1995) the diameter of the patches is expanding at approximately 13 cm per year; this allows progressive changes associated with *Hieracium* invasion into depleted tussock grassland to be studied.

At the sampling site four locations (replicates) were chosen for sampling, each having a circular *Hieracium* patch, a regular halo, and *Hieracium*-free herbfield, as described by McIntosh et al. (1995) and illustrated in Fig. 1. In 1993 the herbfield was dominated by *Leontodon taraxacoides* (13%) with *Hieracium pilosella*, *Rosa rubiginosa*, *Trifolium arvense*, *Anthoxanthum odoratum*, *Muehlenbeckia complexa*, *Melicytus alpinus*, *Carex breviculmis*, *Bromus* spp. and *Wahlenbergia gracilis* (all < 5%; McIntosh et al. 1995). Soil was sampled to a depth of 10 cm, which in pastoral soils has usually been considered as the upper layer for soil microbial biomass and nutrient estimations (Brookes et al. 1985). Using a spade, a topsoil sample of approximately 1 l was taken from each patch centre, halo, and adjacent herbfield (within 0.5 m of the halo), giving four replicates for each "treatment". The samples were stored at 4 °C in plastic bags, hand-sorted to remove vegetation and litter, and sieved moist through a 5-mm sieve. Subsamples of the sieved soil were stored moist at 4 °C for soil microbial biomass C, N and P analysis and the incubation study.

Air-dried samples were used for the total C, N and P analyses. Total C in soils was analysed by a combustion method (Leco Induction Furnace, St Joseph, Mich.). Total soil N was determined using a semi-micro Kjeldahl digestion and by measuring NH_4^+–N in the digests using an autoanalyser procedure. Total P was measured on the Kjeldahl digest.

Soil microbial biomass C

Soil microbial biomass C was determined by a fumigation-extraction method (Vance et al. 1987). Fumigated and non-fumigated soils were extracted with 0.5 M K_2SO_4 for 30 min (1:5 soil:extractant ratio), filtered, and then an aliquot was analysed for C using a TOC 5000 analyser. The oxidizable C obtained from the fumigated samples minus that from the non-fumigated samples was taken to represent the microbial-C flush and converted to microbial-biomass C using the relationship:

Microbial C = C flush/0.41 (Wu et al. 1990)

Soil microbial biomass N

Soil microbial biomass N was measured following the method described by Ross (1992). The K_2SO_4 extracts from fumigated and non-fumigated samples were digested in 0.165 M $K_2S_2O_8$ for 30 min at 121 °C, and NO_3^-–N and NH_4^+–N were measured by autoanalyser procedures. Microbial N was estimated using the relationship:

Microbial N = N flush/0.45 (Jenkinson 1988)

Soil microbial biomass P

Soil microbial biomass P was measured by the method of Brookes et al. (1982) as modified by Ross et al. (1995). Fumigated, non-fumigated and spiked (with P to estimate percentage recovery of P) soil samples were extracted with 0.5 M $NaHCO_3$ for 1 h. An aliquot was decolourized and acidified using phosphate-free charcoal and 1 M HCl (Ross et al. 1995) and phosphate concentration was measured at 882 nm (Murphy and Riley 1962). For each sample, both the extraction and subsequent analyses were performed in triplicate. Microbial biomass P was estimated using the relationship:

Microbial P = (P flush)/(0.4 × % recovery from the spike)

where 0.4 is the average proportion of microbial P recovered from the soil (Brookes et al. 1982).

Incubation

Field-moist subsamples (equivalent to 25 g oven-dry soil) of each treatment replicate were placed in beakers and then incubated in 1.8-l Agee jars containing vials with 10 ml CO_2-free water, avoiding any loss of moisture during incubation. The jars were tightly sealed. Respiration was measured as CO_2 production at weekly/fortnightly intervals for 34 week. On each sampling day, a 1-ml headspace sample was collected through a septum in the lid from each jar, and the CO_2 concentration was measured by gas chromatography. The jars were flushed with ambient air and resealed for the next measurement. A set of controls (without soil) was used as a background reference.

