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An ecosystem-level perspective of allelopathy

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ABSTRACT

Allelopathy is an interference mechanism by which plants release chemicals which affect other plants; while it has often been proposed as a mechanism for influencing plant populations and communities, its acceptance by plant ecologists has been limited because of methodological problems as well as difficulties of relating the results of bioassays used for testing allelopathy to vegetation patterns in the field. Here we argue that the concept of allelopathy is more appropriately applied at the ecosystem-level, rather than the traditional population/community level of resolution. Firstly, we consider the wide ranging effects of secondary metabolites (widely regarded as allelochemicals) on organisms and processes which regulate ecosystem function, including herbivory, decomposition and nutrient mineralization. It is apparent that plants with allelopathic potential against other organisms induce net changes in ecosystem properties, which may in turn impact upon the plant community in the longer term. We then illustrate these concepts using two contrasting examples of how invasive plant species with allelopathic potential may alter ecosystem properties through the production of secondary metabolites, i.e. *Carduus nutans* (nodding thistle) in New Zealand pastures and *Empetrum hermaphroditum* (crowberry) in Swedish boreal forests. In both cases the production of secondary metabolites by the invasive species induces important effects on other organisms and key processes, which help determine how the ecosystem functions and ultimately the structure of the plant community. These examples help demonstrate that the concept of allelopathy is most effectively applied at the ecosystem-level of resolution, rather than at the population-level (i.e. plant-plant interference).

Key words: allelopathy; *Carduus nutans*; competition; crowberry; decomposition; ecosystem properties; *Empetrum hermaphroditum*; herbivory; nodding thistle; population biology

CONTENTS

I. INTRODUCTION

Allelopathy is an interference mechanism in which live or dead plant materials including plant litter release chemicals which exert an effect (usually negative) on associated plants. Many studies have investigated the role of allelopathy in determining associations in plant communities, and the vast majority of these have depended heavily upon the use of laboratory bioassays. The experimental approaches frequently used for studying allelopathy have, however, drawn considerable criticism from many plant ecologists, particularly those who operate at the population level of resolution (e.g. Harper, 1977). Amongst the principal criticisms are that the bioassays used to demonstrate allelopathy do not represent ecological reality (Keeley, 1988), that interpretations of allelopathy can be explained by other phenomena (Henn, Petit & Vernet, 1988; Michelsen *et al.*, 1995), and that the interactions shown by such bioassays do not always conform to patterns of vegetation association observed in the field (Stowe, 1979).

Although the role of secondary metabolites as a determinant of plant populations has only partial acceptance, the significance of these compounds is more widely accepted in other branches of ecology, for example in determining plant-herbivore interactions (Rosenthal & Berenbaum, 1991), in regulating soil biotic interactions (Wardle & Lavelle, 1997) and in determining processes associated with nutrient cycling (Northup *et al.*, 1995) and decomposition (Horner, Gosz & Cates, 1988). Our view is that these types of biotic interactions, which operate mainly at the community and ecosystem level of resolution, do not differ fundamentally in nature from those which regulate plant populations and are therefore not entirely incompatible. There is an increasing appreciation that population-based and ecosystem-based approaches complement each other strongly (Jones & Lawton, 1995) and in this light we believe that the concept of allelopathy can be applied effectively to address ecosystem-level questions.

In this paper, we discuss the potential role of allelopathy in terrestrial ecosystems. In doing this we (1) provide a brief overview of the issues relating to the debates about occurrence of allelopathy in plant populations; (2) describe the probable importance of allelopathy as a factor in ecosystem-level processes and interactions; and (3) present evidence for these concepts using case studies representing two strongly contrasting ecosystems. The ultimate aim will be to demonstrate that allelopathy is most appropriately considered at an ecosystem-level, rather than at a population-level perspective.

II. ALLELOPATHY AND PLANT POPULATIONS

To evaluate the role of allelopathy at the ecosystem level, we firstly need to consider its significance in regulating plant population dynamics and plant growth. Plants serve as the producers of any ecosystem and therefore regulate the functioning of the other components, so interactions regulating plant communities are of fundamental importance at the ecosystem level (Vitousek & Walker, 1989; Oksanen, 1990). We will therefore briefly evaluate the evidence for and against allelopathy operating in plant communities. A detailed and balanced discussion of this aspect is presented by Williamson (1990).

The predominant concern regarding the occurrence of allelopathy is based upon the artificial nature of the bioassays which are usually used to demonstrate it, as has been emphasized by Harper (1977). We are in partial agreement with these concerns; numerous studies have used the results of bioassays involving extracts of fixed concentrations from plant tissues, or involving incorporation of plant material into soil planted with receiver species, as evidence that allelopathy is involved in regulating plant growth and establishment, often without any attempt to relate the amounts or concentrations used with those which would occur in nature. While we do not criticise individual studies here, we emphasize that the allelopathy literature is replete with examples in which the evidence is at best highly disputable. We do not maintain, though, that the generally poor experimentation which sometimes characterizes allelopathy research is in itself evidence that allelopathy does not occur, and the dismissal of allelopathy as a mechanism in patterning vegetation based on these grounds seems extreme (see Wilson & Agnew, 1992).

Studies which have implicated allelopathy in determining plant interactions can also be criticized on the grounds that alternative explanations for observed patterns have not been adequately addressed. Firstly, in relation to bioassays, extracts can also inhibit test species through altering pH and osmotic potential and stimulating microbial growth (Stowe, 1979; Henn *et al.*, 1988; Wardle, Nicholson & Ahmed, 1992). Further, studies in which plant tissues are added to soil usually do not acknowledge the prospect of increases in the soil microbial biomass immobilising nutrients and thus retard the growth of test plants through nutrient starvation (Wardle, 1992). As an extreme example of this we are aware of a number of studies in which plant residues or mulches have been applied in field plots and the resultant inhibition of plants has been presumed to result from the allelopathic potential of the added material; it is intrinsically reasonable to conclude that microbial nutrient uptake is at least partially responsible for such effects (see Powlson, Brookes & Jenkinson, 1987; Allison & Killham, 1988; Ocio, Brookes & Jenkinson, 1991). Secondly, in examples in which allelopathy has been proposed as an explanation for observed inhibition of one plant by another in field conditions, other factors such as the role of herbivores, alteration of light irradience and spectra, and plant-induced changes in microclimate have usually been ignored (see Bartholomew, 1970; Salisbury & Ross, 1978; Carlsson & Callaghan, 1991). Finally, the soil itself is very important in determining the behaviour of secondary metabolites. Bioassays conducted in controlled artificial environments such as Petri dishes in the absence of soil can greatly overestimate the importance of allelopathy because soil significantly deactivates secondary metabolites (Krogmeier & Bremner, 1989) and because of the dilution effect of soil. There are also methodological difficulties in determining the exact concentration of secondary metabolites relative to the levels of active plant roots in the soil. This is confounded by the considerable spatial and temporal variability of secondary metabolites which probably exists (Wardle, Nicholson & Rahman, 1993).

