The ecology of the invasive moss *Campylopus introflexus* in the North York Moors National Park

by

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I hereby declare that the work presented in this thesis is the result of my own investigation and has not been accepted in previous applications for the award of a degree. Exceptions to this declaration are part of the field data used in chapter 4, which was collected and made available to me by Dr. M.B. Usher. The distribution map on *Campylopus introflexus* was provided by P.T. Harding (Biological Records Centre, ITE, Monks Wood). R.C. Palmer (Soil Survey and Land Research Centre, University of York) made available to me the soil and climatological data of the area, and helped me to obtain the corresponding interpolation values for the sampled sites.

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Abstract

Campylopus introflexus is one of the rare examples of invasive bryophytes worldwide. This moss has recently spread, outside its original distributional range in the Southern Hemisphere, into Europe (first recorded in 1941) and into North America (in 1975). *C. introflexus* invasion is important because of its capability of spreading aggressively within newly colonized habitats.

The main goals of the thesis were: (1) to determine the factors controlling the distribution of *C. introflexus* in the North York Moors National Park and (2) to evaluate the potential impact of the moss on the dynamics of the moorland communities, specifically on *Calluna*, its dominant component. It was hypothesised that the interaction should take the form of modifications to the regeneration niche of *Calluna*.

A vegetation survey of the National Park was conducted to analyze the association of *C. introflexus* with the vegetation and other environmental factors. It was found that *C. introflexus* has a wide distribution among *Calluna* dominated communities, but the preferred habitat is where *Calluna* has, on average, 43% cover and 9 cm in height. The carpets of *C. introflexus* tend to fragment producing loose blocks which may provide the moss with an additional form of propagation contributing to its ability to retain colonised territory.

The results of laboratory experiments demonstrated that, despite inducing lower germination, *C. introflexus* has no direct inhibitory effect on *Calluna*. Heather plants growing on moss carpets performed better than those growing on open ground.

A field experiment showed that, although *Calluna* is able to germinate on top of carpets of *C. introflexus*, the seedlings failed to establish themselves. Therefore, heather cover regeneration may be delayed if a carpet of *C. introflexus* more than 1 cm thick develops in the vegetation gaps. Another field experiment showed that *C. introflexus* colonizes, after fire, practically at the same time as the other main components of the moorland. The small moss carpets showed mostly a positive association with the occurrence of *Calluna* seedlings.

Although it is possible for the moss to delay the development of the Callunetum, eventually *Calluna* will outcompete the moss. How does an obviously inferior competitor manages to remain in the community? Disturbance is obviously paramount in this regard but in addition, it is argued, a non-equilibrium rationale to understand the dynamics of the community is useful in this case.

1. Introduction

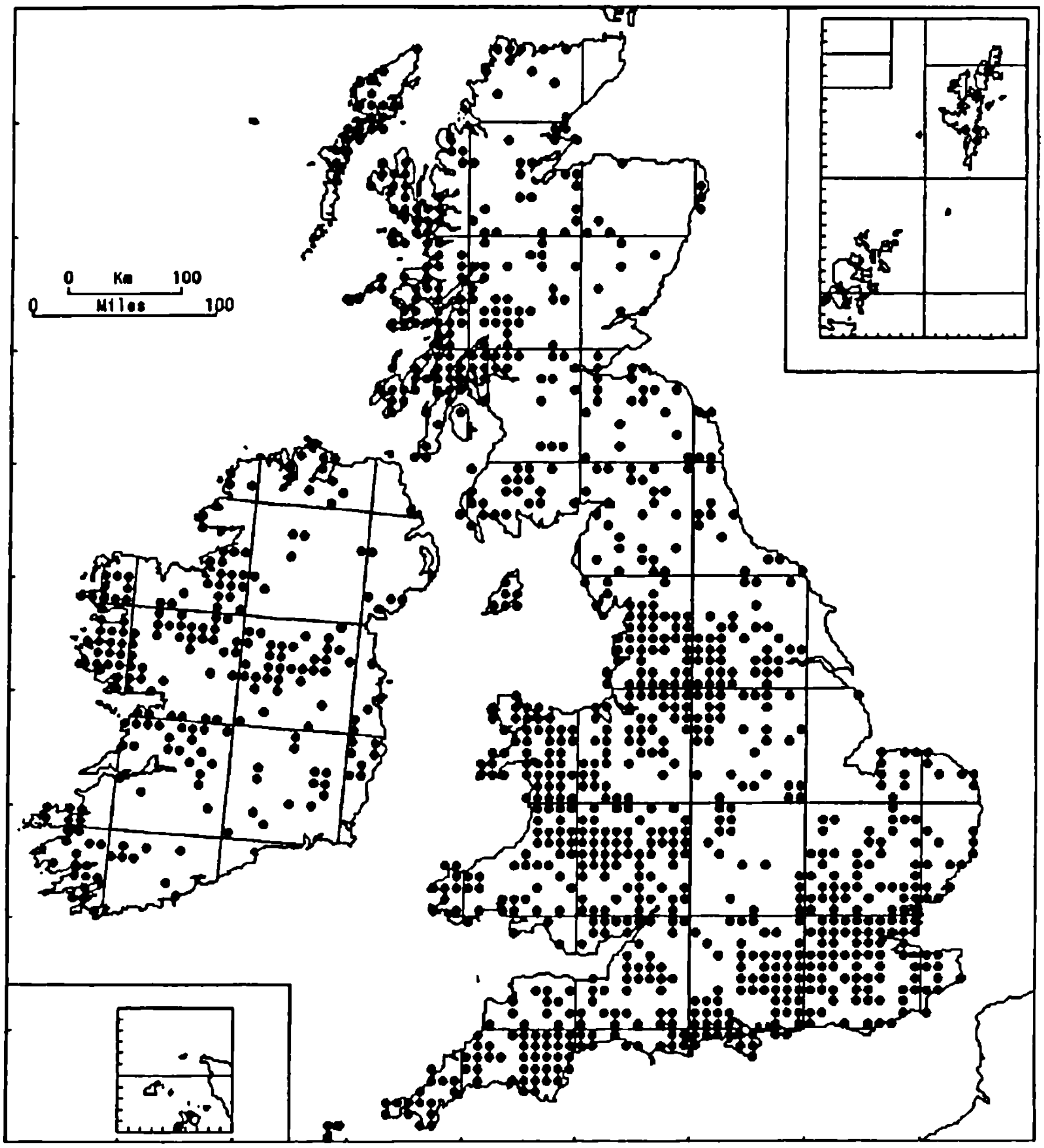
1.1 The invader: *Campylopus introflexus*

Campylopus introflexus (Hedw.) Brid. is a species that has recently spread outside its original distributional range in the Southern Hemisphere, where it is found from subantarctic islands to subtropical regions (Frahm 1984). Initially, *C. introflexus* was considered to be an almost cosmopolitan species, but Giacomini (1955) demonstrated that there were in fact two species: *C. pilifer* Brid. (=*C. polytrichoides* DeNot.) and *C. introflexus*. Some of the characteristics used by Giacomini to differentiate the two species have been questioned by other authors (Richards 1963, Barkman and Mabelis 1968 and Jacques and Lambinon 1968). However, Frahm (1972, 1974 and 1975) and Gradstein & Sipman (1978) have shown that the two species can be differentiated both anatomically and ecologically. The aim of this chapter is to provide a review of the information available on the biology of *C. introflexus* and to examine its role as an invasive plant.

The invasion of the Northern Hemisphere

The first record of *C. introflexus* in Europe dates from 1941, from a locality in Britain (Washington, Sussex). From that date onwards it has been reported with increasing frequency from new localities in the British Isles (Richards 1963, Richards & Smith 1975). By 1970s it had been recorded in 91 British and 39 Irish vice-counties as well as in the Channel Islands. An approximation to the current distribution is illustrated in Figure 1.1 where all the records up to September 1991 held at the Biological Records Centre are included. Elsewhere in Europe it was reported later. For instance in Brittany it was found in 1954 and in The Netherlands

Figure 1.1. Distribution of *Campylopus introflexus* in Britain and Ireland. Based on all the records up to 1990 held at the Biological Records Centre.



are dated around 1960 (Meulen, Hagen & Kruijsen 1987). Richards (1963) suggested that the initial European introduction may have occurred either in Brittany or in the British Isles, from where it afterwards spread; however, he also pointed out that it is possible that this moss may have invaded Europe at several points independently. All the European localities where *C. introflexus* was first recorded are near seaports, suggesting a possible unintentional human introduction (Richards 1963). According to Frahm (1980) this species has also started to expand into North America (the earliest collection in that geographical area was made in California in 1975). Its current world distribution is summarised in Table 1.1 and Figure 1.2.

The recent expansion of the distributional area of *C. introflexus* into the Northern Hemisphere is not the only case in the genus. For a long time *C. pyriformis* was regarded as endemic to the oceanic parts of western Europe, but Corley & Frahm (1982) found that this species was widespread in subantarctic regions of the Southern Hemisphere, with a similar pattern to that of *C. introflexus*, and therefore they suggested that it might also have been introduced into Europe. If this is true the introduction must have happened in the 17th or 18th century (Frahm 1984, Frahm & Arts 1990). Frahm & Arts (1990) have now found *C. pyriformis* in North America (Louisiana and Mississippi), indicating another advance front on the expansion of its geographical range; they considered that it is already naturalized there, but that it has been largely overlooked or mistaken for *C. surinamensis*.

As a whole, *Campylopus* seems to be a remarkably successful genus worldwide. According to Frahm (1990) there are only a few genera of mosses with a number of species comparable to *Campylopus*. According to Smith (1978), *Campylopus* has *ca.* 750 species, which compares only to other large genera like

Table 1.1. Countries where *Campylopus introflexus* has been found.

SOUTHERN HEMISPHERE
Argentina
Chile
Uruguay
Brazil[*]
South Africa
Australia
New Zealand
New Caledonia

NORTHERN HEMISPHERE
British Isles
France (Atlantic coast)
Belgium
The Netherlands
Germany
Denmark
Norway (South)

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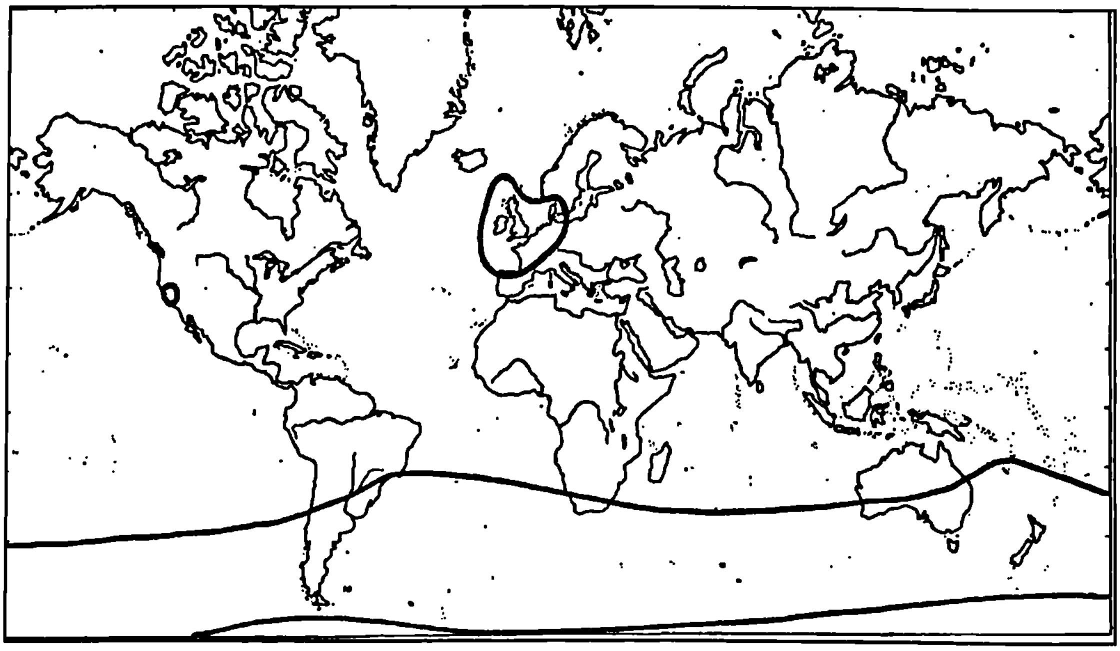
[*] Up to the South East coast, that corresponds to the northern limit of *C. introflexus* in the southern hemisphere (Frahm 1984).

Figure 1.2. World distribution of *Campylopus introflexus* (based on the maps provided by Gradstein & Sipman 1978, and Frahm (1980).



Campylopus has *ca.* 750 species, which compares only to other large genera like *Bryum* (*ca.* 1050 species), *Barbula* (*ca.* 500 species) and *Fissidens* (*ca.* 1000 species?). According to Frahm (1990) recent worldwide revisions of the taxonomy of *Campylopus* have reduce that original figure to less than 200 species (but this has also been the case of other bryophyte taxa); despite this reduction Frahm estimates that 1/3 of all mosses belong to the genus *Campylopus*. Worldwide, species of this genus can be found from sea level to 4,500 m of altitude on a variety of substrates which are, however, always acidic. Compared with other genera of mosses, and especially when considering that 40% of the species in the genus are known only from sterile forms, it is clear that vegetative propagation is relatively important in *Campylopus* (Frahm 1990). The range of vegetative propagation methods in the genus spans from microphyllous branches and deciduous leaves to special brood leaves, broken leaves, stem tips and rhizoidal tubers.

Frahm (1988) suggested that the genus *Campylopus* originated in the Mesozoic era in the southern part of Gondwanaland (corresponding to the subantarctic belt), under relatively cool and moist climatic conditions. Frahm, furthermore, considered that the successful spread of the genus can be explained by the high plasticity of the anatomical structure of the costa, which has allowed the species to adapt to many different ecological situations; because the dorsal lamellae of the costa provide a means to maintain a favourable water balance (species from drier habitats tend to present longer lamellae). Another source of evidence for the proposed origin of the genus is provided by the geographical pattern of the number of species of *Campylopus*. There are numerous species of this genus in the Southern Hemisphere (14 in the Antarctic region, *ca.* 80 in South- and Central-America, *ca* .50 in Africa and *ca.* 30 in Australia and Indonesia) but only a few in the Northern

Hemisphere: *ca.* 15 in North-America and a similar amount in Europe, *ca.* 10 in Asia, and merely one in the Arctic regions (Frahm 1988).

Taxonomy and identity

According to Frahm (1988 and 1990) *C. introflexus*, *C. pilifer* and a third species *C. aureus* (which does not occur in Europe) form a complex of closely related species which, together, occupy the entire Southern Hemisphere and subantarctic islands (from South Georgia to the tropics in SE-Brazil, Réunion and New Caledonia). In some areas where *C. introflexus* and *C. pilifer* overlap hybrids have been found (for example in Northern Argentina and in the Seychelles). This indicates that these two species are genetically very similar. Frahm (1988) suggested that, because of the occurrence of hybrids and the vicariant ranges, these species most probably have developed from the same ancestor. Frahm goes on to suggest that *C. introflexus* may be the ancestor of both *C. pilifer* and *C. aureus* which differentiated when the former invaded the tropical montane regions, extending northwards into the Holarctic during the Tertiary, where they remained in oceanic regions during the climatic changes of the Quaternary.

Within this complex of species, the closest are *C. introflexus* and *C. pilifer*. The substantial affinity between them resulted in the confusion in the identity of the two species mentioned in the introduction to this chapter. Nevertheless, there are consistent morphological and ecological differences. According to Gradstein & Sipman (1978) the main diagnostic characteristic is the structure of the leaf nerve, which in transverse section shows dorsal lamellae composed of only 1 row of cells (occasionally 2) in *C. introflexus* and 2-4 rows of cells in *C. pilifer*. Granstein & Sipman (1978) found another useful difference in the size of the seta, which is between 5 and 8 mm long (occasionally up to 10 mm) in *C. introflexus*, contrasting with 3-5.5 mm (occasionally up to 9 mm) in *C. pilifer*. There are also important phenological differences between these two species. All over their distributional ranges, it is common to find *C. introflexus* specimens with capsules, but *C. pilifer* has only rarely been observed in this stage. Similarly Gradstein & Sipman (1978) found that the spores in *C. introflexus* were never aborted as opposed to the case of *C. pilifer* where they frequently are.

These differences may have ecological significance, on the one hand, because of the common occurrence of capsules Richards (1963) considered that the ability of *C. introflexus* to colonize new habitats could be related to the dispersal by means of spores. On the other hand Frahm (1990) pointed out that, physiologically, the longer costal lamellae can be regarded as an adaptation to relatively dry habitats because of an increased capacity for storing water. Although the participation of this structures on the hydric balance of the moss seems both feasible and important, Proctor (1979) suggested that the storage function is not likely to be significant in this kind of system. He proposed that, instead, their relevance should be related to the need to combine superficial capillary water conduction and gas exchange for photosynthesis in the same leaf surface (although they may serve mechanical functions too).