Metabolic quotient

The microbial respiration:biomass ratio, also known as the metabolic quotient qCO_2 or specific respiration rate, was calculated as the ratio between the CO_2–C produced per hour averaged over the incubation period and the microbial biomass C measured at the begining of incubation.

Unless otherwise stated, results are expressed on the basis of the oven-dry (105 °C) weight of the material. Means ($n = 4$) and standard errors of the means were calculated for organic C, total N and total P, microbial biomass C, N and P and metabolic quotient. Decomposition data were subjected to an analysis of variance to determine the statistical significance of treatment effects, using SYSTAT for Windows software package and the general linear model procedure (Wilkinson 1996). The significance of differences between treatments with time was estimated using repeated measures ANOVA. Results are reported as statistically significant at the 5% probability level.

Results

Soil organic C, total N and total P

Soil organic C and total N contents were higher under *Hieracium* than under the halo or herbfield. This difference was more pronounced for organic C than total N, resulting in significant changes in the C:N ratio (Table 1). The increase in C and N is attributed to a much greater dry matter and likely return to soil under *Hieracium* (McIntosh et al. 1995). The halo around *Hieracium* has been deprived of plant production, resulting in reduced organic C and N contents. Total amounts of organic C and total N found in the soils under the three zones (*Hieracium*, halo and herbfield) showed that *Hieracium* soils had 26% and 11% higher C and N, respectively, than the adjacent herbfield. As *Hieracium* is expanding into the herbfield, this difference is interpreted as a gain of organic C and N under*Hieracium*. In the halo, the amounts of soil organic C and total N were 27% and 21% lower than under the *Hieracium*. Total P values were slightly lower in the halo than under *Hieracium* and herbfield, but the differences were not significant.

Table 1 Chemical and microbial biomass characteristics of the three soil zones under the influence of *Hieracium*. ± indicate standard error with $n = 4$ (*NS* not significant)

Property	Zones			
	Centre of *Hieracium*	Halo around *Hieracium*	Adjacent herbfield	Significant difference
Organic C (g kg^{-1} soil)	20.5 ± 1.8	15.0 ± 1.0	16.3 ± 1.3	**
Total N (g kg^{-1} soil)	1.54 ± 0.14	1.22 ± 0.09	1.39 ± 0.09	**
Total P (g kg^{-1} soil)	0.489 ± 0.002	0.470 ± 0.002	0.498 ± 0.002	NS
Soil C:N ratio	13.3 ± 0.4	12.3 ± 0.2	11.7 ± 0.2	***
Soil C:P ratio	42 ± 3	32 ± 1	33 ± 2	***
Mineral N (mg kg^{-1} soil)	14 ± 1	22 ± 1	33 ± 3	***
Inorganic P (mg kg^{-1} soil)	3 ± 1	3 ± 1	2 ± 1	NS
Microbial C (mg kg^{-1} soil)	498 ± 51	367 ± 31	400 ± 33	*
Microbial N (mg kg^{-1} soil)	98 ± 17	76 ± 12	101 ± 15	*
Microbial P (mg kg^{-1} soil)	21 ± 2	13 ± 2	17 ± 2	**
Microbial C:N ratio	5.1 ± 0.1	4.9 ± 0.5	4.0 ± 0.6	*
Microbial C:P ratio	24 ± 2	28 ± 3	24 ± 1	**
Metabolic quotient (mg CO_2—C g^{-1} biomass C h^{-1})	0.56	0.41	0.49	

* $P < 0.05$; ** $P < 0.001$; *** P

Microbial biomass C, N and P

The microbial biomass C, N and P contents showed variations similar to soil organic matter. However, the differences in microbial biomass C between *Hieracium* and herbfield soils were slightly more pronounced than microbial biomass N, resulting in significant changes in the microbial C:N ratio (Table 1). The changes in mineral N content differed from those of other parameters and varied greatly. Mineral N contents were lowest (14 mg N kg^{-1} soil) under *Hieracium*, and highest (33 mg N kg^{-1} soil) under herbfield. Halo soils had intermediate values (22 mg N kg^{-1} soil).