The concept of allelopathy has also been criticized because of the supposed failure of the results of allelopathy bioassays for particular plant species to correlate with spatial patterning of the same species in the field (although curiously the same requirements are usually not made for studies on plant resource competition; Williamson, 1990). The study of Stowe (1979) is frequently presented as evidence that allelopathy is often ecologically unimportant (e.g. Keeley, 1988). In that study, the observed associations between seven grass species in the field was not significantly correlated with what would be predicted based on the results of laboratory bioassays. In contrast, Wardle, Nicholson & Rahman (1996) found that the effect of 10 grassland forage species on a single test species in field plots was significantly correlated with the results of bioassays of the same 10 species. It is possible that allelopathic effects would be more easily detected in this study than in that of Stowe (1979) because the field plots had a much lower species richness and the soil biochemistry is more likely to be determined by a dominant plant species. There have been few attempts to relate vegetation patterning or the results of plant interference experiments to the results of laboratory allelopathy bioassays in a statistical manner, and while correlation does not mean causation, this appears to be a useful (and largely under-utilized) approach for predicting the role that allelopathy might have in structuring plant communities.

We suggest that the real importance of allelopathy as a plant regulatory mechanism is unclear and this is a result of the types of approaches usually used for investigating it, as well as the difficulties of separating allelopathy from other mechanisms which may cause negative interactions in plant communities [see response of Wardle & Nilsson (1997) to Michelsen *et al.* (1995), for example]. It is uncertain as to whether it is ever possible to demonstrate unequivocally the importance of allelopathy at the population level using currently accepted methodologies, and a conceptual framework where these types of interactions can be considered in a broader, ecosystem-level context might help to clarify these issues.

III. ALLELOPATHY AND ECOSYSTEMS

Ecosystems consist of groups of organisms which interact with each other and with their environment. As such, the various components of a given ecosystem are often closely interlinked and factors which alter one component will often have flow-through effects on other components (e.g. Hairston, Smith & Slobodkin., 1960; Aber & Melillo, 1991; Abrams *et al.*, 1996). In this light it is reasonable to expect that secondary metabolites produced by plants may alter other ecosystem components which in turn drive fundamental processes and interactions, thus determining ecosystem function and ultimately the nature of the plant community. We suggest that the evidence for secondary metabolites (i.e. allelochemicals) participating in these sorts of relationships is generally considerably stronger than in direct plant–plant interactions, probably in part because of methodological difficulties in demonstrating the importance of allelopathy in inter-plant associations. We now discuss these relationships.

Herbivores are often important in determining vegetation composition but are in turn usually also strongly regulated by the rate of net primary productivity (Oesterheld, Sala & McNaughton, 1992; Power, 1992). Although the herbivore biomass across ecosystems is correlated with plant production (McNaughton *et al.*, 1989), at a finer level of resolution secondary metabolites are well known to regulate herbivore populations and consequently feeding activity (Coley, Bryant & Chapin, 1985). We emphasize, however, that secondary metabolites do not act in isolation and plants which are of low palatability and have high levels of secondary metabolites also have other characteristics which make them unfavourable to herbivores such as low nitrogen status, structural complexity and large amounts of high molecular weight compounds (e.g. cellulose, lignin) (Bryant, Chapin & Klein, 1983; Bryant, 1987; Pastor *et al.*, 1993). Plant factors regulating herbivores are therefore complex and the precise mechanisms (including the direct role of secondary metabolites) are difficult to identify, although it is apparent that plant antiherbivore defences involve the simultaneous presence of several characteristics including allelochemicals (see Harborne, 1997). Production of relatively unpalatable foliage in turn is often reflective of site conditions, and plants that are less favourable to herbivores are often associated with stressful environments (Grime, 1979; Coley *et al.*, 1985). There is also evidence that plant species which are less palatable (especially those which are adapted for stressful and late-successional environments) often have a competitive advantage over other species in situations of heavy browsing, resulting in their domination of the plant community (e.g. Hanley & Taber, 1980; Pastor *et al.*, 1988). In such situations, metabolites such as polyphenolics probably exert important effects in altering the competitive balance between plant species simply through affecting their relative resistance to herbivory.

Secondary metabolites produced by herbivores may also determine the outcomes of plant–plant interactions. An intriguing example of this occurs in the Peruvian Amazon, in which individual trees of the species *Tococa occidentalis* provide food and habitat for ants of the genus *Myrmelachista*. These ants in turn kill all surrounding, potentially competing plants by biting them and transmitting toxins (Morawetz, Henzi & Wallnofer, 1992). This represents a complex co-evolutionary system in which one plant chemically suppresses another through an intermediary agent.

Most net primary production is not consumed by herbivores but instead enters the soil system as plant litter (McNaughton *et al.*, 1989). This material is mainly decomposed or transformed by the soil saprophytic microflora with the net result of the eventual release of CO_2 and nutrients. This decomposition process is regulated mainly by climate across broad ecosystem types but at finer scales of resolution it is determined to a large extent by litter quality (Lavelle *et al.*, 1993; Couteaux, Bottner & Berg, 1995; Heal, Anderson & Swift, 1997). There has been considerable interest in evaluating litter quality controls of decomposition but amongst the most widely accepted properties are carbon/nitrogen ratios, lignin content or lignin/nitrogen ratios, structural properties, and concentrations of secondary metabolites such as polyphenolics (e.g. Melillo, Aber & Muratore, 1982; McClaugherty, 1983; Andren & Paustian, 1987; Taylor, Parkinson & Parsons, 1989). It is apparent from the literature that these controls of decomposition are closely correlated with each other (Vanlauwe *et al.*, 1997) and that they probably act in tandem, implicating allelochemicals as having a role in regulating plant litter breakdown.