A general description of the morphology of *C. introflexus* is, according to Smith (1978), as follows (Figure 1.3). The gametophytes of this moss are plants 0.5-5.0 cm tall, with swollen perichaetia or perigonial nodes and slender internodes. They have a reddish-brown tomentum which is often rather scanty. The leaves are between 2.5 and 6.5 mm long, straight, erecto-patent when moist, more tightly appressed when dry. Their shape is variable, usually lanceolate, subulate or acuminate, with entire blades. The leaves have a prominent nerve that is excurrent

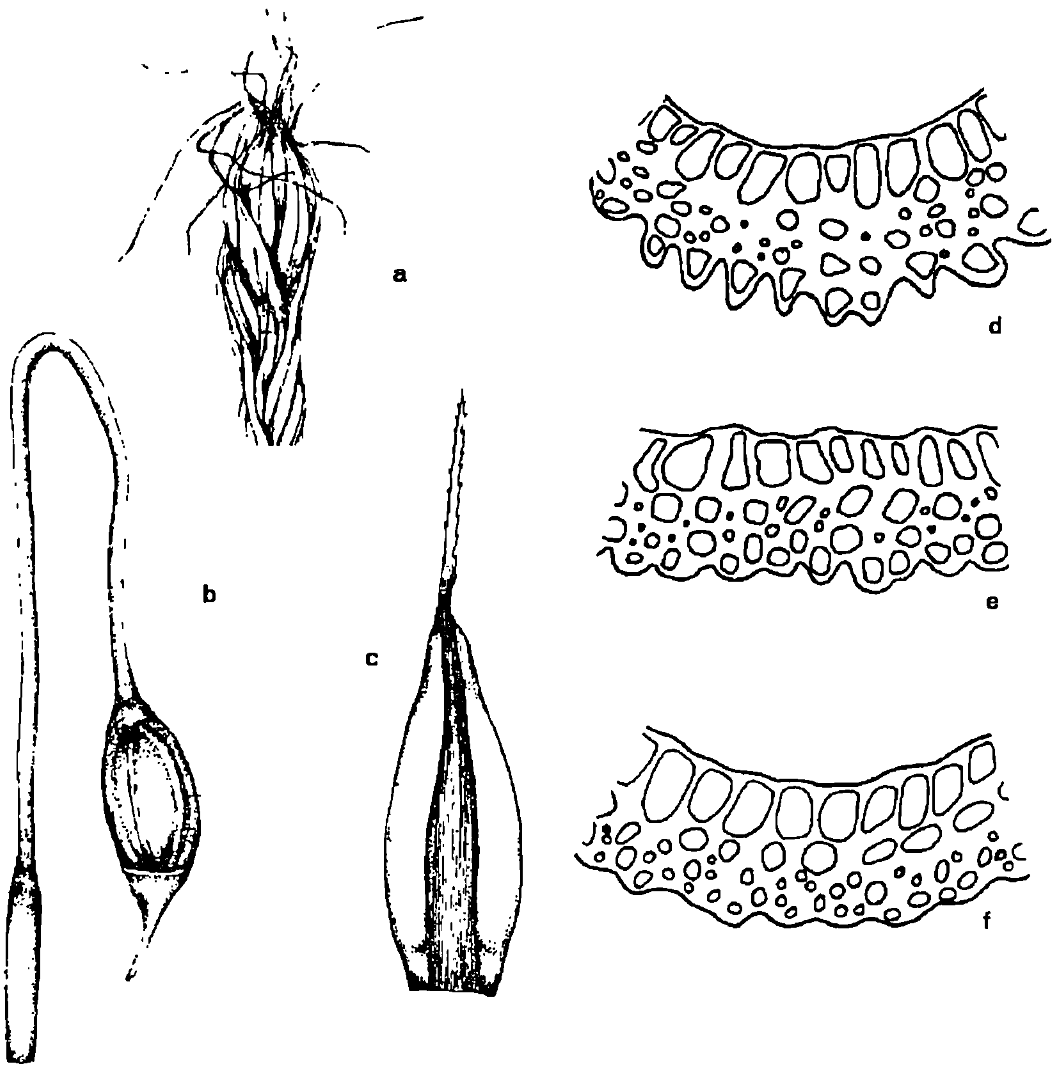


Figure 1.3. Main morphological structures of *Campylopus introflexus*: (a) dry shoot tip, (b) capsule (*ca.* ×17), (c) leaf (*ca.* ×17), (d-f) leaf cross section showing lamella (*ca.* ×480): (d) near leaf tip, (e) midle of the leaf and (f) near leaf base (drawings adapted from Smith 1978).

in a toothed hyaline hair-point which is between 3/4 and 1/2 of the length of the rest of the leaf but sometimes very short or lacking in some leaves, especially in the internodes. The hair points are strongly squarrose, particularly on nodal leaves. The form of vegetative reproduction in *C. introflexus* is by means of deciduous leaves and stem tips. It can form dense carpets (Figure 1.4) that break up easily, especially when they are thick (more than 2 or 3 cm deep).

Ecology

The ecology of *C. introflexus* and *C. pilifer* provides further support to the consideration of them as different species (Table 1.2). Both species occur where the climate is humid (at least periodically). *C. pilifer* seems to be restricted to places where the soil is dry, acid, nutrient-poor and with a low organic matter content. It prefers fairly open conditions and rarely occurs on the bases of trees or on rotten wood (Gradstein & Sipman 1978). According to Richards (1963), *C. introflexus* in Britain has a wider ecological range than *C. pilifer*. The most common habitat of *C. introflexus* in the British Isles seems to be peat on blanket bogs and moist heaths and moors. It has been found growing on fen peat at pH 6.5 to 7.0 and is possibly less oligotrophic and calcifuge than *C. pilifer*. The wider ecological amplitude of *C. introflexus* is also clear elsewhere. Worldwide it grows better at low elevations, usually below 1000 m altitude; it can develop over soils ranging from dry to humid, which are usually non-calcareous and nutrient-poor. These soils could range from peat to mineral. The suggestion by Richards (1963) that *C. introflexus* is less calcifuge than *C. pilifer* seems to be confirmed by the fact that it has been found growing on calcareous dunes in The Netherlands (Meulen, Hagen & Kruijsen 1987). *C. introflexus* also prefers open situations but, in contrast with *C. pilifer*, can often

Table 1.2. Ecological requirements of *Campylopus introflexus* and *C. pilifer*.

Factor	*C. pilifer*	*C. introflexus*
Climate	Humid	Humid
Altitude	< 3500 m	< 1000 m
Habitats:		
open sites	frequent	frequent
tree bases	rare	frequent
rotten wood	rare	frequent
Soil moisture	low	low to high
Soil nutrients	low	low
Soil pH	acidic	acidic to neutral
Soil contents of organic mater	low	low to high

Figure 1.4. Carpet of *C. introflexus* in a slope near Hutton-Le-Hole in the North York Moors National Park. This broken aspect is common in late spring and summer. During the winter the carpet re-establishes itself forming a more continuous layer.

be found growing on bases of trees or on rotten wood. In Europe *C. introflexus* is favoured by disturbance, possibly because of the lower competitive pressure that the perturbation produces (Gradstein & Sipman 1978). It is however, not restricted to disturbed habitats. Clément & Touffet (1988) found that, in Brittany, *C. introflexus* is a xerophitic species very tolerant to soil constraints, but they also found that its propagation was relatively slow.

1.2 The problem

Weeda (1987) reported 220 vascular plants and 3 mosses that were neophytes in The Netherlands, and from this total only *C. introflexus* and two vascular plants were spreading aggressively independent of human interference. Meulen, Hagen & Kruijsen (1987) described, also in The Netherlands, coastal dunes with extensive carpets of *C. introflexus* (2 to 10 cm thick), covering from 25% to 100% of the ground. They noted that under these conditions other species, even grasses and forbes, become scarce (but *Cladonia* spp. could be abundant on top of the moss carpet). The same authors indicated that the infested costal dunes could be calcareous or non calcareous, and also that the invaded sites were not necessarily subjected to human disturbance. However, dune communities are clearly prone to natural perturbation and are thus consistent with the general consideration that *C. introflexus* is favoured by disturbance. In addition, Joenje (1987) pointed out that any of the natural communities in The Netherlands, that have been invaded by alien species, can be described in general as open ecosystems of extreme or dynamic environments (*i.e.* governed by abiotic factors such as drought, salinity, low nutrient status, or recurrent physical disturbances).

It is interesting to consider whether similar aggressive behaviour by the moss can occur in other communities. It is generally agreed that the communities that are most vulnerable to invasion by alien species are those from mesic environments, particularly during initial stages of succession (Joenje 1987, Rejmánek 1989). This seems to be due to the fact that most invasive species are ruderals. Indeed this seems to be the case in the example from The Netherlands where the aggressive invasion by *C. introflexus* occurs during the early stages of the colonisation of sand dunes. Therefore, disturbance seems to be a crucial factor predisposing a community to invasion by pushing it into a process of secondary succession. However, because it often is human disturbance that initiates the sequence, a more intensive human-mediated import of propagules at the beginning of the process can be expected, and hence it is not clear if these successional stages are themselves more susceptible to invasions (Rejmánek 1989).

Because of the significance of disturbance for the process of invasion, it is important to provide a clear definition of the concept. In this work the one proposed by Grime (1979) is used: 'Disturbance consists of the mechanisms which limit the plant biomass by causing its partial or total destruction'. Rejmánek (1989) pointed out that the probability of successful invasion by an alien species seems to be crucially dependent on the extent and type of disturbance, on the number of incoming propagules of the non-native species and on the length of time the community is exposed to that import of propagules. Rejmánek considered that the amount of open space created by the destruction of biomass might be the only really general factor responsible for plant invasions, because it has been observed in some situations that the total amount of biomass or cover are good indices of community resistance to invasions, in preference to species composition or number of species.

Rejmánek (1989) constructed a model to explore the conditions that make a community susceptible to an invasion. The model was based on Lotka-Volterra competition equations for four species (one of them a neophyte) with one dimensional diffusion and a discrete stochastic harvest varying both spatially and temporally. He found that even if the invader is a weaker competitor than the rest of the species, some regimes of disturbance allow its invasion. Moreover, the invasion might be successful even if an external source of propagules exists only temporarily and the invader does not disperse faster than most of the native species. There should be little doubt that disturbance facilitates invasion; after all this is the basis of the procedures that humans have used for centuries to introduce plants (some of them weak competitors) into a wide variety of habitats. It was also human disturbance that opened up the forests to the invasion of the local Gramineae and Ericaceae and eventually eliminated the trees from the landscape in many places. Further human activities kept these communities in a successional stage that eventually gave rise to heathlands (Gimingham 1972).

Given the ecological behaviour of *C. introflexus* in Britain it could be expected to have the potential of producing an impact, similar to that in The Netherlands, on heathlands and moorlands where it is already widespread. Burning and cutting of the vegetation are forms of disturbance traditionally used in the management of heathlands with the purpose of reducing a closed canopy to an open situation where vigorous regrowth of the vegetation can take place. This practice seems to give a good opportunity for the invasion of *C. introflexus*. Indeed, extensive carpets of the moss have been observed in some places of the British Islands; for example in County Galway (Ireland) it has been found covering an extensive area of exposed peat to the exclusion of all other bryophytes (Richards

1963). A similar situation has been observed in some heathland areas of the North York Moors National Park. Therefore, if the moss is to have an impact on a heathland community it should take place early in the succession and should result in an alteration of the 'normal' course of the successional process. It is possible that the moss could have an impact on the regeneration process of moorland communities, at least slowing down its rate of recovery following fire or cutting.

1.3 Hypothetical mechanisms of interaction

It is reasonable to expect that the initial stages of development of the moorland are susceptible to invasion by alien species and thus it is not surprising to find that *C. introflexus* occurs in this stage of the Callunetum. However, it is more difficult to predict what the extent of the impact of the invasion may be (Crawley 1987). Joenje (1987) pointed out that invaders establishing in new areas often show a lag-phase, then increase (apparently without controlling biotic interactions) wedging their way into native ecosystems where they take hold of ecologically unoccupied space and, in some cases, after having reached high densities their numbers are reduced by the attack of some disease or by predation. Similarly Rejmánek (1989) observed that, in general, the cover of invading species tends to peak between 5 and 10 year after an initial perturbation and then declines. It seems that this successional 'repairing' function of native vegetation is rather universal in continental situations, but on islands it seems to be much slower, incomplete or even absent (the reasons for this difference are complex and still not fully understood). On the other hand not all neophyte species have a disruptive effect on the communities where they have arrived. For instance *Orthodontium lineare* is another neophyte moss introduced into the British Isles at the beginning of this century that has spread widely in western and central Europe. Nevertheless, it has caused no apparent interference in the habitats where it has established itself (Hedenäs *et al.* 1989).

Joenje (1987) has suggested that the degree of invasive success of a neophyte may be related inversely to the number of functional links the species has in its native community. This is inferred from the observation that generalists are usually better invaders. Grubb (1989) pointed out that colonizing plants have distinctive growth-forms corresponding to the substrate types where they establish; in particular, the pioneer species that are more successful in sites that are poor in resources or have unstable substrates (as a result of tides, wind or other erosion factors) are typically long-lived. Another important characteristic of a pioneer species is its ability to arrive at newly-created open sites as quickly as possible, which usually implies effective means of dispersal through space (small seeds or spores and wind dispersion) but the availability of a propagule pool *in situ* is another possibility (dispersal through time). *C. introflexus* is a perennial moss with spores between 10-14 µm (smaller than the average for the mosses) which prefers open conditions in a wide range of environmental combinations and with an ability to profit from disturbance. Therefore, *C. introflexus* may be defined as both a generalist and a pioneer species. Similarly, Verdus (1979) has shown that the growth of the vegetative offshoots of *C. introflexus* under humid conditions give rise to the development of a large number of gametophytic branches, which could contribute to explain (together with the wide production of spores) the rapid and dense colonization of bare ground. All this support the idea that *C. introflexus* is a pioneer species. However, Verdus (1979) has also suggested that the persistence of the plant in the areas where it has colonized, is different from the usual behaviour of pioneer species, which tend to be gradually replaced by more competitive species. Because of this behaviour, Verdus considered that *C. introflexus* is different to other pioneer species and closer to the behaviour of *Dicranum montanum* Hedw. (=*Orthodicranum montanum* (Hedw.) Loeske) and *Orthodontium lineare* Schwaegr., which are two other species in the process of expanding their distributional areas.

Because moorlands are communities with economic importance, and taking into account the effects that the moss has had in some costal dunes in The Netherlands, the possibility of a 'negative' impact on the dynamics of the community has to be particularly considered. Heathland management aims at rapid regeneration, minimizing seral stages, maintaining the production of edible *Calluna vulgaris* (L.) Hull[1] material for sheep and grouse. It is known that when regeneration is delayed (for example when burning has been mis-managed) the consequences may be erosion and the establishment of unwanted species, like *Pteridium aquilinum* (Gimingham 1972). In cases of severe fire damage the *Calluna* seed bank can be completely destroyed, leading to a slow regeneration where the colonizing community may be, for a long time, confined mainly to lichens and mosses such as *Polytrichum juniperinum* or *P. commune* (Gimingham 1972, Maltby, Legg & Proctor 1990).

At the population level, it seems evident that the concept of competition lies at the core of the interaction between the moss and the other plants. Unfortunately, many different interpretations of what competition is have been used which, in turn, have made its effect on natural populations very difficult to demonstrate (Keddy 1989). Because of this, there has been for a long time much confusion about its meaning, to the point that Harper (1961) proposed that the use of the term should be abandoned. However, Grime (1979) considered that competition is too important a

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[1] Subsequently referred to only by the generic name.

concept to be disregarded. His definition of competition states that it is 'the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space', and it is this interpretation that will be given to the term in this work. Although, a coherent body of competition theory should be useful to understand the impact of the invasion by *C. introflexus*, such framework is currently not available (Keddy 1989).

At the ecological community level, it can be expected that the impact of the moss invasion in the heathlands may lead, if it is extensive enough, to the disruption of the development of the moorland community. Considering the successional models of Connell and Slatyer (1977) the impact of the invading moss should correspond to the inhibition model, which consists of either a complete suppression or a reduced establishing capacity of one species due to the presence of another. If this inhibition model applies and considering that given the alien origin of *C. introflexus* it is likely that there would be few natural enemies of the moss in Europe, a substantially long-lived stage of moss dominance can be envisaged. It is believed that preempting the space available for colonization provides the best opportunity for *C. introflexus* to be able to exclude other species, because as soon as other plants get established, particularly vascular species, it is certain that they will eventually exert a competitive dominance over the moss, possibly leading to its local exclusion.

There are several examples where the inhibition model has been found to apply. For instance Whitmore (1985) mentioned an abandoned forest field in Kepong, Malaysia where a fern blanket kept the trees at bay for over 10 years, before the ferns were shaded out. *Calluna* is another example in forest plantations of *Picea sitchensis*, where it is known to inhibit the development of this tree species; the effect of *Calluna* has been attributed to an allelopathic effect on the tree (Gimingham 1972). However, Finegan (1984) pointed out that the inhibition model may not be a general phenomenon, at least in forest succession, because it seems to apply to areas that are not typical (they are usually small or extremely small and sometimes have an unusual management history). *Pteridium aquilinum* provides another example. This fern is having a profound effect on heathlands (among other communities), where its vigorous growth and presumed allelopathic effect are combined to exclude many of the original components of the heathland, including *Calluna* (Gimingham 1972). The bracken has been considered as a 'permanent ecological opportunist' and as one of the world's worst weeds (Heywood 1989). Some of the reasons for its success are its high disease resistance, low palatability to herbivores, its allelopathic effect on competing species, the effectiveness of the long distance dispersal by its minute spores, its long vegetative lifespan, its tolerance of burning, its wide edaphic and climatic tolerance and its broad cytological and genetical variability (Smith and Taylor 1986). However, Grime (1979) pointed out that sites dominated by *P. aquilinum* are characterized by the presence of a very dense accumulation of litter which shows comparatively little variation with season (in contrast to the phenology of the aerial cover); therefore, Grime suggested that the litter, either by shading or by physical impedence of germination, establishment and growth, restricts the frequency of other species (especially smaller or slower-growing species). In all the forest examples mentioned above the inhibition is carried out by a normally subordinated component of the community. The explanation of this effect can be found by considering that any plant goes through a series of stages during its development. Each one of these stages puts the plant in a particular kind of interaction with a subset of the local biota. In the forest cases it is the interaction between the early stages of development of the trees and the understorey components that results in the suppression of the former. Similarly, in the case of *P. aquilinum* it is the effect of the fern's litter on the early development stages of other species that produces the inhibition (probably magnified by allelopathy). This suggests that this type of interaction should be analyzed by considering the effects that the inhibitor has on the regeneration niche (*sensu* Grubb 1977) of the species involved.