Organic matter respiration

The CO_2—C respired from the *Hieracium*, halo and herbfield soils during the 34-week incubation amounted to 1.58, 0.85 and 1.11 g kg^{-1}, respectively (Fig. 2), and comprised 7.7, 5.7 and 6.8% of the initial soil C. The *Hieracium* soil had the greatest rate of CO_2 respired, and the halo soil the lowest, throughout the incubation. Trends in soil respiration were similar in all soils and for each soil the rates of CO_2 respired declined with incubation period. There were three phases apparent during the incubation (Table 2). During the first 5 weeks (phase I) of the incubation, respiration rate was rapid (8.9 to 14.2 mg CO_2—C kg^{-1} soil day^{-1}). The initial active decomposition was followed by a slower secondary metabolism (phase II, weeks 5–20) with respiration rate dropping to between 3.0 and 5.9 mg CO_2—C kg^{-1} soil day^{-1}. For phase III (weeks 20–34) the respiration rate was much slower in the respective soils (2.2 to 4.5 mg CO_2—C kg^{-1} soil day^{-1}).

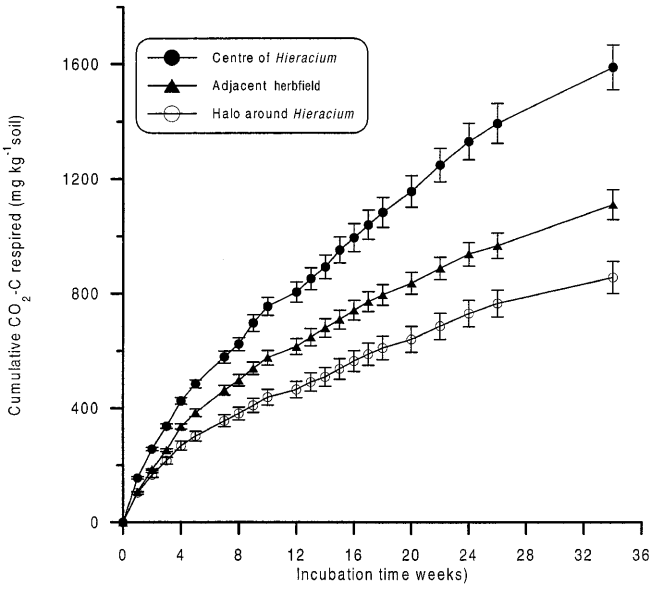

Fig. 2 Evolution of CO_2–C in soils from under *Hieracium*, the halo, and adjacent herbfield during 34-week incubation. Each value represents the mean of four replicates with the standard error shown by *vertical bars*

Metabolic quotient

Metabolic quotient values showed similar trends to those of microbial biomass values. They tended to be the highest in *Hieracium* soils (0.56 mg CO_2—C g^{-1} biomass C h^{-1}), lowest in halo soils (0.41 mg CO_2—C g^{-1} biomass C h^{-1}), and intermediate in herbfield soils (0.49 mg CO_2—C g^{-1} biomass C h^{-1}). The differences observed in the size of the microbial biomass in the soils under the three zones (*Hieracium*, halo and herbfield) were not paralleled by changes in soil respiration, indicating microbial biomass activities to be different. The high qCO_2 values in soil under *Hieracium* suggest that during mineralisation of organic matter microbes divert more C to respiration than to new microbial biomass, causing more C loss than from microbes in halo soils.

Discussion

Soil chemical and biological properties were markedly affected by the growth of *Hieracium*. In the field we found that the soil microbial biomass C, N and P, and soil C and N pools were greatest underneath *Hieracium* plants. Our results suggest that soil processes under this plant are profoundly different from those occurring in herbfield (depleted tussock grassland) soils which may be only a metre away (Fig. 1).