The soil microflora is regulated by litter quality (including concentrations of secondary metabolites) and this in turn determines decomposition processes (Flanagan & Van Cleve, 1983). As an example of these effects at the broad ecosystem level of resolution, the soil microbial biomass of boreal conifer forests is anomalously low and this is almost certainly a consequence of the poor litter quality produced in such ecosystems (Wardle, 1992). At a much finer scale of resolution Robinson *et al.* (1994) found that internode and leaf material of dead wheat plants supported vastly different fungal communities and this was reflective of large differences in substrate quality. The nature of litter quality, including the concentration of secondary metabolites, results in vegetation type having a dominant effect on the soil microbial community (e.g. Widden, 1986); this in turn can have extremely important feed-back effects on nutrient mineralisation and plant growth and nutrient acquisition, ultimately affecting plant community structure (Wardle *et al.*, 1997*b*).

Although the soil microflora is the biotic component directly responsible for decomposition and mineralisation processes, the soil fauna is usually of considerable importance in regulating these processes through influencing the growth and activity of soil microbes. The nature of these interactions is itself governed by litter quality. For example, the ability of certain microfauna (e.g. protozoa, bacterial- and fungal-feeding nematodes) to mineralize nutrients immobilized in microbial tissue through predation is in itself probably strongly regulated by substrate quality (e.g. Darbyshire *et al*., 1994; Griffiths, 1994). Feeding activity by certain mesofauna such as springtails and oribatid mites on fungi is also determined by resource status; for example, some springtails actively seek out microscopic patches occupied by greater amounts of hyphae (indicative of higher resource status) (Bengtsson, Hedlund & Rundgren, 1994) and preferentially consume fungal species which are associated with litter of higher quality (Klironomas, Widden & Deslandes, 1992). Earthworms, which are often of fundamental importance in regulating microbial activity through the structures that they create, are usually associated with vegetation which produces litter of high quality, and tend to avoid systems dominated by low-quality vegetation including those which produce litter with high phenolic concentrations (Satchell, 1967; Boettcher & Kalisz, 1991; Wardle & Lavelle, 1997).

The regulation of microbial–faunal interactions by resource quality is critical in determining the availability of nutrients for plant growth. For example, it has been shown that microfaunal predation allows uptake by plants of nutrients which would otherwise remain immobilized in bacterial cells (Kuikman & Van Veen, 1989). Similarly, the enhanced availability of nutrients caused by arthropod feeding activity in situations of low nutrient availability (see Teuben, 1991) can substantially enhance plant growth and nutrient concentration (e.g. Setälä, 1995; Setälä & Huhta, 1991). Larger organisms can also cause similar effects; for example, earthworms can induce considerable increments in plant growth when inoculated into field plots (Lavelle, 1994) and enhance plant nutrient acquisition (Spain, Lavelle & Mariotti, 1992). Those organisms which can build physical structures (i.e. 'ecosystem engineers': see Jones, Lawton & Shachak, 1994; Gurney & Lawton, 1996) can also be significant determinants of plant growth and community structure. This is apparent through the ability of earthworms to transfer buried seeds of certain plant species preferentially to the soil surface (Thompson, Green & Jewels, 1994) and through the effects of mounds created by termites on altering the spatial distribution of different plant functional groups (Spain & McIvor, 1988). Since it is apparent that the quality of plant litter is critical in regulating plant growth and community composition through biotic interactions in the decomposer subsystem, and that compounds believed to be allelopathic in nature (such as phenolics) are major determinants of litter quality, we suggest that the allelopathic nature of some types of plant litter could contribute significantly to shaping plant communities through these sorts of mechanisms.

Foliage which has a chemical constitution which makes it of low palatabilty to herbivores also ultimately results in litter which is undesirable for microbes and soil animals and therefore decomposes slowly (see Hobbie, 1992). It has also recently been shown quantitatively, using a comparative approach, that plant species which decompose more slowly are also less palatable to invertebrate herbivores (Grime *et al*., 1996). In this context we suggest that plants producing tissues with unfavourable foliage and litter characteristics also contain high levels of secondary metabolites, and could therefore conceivably have a greater allelopathic potential. Plants with the dual ability to resist herbivory and produce poor quality litter may thus be expected to have strong ecosystem-level effects. Although few studies have specifically investigated this aspect, those which have addressed this hypothesis have generally found strong support for it. Probably the strongest evidence for this effect is in the study of Pastor *et al*. (1988) in a paper appropriately entitled 'Moose, microbes, and the boreal forest'. In their study, exclosure plots were established to exclude browsing by moose (*Alces alces*), and the response of various properties indicative of ecosystem function were subsequently evaluated. Moose preferentially browsed deciduous species such as aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and birch (*Betula papyrifera*), resulting in these species being suppressed and the forest consequently being dominated by less-palatable spruce species (*Picea glauca* and *P. mariana*). Spruce also produces litter with a vastly inferior quality to that of deciduous species and domination by spruce therefore resulted in a general deterioration of properties generally believed to be associated with superior soil quality, e.g. soil C, N, nitrogen mineralisation rate and microbial biomass and respiration. The ultimate effect was retarded development of the soil profile. Since spruce needles and litter could be expected to contain considerably higher levels of secondary metabolites (such as phenolics: Van Praag *et al*., 1991; Gallet, 1994; Gallet & Lebreton, 1995) than needles and litter of the other species it would appear that allelochemicals contributed to a decline in ecosystem performance through adversely affecting other biotic components. Extending this hypothesis further, we suggest that allelochemicals are part of a complex in plant material which also involves other constituents such as lignin, structural materials, etc. and that this complex simultaneously determines the effect that a plant species may have on herbivory, litter decomposition, other plant species and ultimately ecosystem function. In other words, a plant which has adverse effects on one biotic component of the ecosystem is also likely to have adverse effects on other biotic components. We believe that allelopathic effects therefore have consequences that are more wide-ranging than simply determining the outcome of plant–plant interference, and understanding these sorts of interactions could greatly enhance our knowledge of the way in which allelopathy operates.