C. introflexus is obviously an inferior competitor in comparison with the rest of the vascular species from the moorlands; however, it may be able to compete for space during the early stages of the secondary succession, provoking a substantial change in the regeneration niche of the species of the heathland community which may result in an inhibition of its normal regeneration. This aspect of the ecology of *C. introflexus* was the basis of the main objective of this research, which essentially aimed at documenting the extent to which the moss may interfere with the regeneration niche, particularly of *Calluna*, the physiognomic dominant of the heathland community.

2. Aims of the research

This research project was located on the North York Moors National Park, where *Campylopus introflexus* is currently widespread. To assess the distribution of the moss it was considered important to explore the ecological preferences of the moss in the National Park. At the same time it was judged important to determine how quickly *C. introflexus* colonizes new areas and the effect that its development may have on the establishment of other species. The main suppression of other plant species by *C. introflexus* was expected to be related with physical limitations on both the germination and the establishment of seedlings. In particular, it was hypothesized that *C. introflexus* may affect either the germination of *Calluna* seeds, seedling establishment (because moss carpets are a poor substrate for young plants) or seedling growth rate (through direct competition for nutrients, water, or some allelopathic effect). Therefore, the aims of this work are:

1. To explore the ecological preferences of *C. introflexus* in the North York Moors National Park.
2. To determine the effect of the moss carpet on the germination of *Calluna* seeds.
3. To asses the possible effect of *C. introflexus* carpets on the performance of *Calluna* seedlings.
4. To asses the effect of *C. introflexus* on the establishment of *Calluna* and the regeneration process of a moorland community within 18 months after a fire.

3. Description of the study area

The North York Moors National Park is an isolated area of upland covering approximately 1425 km^2 in northeast England (Maltby, Legg and Proctor 1990). The area has ecological and conservation importance because it contains the largest area of *Calluna* dominated moorland in both England and Wales (Figure 3.1). The dominant physiognomy is that of an extensive plateau with maximum altitude of 454 m (on Urra Moor). The superficial geology is composed mainly by Middle Jurassic grits, sandstones and clay shales dissected by abrupt valleys. There is a general absence of glacial deposits which explains the great importance of the solid rocks in the formation of soils (Carrol & Bendelow 1981). Although the climate is humid, the annual totals of precipitation for the moorland plateau are relatively low, between 1000 to 1100 mm on average, compared with other upland areas in britain. There is rainfall all the year round, but in the summer the precipitation is normally higher. Temperatures are generally low. In winter the average mean air temperature is around 1 and 2°C (dropping by about 0.3°C each 100 m altitude increase). In summer the air temperature rises to approximately 13 and 14°C. Annual evapotranspiration may exceed rainfall between late spring and mid-summer, during this period plant growth is dependent on water held in the soil (Carroll & Bendelow 1981, Maltby, Legg and Proctor 1990). Frost is common (but varies depending on the local terrain characteristics) averaging 75 days a year (Maltby, Legg and Proctor 1990).

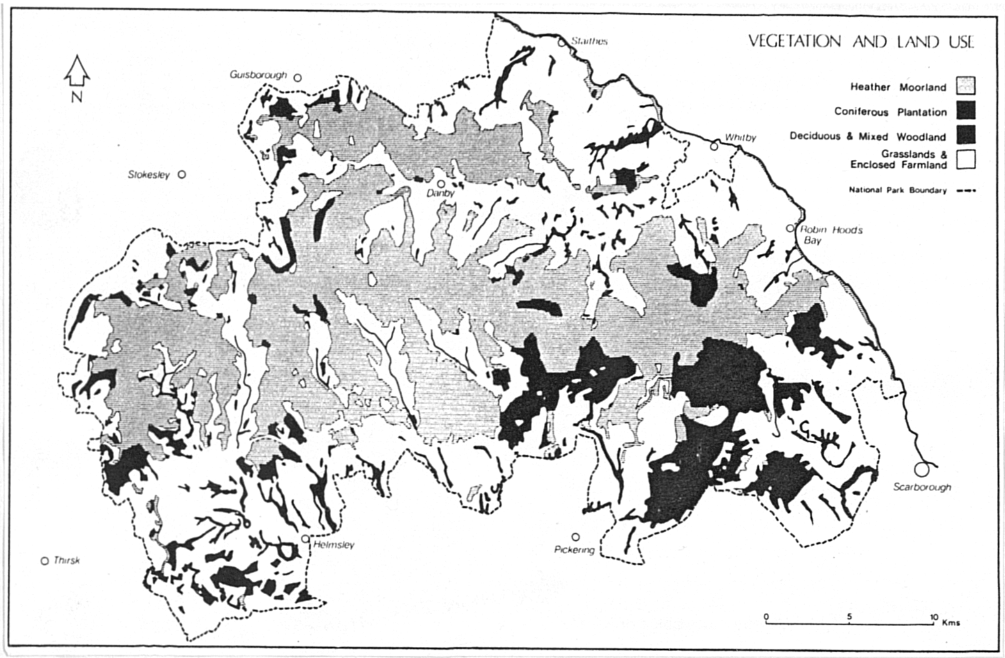
There are four broad types of land use in the North York Moors National Park (North York Moors National Park Department 1984), namely moorland dominated by *Calluna*, which covers 35% (approximately 518 km^2) of the Park,

Figure 3.1. Distribution of upland habitat (rough pasture and moorland). Almost 30% of Britain's surface is upland. Illustration adapted from Thompson, Stroud & Pienkowski (1988).

coniferous plantations (20%), broadleaved and mixed woodland (5%) and farmland (40%). The *Calluna* moorland is managed by prescribed rotational burning as grouse moor and sheep grazing. These moorlands have developed over Jurassic rocks and under low rainfall conditions, contrasting with the general rule that moorlands develop in uplands over geologically old rocks, with high rainfall. The moors of the park are anthropogenic, being the result of human activities during prehistoric and historic times. The map of present vegetation and land-use is summarised in Figure 3.2 Typically, heather moorlands are nearly monocultures of *Calluna.*

The history of moorland vegetation has been documented by studies of pollen in deep peat deposits. The results of one of these studies, conducted by Eyre (1973), showed that the low layers of peat accumulated prior to 8400 B.C. and that very little tree pollen was present. This finding suggests that bogs formed in hollows and poorly drained depressions and that the remainder of the landscape was a treeless tundra. However, the same analysis showed that from 8400 to 7500 B.C. important changes occurred: birch (*Betula* sp.) forest spread up slopes and onto the plateaux and the tundra only survived on high and exposed ground. After approximately 7500 B.C. there was a massive invasion of pine (*Pinus sylvestris*) and hazel (*Corylus avellana*), although birch was still important. This phase was the start of the wide development of forests and marked the end of the tundra. By 5000 B.C. the pine was replaced by oak (*Quercus petrea*), elm (*Ulmus* spp.) and lime (*Tilia* spp.); at the same time, because of the higher amount of rainfall in this period, alder (*Alnus glutinosa*) increased. Because of the growing water-logging of the soils the forest ceased to regenerate and the bogs expanded. Eyre pointed out that the activities of Mesolithic hunting societies hindered forest regeneration. Bracken spores are found in peat of this age, which Eyre interpreted as an indication that forest was being

Figure 3.2. Vegetation and land use in the North York Moors National Park. There is a strong correlation between vegetation and geology in the area (illustration taken from Atherden & Simmons 1989).



thinned on well drained slopes. After 3000 B.C. forest clearance began and elm declined as birch and ash (*Fraxinus excelsior*) increased. The ratio of tree to non-tree pollen fell, the proportion of bracken spores soar and there was a great increase in heather and grass pollen. With the arrival of Bronze age people, after 1500 B.C., there was a great flood of heather and grass pollen, suggesting large-scale deforestation of the uplands. The wetter and cooler climate setting in by 500 B.C. increased the rate of leaching and pan formation, a degradation process that has continued since then. Although heather populations were already spreading Atherden (1976) considered that the largest expansion of *Calluna* in the area followed the major forest clearance of the Iron Age and Romano-British periods, but she also pointed out that the dominant heather moorland covering vast areas of the region today is a development of the last two centuries.

Calluna used to be a common understorey plant in ancient forests, but once free of forest shade the plant developed very successfully. *Calluna* dominance in dwarf shrub communities varies greatly. This variation is dependent on substrate characteristics as well as management practices (Watt 1955, Gimingham 1972, Equihua 1990, Maltby, Legg & Proctor 1990). The moorland that develops on the soils that are better drained and have only a thin layer of peaty humus has, apart from the dominant *Calluna*, the contribution of *Erica cinerea* and *Vaccinium myrtillus*. The actual composition will vary according with the development stage of *Calluna*, with larger plant diversity in the pioneer and degenerated stages (Equihua 1990). The wetter areas have abundant representation of *Erica tetralix*, *Eriophorum vaginatum*, *Agrostis canina*, *Juncus effusus*, *Sphagnum* spp. and *Polytrichum commune*.

Regular burning of heather has been in operation since about 1800 and possibly earlier to keep the herbage in a productive condition for sheep grazing (Gimingham 1972). However, the practice of rotational burning was developed in Victorian times to increase the grouse bags for sport shooting (Gimingham 1972, Statham 1989). The resulting mosaic of different development stages of *Calluna* makes it possible to support larger populations of grouse. At the same time, this practice is suitable for sheep grazing (Maltby, Legg & Proctor 1990). The intensity of sheep-grazing is approximately 0.5 sheep ha^{-1}; however, because of the selective behaviour of sheep the flocks probably concentrate in less that 20% of the area available, which in turn means that local grazing may vary between nearly zero and around 2.5 sheep ha^{-1} (Maltby, Legg & Proctor 1990). The optimum rotation for burning indicates that heather should be burnt every 10-15 years (Gimingham 1972), but this has become increasingly difficult since the Second World War because of both the shortage and the high cost of manpower. This situation is cause of concern in the North York Moors because it has been estimated that nearly 27% of heather is outside the limits of normal management practice (North York Moors National Park Authority 1986).

According to the Biological Records Centre, *C. introflexus* was present in the National Park in 1967. There is a total of seven entries within the area of the National Park (from observations made in 1967 and 1977). A survey conducted by M.B. Usher in 1987 (described in Equihua 1990) found the moss in other 15 localities. There is no further information on the development of the invasion by the moss in the North York Moors National Park. Because of the relevance of the area, it seems important to ascertain the potential impact of *C. introflexus* on the moorland habitat and to document the current status of the invader in the Park.

4. Ecological preferences of *Campylopus introflexus* in the North York Moors National Park

4.1 Introduction

In Europe, the neophyte moss *Campylopus introflexus* has been especially successful establishing itself in disturbed habitats, like many other invasive plants have. However, it is not restricted to these conditions. *C. introflexus* is a species that occurs where the climate is humid (at least periodically). Its most common habitat in the British Isles seems to be peat or blanket bogs and moist heaths and moors, but, although it prefers acidic conditions, it has been found growing on fen peat at pH 6.5 to 7.0 (Richards 1963), which suggests that it is possibly less oligotrophic and calcifuge than its closest relative, *C. pilifer*. *C. introflexus* prefers open situations but often it can be found growing on bases of trees or on rotten wood. It can develop over soils ranging from dry to humid, which could also range from peat to mineral.

Although *C. introflexus* had been found in the North York Moors area by 1967, it is not until 1987 that it was drawn to the attention of the National Park Authorities by M.B. Usher (pers. comm.), highlighting its invasive potential. The case of the North York Moors is important because the Park contains the largest single tract of heather-dominated moorland in England and Wales (approximately 500 km^2). It is subject to various forms of disturbance, especially those associated with sheep grazing and tourist activities. The heather is managed by rotational burning to encourage high densities of red grouse (*Lagopus lagopus scoticus*) for sport shooting (North York Moors National Park Committee 1991). This combination of factors makes the area very suitable for the spread of *C. introflexus*.

The extent of the impact that the invasion by the moss may have on the heather communities of the Park is not known. However, it is known that *C. introflexus* invasion in the Netherlands may lead to the development of stands where a thick moss carpet has established to the extent of excluding vascular plants (Meulen, Hagen & Kruijsen 1987). A similar situation has been observed in Ireland (Richards 1963), but probably not to the extent of the situation that has developed in the Netherlands.

It is clear from the summary made above on the ecology of *C. introflexus* (and also from chapter 1), that this moss has a wide ecological tolerance but, for the objectives of this research, it was important to have a more precise account of the conditions that are associated with changes in the performance of the moss, particularly in the area of the North York Moors. Therefore, the aims of this chapter are to examine the ecological preferences of the moss in the North York Moors National Park as well as to analyze the association of relevant environmental factors with the cover and thickness of the moss carpets.

4.2 Methods

The ecological preferences of *Campylopus introflexus* in the Park were analyzed using a sample composed as follows (Table 4.1). 58 plots recorded by M.B. Usher in 1987 (described in Equihua 1990) with the aim to survey a wide spectrum of heather moorland types in the Park (but avoiding bracken-dominated areas). Another 25 plots included were the control sites from a burning versus cutting experiment (Usher & Gardner 1991). A further 20 plots were sampled to provide representation of stands with larger cover of *C. introflexus*. The thickness of the carpet was measured in these latter 20 plots (but not in the rest of the sample).

Table 4.1. List of localities sampled in the North York Moors National Park.

Locality	National Grid Reference	Number of samples
Vegetation survey		
Castleton Rigg	NZ6804	4
Egton Moor	NZ7501, 7602 & 7901	13
Fylingdales Moor	SE8897	4
Glaisdale Moor	NZ7300 & 7301	5
Kildale Moor	NZ6111 & 6408	6
Lealholm Moor	NZ7509 & 7510	4
Levisham Moor	SE8494	5
Rosedale Moor	SE7199 & NZ7100	6
Spaunton Moor	SE7095	6
Westerdale Moor	NZ6506	4
Control plots from the burning/cutting experiment		
Danby Low Moor	NZ7210	10
Danby High Moor	NZ7001 & 7002	10
Kildale Moor	NZ6111 & 6210	5
***C. introflexus* survey**		
Danby Low Moor	NZ7309	1
Danby High Moor	NZ7002	1
East Moor	SE6092	1
Egton Moor	SE8099	1
Glaisdale Moor	NZ7400	1
Goathland Moor	NZ8502 & NZ8402	2
Hartoft Moor	SE7396	1
Hutton Ridge	SE7090	1
Kildale Moor	NZ6111	1
Lealholm Moor	NZ7409	1
Levisham Moor	SE8494	2
Rosedale Moor	SE7499	1
Shaw Ridge (Moor House)	SE6394	1
Spaunton Moor	SE7192	2
Two Howes Rigg	SE8399	1
Wheeldale Moor	SE7995 & SE8098	2

In all of the 103 plots the same sampling procedure was applied (this had originally been devised in 1987, and was retained so that comparative data were collected). Sites were selected subjectively. Within each site a 12 m sampling transect was laid down and marked at 4 m intervals. On each side of these marks, 0.5 m away from the transect, a 0.5 m square sampling quadrat was placed. The quadrat was divided into a grid of 25 equal squares. The number of grid squares where each species was present was recorded, summed for all eight quadrats and the result was expressed as a percentage occurrence of each species in the 200 10 cm x 10 cm squares, rounded to the nearest integer. The moss thickness was estimated measuring the maximum value in each quadrat and then taking the average of the eight measures for each plot.

All of the species occurring in less than 5% of the plots, together with *C. introflexus* itself, were excluded from the vegetation analysis that is described below. To explore the relationships of the vegetation and the other environmental factors with the distribution of *C. introflexus*, the moss data together with the environmental factors, described below, were incorporated as external variables in the analysis.

The environmental variables considered were: the height of *Calluna*, altitude, rainfall totals (annual and for the summer), the averages of potential solar radiation for December (as representative of winter), June (representative of summer) and the annual average. Similarly, the slope, aspect (the four main compass directions as classes), soil type and its wetness class were also incorporated. The information about the rainfall data were obtained from the Soil Survey of England and Wales (R.C. Palmer pers. comm.). The potential radiation values were calculated using the data of latitude, slope orientation, and its inclination according to the procedure described by Swift (1976). These values correspond to the expected average radiation incident on the ground, disregarding the effect of the atmosphere. The soils information was extracted from the maps by Carroll & Bendelow (1981) and is summarized in Table 4.2 for the soil types found in the sample only. It should be noted that in the area as a whole there is a predominance of soils either in wetness class I (40% of the area mapped by Carroll & Bendelow 1981) or in wetness class VI (33% of the mapped area).

The vegetation analysis was carried out to produce a classification of plant communities. The classification was obtained using the fuzzy *c*-means technique (Bezdek 1987, Equihua 1990). This approach, like the more conventional methods (refered to as 'hard' here), produces a classification that consists of groups defined in terms of species composition. However, instead of the samples being members of a single group, they can be allocated partially to several of the groups considered; for instance, samples typical of a group will have membership values close to one in the group, and near-zero membership values for all other groups. The main advantages of this procedure are that, while the vegetation description is made in the intuitively appealing fashion of recognizable species groups, overlap between the groups can be considered and it is possible to retain some information about the heterogeneity of the plant communities, which can be considerable and important for analytical purposes.

The fuzzy c*-means algorithm*

The fuzzy c-means algorithm is based on minimizing the within group sum of squares, J_m (U, V, A), which is given by

Table 4.2. Summary of the main features of the soils found in the vegetation sample in the North York Moors National Park according to Carrol & Bendelow (1981). Not all soil groups described by Carrol & Bendelow are in the table. Only those found in the vegetation sample are included. The area mapped by these authors was the region of the National Park above 183 m altitude. The pH values are those measured in water (1:2.5). Wetness classes are I the driest and VI the wettest (see soil wetness table at the bottom, after Jarvis *et al.* 1984).