The degree of accumulation of organic matter in soil depends on the relationship between C input and decomposition rates. This results from a complex interaction of ecosystem properties involving substrate quali-

Table 2 C mineralization rates (mg CO_2–C respired kg^{-1} soil) and net N mineralization in soils under *Hieracium*, in the halo, and under adjacent herbfied during 34-week incubation. ± indicate standard error with $n=4$ (*nd* not determined)

	C mineralization rate (day^{-1}) during			Net N mineralized during incubation (mg N g^{-1} soil N)
	0–5 week (phase I)	5–20 week (phase II)	20–34 week (phase III)	
Centre of *Hieracium*	14.2 ± 0.9	5.9 ± 0.6	4.5 ± 0.5	57
Halo around *Hieracium*	8.9 ± 1.1	3.0 ± 0.5	2.2 ± 0.7	74
Adjacent herbfield	11.3 ± 0.8	3.6 ± 0.3	2.9 ± 0.4	71
Significant difference	***	**	**	nd

* $P<0.05$; ** $P<0.001$; *** P

ty, soil matrix (Saggar et al. 1996, 1997, 1999), climate and topography, and the community structure of decomposing organisms (Djajakirana and Joergensen 1996). *Hieracium* is a perennial and returns more C and N to the soil from dying leaves and roots than annual plants in the surrounding herbfield (McIntosh et al. 1995). Our study clearly showed the influence of plant species on soil organic matter accumulation (Table 1) and respiration (Fig. 2).

Our data on the decomposition of organic matter in these zones showed that the *Hieracium* soil had the greatest rate of CO_2 respired, and the halo soil had the lowest, throughout the 34-week incubation period. Rates of CO_2 respired declined rapidly after 5 weeks (Fig. 2) in all soils. Higher CO_2 production during the first phase may be due partly to the disturbance of the soil during sampling, sieving and processing resulting in greater availability of metabolically accessible compounds, and partly to incubating under laboratory conditions. The *Hieracium* soil with more labile organic matter inputs resulted in greater availbility of metabolically accessible compounds during this phase. Therefore, the proportional decline was greater in the halo and herbfield soils than in the *Hieracium* soil, suggesting the more labile nature of organic matter in *Hieracium* soil. We found that the rates of C mineralization from the *Hieracium* soil were about twice those from the halo soil and one-and-a-half times those from the herbfield soil. The organic matter from the *Hieracium* soil had higher C:N and C:P ratios (Table 1), while the organic matter from halo and tussock soils had lower ratios. The higher rate of mineralization from *Hieracium* soil is therefore probably related to the greater inputs and consequently higher proportion of relatively young plant materials (e.g. dead leaves and recent roots) in *Hieracium* soil, which presumably contained substrates such as sugars, amino acids and organic acids that were readily metabolized, leading to the greater concentration of microbial biomass.

All the soils, in the present study, had much smaller qCO_2 values than those reported for mineral forest soil (Anderson and Domsch 1993) and forest litter from *Pinus radiata* growing in P-deficient soils fertilized with different amounts of superphosphate (Saggar et al. 1998). It is difficult to compare the estimated qCO_2 with other data since no quantitative data are available on herbfield and *Hieracium* soils in New Zealand. However, our qCO_2 measurements are similar to the value (0.51 mg CO_2—C g^{-1} biomass C h^{-1}) reported by Lovell and Jarvis (1996) for a permanent pasture UK soil and are in the range for tussock grassland soils elsewhere in the South Island high country (McIntosh et al. 1999).