Ultimately the effects of secondary metabolites on organismic interactions contribute to effects on processes such as nutrient cycling. This is apparent, for example, in studies which have implicated allelopathy as a control of steps in the nitrogen cycle, such as the classical work of Rice & Pancholy (1972, 1973) which shows allelopathic control of nitrification, and those studies which have demonstrated the sensitivity of nitrogen-fixing bacteria to secondary metabolites (Weston & Putnam, 1985). Symbiotic interactions between plants and mycorrhizal fungi can also be regulated strongly by allelochemicals (Rose *et al.*, 1983; Perry & Choquette, 1987; Coté & Thibault, 1988) and this may in turn determine the capacity of mycorrhizal hyphae to assist in plant acquisition of nutrients (Nilsson *et al.*, 1993). These interactions are, in turn, related to other organisms such as those present in the decomposer subsystem: for example, it has been shown that grazing by soil animals of both ectomycorrhizal hyphae (Setälä, 1995) and endomycorrhizal hyphae (Klironomas & Kendrick, 1995) can be of fundamental importance in determining the effectiveness of mycorrhizal associations. In light of the above discussion, it seems reasonable to conclude that secondary metabolites may have a role in governing these types of interactions. Allelochemicals are also likely to regulate nutrient cycling through determining the nature of nutrient uptake by plants; for example, it has been shown that the tree species *Pinus muricata* produces high levels of dissolved organic nitrogen when growing in infertile soils, and that this form of nitrogen can be taken up by mycorrhizal hyphae and plant roots (thus bypassing the nitrogen mineralisation step). This mechanism is probably regulated by high production rates of polyphenolics in nutrient-stressed situations (Chapin, 1995; Northup *et al.*, 1995). Plants with such a strategy may have a significant competitive advantage in nutrient-limited situations, thus encouraging their dominance (Kaye & Hart, 1997).

IV. CASE STUDIES OF INVASIVE PLANTS

In this section, we aim to address and link the probable effects of allelopathy at the population and ecosystem levels of resolution using two examples showing how invasive plants can alter other ecosystem components by the production of secondary metabolites. These examples are from vastly different ecosystem types; with one involving effects relating to a ruderal plant, the nodding or musk thistle *Carduus nutans*, and the other relating to a stress tolerator, the crowberry *Empetrum hermaphroditum*.

(1) Carduus nutans *and New Zealand dairy pastures*

New Zealand dairy pastures are dominated by introduced forage species, principally *Lolium perenne* (perennial ryegrass) and *Trifolium repens* (white clover). *Trifolium repens* is of particular importance in the pasture ecosystem because of its capacity to fix considerable amounts of nitrogen. A major problem associated with such pastures is that they can encourage significant ingress of other weedy species, especially when the forage species have been weakened by stress or disturbance, and a high intensity of vegetation gaps results (Panetta & Wardle, 1992). One such weed, which is particularly problematic in dairy pastures of the Waikato district, is *C. nutans* which can rapidly invade pasture and significantly reduce the availability of forage to livestock (Popay & Medd, 1990).

Establishment of *C. nutans* occurs mainly in autumn and seedlings establish preferentially in gaps of approximately 5 cm in diameter (Panetta & Wardle, 1992). Individual plants then undergo rapid growth, forming a rosette which can occupy an area of over 1 m in diameter. Following this, the plants produce flowering stems at which time the rosette leaves die and decompose; this can occur either during the first or second summer depending on interference pressure from forage species (Wardle *et al.*, 1995*a*) and vernalization requirements (Medd & Lovett, 1978). Decomposition of rosette tissue occurs extremely rapidly and has been determined as having a half-life of 15 days; this is probably attributable to the extremely high nitrogen content of this material (Nicholson & Wardle, 1994). Coincident with this decomposition is substantial suppression and sometimes death of pasture,