					Superficial	
Mapped soil unit	Soil series	Soil group	Wetness class	Map area (%)	Ph	Organic Carbon (%)
C2	Stow	Non-calcareous pelosols	II/III	9	3.7	20.0
G1	Anglezarke	Loamy podzols or stagnopodzols	I	3	3.4	45.0
H1	Howe	Gley-podzols in drift	V	3	3.6	18.0
J2	Hambleton	Stagnopodzols	I	3	3.3	43.0
J5	Maw	Loamy stagnopodzols	I	13	3.8	10.0
K3	Rowsham	Loamy clayey stagnogley soils	III/IV	4	6.1	2.3
L1	Onecote	Stagnohumic gley soils	VI	26	3.7	13.0
M1	Winter Hill	Raw peat soils	VI	5	2.7	44.0

Soil wetness

	Number of days the soil is waterlogged	
Wetness class	Within 70cm	Within 40cm
I	< 30	-
II	> 20 & < 90	-
III	> 90 & < 180	-
IV	> 180	< 180
V	> 335	> 180 & < 335
VI	> 335	> 335

$$J_m (U, V, A) = \sum_{i=1}^{n} \sum_{j=1}^{c} (u_{ij})^m (d_{ijA})^2 \qquad (1)$$

where

$$(d_{ijA})^2 = || x_i - v_j ||_A^2 = (x_i - v_j)' A (x_i - v_j)$$

is a distance measure calculated as a norm induced metric, **A** is the norm inducing matrix (any matrix of dimension p, where p is the number of attributes considered), m is the 'fuzziness parameter' ($1 \le m < \infty$), $\mathbf{x}_i$ is the vector of attribute measurements made on individual i (i=1, 2,...,n), the vector $\mathbf{v}_j$ is the centroid of cluster j (j=1, 2,...,c}, u_{ij} is the membership value of the individual i on cluster j, **U** is the matrix of memberships, **V** is the matrix of cluster centroids ($\mathbf{U}=\{u_{ij}\}$ and $\mathbf{V}=\{\mathbf{v}_j\}$).

The clustering is hard when m=1 and becomes fuzzier as m approaches ∞ (Bezdek 1981). Although m may have a wide range of values it has been found, purely on the basis of empirical results, that values around 2 produce satisfactory results (Dunn 1974b, Bezdek 1981, Granath 1984, McBratney & Moore 1985). This can be justified because, although a hard partition is considered not to be appropriate to represent ecological communities, a completely fuzzy partition (where all the memberships are $1/c$) is clearly not desirable either. Thus, what is required is a balance between 'hardness' and 'fuzzyness', which is usually achieved when m takes values around 2. To minimize equation (1) the following two conditions must be satisfied

$$v_j = \frac{\sum_{i=1}^{n} (u_{ij})^m X_i}{\sum_{i=1}^{n} (u_{ij})^m} \tag{2}$$

$$u_{ij} = \left\{ \sum_{k=1}^{c} \left[\frac{(d_{ijA})^2}{(d_{ikA})^2} \right]^{1/(m-1)} \right\}^{-1} . \tag{3}$$

The fuzzy *c*-means algorithm (Bezdek 1974, 1981) consists of solving these equations iteratively, given a number of clusters, *c*, a value for the parameter *m* and a norm inducing matrix, A. The classification produced is non-hierarchical.

Equations (2) and (3) are the necessary conditions for **U** and **V** to be associated with a *local* minimum or saddle point of equation (1). When $\mathbf{x}_i = \mathbf{v}_j$, which implies $d_{ij} = 0$, u_{ij} cannot be calculated using equation (3). This condition is called a 'singularity' (Bezdek 1981). Whenever a singularity occurs, the corresponding individual must have no membership value in any cluster where $d_{ijA} > 0$. The membership in the clusters where $d_{ijA} = 0$ is arbitrary (up to the constraint of the algorithm that the membership values must add up to 1 for each individual). Given the local convergence properties of this clustering approach, it is clear that different starting membership configurations may converge to different minimizers. It is therefore important to specify the starting strategy.

As stated above, there are two main parameters that need to be specified when using the fuzzy *c*-means procedure: the number of clusters to produce, *c*, and the fuzziness parameter, *m*. McBratney & Moor (1985) suggested that a good classification involves the selection of a particular combination of these two parameters simultaneously. In the example described in Equihua (1990) the classification was produced using correspondence analysis ordination axes (Hill 1974) as the bases of the clustering and a fuzziness parameter of 2. However, following the suggestion by McBratney & Moor (1985) it was found that, with the 103 plots of the vegetation dataset, a value of 1.5 made it possible to derive a satisfactory classification based on the original set of species. The classification was produced using the Euclidean norm to give preference to better represented species and was applied to the percentage cover data. The iteration process was initiated using the following procedure (Equihua 1990): (1) the dominant correspondence analysis axis was divided into c segments of equal length and (2) the observations found in each segment were given an arbitrary membership of 0.9 in the cluster corresponding to that segment and a membership value of $0.1/(c\text{-}1)$ for each of the remaining clusters.

Evaluation of the associations

The significance of the relationships between the moss cover and the environmental factors detected by the clustering was assessed using generalised linear models (Aitkin *et al.* 1989). In the case of the cover estimates of *C. introflexus* the original scores (frequency of presence in the 200 grid squares) were used. The model applied assumed a binomial distribution (with logit link). During the analysis it was found that there was a strong overdispersion, which limits the validity of the model. To allow for this overdispersion the quasi-likelihood approach was used (Baker & Nelder 1986; Aitkin *et al.* 1989). In this case the quasi-likelihood approach consisted of fitting a model where the basic error distribution is taken to be binomial but the scale factor, instead of being fixed to 1, is estimated from the sample as the residual deviance divided by the degrees of freedom (*i.e.* the mean residual deviance).

The vegetation groups were used to build a basic regression model and then the other environmental factors were included in the regression if found significant (with $P \leq 0.10$ as criterion) in a forward selection procedure. Soil type, wetness class and aspect were represented by dummy variables which took the value '1' when the condition was present and '0' otherwise. When the categories showed similar coefficients in the model, the possibility of collapsing the corresponding categories together into a single term to simplify the model was tested. If the change in deviance was found to be not significant the new term replaced the original dummy variates in the model. Because the vegetation groups are constrained to add to one, at most c-1 groups can be included in the regression model; also, as in the case of the dummy variates, when categories showed similar regression coefficients, the possibility of using a single term to represent all of them together was tested.

Desiccation survival of the moss carpets

When surveying the North York Moors for the occurence of *C. introflexus* it was remarkable to observe that the carpets of *C. introflexus* tend to be fragmented and detached from the substrate, specially when the carpets are thick and extensive. These fragments are viable and they may be reactivated when suitable conditions arise. An estimate of the survival rate of detached fragments of *C. introflexus* was obtained by incubating a number of dry fragments from a *C. introflexus* carpet. These fragments had been found detached on the ground (the carpet was approximately 2 cm thick) in July 1990 and were kept dry in polythene bags for four months. A sample of 70 moss shoots from these fragments was placed on moistened filter paper in 7 petri dishes (10 shoots in each dish). The petri dishes were placed in a growth chamber at 20°C (night depression of 5°C), 60% humidity and light period of 16h. The filter paper was kept moist all the time. A set of fresh moss shoots were prepared in a similar manner as a control.

4.3 Results

Vegetation analysis

The vegetation classification used comprised 7 groups (Table 4.3). The first two of them are associated with the vegetation of wet conditions where species like *Agrostis canina, Juncus effusus Eriophorum angustifolium, Eriophorum vaginatum* and *Sphagnum* spp. are abundant. These are bogs (group 1) and damp heath communities (group 2). The remaining five groups are hypothesized to correspond to different stages of the development cycle of *Calluna* (Table 4.3). Groups 3 and 4 are regarded as representative of mature heather communities, they are where *Calluna* is fully developed and the participation of other species is reduced. It seemed that group 3 describes mature heather communities under moister conditions than those of group 4, because the former group has a relatively larger representation of species, including *E. tetralix*, than the latter. Groups 5 and 6 are interpreted to be building heather communities, probably again with group 5 representing the composition under moister conditions (*E. tetralix*, *P. commune* and *Sphagnum* spp. are relatively abundant) than those in group 6. Group 7 is described as representing pioneer heather communities.

Using the procedure described in Equihua (1990) the centroids of the set of environmental variables and the cover of *C. introflexus* were calculated (Table 4.4).

Table 4.3. Average species composition (centroids) of the groups identified by fuzzy clustering. The values are percentage cover. The species are sorted according to their indicator value within each group. The larger the contrast of a species cover among the groups the better indicator that species is. The best indicator species are shown in bold percentage cover within the group that they are associated with.

	Fuzzy group						
Species	1	2	3	4	5	6	7
Juncus effusus	**77.5**	1.6	1.0	0.2	5.4	0.5	1.2
Carex echinata	**13.5**	1.1	0.1	0.0	0.9	0.0	0.1
Agrostis canina	**59.7**	2.8	0.9	0.4	4.6	0.6	0.8
Potentilla erecta	**3.5**	0.2	0.2	0.0	0.2	0.0	0.1
Galium saxatile	**14.4**	0.1	1.6	0.4	1.3	0.1	0.3
Juncus bulbosus	7.0	2.4	0.1	0.0	1.2	0.1	0.7
Nardus stricta	5.5	3.4	0.7	0.3	1.2	0.7	1.9
Polytrichum commune	55.3	24.1	3.7	1.5	46.9	1.9	6.1
Deschampsia flexuosa	2.3	0.1	0.3	0.7	1.9	1.0	0.9
Eriophorum angustifolium	4.8	**91.1**	0.4	0.3	3.5	0.3	1.1
Eriophorum vaginatum	0.1	**6.4**	0.1	0.1	0.5	0.2	0.1
Erica tetralix	4.9	**47.6**	3.1	1.8	6.5	2.6	2.8
Sphagun spp.	70.9	75.5	2.2	0.4	8.6	0.9	2.3
Eurhynchium praelongum	0.0	0.3	0.1	0.2	0.2	0.0	0.0
Vaccinium myrtillus	2.1	2.9	**44.2**	2.5	6.5	2.7	6.0
Dicranum scoparium	0.0	0.4	4.4	4.3	1.1	3.6	1.2
Hypnum jutlandicum	0.1	4.7	5.1	3.4	1.1	2.5	1.0
Pohlia nutans	0.6	0.1	9.9	7.8	9.1	8.0	1.9
Calluna vulgaris	12.2	49.8	94.9	**97.0**	80.0	89.7	42.8
Gymnocolea inflata	0.1	0.1	2.2	1.2	**5.0**	0.5	0.4
Cephalozia bicuspidata	0.0	2.5	1.3	0.7	**5.9**	0.7	0.6
Juncus squarrosus	0.3	0.2	0.9	0.6	2.8	0.5	1.8
Plagiothecium undulatum	0.1	0.2	0.2	0.5	0.7	0.3	0.1
Empetrum nigrum	0.5	0.2	2.0	1.0	3.0	0.6	1.7
Carex nigra	0.0	0.7	0.3	0.3	0.9	0.8	0.1
Cephaloziella divaricata	0.0	0.0	0.0	0.2	0.0	**0.5**	0.0
Campylopus paradoxus	0.0	0.1	5.2	3.9	6.5	**30.6**	8.5
Orthodontium lineare	0.0	0.0	1.0	0.3	0.4	1.4	0.0
Lophozia ventricosa	0.0	0.0	0.1	0.0	0.0	0.2	0.1
Erica cinerea	0.0	0.0	1.1	2.9	0.9	3.4	0.8
Polytrichum juniperinum	0.0	0.0	0.5	0.4	1.8	0.5	**6.3**
Carex pilulifera	0.0	0.0	0.4	0.6	0.3	0.4	2.3
Calypogeia muellerana	0.0	0.7	0.5	0.0	0.5	0.0	1.6
Agrostis capillaris	0.0	0.0	3.0	0.8	2.6	0.6	5.1

Table 4.4. Centroids of external variables associated with the species groups of the fuzzy clustering (see Table 4.3). The values were calculated as weighted averages, where the weights are a function of the membership values produced by the fuzzy clustering applied to the species data.

	Vegetation groups						
External variates	1	2	3	4	5	6	7
C. introflexus cover (%)	0	0	3	11	9	13	59
Height of vegetation	49	22	34	31	23	19	9
Altitude (m)	257	253	342	308	301	302	269
Slope (degrees)	4	3	4	4	4	4	4
Average annual rainfall	942	913	1027	975	980	977	959
Average summer rainfall	438	419	467	449	451	449	442
Potential radiation							
Annual	379	381	372	380	380	388	390
June	684	684	682	684	684	685	686
December	88	91	81	91	90	101	103
Aspect							
N	20	0	35	37	26	30	8
S	0	34	16	19	4	22	36
E	75	66	47	30	39	29	45
W	4	0	2	14	30	18	12
Soil types							
C2	0	0	1	1	0	1	0
G1	0	0	0	3	3	1	15
H1	0	0	1	5	1	11	0
J2	0	0	1	8	0	21	0
J5	1	0	16	45	44	34	36
K3	0	0	4	0	0	1	0
L1	95	99	38	17	26	16	15
M1	5	0	41	20	29	17	33
Soil wetness class							
I	1	0	17	56	45	55	51
II/III	0	0	1	1	0	1	0
III/IV	0	0	4	0	0	1	0
V	0	0	1	5	1	11	0
VI	99	100	79	38	54	34	48

The results of these calculations give further support to the interpretation of the groups advanced above. Clearly groups 1 and 2 appeared strongly associated with wet soils (wetness class VI). In the area the waterlogging is due to the topography rather than to an excess of rainfall; this is clearly suggested in the results of the classification because the average amounts of rainfall are the smallest for these two groups and also the altitudes are the lowest. This is consistent with the fact that damp habitats, in the North York Moors, tend to occur in depressions and valleys where rainfall is supplemented by run off or drainage from the surrounding heathlands. The interpretation of the heather dominated groups, groups 3 to 7, is supported by the values of vegetation height which in this communities is related to the size of *Calluna* and, therefore, with its age (and the shape of the plants). The proposition that the pair of mature heather groups, groups 3 and 4, represent a moisture contrast is also supported by considering their associated soil wetness classes and, to a lesser extent, by the contrast in the amounts of rainfall detected. A similar pattern provides support for the interpretation presented for the pair of building heather communities, groups 5 and 6. The results suggest that the group of pioneer stage *Calluna*, appears to be more common at lower altitude than the rest of the heather dominated groups. This could mean that they are subject to more intense disturbance, because they would be located in places more accessible to visitors or nearer to populated areas, or it may be an artifact of the subjective system used in the selection of the sample plots listed in Table 4.1.

There is a clear indication in Table 4.4 of the ecological preferences of *C. introflexus* in the North York Moors. The moss appears to strongly avoid the wettest habitats (as represented by groups 1 and 2). Its larger abundance appeared associated to moorland communities in a late pioneer stage where the cover of *Calluna* was approximately 43% and its individuals were, on average, 9 cm tall. However, the results also made it clear that the moss can be found in communities at any stage of development, probably with slightly more abundance in relatively drier communities (groups 4 and 6 when compared with groups 3 and 5 respectively. This seems also interesting because it is consistent with the result of the analysis which suggests that *C. introflexus* is absent or very rare in the dampest habitats.

Assessment of moss associations

The significance of the relationships between the moss cover and the environmental factors was assessed using the regression approach based on generalised linear models. The model was applied to the original scores of *C. introflexus* as response variate. By testing the individual vegetation groups it was found that the model can be simplified into the following terms: the pioneer heather (group 7) and a composite term (that accounts for groups 4, 5 and 6 simultaneously), the remaining groups (all from wet conditions) are accounted for by the constant term in the model. The environmental variables that were found subsequently significant were (Table 4.5): soil groups L1 (stagnohumic gley soils of the Onecote series) and G1 (loamy podzols of the Anglezarke series) combined (and thus a single term contrasting soil types L1 and G1 with all the others was included in the model), the height of the vegetation, soil wetness class I (dry, versus all the others) and the aspect of the site (east orientation versus all the others). All these terms appeared positively associated with the cover of *C. introflexus*, except for the height of the vegetation and the aspect term (Table 4.5). These results follow closely what was deduced from the analysis of the fuzzy clustering, suggesting that the association patterns discussed there are significant. However, the regression model showed an important amount of residual deviance (the mean residual deviance was 33.48), which

Table 4.5. Summary of the regression on cover of *C. introflexus* (binomial model with logit link). The final model fitted showed a large amount of overdispersion. To compensate for it the scale parameter was estimated to be 33.48 (with 95 degrees of freedom) which was used to divide the deviances to test for significance (using the *F* distribution as reference, with 1/95 degrees of freedom). Based on this criterion no other environmental factor was found to contribute significantly to the fit of the model.

Source	Deviance	*F*	Regression coefficients
Constant	-	-	-9.89
Soils L1 & G1	1953.22	58.34**	3.32
Group 7	1577.91	47.13**	12.03
Groups 4, 5 & 6	730.87	21.83**	7.90
Height of vegetation	407.79	12.18**	-0.07
Soil wetness I	146.64	6.87*	1.01
Aspect (facing E)	229.91	4.38*	-1.11

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.001$.

indicates a substantial lack of fit. The lack of fit of the model could possibly be due to the binomial model assumption being inappropriate or to the absence of a representation of an important environmental factor in the model. By inspection of the residuals (Figure 4.1) it was evident that important deviations from the model were associated with an incapacity to predict medium range frequency values, but the extreme conditions seemed to be well identified. Despite this objection to the model, its results are regarded as providing satisfactory support to the relationships deduced from the fuzzy clustering, especially considering the exploratory goals of the chapter.