Our aim in the present study was to determine the pattern of change in microbial biomass C, N and P and metabolic quotient in the different soil zones resulting from *Hieracium* invasion of depleted tussock grasslands and to determine whether progressive *Hieracium* invasion was correlated with the "quality" of organic matter inputs. The significant changes in microbial biomass and qCO_2 are clearly associated with the invasive growth of *Hieracium* into the halo towards the herbfield. The lower microbial biomass and qCO_2 in the soil beneath the halo of bare ground around patches of *Hieracium* may be caused by the absence of C inputs. The qCO_2 data provide a means of determining whether microbial biomass in *Hieracium* soil was more metabolically active. The increase in qCO_2 following *Hieracium* invasion must reflect an increase in the ratio of active:dormant components of the biomass. This ratio may also have been modified by the differences in the composition of organic matter between *Hieracium*, halo and herbfield. The qualitative changes within microbial population are expected to affect the microbial biomass C:N ratio. The higher C:N ratio in *Hieracium* soil obtained in the present study would suggest an increase in the proportion of fungi present (Anderson and Domsch 1980). More acid soils found under *Hieracium* than under herbfield (McIntosh et al. 1995) would also support the hypothesis that *Hieracium* soils have a greater proportion of fungal biomass.

Measurement of mineral N showed that *Hieracium* soils had about half as much mineral N as herbfield soils (Table 1), with halo soils having intermediate values, even though *Hieracium* soils had more microbial and total N. This suggests that as *Hieracium* invades tussock grasslands, it "mops up" mineral N and transforms it into organic forms. Over the 34-week incubation there was an increase in mineral N (net mineralization) in all the soils. However the amount of N mineralized during an 34-week laboratory incubation was considerably lower from the *Hieracium* soil (57 mg N g^{-1} soil N) than from herbfield and halo soils (74 and 71 mg N g^{-1} soil N, respectively), confirming that the nature of organic N in soil beneath *Hieracium* is different from soil under the adjoining halo and herbfield, i.e. *Hieracium* is able both to increase N in soils under it, and also "store" this N in less labile form than in the adjacent herbfield. It seems plausible that specific compounds such as polyphenols and lignins released by *Hieracium* are not only responsible for increased total N but also control the form and amount of N released during organic matter transformations. Soil acidification (McIntosh et al. 1995) is an incidental effect of this transformation of soil organic matter and does not appear to be the primary cause of the competitive advantage of *Hieracium*.

This study has highlighted the importance of *Hieracium* as a "powerful engine" for transforming soil organic matter and forms of N, and points to several aspects that need to be addressed in future research. *Hieracium*, now common over 42% of the South Island high country (Hunter et al. 1992), has the ability to acquire N from surrounding soils, and this ability to confine N and control the N cycle probably accounts for its outstanding success in invading N-deficient environments like the South Island high country of New Zealand. The halo and herbfield soils had significantly low-

er total N values than *Hieracium* soils (Table 1) despite higher mineral and mineralizable N contents. This probably reflects the lower ability of the herbfield plants to uptake availble N than *Hieracium* which not only consumes the mineral N from the soil beneath it but also "mops" some from the soils under halo. Spatial trends show how the patches progressively modify soils of the surrounding herbfield as *Hieracium* patches expand (McIntosh et al. 1995).

A new uptake pathway for soil N in infertile (N-deficient) acid environments has recently been proposed (Northup et al. 1995), in which dissolved organic N in the form of a complex with polyphenols is able to be directly taken up by plants. Direct uptake of organic N (amino acids, polypeptides etc.; Chapin et al. 1993; Schimel and Chapin 1996; Leadley et al. 1997) either by plants or in association with vesicular-arbuscular mycorrhiza, short-circuits the N mineralization step – traditionally considered as limiting terrestrial N cycling. It seems plausible that enhanced N uptake by *Hieracium* mediated by polyphenol "leakage" into the soil from roots contributes to the outstanding invasion success of this plant. The question remains however: what drives *Hieracium*? Can polyphenols, known to be a significant component of *Hieracium* tissue (Makepeace et al. 1985), mediate N uptake of *Hieracium* by polyphenol "leakage" into the soil from roots? This leads to a further question: can polyphenols and lignins confine N in organic matter and thereby control N transformations? Recent work indicates that classes of organic N compounds can be distinguished with ^{15}N-NMR (Kôgel-Knabner 1995). As the nature and structure of compounds released by *Hieracium* are not well understood, biochemical techniques including ^{13}C-NMR and ^{15}N-NMR, and infrared spectoscopy could be explored to characterize these specific compounds. Studies addressing these issues are the focus of our current research.

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