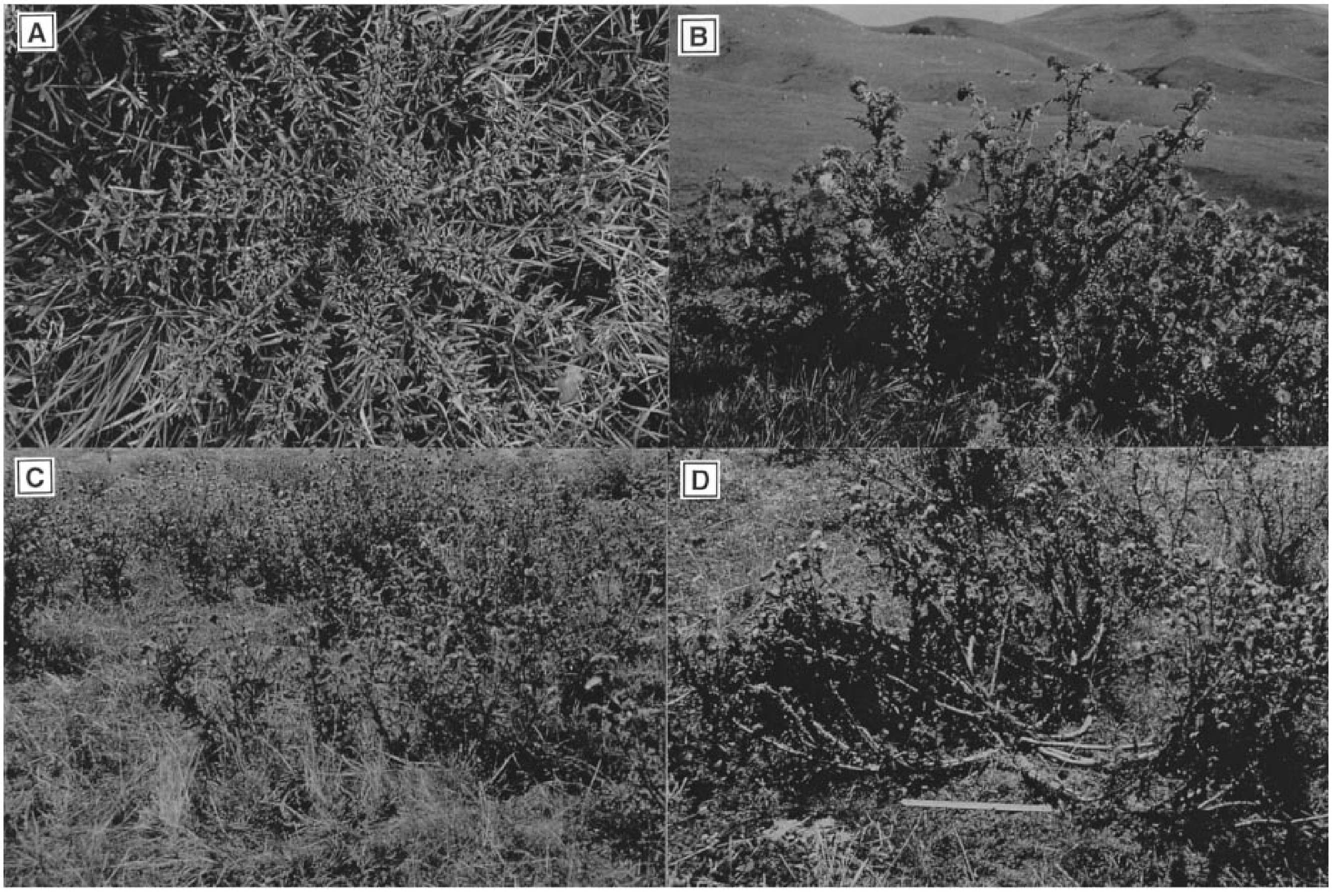

Fig. 1. *Carduus nutans* (nodding thistle) in Waikato, New Zealand, dairy pastures. (A) Full-sized *C. nutans* rosette prior to formation of flowering stems. (B) *C. nutans* in full flower. (C) Dense patch of flowering *C. nutans* plants characteristic of later stages of invasion. (D) Bare patch under flowering *C. nutans* plant indicative of the zone previously occupied by the rosette leaves.

resulting in significant bare patches in the zone previously occupied by the rosette leaves (Fig. 1). The use of allelopathy bioassays (in which concentrations of materials have been related to rosette tissue mass in the field) suggests that *C. nutans* is highly allelopathic and that this may help to explain the bare patches (Wardle *et al*., 1993). The nature of this allelopathy seems highly selective and legume species appear to be considerably more sensitive than grass species.

These trends have been confirmed by field experiments. Wardle *et al*. (1994) conducted an experiment in which changes in certain properties, including production of forage species, were evaluated under *C. nutans* rosettes, in the pasture adjacent to the rosettes and in nearby unaffected pasture; these measurements were continued until after the *C. nutans* plants had died. *L. perenne* was not consistently inhibited by *C. nutans* while *T. repens* usually underwent severe inhibition but only after the *C. nutans* rosette leaves had begun to decompose. The rate of symbiotic nitrogen fixation by *T. repens* was particularly adversely affected by *C. nutans* rosette tissue (significantly more so than for the *T. repens* plants themselves) and greenhouse experiments confirmed that this was also linked to a reduction in *T. repens* nodulation in the presence of decomposing *C. nutans* rosette leaves. The use of partitions in these experiments to separate above-ground and below-ground interference effects of individual *C. nutans* plants on *T. repens* plants at different *C. nutans* life-history stages confirmed that these effects were only apparent when above-ground interactions were permitted and decomposing *C. nutans* rosette leaves were present. Although invasive plants which benefit from disturbance are often presumed to be associated with ecosystem nitrogen build-up (Vitousek & Walker, 1989), we suggest that *C. nutans* induces long-term decline of soil nitrogen input and that this results from currently unidentified secondary metabolites which are released from decomposing rosette leaves and to which legumes and the nitrogen-fixing process are particularly susceptible.

We also believe these effects to have an allelopathic basis because other factors can be effectively eliminated. These interference effects do not occur when only root interference is permitted (Wardle *et al*., 1994) indicating that resource competition is not involved. Light interference from rosette plants is unlikely since interference is strongest after the rosette leaves have decomposed and are intercepting considerably less light than were the actively growing plants. Facilitation of herbivores by *C. nutans* (see Bartholomew, 1970) is unlikely since the numbers of herbivorous invertebrates are very low under individual plants (we have confirmed this by using pitfall traps) and small herbivorous vertebrates are extremely scarce. Although decomposing plant material may enhance microbial nutrient immobilisation (Harper, 1977; Michelsen *et al*., 1995), in the case of *C. nutans* decomposing leaves cause an enhancement of soil microbial biomass which, although detectable (Wardle *et al*., 1994), is well below the level required to induce nutrient starvation in associated plants.

The effects that *C. nutans* has on the pasture ecosystem through selectively suppressing *T. repens* and symbiotic nitrogen fixation also contribute to *C. nutans* population dynamics. The suppression of *T. repens* by *C. nutans* rosettes persists for some time after the thistle has set seed and died. Since nearly all of the seeds produced by *C. nutans* individuals land very close to the parent plant (Kelly, Cameron & Alex, 1988), and *C. nutans* seedlings preferentially establish in small vegetation gaps in the pasture, the gaps provided by suppression of *T. repens* result in an ideal environment for the establishment of new cohorts of *C. nutans* seedlings. *C. nutans* also appears to tolerate low nitrogen conditions better than most forage species, so reduction of nitrogen fixation by this species may also benefit subsequent *C. nutans* cohorts. Wardle *et al*. (1994) found that *C. nutans* seedling densities were approximately 18 times greater in patches previously occupied by individual thistles than in corresponding unaffected patches of pasture. While invasion of pasture by *C. nutans* initially involves the establishment of a few individuals, these individuals can contribute to significant population growth through mechanisms which involve allelopathy affecting ecosystem-level processes, contributing to a vastly different plant community with greatly altered ecosystem properties.

The relationship between *C. nutans* and forage species appears to be reciprocal. When *L. perenne* is grown in monoculture it can exert severe effects on *C. nutans* establishment and growth while *T. repens* has a considerably smaller effect (Wardle *et al*., 1995*a*); these effects appear to be related to the differential allelopathic potential of these two forage species (Wardle *et al*., 1996). We therefore suggest that the ability of *C. nutans* to alter ecosystem properties in the way described above is in turn regulated by the allelopathic potential of *L. perenne*.