Carpet thickness

The data on thickness of the carpets of *C. introflexus* are summarized in Table 4.6. The dataset was analysed in a similar manner to the cover data but, because this information was only available for 20 plots, the calculation of the centroids was not carried out. Instead, the regression approach was used (assuming a normal distribution in this case). The model fitted accounted for 80% of the variance and consisted of *Calluna* height and four vegetation terms (Table 4.7): group 4, group 5, group 6 and group 7. The model suggests that the carpet tends to be thicker under moist building stage heather communities (group 5). That the moss carpets are thicker in building stage heather communities seems reasonable because it is not until the heather canopy closes that the growth of the moss starts to be interfered with. More difficult to explain is the contradiction with the results of the moss cover, where it was shown that the moss is less developed in moister habitats. However, the following interpretation is offered. It is possible that the protection from desiccation, that would be provided by a fuller *Calluna* canopy (especially in moister conditions), would allow a better growth of the moss shoots while, at the same time, it will be limiting the area available for the moss to develop. The result of this

Figure 4.1. Residuals versus fitted values of the binomial regression model for cover. It is apparent that there is some lack of fit of the model, specially at cover values in the middle range.

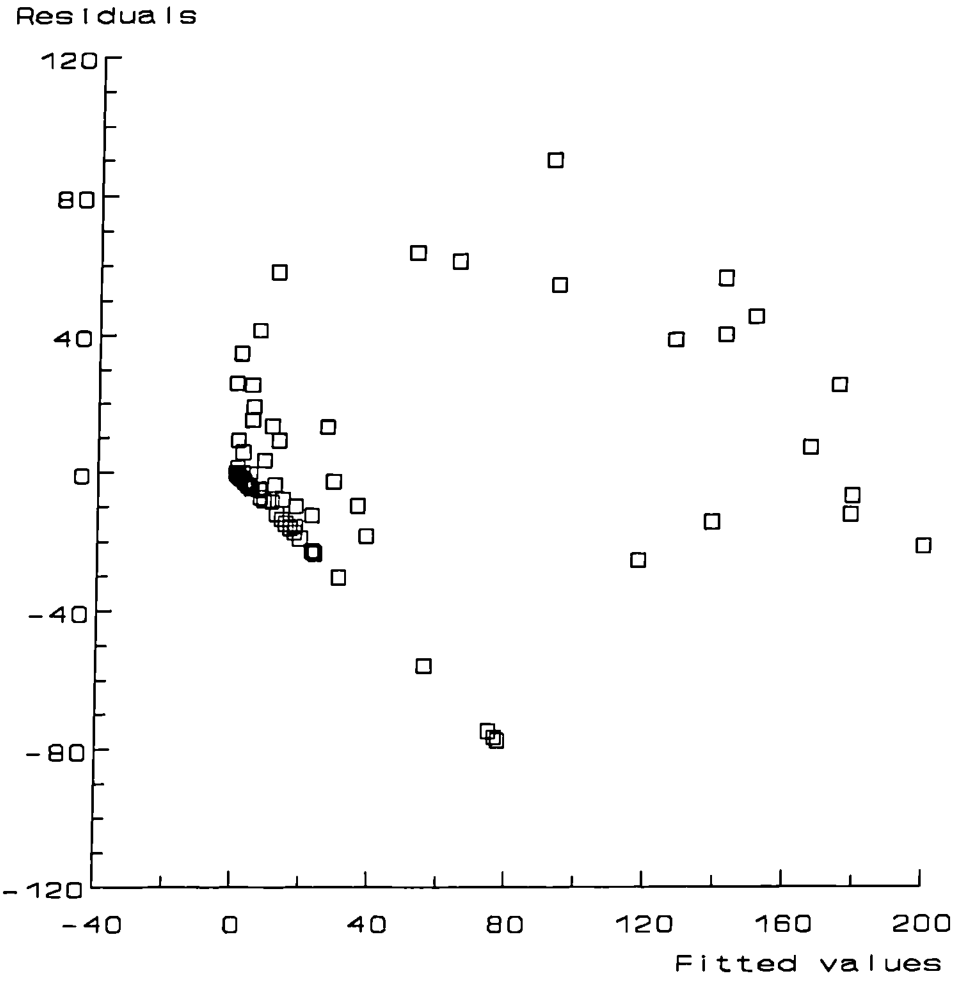


Table 4.6. Summary of the sample plots to estimate *C. introflexus* carpet thickness.

				Campylopus introflexus		
		Calluna		Thickness		
Site (N.G.R.)	Altitude (m)	Height (cm)	Cover (%)	Maximum (cm)	Average (cm)	Cover (%)
NZ610116	265	7.8	34	3.0	2.4	91
NZ705022	403	9.3	45	2.0	0.9	54
NZ717926	230	7.4	76	2.7	2.2	83
NZ736093	299	6.4	82	0.9	0.4	91
NZ748094	260	7.6	75	2.7	2.4	98
NZ749006	325	41.3	100	1.5	0.8	18
NZ848029	275	6.5	59	2.4	1.7	87
NZ854027	285	17.8	92	3.0	1.7	74
SE609922	243	29.1	100	1.0	0.1	6
SE636947	275	22.9	100	0.0	0.0	0
SE707905	135	1.6	2	3.4	2.7	100
SE718924	218	7.8	43	2.7	2.0	89
SE738968	301	22.1	89	1.2	0.9	62
SE746992	318	7.4	30	1.5	0.8	46
SE798956	241	23.5	91	5.2	2.8	63
SE802997	225	14.5	76	3.0	2.2	83
SE803983	230	10.8	65	3.5	2.0	86
SE831999	195	4.6	85	2.5	2.3	99
SE846940	260	37.3	94	1.6	0.5	15
SE847941	265	10.0	74	0.5	0.3	35

Table 4.7. Summary of the fit of the final model to describe the association between thickness of the carpets of *C. introflexus* and the environmental factors. The model explained 80% of the total variance. The error mean square was 0.233 (with 14 degrees of freedom). The assumption of normality was assessed using the Filliben correlation coefficient. It was found to be 0.992, which suggests a satisfactory agreement to the normal distribution assumption (within 95% confidence level).

Source	*F*	Regression estimates
Constant	-	-3.97
Group 5	26.10***	30.35
Group 4	15.30**	6.20
Group 7	11.48**	5.48
Calluna height	7.12*	-0.04
Group 6	4.81*	3.68

* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.

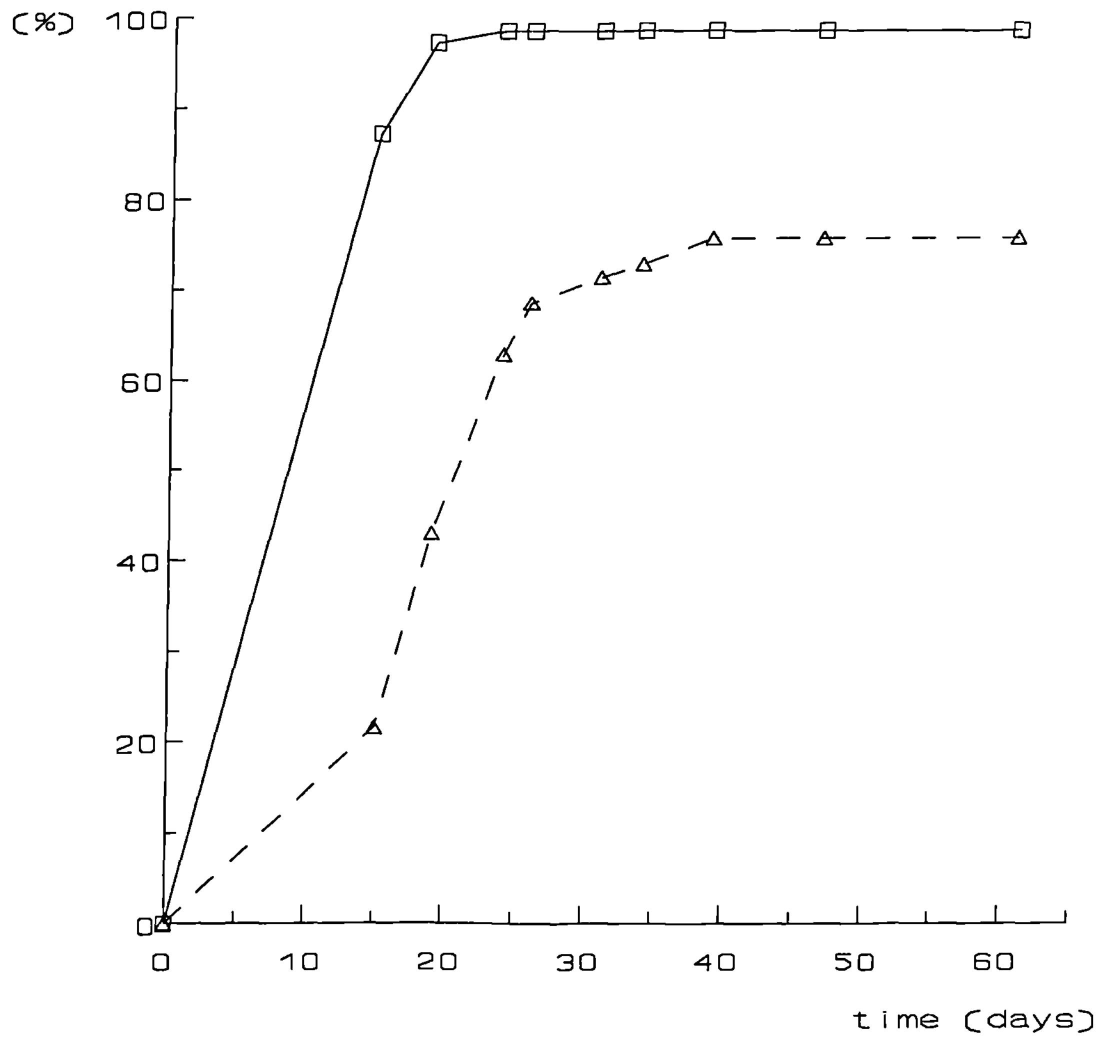
would be that the maximum carpet thickness would not coincide with the condition with maximum moss cover (identified to be a heather community in a pioneer stage, group 7). The only other environmental factor that was found to be significantly associated to the thickness of the moss was the height of *Calluna*, which has a negative effect on the carpet, suggesting that mature heather communities are unsuitable habitats for the growth of the moss ar that the moss stands are degenerating and becoming thinner under taller *Calluna*. On the other hand it has to be observed that the effect is small (although statistically significant). In interpreting this result it has to be borne in mind that the effect that the height of *Calluna* has may be partially accounted for by other terms already in the model (because they are not statistically independent from each other).

Moss carpets survival

It was mentioned before (see chapter 1) that a distinctive feature of the carpets of *C. introflexus* is that they appear to be prone to fragment and detach from the substrate when they become thick enough. Meulen, Hagen & Kruijsen (1987) mentioned that these loose blocks may be turned upside down either by birds in search of insects or because of mechanical tension in the moss itself (possibly due to alternate wetting and drying in cracks of the carpet). According to these authors, the moss blocks can stay alive for many years.

The evaluation of the viability of the carpet fragment of *C. introflexus* showed that after approximately three weeks 99% of the fresh shoots had produced new branches whereas it took nearly one month for the dried specimens to reach 73% 'germination' (Figure 4.2). Despite the decline in vitality that this results show, there is a clear indication that *C. introflexus* can withstand successfully both detachment

Figure 4.2. Proportion of shoots of *C. introflexus* that produced new branches when incubated on moistened filter paper in petri dishes. The continuous line corresponds to fresh moss and the broken line to dry moss. The dry specimens were collected in the North York Moors National Park as dry carpet fragments and kept in that condition in polythene bags for 4 months before the incubation began.



from the substrate and dehydration for a considerable length of time. The moss shows a relatively quick response to suitable conditions, producing new branches and protonema extensions. This also implies that detached fragments can act as 'propagules' of a well developed carpet holding colonized habitat, complementing the propagation by spores or other propagules (deciduous shoot tips). It is known that *C. introflexus* produces an abundance of propagules and also that, in contrast to its nearest relative *C. pilifer*, it is common to find it producing capsules. The abundant production of both spores and propagules may explain the successful colonisation of new sites by *C. introflexus*. However, the persistence of the moss in the colonised places may be the result of the potential of this species to produce loose blocks of carpet as an additional form of propagation.

4.4 Discussion

The results showed that there is a clear relationship between the vegetation of the National Park and the distribution and carpet thickness of *C. introflexus*. Although the wide ecological tolerance of the moss recognized elsewhere (Richard 1963, Richards & Smith 1975) is also apparent on the North York Moors, the moss seems to have some preference for relatively drier conditions. This suggestion is in agreement with what Clément & Touffet (1988) found about the behaviour of *C. introflexus* in regenerating heathlands in Britanny. They regarded *C. introflexus* as a xerophytic species which was also very tolerant to soil constraints. The preference of the moss for open situations is also evident in the area, but this does not imply that it is absent from places with a large cover of *Calluna*, as the results made also clear. In the field, it was possible to observe individuals of *C. introflexus* (up to 5.2 cm long) thriving under the canopy of large heather plants (approximately 30 cm height), although, at the same time, dead carpets were found under these same conditions.

It was expected to find that the main factors associated with the distribution of the moss should be related with the soil conditions and the vegetation structure. This conjecture seems largely confirmed. It was found that they are indeed important, but, at the same time some unaccounted factor seemed to be still missing. This missing factor may be some measure of the intensity of disturbance of a site (*i.e.* its management history) or perhaps the fact that the moss is not present, yet, in all the places where it might be growing (*i.e.* an element of stochasticity in where the moss has actually colonized). Nonetheless, it is considered that, in general, the results summarize adequately the main relationships of the moss with the vegetation and the soil in the area. They are in agreement with what could be expected from what is known of the ecology of the moss.

Although the moss was found to be widespread in the North York Moors, the results of this chapter showed that its presence in the area has not reached, generally, the levels that the invasion has shown in places like The Netherlands (Meulen, Hagen & Kruijsen 1987). It is possible to observe stands with extensive cover of the moss in the Park, apparently to the exclusion of other plant species, but this is not a common sight.

The tendency to produce loose blocks could be hypothesised to provide important competitive advantages to *C. introflexus*, which could explain its ability to retain and expand in colonized habitat. A somewhat similar behaviour is that mentioned by Mägdefrau (1982) in describing what are called 'glacier mice' in Iceland; these are special cushion forms of species of *Andreaea* and *Grimmia.*

Glacier mice are formed when cushion fragments are levered up from their substrate by ice action and then tumble about, pushed by the wind, which promotes a radial growth and a free life form. One interesting feature of the loose block behaviour is that the carpet becomes an unstable substrate for other species. Even when other plants become established on top of the carpet, the loose block dynamics may destroy those colonizers by up-rooting them or by covering them.

As argued above, the formation of loose blocks in *C. introflexus* might be an adaptation of the moss to retain colonised habitat. This species can produce carpets between 0.5 and 10 cm thick (probably up to approximately 5 cm in the British Isles). However, its attachment to the ground is weak. Moore & Scott (1979) found that the rhizoids of *C. introflexus* have a low breaking resistance, only 3.9 ± 1.0 kg cm^{-2}, which is the lowest of those measured by these authors (the next lowest is *Thuidium furfurosum* with 27.5 ± 5.4 kg cm^{-2}). They also found that the rhizoids of *C. introflexus* did not hold any significant amount of sand. Another morphological feature of this species, common to almost all the species in the genus, is the disposition of the seta which holds the capsule buried in the leaves before maturation and only becomes erect when the capsule is ripe. This feature may be important in association with the loose blocks as a propagation adaptation because in this way the capsules would be protected even when a moss carpet becomes detached and tumbles about. An analogous situation to this aspect of the carpet fragmentation of *C. introflexus* has been observed in the vascular weed *Salsola kali* L. (Chenopodiaceæ); according to Young & Evans (1990) one important feature of the life cycle of *S. kali* is its tumbling stage. The plants start to die with the first frost. When the ground becomes frozen the winds break the already dry and fragile stems of the weed, liberating it to be carried along scattering seeds on its way. A result of this tumbling action is the dispersal of the seeds, which were protected within the plant skeleton. Young & Evans considered that these features have combined in *S. kali* to produce a very successful weed. A similar combination of features is found in *C. introflexus* which may be important in an understanding of its successful invasion of Europe and its ability, in some cases, to exclude other plant species.

5. Impact of a *Campylopus introflexus* carpet on *Calluna vulgaris* germination and growth

5.1 Introduction

Campylopus introflexus (Hedw.) Brid. was originally distributed in the temperate regions of the southern hemisphere (Gradstein & Sipman 1978; Meulen, Hagen & Kruijsen 1987), but in 1941 it was recorded for the first time in Britain. From 1949 onwards it was reported with increasing frequency from new localities in the British Isles (Richards 1963, Richards & Smith 1975). Elsewhere in Europe it was reported later; for instance in The Netherlands the infestation is dated around 1960 (Meulen, Hagen & Kruijsen 1987). According to Richards (1963), it is likely that the first European foothold of *C. introflexus* was either in Brittany or in the British Isles, from where it afterwards spread; however, the same author pointed out that it is also possible that this moss may have invaded Europe at several points independently. All the European localities where *C. introflexus* was first recorded are near seaports (Richards 1963).

C. introflexus grows better at low elevations (usually below 1000 m altitude), over dry to humid soils which are non-calcareous and nutrient-poor. These soils could range from peat to mineral. It prefers open situations and it is also found on bases of trees or on rotten wood. In Europe the species is favoured by disturbance, possibly because of the lower competitive pressure that the perturbation produces (Gradstein & Sipman 1978). According to Richards (1963), *C. introflexus* in Britain has a wider ecological range than its closest native European relative, *Campylopus pilifer* Brid. The most common habitat of *C. introflexus* seems to be peat on blanket bogs and on moist heaths and moors. It has, however, been found growing on fen peat with a pH of 6.5 to 7.0 and is possibly less oligotrophic and less calcifuge than *C. pilifer*.

van der Meulen *et al.* (1987) reported the occurrence of extensive carpets of *C. introflexus* (2 to 10 cm thick) in The Netherlands, covering from 25 to 100 percent of the ground surface. Under these conditions other species, even grasses and forbs, become scarce (but *Cladonia* spp. could be abundant on top of the moss carpet). These authors indicated that the sites infested are costal dunes which could be calcareous or non calcareous, and also that the sites invaded are not necessarily subjected to human disturbance. Given the ecological behaviour of *C. introflexus* in Britain it could be expected to have a similar impact on heathlands and moorlands. Indeed, extensive carpets of *C. introflexus* can be observed, for example in some areas of the North York Moors National Park. Hobbs & Gimingham (1987) have found that the establishment of *Calluna* seedlings may be prevented by the presence of mats of mosses and litter, which are poor substrates for seed germination. *Cladonia* spp. can produce the same effect (Hobbs 1985); lichens, when growing in dense patches, can inhibit germination or establishment of other heath species and thus maintain lichen mats within otherwise closed heather stands.