Finally, we emphasize that the effects described above appear specific to *C. nutans* and do not appear to apply to other broadleaf weeds in these pastures. Several species widely regarded as weeds in pastures do not significantly influence the growth of forage plants (Wardle & Nicholson, 1996) and may contribute to encouraging improved soil biological characteristics which probably benefit the pasture ecosystem. A more detailed study on *Senecio jacobaea* (ragwort), which has a similar growth pattern and life history as *C. nutans*, revealed that while this species may show some slight allelopathic effects (Ahmed & Wardle, 1994), in field conditions it does not reduce *T. repens* growth and nitrogen fixation in the same way as *C. nutans* (Wardle, Nicholson & Rahman, 1995*b*). In fact, individual *S. jacobaea* plants can actually stimulate forage plant growth (probably through improving microclimatic conditions in the area it occupies) and enhance the soil microbial biomass and soil animals critical for assisting nutrient cycling.

(2) **Empetrum hermaphroditum** ***and the Swedish boreal forest***

The boreal forests of northern Sweden are essentially pyrogenic in nature, with fire occurring on average approximately every 50–100 years (Zackrisson, 1977). Fire has a fundamental role in rejuvenating this system by providing conditions conducive for seedling establishment of *Pinus sylvestris* (Scots pine), through mineralising nutrients and reducing the depth of the humus layer (Van Cleve & Viereck, 1981; Tamm, 1991; Schimmel & Granström, 1996), and through the sorptive properties of the charcoal it produces (Zackrisson, Nilsson & Wardle, 1996). In systems with long fire return intervals, different vegetation types often begin to dominate, with an increased frequency of *Picea abies* (Norway spruce) and the dwarf shrub *E. hermaphroditum* (Fig. 2). These changes can be interpreted as being late-successional and are usually associated with greater humus build-up and diminished tree productivity (Sirén, 1955; Tamm, 1991).

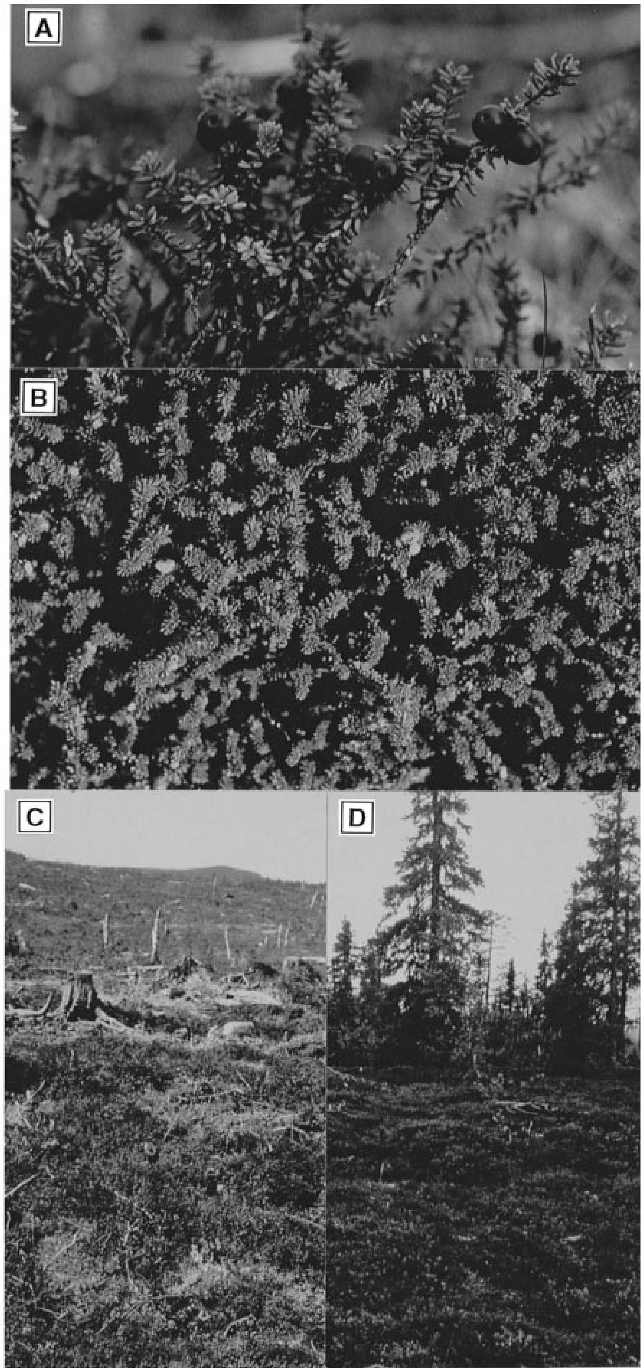

Fig. 2. *Empetrum hermaphroditum* (crowberry) in the Swedish boreal forest. (A) *E. hermaphroditum* foliage and berries. (B) *E. hermaphroditum* foliage. (C) Clearcut forest with limited regeneration and the ground cover dominated by *E. hermaphroditum*. (D) Late-successional forest with *E. hermaphroditum* domination.

Empetrum hermaphroditum is a stress-tolerant plant which establishes in the comparatively harsh conditions of late-successional ecosystems, probably because of the diminished competitive pressure of other species (see Grime, 1979). It initially establishes from seeds in post-fire successions, expands as individually located clones, and ultimately dominates the ground-layer vegetation. This pattern is reversed by fire disturbances; for example, *E. hermaphroditum* is extremely intolerant of wildfire (Vakurov, 1975). In contrast, it is often encouraged by anthropogenic disturbances such as clear-cutting. This expansion appears to coincide with enhanced allelopathic effects of *E. hermaphroditum* and this is supported by the results of allelopathy bioassay and field experiments (Zackrisson & Nilsson, 1992; Nilsson & Zackrisson, 1992; Nilsson, Gallet & Wallstedt, 1998). The allelopathic effect of *E. hermaphroditum* against associated species is consistent with the results of experiments which have shown that the seed germination and seedling growth of *P. sylvestris* is vastly reduced under *E. hermaphroditum* vegetation compared with other ground-layer vegetation types (Zackrisson *et al.*, 1995). This apparent allelopathic effect appears to be associated with the release of substances from glands on the surface of *E. hermaphroditum* leaves (Zackrisson & Nilsson, 1992; Nilsson *et al.*, 1997). Inhibitory effects of *E. hermaphroditum* appear to be linked to phenolic compounds, and in particular to batatasin III, a stilbene which occurs in anomalously high concentrations in *E. hermaphroditum* leaves and aqueous leaf extracts (Odén *et al.* 1992; Wallstedt *et al.*, 1997). These inhibitory effects appear to reduce seed germination, growth and nutrient acquisition of tree seedlings, and there is evidence of a tripartite interaction in which *E. hermaphroditum*, the moss *Pleurozium schreberi* and extramatrical ericoid mycorrhizal hyphae appear to act in combination to suppress tree seedling regeneration (Zackrisson *et al.*, 1997).

Although the allelopathic effects of *E. hermaphroditum* result from both live and dead leaf material, they appear to be strongest in humus under individual clones. Nilsson (1994) added activated carbon to field plots and greenhouse mesocosms and found that this diminished the inhibitory effect of *E. hermaphroditum* on *P. sylvestris*. This suggests that the carbon adsorbed secondary metabolites present at the humus surface which ultimately originated from *E. hermaphroditum*. Since resource competition was controlled, the partial reduction of inhibition caused by activated carbon addition is therefore attributed to reduced allelopathic effects.

Charcoal recently produced by wildfire also has the capacity to adsorb secondary metabolites produced by *E. hermaphroditum*, thus reducing its allelo-

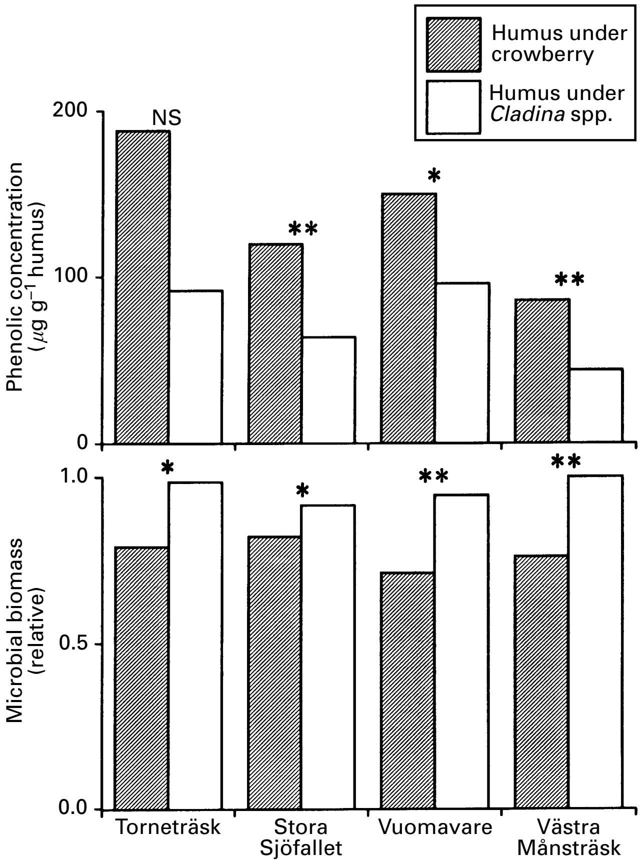

Fig. 3. Concentration of phenolics and relative microbial biomass in humus under crowberry (*E. hermaphroditum*) and under *Cladina* spp. at four sites in northern Sweden. *, ** indicate that differences between the crowberry and *Cladina* spp. differ significantly at $P = 0.05$ and 0.01 respectively; NS indicates no significant difference at $P = 0.05$. (Analyses performed using paired t-tests, for $n = 5$.)

pathic effects against other plant species and soil biological processes (Zackrisson *et al.*, 1996; see also Moore, 1996). Following fire, charcoal is produced in sufficient amounts to have important ecological effects; its sorptive ability diminishes over the next century due to increasing occlusion by organic debris, although this occlusion is reversed by subsequent heating (e.g. by further fires) which reactivates the charcoal. The reduction of charcoal activity over time is coincident with increased density of *E. hermaphroditum* and ultimately with increased allelopathic effects.

Secondary metabolites from *E. hermaphroditum* are critical not only in influencing populations of other plant species but also in determining other biotic components of the ecosystem. For example, the fungal component of the *P. sylvestris* mycorrhizal symbiosis is strongly impaired by *E. hermaphroditum* extracts and this reduces nitrogen acquisition by pine seedlings (Nilsson *et al.*, 1993). In relation to above-ground primary consumers, *E. hermaphroditum* is largely avoided by herbivores (Grime, Hodgson & Hunt, 1988) and this could be expected to result in simpler food webs in systems dominated by this species. In the below-ground system, litter and humus produced by *E. hermaphroditum* appear to be highly unfavourable to the decomposer biota. These inhibitory effects are attributable to the very poor quality of foliage and litter of *E. hermaphroditum*, with secondary metabolites almost certainly having an important role. The humus under *E. hermaphroditum* appears to provide a highly unfavourable environment for microbial activity with the decomposition rate of test litter placed in *E. hermaphroditum* humus being only 70% of that placed in *Vaccinium myrtillus* (bilberry) humus (Wardle & Lavelle, 1997). This is related to the low levels of microbial biomass in *E. hermaphroditum* humus relative to that in humus under different ground cover such as the lichens *Cladina* spp. (Fig. 3). We have also observed severely reduced populations of soil animals, particularly macrofauna, in *E. hermaphroditum* humus. This suppression of soil organisms is not due to the nitrogen status of *E. hermaphroditum* litter but is more likely to be due to the high levels of phenolics present (Fig. 3). We therefore suggest that polyphenolics produced in *E. hermaphroditum* foliage have important effects on a range of components of the boreal forest ecosystem including other plant species, above-ground consumers, the soil biota and decomposition processes.