However, mosses may play a positive role in a community. Gimingham (1972) observed that the abundance of *Calluna* seedlings was associated with the amount of *Campylopus paradoxus* Wils. (=*C. flexuosus*) present, nevertheless, it is uncertain whether the presence of the moss provided beneficial conditions for the germination of heather, or whether it was just a coincidental co-occurrence. According to Keizèr, Tooren & During (1985), seedling mortality of some species was lower with high bryophyte cover on chalk grassland in The Netherlands but at the same time seed germination was diminished. Tooren, Hertog & Verhaar (1987) studying chalk grassland suggested that bryophytes may be important in the nutrient cycle of the ecosystem, because their activity period is in winter, when the vascular plants are inactive. This timing of the activity could prevent or reduce the leaching of nutrient during the winter period.

The potential impact of the invasion of *C. introflexus* on the moorland seems likely to be related to the effect that the moss carpets could have on the germination and establishment of *Calluna* seedlings, thus suppressing the *Calluna* regrowth capability. It is hypothesized that *Campylopus introflexus* may affect either the germination of *Calluna* seeds or seedling establishment (because moss carpets are a poor substrate for young plants) or growth rate (through direct competition for nutrients, through inhibition of mycorrhizal development, which could mean mainly a lower intake of phosphorus and nitrogen by *Calluna*, or by some other chemical (allelopathic) effect. However, the main mechanism of suppression of other plant species by *C. introflexus* is expected to be related to physical limits set upon the germination and establishment of seedlings.

Calluna seeds are approximately 600 × 350 µm in size. They are produced in the autumn and are mainly dispersed by wind (Webb 1986). Gimingham (1960) reported that germination depends upon an adequate and maintained water supply; but Pons (1989) found that repeated hydration and dehydration neither affected viability of the seeds nor inhibited better germination when suitable conditions subsequently arose. Seed germination is also affected by both temperature and light (even in short bursts). There is no germination in darkness (Gimingham 1972). In the field, with an adequate moisture supply, germination is better on mineral than on organic substrata and is better on a consolidated substrate than a loose one. This has been attributed to better water retention characteristics together with the better exposure to light on a smoother surface (Gimingham, 1960). According to Gimingham (1960), germination is possible among mosses like *Sphagnum* spp. *Aulacomnium palustre* (Hedw.) Schwaegr. and *Dicranum scoparium* Hedw. if there is water available at the base; but without this there is no germination on the latter two species. If water is provided only from above, germination of *Calluna* seeds can occur on *Sphagnum* spp., *Hylocomium splendens* (Hedw.) and *Pleurozium schreberi* (Brid.) Mitt. (Gimingham 1960).

The germination of *Calluna* seeds is usually slow; the first germination occurs after 8 to 15 days, it takes around one month to reach 50% germination and about two months to get to 96% germination (Gimingham 1960, Pons 1989). According to Pons (1989), *Calluna* seeds show a form of dormancy, because they require specific conditions to germinate (high photon flux density, large red/far-red ratio and long exposure times to light). These conditions are not likely to be fulfilled in autumn under a closed canopy, a thick layer of litter or within a dense moss carpet, and hence a large amount of seed will be incorporated into the seed bank. However, Pons (1989) has shown that repeatedly imbibing and then drying the seed increased both the rate and the percentage of germination. This treatment also had an effect on the requirement of light, reducing the exposure time from several days to less than one day. Considering these results the seeds are more likely to germinate after a period of burial in the seed bank, provided that they are then exposed to light.

It has been suggested that disturbance favours the invasion of *C. introflexus*. Also, the results of a survey of the distribution of this moss in relation to environmental factors in the North York Moors National Park (chapter 4), have shown that *C. introflexus* reaches its greatest frequency in patches of heather between the late pioneer and early building stages. Therefore, it is likely that the moss could have an impact on the regeneration process of the moorland community, at least slowing down its rate of recovery following fire or cutting. The establishment of *Calluna*, the main component of the vegetation, takes place from both vegetative development of new shoots from surviving stem bases and from seed. Sometimes the vegetative contribution can be the most important, as for example after cutting, but the proportion of seed germination is always substantial, specially after fire in old stands. Therefore, it was considered important to evaluate the effect of the moss on the establishment of new *Calluna* individuals from seed by direct interference either on the germination or on the growth of the seedlings, which is the aim of this chapter.

5.2 Methods

To establish the presence of a seed bank of *Calluna* on the carpets of *C. introflexus* a small sample was taken. Four blocks of soil with moss carpet, approximately 20 cm square and 10 cm thick (average thickness of the moss layer was between 1.3 and 1.9 cm), were collected from Kildale Moor in the North York Moors National Park (National Grid Reference NZ 612113). The area had a cover of approximately 45% of *Calluna* (gaps were about 1 m in diameter) and 48% of *C. introflexus*. The blocks were placed in seed trays filled with micafil under greenhouse conditions and daily watering.

To assess the effect of the presence of a moss carpet on the germination of *Calluna* seeds, the following experiment was designed so as to contrast the amount of germination on moss carpet blocks with that on bare ground. Considering the observation by Gimingham (1960) mentioned above that germination is possible among some mosses if there is water available at the base but not when it is only provided from above, two different regimes of watering were used: watering daily from above and continuous supply of water at the base of the pots. Each treatment was replicated 5 times. The pots used were 1 l capacity, square, 10 cm on side. The seed of *Calluna*, the moss and the soil were collected from Kildale Moor. All moss blocks used were approximately 2 cm thick, with about 2 cm of original soil at the base. The moss carpet collected for this experiment was gathered from an area with extensive cover of moss, where very little *Calluna* was present. The closest *Calluna* bush was over 3 m distant. The pots were prepared filling them with soil collected from the area on top of a layer of micafil (2 cm thick); the pots with moss carpet were prepared placing a complete moss block on top of the soil layer. All the pots, with and without moss, were filled up to approximately 10 cm height. The seed was obtained from air dried flowering branches. First, the capsules were separated from the branches and sieved (5 mm mesh), then the seed was extracted from the capsules using a sieve (0.8 mm mesh) and soft hand pressure to force the capsules open; finally, the seed was separated from the capsule remains by vibration. 25 mg of seed (approximately 1060 seeds) were placed in each pot. To account for the germination from the pre-existing seed bank in both the soil samples and the moss blocks, a whole replicate of the experiment was prepared with unseeded pots (another set of 20 pots). The pots were placed in a randomized arrangement in the greenhouse (hence the experiment has a 2^3 factorial design). Two samples of 25 mg of seed were placed on moist filter paper in petri dishes to estimate the maximum potential germination of the seed.

If there is an effect of the moss on the germination rate of *Calluna* seeds it could be due to an allelopathic interaction. To test this possibility two more experiments were conducted. First, 10 lots of 100 seeds of *Calluna* were placed in petri dishes with filter paper that was kept moist all the time. Five of them were watered with deionized water and the other five were watered with a solution obtained from soaking 50 g of fragments of *Campylopus introflexus* carpet in 2 l of deionized water for 1 hour. The solution was then filtered using Whatman paper No. 1, and kept in the fridge while not in use. The pH of the resulting solution was 6.65. Second, again 100 seeds per plate were used, but this time individual moss shoots were placed in the petri dishes together with the seeds. Three conditions were tested in this way (no moss, 3 shoots and 6 shoots) and these treatments were replicated five times. All these petri dishes were incubated in a growth chamber at 20°C (night depression 5°C), humidity 60% and light period of 16h. Seeds were considered as 'germinated' when the radicles started to show, they were then counted and eliminated from the plates.

5.3 Results

The results of the incubation of moss carpet blocks showed that an active seed bank can exist within carpets of *C. introflexus*. After 55 days of incubation, seedlings started to show on all of the blocks and after nearly 100 days there were between 9 and 160 seedling per block (0.023 and 0.4 seedlings cm^{-2} respectively). The results of the germination experiment were consistent with this observation (Table 5.1), however the numbers were consistently smaller (on average between 0.004 and 0.01 seedlings cm^{-2}). This suggests that the size of the moss patch could have an effect on the seed bank stored in the carpets. On the other hand, whether or not this seed bank could be activated under field conditions remains to be ascertained. It is also clear that either its response to favorable watering conditions is more limited or else its size is smaller to that on bare ground.

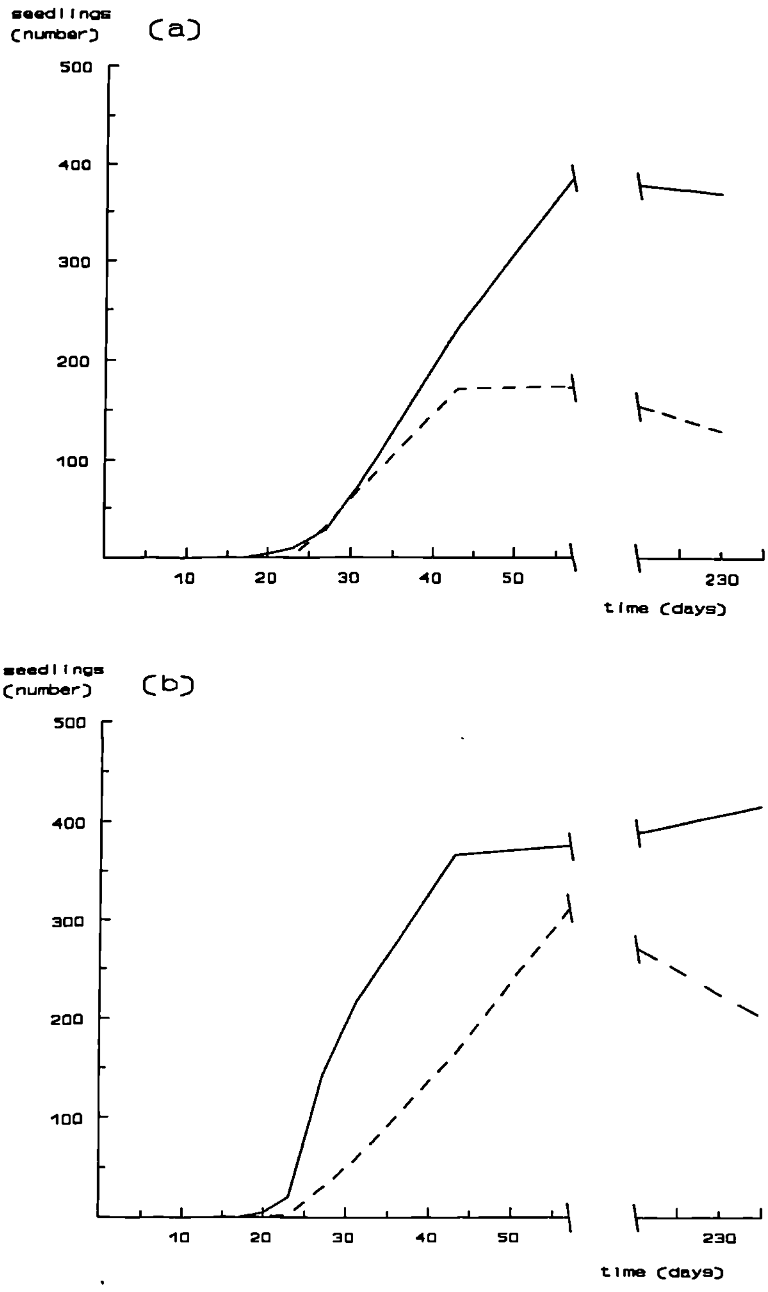
Table 5.1. Average number of harvested seedlings per pot for each treatment. The average counts of the unseeded pots were subtracted from the counts of the seeded pots to allow for the contribution from the pre-existing seed bank. One observation from the treatment with bare ground and with water supplied from above was discarded (see text for justification). Germination on blank petri dishes was 755 seeds on average, representing approximately 71% germination of the added seeds.

	No moss		Moss	
Data set	Water above	Water base	Water above	Water base
Unseeded pots	24.2	12.4	0.4	1.0
Seeded pots	457.3	441.8	131.4	203.0
Corrected values	433.1	429.4	131.0	202.0

After 57 days any further germination in the petri dishes ceased and, at this time, the seedlings in the pots were counted non destructively for the last time (Figure 5.1). The heather plants were finally harvested after 231 days of growth. From the harvest the following information was recorded: number of plants, maximum height, dry weight and weight of flowering structures and fruits.

The counts of harvested plants were corrected for contribution from the seed bank by subtracting the average estimated from the unseeded pots for each treatment combination (Table 5.1). These data were analysed using generalised linear models assuming a Poisson distribution and logarithmic link function (log-linear model). An important amount of overdispersion was found, which suggested a departure from the assumption of a Poisson distribution as the random component of the model. To allow for this overdispersion the quasi-likelihood approach was used (Baker & Nelder 1986; Aitkin *et al.* 1989). A justification of the use of this approach is that the probability model that describes the number of counts best might be the negative binomial distribution, with variance $(1 + \mu/k)\ \mu$, where μ is the mean and k is the shape parameter of the distribution. If $\lambda = (1 + \mu/k)$, where $\lambda>1$ ($\lambda=1$ in the Poisson case), then the variance ($\lambda\mu$) is proportional to, rather than equal to, the mean (Baker & Nelder 1986). Therefore, in this case the quasi-likelihood approach consists of fitting a model where the basic error distribution is taken to be Poisson but the scale factor, instead of being fixed to 1, is estimated from the sample as the residual deviance divided by the degrees of freedom. Another difficulty found when modelling these data was that one observation had a very small value in comparison with the other replicates in its treatment. It was decided to eliminate this observation from the analysis because it was a pot that was affected when glass broke in the greenhouse (the observation was from the combination no moss and water at the

Fig. 5.1. Effect of a carpet of *Campylopus introflexus* on the germination and survival of seedlings of *Calluna vulgaris*. The values plotted are the average number of living plants. Dashed lines indicate plants on a moss carpet and the continuous lines plants on bare ground. Plot (a) shows the data when water was provided only from above, and (b) the values when water was provided continuously at the base.



base). However, similar conclusions were reached when using the complete dataset.

The amount of germination observed in the petri dishes was on average 755 seedlings per dish, or approximately 71% of the added seed. This proportion is taken as an estimate of the maximum amount of germination to be expected with the seed used. From the values shown in Table 5.1 it can be seen that about 60% is the maximum germination of the germinable seed that is reached in the best case. This is consistent with the fact that *Calluna* normally forms a large seed bank. Considering the effect of the treatments, the results suggest a consistent significant depressive effect of the moss carpet on the germination of *Calluna* (Figure 5.2 and Table 5.2), since neither the interaction term nor the main effect of water supply were significant. The experiments to test an allelopathic effect gave no indication of moss effect (Figures 5.3 and 5.4). In the case of the solution of moss the difference in total germination between the control and the treatment was only one seedling. The experiment with moss shoots was analysed with log-linear models. The deviance associated with moss effect was 0.788 with 2 degrees of freedom which, being a χ^2 distribution, is not significant.

The moss carpet produced a reduction of about 60% in the germination of *Calluna*, with respect to that observed on open ground, but this was not due to a chemical inhibition produced by the moss; therefore, it seems clear that the physical conditions within the moss carpet are likely to be responsible for this reduction in germination. It is perhaps surprising that the germination was not lower, as would be expected because of the lack of light within the moss carpet. The carpet of *C. introflexus* is very dense with a great overlap between leaves of adjacent shoots even when dry (Moore & Scott 1979) and the seeds of *Calluna* are very small. Because of this morphological characteristic, a proportion of the seeds is trapped on the top

Fig. 5.2. Number of seedlings at the time of harvesting (231 days after experiment initiation). The values are expressed as the percentage of the germination observed on the blank plates. The 'notches' on the box-plots mark the span of a 95% confidence interval for the median. Notice that in this case the intervals extended beyond the span of the box itself. There was an observation with unusually large counts which is marked as a circle. The first treatment combination showed particularly large dispersion as suggested by the size of the box. The observation that showed the samallest number of seedling was recorded for the first treatment. This observation was omitted in the subsequent analyses because it was suspected to be an outlier.