The retardation of the decomposer subsystem by secondary metabolites of *E. hermaphroditum* has important consequences for ecosystem function. In systems dominated by this species and with diminished fire frequency, there is considerable humus accumulation. Recent studies on lake islands in northern Sweden (Wardle *et al.*, 1997*b*) indicate that islands with long-term domination by *E. hermaphroditum* have humus depths of up to 1.2 m, while islands dominated by other ground-layer species have only approximately 5 cm of humus. This accumulation of humus under *E. hermaphroditum* is coincident with higher water-soluble phenolic concentrations, reduced microbial activity and reduced rates of decomposition and nitrogen mineralisation. Further, large amounts of nitrogen are locked up in the humus of those islands dominated by *E. hermaphroditum*, and plant acquisition of nitrogen from the humus is significantly reduced. Adverse effects of *E. hermaphroditum* are also apparent

Table 1. *Comparison of properties related to allelopathic effects at the ecosystem level between* Carduus nutans *in New Zealand dairy pastures and* Empetrum hermaphroditum *in Swedish boreal forests*

	C. nutans	*E. hermaphroditum*
Strategy (*sensu* Grime, 1979)	Competitive ruderal	Stress tolerator
Response to disturbance	Positive	Negative (fire), positive (clearcutting)
Nature of spread	From individuals serving as foci	Mainly clonal spread
Shoot:root ratio	Much greater than associated species	Much greater than associated species
Response to nutrient enrichment	Reduced through increased competition from other species	Reduced through increased competition from other species
Source of allelopathic effects	Decomposition of leaf litter	Leaf leachates, decomposing leaves
Target species for allelopathic effects	White clover	Scots pine and birch seeds and seedlings
Effect on symbioses of target species	Reduces clover-*Rhizobium* nitrogen fixation	Reduces effectiveness of pine ectomycorrhizal system
Preference by herbivores	Less preferred than forage species	Almost entirely avoided
Effect on soil microbial biomass	Slightly positive	Negative
Effect on soil animals	Positive	Highly negative
Decomposition of material	Extremely rapid	Slow
Contribution to humus accumulation	Negligible	Considerable
Diversity of plant community	Low ($\leqslant$ three main species)	Low ($\leqslant$ three main species)

in areas where clearcutting of forest has been performed and prescribed burning not conducted. This type of management leads to considerable domination of the ground layer by *E. hermaphroditum*, and this is extremely detrimental to tree establishment. The consequence is an ecosystem which has an entirely different stable equilibrium with vastly reduced productivity and tree cover (Fig. 2).

(3) *Parallels between* C. nutans *and* E. hermaphroditum?

We have considered biotic interactions involving invasive plants in two greatly different ecosystems in which we believe allelopathy has significant effects on ecosystem properties. Both these invasive plants create patch effects, resulting in the modification of the environment under individual plants. There are important differences between the nature of allelopathic effects in the two systems but also there are some notable parallels (Table 1). In *C. nutans*, the effect disproportionately influences a particular species (*T. repens*) and a specific process (symbiotic nitrogen fixation) and is generally not strongly negative to other biotic components of the pasture system. In contrast, *E. hermaphroditum* produces metabolites which affect a wide range of organisms. These differences appear linked to the differing ecological strategies of the two species; the allelopathic effect of *C. nutans* has the net effect of promoting subsequent thistle cohorts, while the effects of *E. hermaphroditum* are more general and thus more consistent with its role as a stress tolerator (see Coley *et al.*, 1985). Despite these differences, similarities also exist. For example, in both cases effectiveness of symbiotic associations involving the species are particularly susceptible and this results in reduced nutrient acquisition and thus reduced competitive ability of the target plants. Both examples show that allelopathic effects are more appropriately considered in an ecosystem-level context, rather than simply considered as an association between two plant species.

Another parallel between both systems is that they are characterized by a relatively low plant species diversity, with one or two species dominating most of the plant biomass present. This enables one plant species to dominate the biochemistry of the soil under it in large patches, allowing it to affect other plants and processes significantly. We suggest that allelopathy is much less likely to occur in a community with high plant diversity because no one species would have the opportunity to dominate the nature of the metabolites entering the ecosystem. In this context, it is apparent that the more persuasive examples of allelopathy in the literature involve situations in which there is relatively low species diversity and one plant species can dominate patches in the community (e.g. Muller, 1966, 1969; Richardson & Williamson, 1988; Williamson, Richardson & Fischer, 1992). The study of Stowe (1979), which failed to find evidence for allelopathic effects (and is often therefore quoted by critics of allelopathic research) was conducted in a high-diversity grassland community in which allelopathic effects would be expected to be unimportant. Enriched plant diversity has been proposed as having possible effects in enhancing community stability (McNaughton, 1993) and maintaining components of ecosystem function (Naeem *et al*., 1994; Tilman, Wedin & Knops, 1996; but see Huston, 1997; Wardle, Bonner & Nicholson 1997*a*). We believe that in a species-rich community, allelopathic plant species are less likely to have a dominating effect on plant community structure, and that there is less opportunity of ecosystem function being impaired by the secondary metabolites of a single plant species.

V. CONCLUSIONS

1 Allelopathy has frequently been proposed as a potential mechanism for structuring plant communities. Most studies which have specifically investigated allelopathy have evaluated its role in plant-plant interactions, but acceptance of allelopathy in plant population biology is limited largely because of problems associated with methodology, and difficulties of relating results of bioassays for testing allelopathy to patterns of vegetation association in the field.

2 While there are some instances in which there is evidence of plants affecting each other at an individual level through producing phytotoxins, plants with allelopathic potential are more likely to have wide-ranging influences at the ecosystem level because the secondary metabolites which they produce are also likely to be unfavourable to other organisms such as symbiotic and saprophytic microflora, soil animals and herbivores.

3 The effects of plants with allelopathic potential on other organisms may ultimately result in net changes in ecosystem processes and function, which may be important in shaping plant community structure in the long term.

4 These concepts are illustrated through the use of two widely contrasting examples in which invasive plant species with demonstrated allelopathic potential can alter aspects of ecosystem function through the production of phytotoxins, i.e. *Carduus nutans* (nodding thistle) in New Zealand dairy pastures, and *Empetrum hermaphroditum* (crowberry) in Swedish boreal forests. Comparison of these two systems demonstrates that the effects of secondary metabolites produced by allelopathic plants are far more wide ranging than simply altering the success of other plants.

5 It is concluded that the effects of the production of secondary metabolites by plants with allelopathic potential are better appreciated at an ecosystem level rather than a population level (e.g. plant-plant interference) context.

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