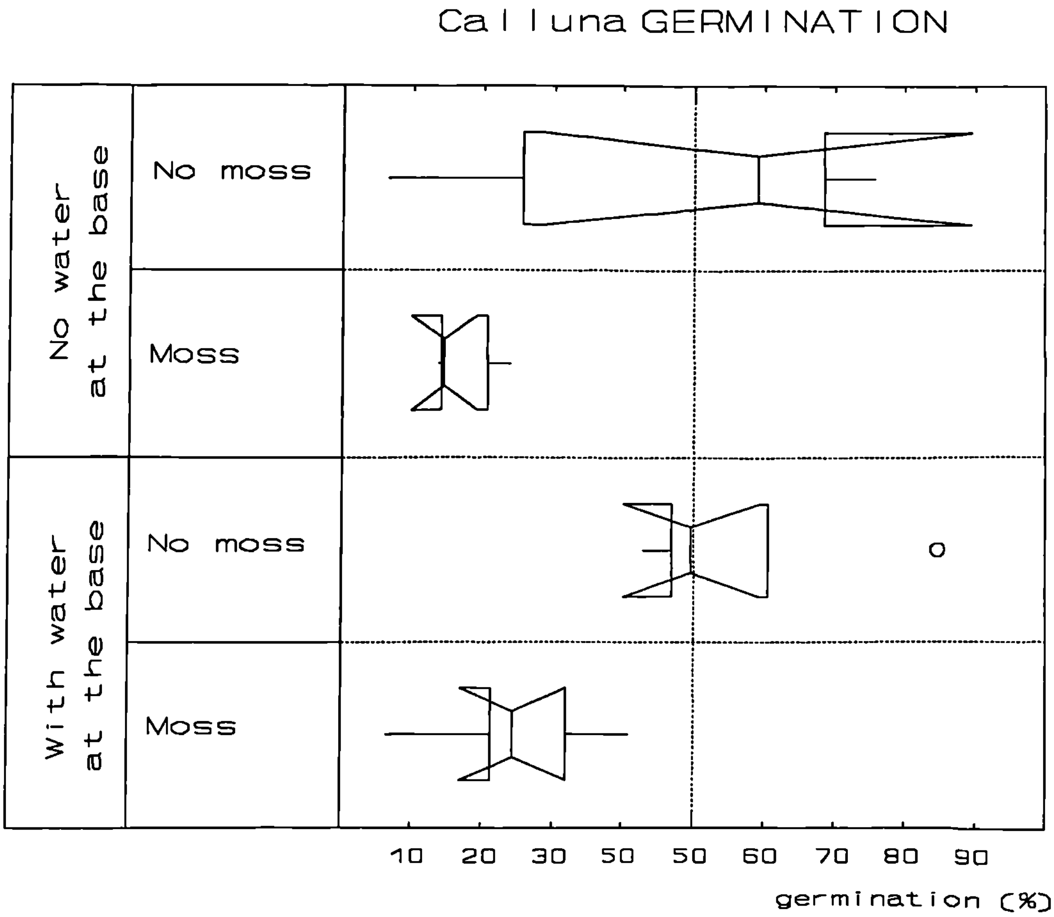


Table 5.2. Harvested seedling counts analysis using log-linear models. Critical χ^2 for all the deviances in the table is 3.84 (with 1 degree of freedom, $p=0.05$). An overdispersion parameter of 33.71 was assumed (see text for explanation).

Source	DF	Deviance
Moss	1	33.75^{*}
Watering	1	0.61^{ns}
Interaction	1	1.64^{ns}

[ns] Not significant
[*] $p \leq 0.0001$

Fig. 5.3. Germination of *Calluna* seeds treated with the solution obtained from soaking fragment of *Campylopus introflexus* in deionised water. There was no evidence of significant differences between the treatment and the control (deionised water only).

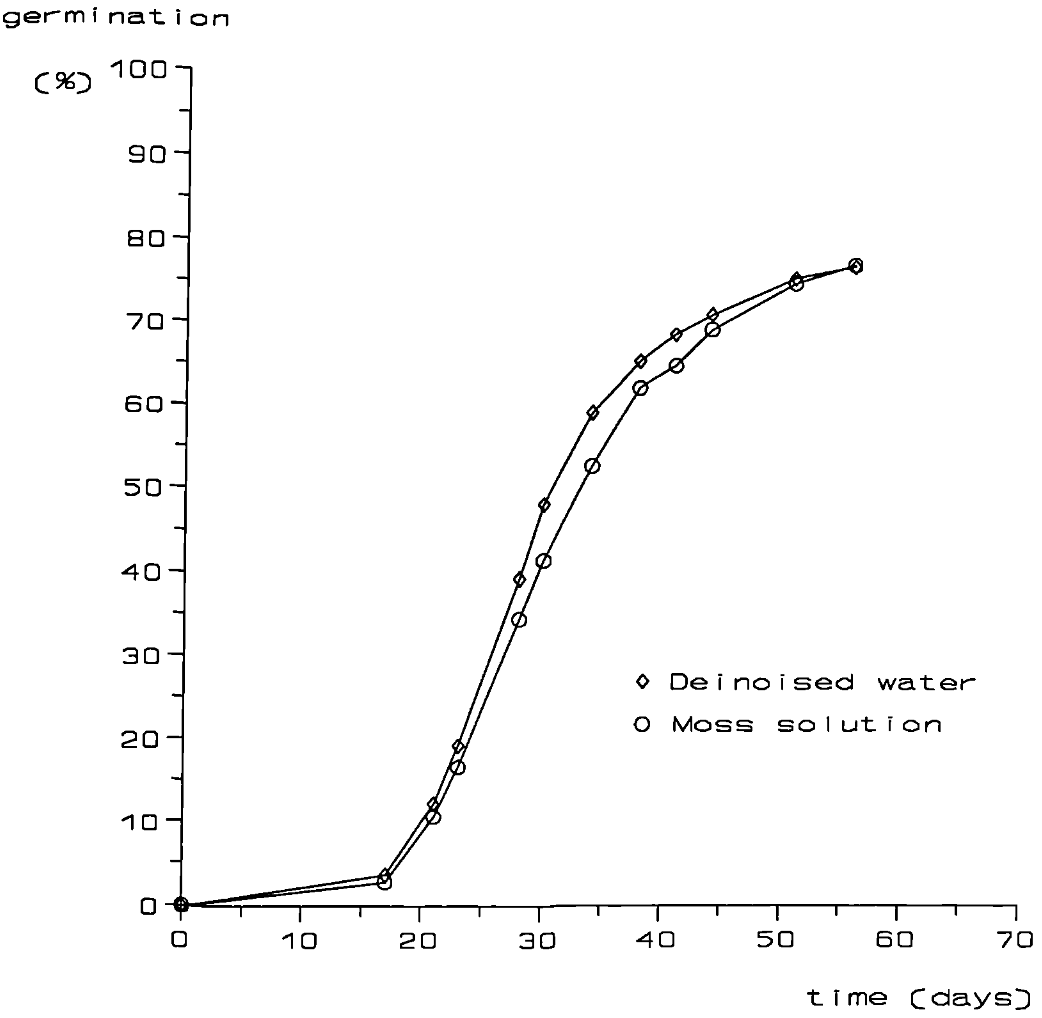
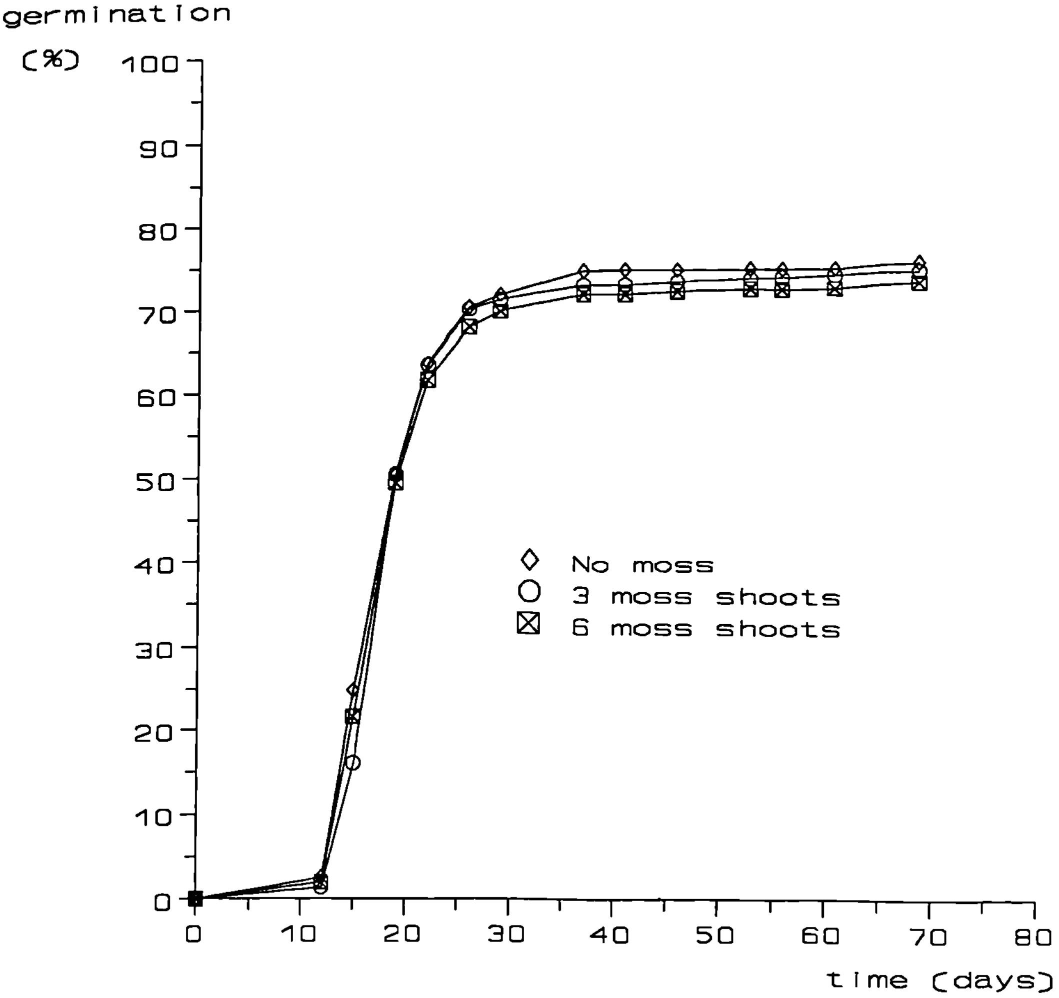


Fig. 5.4. Germination of *Calluna* seeds incubated in petri dishes together with shoots of *Campylopus introflexus*. There was no evidence of differences in the number of germinating seeds between the treatments and the control.



of the moss shoots (at the bases of the leaves) where they may germinate if enough water is available from either the atmosphere or the soil. It is also interesting to consider that these trapped seeds would be subject to a regime of repeated hydration and dehydration which, according to Pons (1989), would reduce the requirement of light for germination.

The other three attributes of the harvested plants that were measured are summarized in Table 5.3. As the plant density affects the performance of the plants, it was decided to include the number of seedlings as a covariable. These data were analysed using an analysis of covariance and, to cope with problems of heterogeneity of variances and normality, a suitable Box-Cox transformation was chosen (Aitkin *et al.* 1989). The assumptions of normality and homogeneity of variances were tested with the Filliben correlation coefficient and Hartley's F_{max} ratio respectively (Aitkin *et al.* 1989); the results of these analyses are summarised in Table 5.4.

For the maximum height of the plants a log transformation was found appropriate. The interaction term was found to be significant. This is because, while there was no difference in the maximum height of the plants due to the form of the water supply when growing on moss carpets, in the absence of the moss carpet the plants were significantly smaller when water was supplied continuously at the base. The main effects of moss and water are also highly significant which is due to the fact that, despite the interaction effect, the depressive effect of the moss carpet on the number of plants is consistently maintained. On the other hand the maximum height of the plants was substantially larger when growing on moss carpets irrespective of the form of the water supply. This was due partially to the lower plant density that resulted on the carpets (density effect was found to be significant). However, the analysis suggests also that there should be conditions for a better nutrient intake,

Table 5.3. Treatment means for the variables measured on the harvested plants of *Calluna*. To account for the density effects on the performance of the plants, a set of corrected values was calculated taking the linear regression on density and then computing the fitted values for the average density.

	No moss		Moss	
	Water above	Water base	Water above	Water base
Raw data				
Height (cm)	11.4	6.2	19.3	20.4
Dry biomass (g)	3.6	1.3	3.0	2.4
Flowering parts (g)	0.059	0.005	0.305	0.356
Corrected for density				
Height (cm)	12.3	7.2	15.3	17.8
Dry biomass (g)	3.3	1.1	3.3	2.5
Flowering parts (g)	0.066	0.018	0.193	0.290

Table 5.4. Results of the analysis of covariance and tests of its assumptions. The critical value of Hartley's F_{max} for the hypothesis of homogeneity of variances is 19.2 (P=0.05, 4 degrees of freedom and 4 treatments). The critical value of Filliben correlation is 0.950 (for n=20 and P=0.05), a lower correlation value would mean serious departure from the normality assumption.

		F ratios					
Attribute	Transformation	Moss	Water	Interaction M.W	Density	Filliben correl (%)	Hartley's F_{max}
Height	Log	10.982^{***}	42.416^{***}	7.948^{**}	5.483^{*}	99.5	1.592
Dry biomass	Log	3.125^{ns}	18.990^{***}	8.448^{**}	1.118^{ns}	98.0	5.810
Flowering parts	Square root	23.119^{***}	0.059^{ns}	6.528^{*}	11.237^{***}	98.9	6.706

^{ns} Not significant
* $P \leq 0.050$
** $P \leq 0.025$
*** $P \leq 0.010$

because the plants are found to be significantly higher after the effect of density has been accounted for. A complement to this result is the series of dry mass determinations, which were also log-transformed for the analysis. As in the case of the maximum plant height, the interaction term was found to be significant and the explanation is the same; no significant difference in biomass between the forms of water supply when growing on moss carpets, but a significant difference in the absence of the carpet. However, in the case of the dry mass it was also found that all the treatments produced similar amounts of biomass except when water was supplied at the base in the absence of a moss carpet, in which case the dry mass was significantly smaller (about 60% less). This result is in agreement with what has been found in natural conditions (Gimingham 1960), where it has been observed that *Calluna* cannot withstand water-logged soil conditions very well.

The dry mass of reproductive structures was analysed using a square root transformation. The only significant factor in this case was the moss carpet, due to a production of flowers and fruits about 10 times larger when the carpet was present than when it was absent. All of these results indicate that, once a *Calluna* seed has germinated on a carpet of *C. introflexus*, the new plant can be expected to have a good performance, which is in agreement with the results of Keizer *et al.* (1985) and Tooren *et al.* (1987). It is important to mention that the root systems of the seedlings growing on moss carpets were very ramified within the carpet itself.

5.4 Discussion

The carpets of *C. introflexus* have a significant negative effect on the germination of the seeds of *Calluna* but a positive one on the post-germination performance of the seedlings. The depressive impact on the germination is mainly due to a proportion of seeds that is lost because they sink in the carpet and are then deprived of light. However, another proportion of seeds is trapped near the apices of the moss shoots where they may germinate, provided that enough water is available. The germination of the seeds under these circumstances requires further consideration because it can be seen that it is a risky position for the seedling to grow from. There are two main problems. First, the carpet can dry quickly in the absence of an adequate water supply. Second, the carpets tend to fragment, up-rooting the plants that are growing on top of the carpet, as has been observed in the field (Figure 5.5). This fragmentation process has been attributed informally to the action of birds (F. Cook, personal communication) but it is considered here that it is more likely to be a spontaneous process that occurs when the carpet has reached a certain thickness, as van der Meulen *et al.* (1987) have also suggested. According to Moore & Scott (1979), the rhizoids of *C. introflexus* are relatively sparse and weak with a breaking strain of only 3.9 kg cm^{-2}, which is far less than that estimated for the other three species examined by these authors (the next closest, *Thuidium furfurosum*, was found to be 27.5 kg cm^{-2}). This suggests that it is possible that the drag produced by the wind, or perhaps by running water, on a carpet of a certain thickness could be enough to separate fragments from the soil. It is possible that at a latter stage the birds contribute to the fragmentation of the carpet in their search for tipulid larve in the winter months.

Although the number of seedlings produced on a carpet of *C. introflexus* is diminished, their performance can be better, which could compensate for the initial drop in germination. Under greenhouse conditions not only can they grow more quickly but also they mature and reproduce earlier. At the end of almost 8 months the plants that grew on moss carpets produced about 10 times more reproductive

Fig. 5.5. Example of an individual of *Calluna* that was up-rooted when the carpet of *Campylopus introflexus*, on which it had established, became fragmented and separated from the ground.

biomass than those growing on bare ground. However, under field conditions the growth is largely slowed down. Therefore, even when the same behaviour can hold true, there is a further risk derived from the span of time required by a seedling to become well established in the firm soil beneath a moss carpet. The support that the seedling has to develop must be enough to withstand the pulling force generated by a fragmenting carpet, with which it is closely interwoven because of the proliferation of the fine roots of the seedling. Also, grazing comes into play with a selective negative impact on the seedlings and young plants of *Calluna*, which will reduce even more its numbers and growth rate. The results on the size of the seed bank in carpets of *C. introflexus* suggest that the moss may also interfere the dispersion of *Calluna* seeds, as the carpet cover expands the fewer seeds are available for germination. Therefore, it seems possible that, under field conditions, the moss carpet may obstruct the establishment of *Calluna*.

The results of this work suggest that there is no distinct evidence that *C. introflexus* suppresses *Calluna* on the basis of the effects on germination and subsequent seedling growth. It has been demonstrated that the positive and negative effects, which have been described, compensate each other. However, under field conditions the impact of the moss is expected to be amplified. On the basis of informal field observations, it seems important to investigate the effect that the dynamics of the carpet itself could have on the competition process. A number of aspects are important here. Some preliminary results (chapter 4) suggested that *C. introflexus* can survive prolonged desiccation and also that detached carpet fragments can reestablish, once suitable conditions arise. This is a form of propagation used by *C. introflexus* which could convey competitive advantages, because of the resulting ability to eliminate young individuals of other species either by up-rooting or by covering them.

6. Establishment of *Calluna* seedlings on carpets of *Campylopus introflexus* under field conditions

6.1 Introduction

The invasion of the moss *Campylopus introflexus* from the Southern Hemisphere into Northern Europe has been very successful. Since 1941, when it was first found in England, it has expanded widely not only in the British Islands but also in oceanic portions of Northern Europe. In some localities the invasion has developed in the form of extensive stands covered with a thick carpet that makes difficult the establishment of other plants (in some instances even vascular plants). This has been the case in coastal dunes in The Netherlands (Meulen, Hagen & Kruijsen 1987), in a bog in Ireland (Richards 1963) and in heathlands in Brittany (Clément & Touffet 1988). There are other mosses that have invaded Europe during this century; an important example is *Orthodontium lineare* Schwaegr (which coincidentally also came from the Southern Hemisphere). However, in contrast with *C. introflexus*, *O. lineare* grows mostly on temporary substrates and it is often overgrown by other species on the same substrata; only occasionally *O. lieneare* is able to overgrow other mosses (Hedenäs *et al.* 1989a and 1989b). *C. introflexus* seems to be singularly capable of displaying an aggressive behaviour. Therefore, it is interesting to evaluate the potential of the moss to develop to such an extent as to interfere with the development of the communities that it is colonising.

C. introflexus has been found growing widely in the North York Moors National Park (chapter 4). In some parts of the Park it has been observed forming thick and extensive carpets where very few other species are present, and it was considered interesting to assess the potential of the moss to hinder the development of the moorland. It is hypothesised that an obstructive interaction with the vascular components is more likely to take place on the establishment of new plants from seed i.e., interfering with the regeneration niche (Grubb 1977) of the species. Because *Calluna* is commonly the dominant species of the moorland community it was the interaction with this species which was analyzed in most detail.

The seeds of *Calluna* are very small (approximately 500 µm in diameter), which makes them susceptible to plunge into the carpets of *C. introflexus* (usually more than 5 cm thick). The critical requirement for *Calluna* seed germination is a sustained source of humidity, long exposure to strong light helps although it is probably not essential, and fluctuating temperatures promote it (Gimingham 1972, Pons 1989). Gimingham (1972) has also pointed out that the germination of heather is better on organic than on mineral soils but that at the same time a consolidated substrate is better than a loose one. Pons (1989) found that when seeds of *Calluna* are exposed to repeated hydration and dehydration (likely to happen under field conditions) there is no loss in the germination capability of the seeds; on the contrary, it produced a relaxation on the requirement of abundant light supply. The establishment of the seedlings have similar requirements, but with a narrower tolerance, to those of seed germination. Moisture availability is again critical and a good supply of water is also required. Gimingham (1972) pointed out that the seedlings of *Calluna* cannot survive if the surface of the substrate dries out (beyond field capacity) or if a high saturation deficit develops in the air-layer close to the ground during the early phases of growth. *Calluna* is a species adjusted to colonize bare areas rather than closed communities, and hence its seedlings are more commonly found, for instance, in gaps or in areas cleared by fire or cutting (Gimingham 1972).

Contrary to the suggestion that *C. introflexus* may interfere the establishment of *Calluna* seedlings, it has been observed that mosses may have a positive association with the occurrence of heather seedlings. Gimingham (1972) observed, in a locality in north-east Scotland, small depressions with clumps of *Calluna* seedlings occurring together with dense growth of the moss *Campylopus paradoxus* Wils. (=*C. flexuosus*). He suggested that probably both the depression and the moss contributed to the maintenance of favourable moisture conditions in the proximate air-layer and in the substratum. Mallik, Hobbs & Rahman (1988) found a positive association between *Ceratodon purpureus* (Hedw.) Brid. and the seedlings of both *Calluna* and *Erica tetralix* L. in a stand where a fire left a substrate consisting mostly of bare mineral soil. A positive role of mosses has been reported for other communities. According to Keizer, Tooren & During (1985), in chalk grasslands, seedling mortality of some species was found to be lower when a high bryophyte cover was present, despite a lower level of germination. Indeed, *C. introflexus* may have a similar positive effect. The results of a previous greenhouse trial (chapter 5), suggested that germination and establishment of *Calluna* seedlings is possible on carpets of *C. introflexus*. It was observed that the presence of the moss carpet produced a strong reduction on the amount of heather seed germination (approximately 60% less than that obtained on open ground), which was demonstrated not to be due to an allelopathic inhibition. However, despite the lower amount of germination, it was found that the seedlings developed quicker when growing on a moss carpet.

Therefore, the aims of this chapter are to explore the relationships between the occurrence of *Calluna* seedlings and the carpets of *C. introflexus* as well as to determine the impact that the carpets have on the germination and establishment of *Calluna* under field conditions.

6.2 Methods

To examine the relationships between the carpets of *C. introflexus* and the establishment of seedlings of *Calluna* a survey was conducted in July 1989 in a stand where the moss was growing abundantly at Kildale Moor in the North York Moors National Park (National Grid Reference NZ612113). The variates measured were the frequency of both *C. introflexus* and *Calluna*, the thickness of the moss carpet, the number of *Calluna* seedlings and their height. The sample was taken in a systematic way over a grid of 7 × 9 points covering a rectangle approximately 15 × 25 m. On each point a square quadrat 25 cm on side was placed and the frequency of *C. introflexus* and *Calluna* estimated as the proportion of 5 cm squares where the heather and the moss were growing, all seedlings in the quadrat were counted and their height measured, the thickness of the moss cushions was estimated calculating the average length of a sample of individuals taken from different carpet points within the quadrat.

After the survey was conducted a fence was erected around the rectangle to prevent sheep grazing. Inside this plot an experiment was carried out to determine the impact that the carpets of *C. introflexus* have on the germination of *Calluna* under field conditions. The experiment aimed to contrast the amount of germination of *Calluna* occurring on open ground versus that taking place on moss carpets. In addition to the carpet treatment the artificial addition of 25 mg of *Calluna* seed (*ca.*

1060 seeds) was incorporated into the experiment, to allow for a possible difference in seed availability. The seed of *Calluna* that was added to the plots was obtained from air dried flowering branches collected in the same area during November 1989. To obtain the seed the following procedure was followed. The capsules were separated from the branches, and then the seed was extracted from the capsules using a sieve (800 µm mesh) and soft hand pressure to force the capsules open; finally, the seed was separated from the capsule remains by vibration. The seed was kept in plastic boxes in the dark. The experiment was laid out selecting 10 areas approximately 50 cm in diameter where the cover and thickness of *C. introflexus* carpet were relatively homogeneous (the carpet thickness ranged between 1 and 3.5 cm approximately among the blocks and its cover was 100% or very nearly so); within each one of these blocks four squares 10 cm on side were marked. The treatments were assigned randomly to the plots, those receiving the 'open ground' treatment were obtained by removing completely the carpet of *C. introflexus* present in the plot. The experiment was initiated in October 1990 and the germination was monitored regularly until July 1991. On each sampling date the seedlings present were counted disturbing them as little as possible. As an estimate of the performance of the seedlings, the maximum length of the seedlings was recorded at the end of the experiment. The maximum potential germination of the seed lot was assessed by placing 25 mg of seed in each of four Petri dishes with moistened filter paper. Two of these dishes were kept in the field and the other two under greenhouse conditions.

6.3 Results

The distribution of the frequency of both *C. introflexus* and *Calluna* in the stand is summarised in Figures 6.1 and 6.2. The overall statistics of the variates

Figure 6.1. Spatial distribution of *Calluna* in the experimental plot at Kildale moor (National Grid Reference NZ612113). The contours represent frequency of heather determined on a grid of 25 squares within quadrats 25cm on side. Minima are indicated by contour lines with hachure.

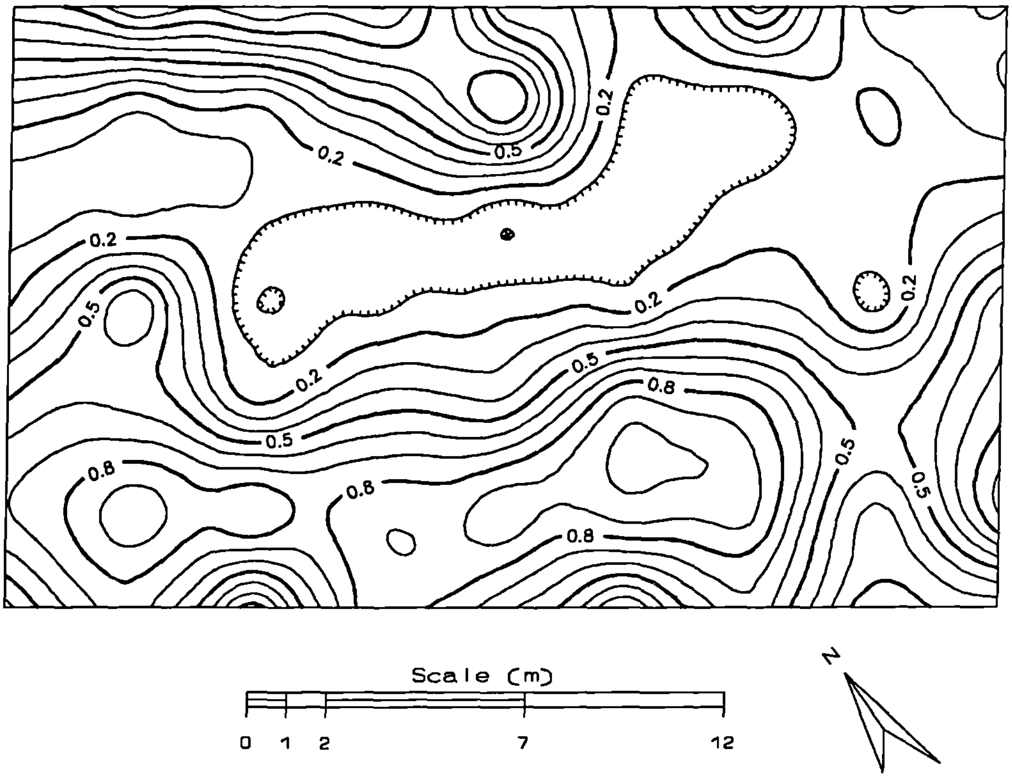
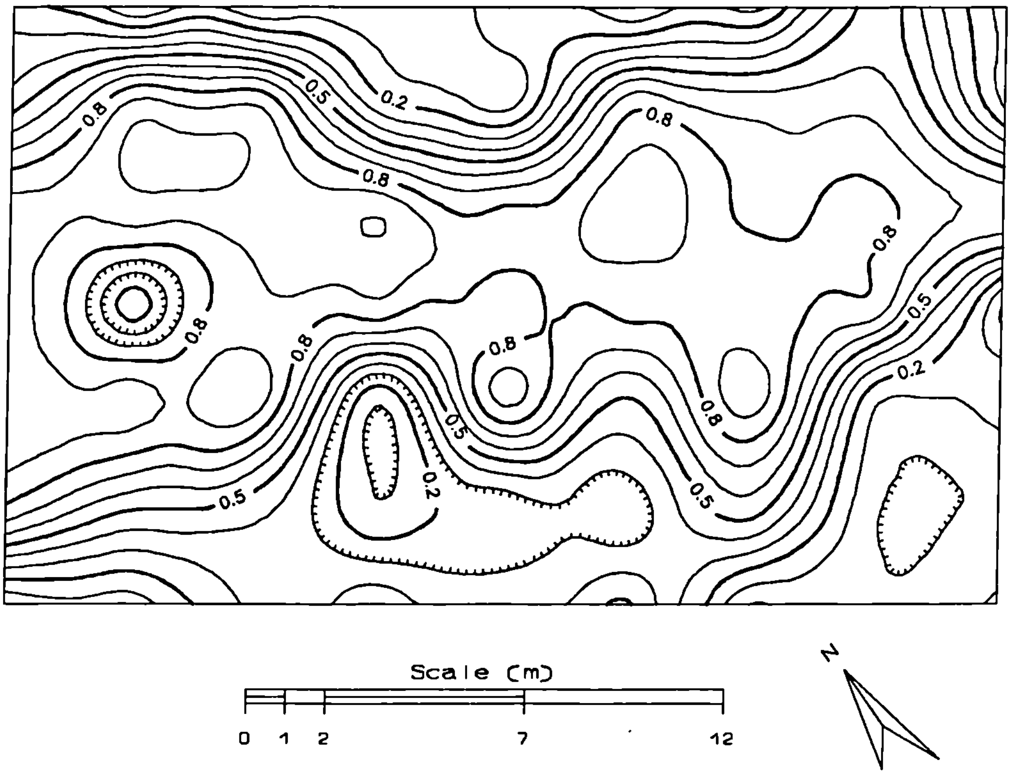


Figure 6.2. Spatial distribution of *C. introflexus* in the experimental plot at Kildale moor. The contours represent frequency of moss carpet ocurring on a grid of 25 squares within quadrats 25cm on side. Minima are indicated by contour lines with hachure.



measured are presented in Table 6.1. Comparing Figures. 6.1 and 6.2 it is apparent that, as could be expected, there is a strong negative association between *Calluna* and *C. introflexus*.

The relationship between the average length per quadrat of the seedlings of *Calluna* and the abundance of heather seedlings, the thickness of *C.introflexus* and the frequency of both *Calluna* and the moss was analyzed using a quadratic polynomial on these variates. The model fitted showed that the size of the seedlings of heather was poorly associated with the frequency of the heather as well as with the frequency and size of the moss carpet, since only approximately 16% of the variance was accounted for by the model including these three variates. In contrast, the abundance of seedlings of heather showed a better association, since approximately 35% of the variance was accounted for by the quadratic model on seedling abundance. However, the residuals of the model suggested a poor fit and strong departure from normality. Using the Box-Cox procedure (Aitkin *et al.* 1989), it was not possible to find a suitable transformation to improve the model. Therefore, it seems only safe to suggest that the seedlings of *Calluna* grow better where they are more likely to occur; which is obvious considering the high similarity in ecological requirements of both germination and seedling establishment of *Calluna*.

The association between the abundance of *Calluna* seedlings with the amount of heather cover and with both the amount and size of *C. introflexus* carpet was analyzed using generalised linear models (GLM) with assumed Poisson distribution and logarithmic link function (Aitkin *et al.* 1989). The results of the analysis are shown in Table 6.2. A small amount of overdispersion was observed suggesting that the assumption of a Poisson random component of the model was unsatisfactory. To

Table 6.1. Overall statistics of the variables sampled in the permanent plot set up at Kildale Moor.

Variable	Mean	Standard error	Maximum
Number of seedlings	3	0.61	19
Average height of seedlings(mm)	5	0.75	22
Frequency of *Calluna* (%)	43.4	4.56	100
Frequency of moss carpet (%)	48.9	4.90	100
Thickness of moss carpet (mm)	7	0.70	28

Table 6.2. Regression analyses to explore the relationships of the number of *Calluna* seedlings with both the frequency and with the thickness of *C. introflexus* carpets as well as the amount of cover by adult heather. The key for the models is: CC=*Calluna* frequency, CM= moss carpet frequency, TM=thickness of the moss carpet. Deviances are χ^2 distributed but, because of overdispersion, they have to be first divided by the scale factor indicated and then compared against the corresponding *F* distribution.

Source	Degrees of freedom	Deviance	Scale (df)
Full quadratic model: CC+CM+TM+CC²+CM²+TM²+CCxCM+CCxTM+CMxTM			
Error	53	264.5	
All quadratic terms	3	21.9^{ns}	4.99 (53)
All interaction terms	3	58.9^{**}	5.11 (56)
CC x TM	1	28.5^{**}	
CC x CM	1	3.3^{ns}	
CM x TM	1	2.2^{ns}	
Linear terms (only one can be tested)			
CC	1	6.0^{ns}	5.08 (58)
Final model: CC+TM+CCxTM			
Error	59	300.9	

^{ns} Not significant: $P>0.05$.
* Significant at $P\leq 0.05$.
** Significant at $P\leq 0.025$.

allow for this departure of the Poisson assumption the quasi-likelihood approach was used (Aitkin *et al.* 1989). This approach is justified considering that the negative binomial distribution may be more adequate to describe the counts of seedlings; if that is the case the variance is given by $(1+\mu/k)\mu$ (where μ is the mean and k is the shape parameter of the distribution). If a scale parameter is defined as $\lambda=(1+\mu/k)$, where $\lambda>1$ ($\lambda=1$ in the Poisson case), then the variance ($\lambda\mu$) is proportional to, rather than equal to, the mean (Baker & Nelder 1986). Therefore, in this case the quasi-likelihood approach consists of fitting a model where the basic error distribution is taken to be Poisson but the scale factor, instead of being fixed to 1, is estimated from the sample as the residual deviance divided by the degrees of freedom. A drawback of the approach is that the goodness of fit of the model cannot be assessed any more. As an additional reference for the analysis, a binomial GLM model with logit link was fitted to the presence of seedlings (Table 6.3).

The results of the two models are consistent in suggesting that both the presence and the abundance of the seedlings of *Calluna* are related to both the frequency of mature heather and the size of the moss carpet (Figures 6.3, 6.4). It is considered that, because of the time of the year when the sample was taken (summer), the seedlings found were likely recruits of the heather population, it is then interesting that the seedlings were more frequent where mature plants of *Calluna* offered larger cover. At the same time there is a negative relationship between both occurrence and abundance of seedlings with carpet size when the cover of *Calluna* was low. This moss interference is ameliorated or completely reverted as the cover of heather increases, which suggests that the effect of the moss may only become inhibitory in the gaps of a regenerating moorland where the moss is growing extensively. This is important because it is there where seedlings generally occur

Table 6.3. Regression analysis of the probability of occurrence of heather seedlings in relation to frequency of both *Calluna* and carpets of *C.introflexus* as well as the thickness of the moss carpets. The explanations of the abbreviations used are provided in Table 6.2.

Source	Degrees of freedom	Deviance
Full quadratic model: CC+CM+TM+CC^2+CM^2+TM^2+CCxCM+CCxTM+CMxTM		
Error	53	51.3
All interaction terms	3	8.6^{*}
CC x CM	1	0.3^{ns}
CM x TM	1	1.1^{ns}
CC x TM	1	7.2^{**}
All quadratic terms	3	12.6^{**}
CM^2	1	0.0^{ns}
CC^2	1	0.6^{ns}
TM^2	1	12.2^{***}
Linear terms (only one can be tested)		
CM	1	1.3^{ns}
Final model: CC+TM+TM^2+CCxTM		
Error	58	54.7

^{ns} Not significant: $P > 0.05$.
* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.

Figure 6.3. Expected number of *Calluna* seedlings as a function of adult heather frequency and the thickness of the carpet of *C. introflexus*. The function is only calculated within the convex hull of the sampled space. Contour lines are ilustrated at intervals of one seedling.

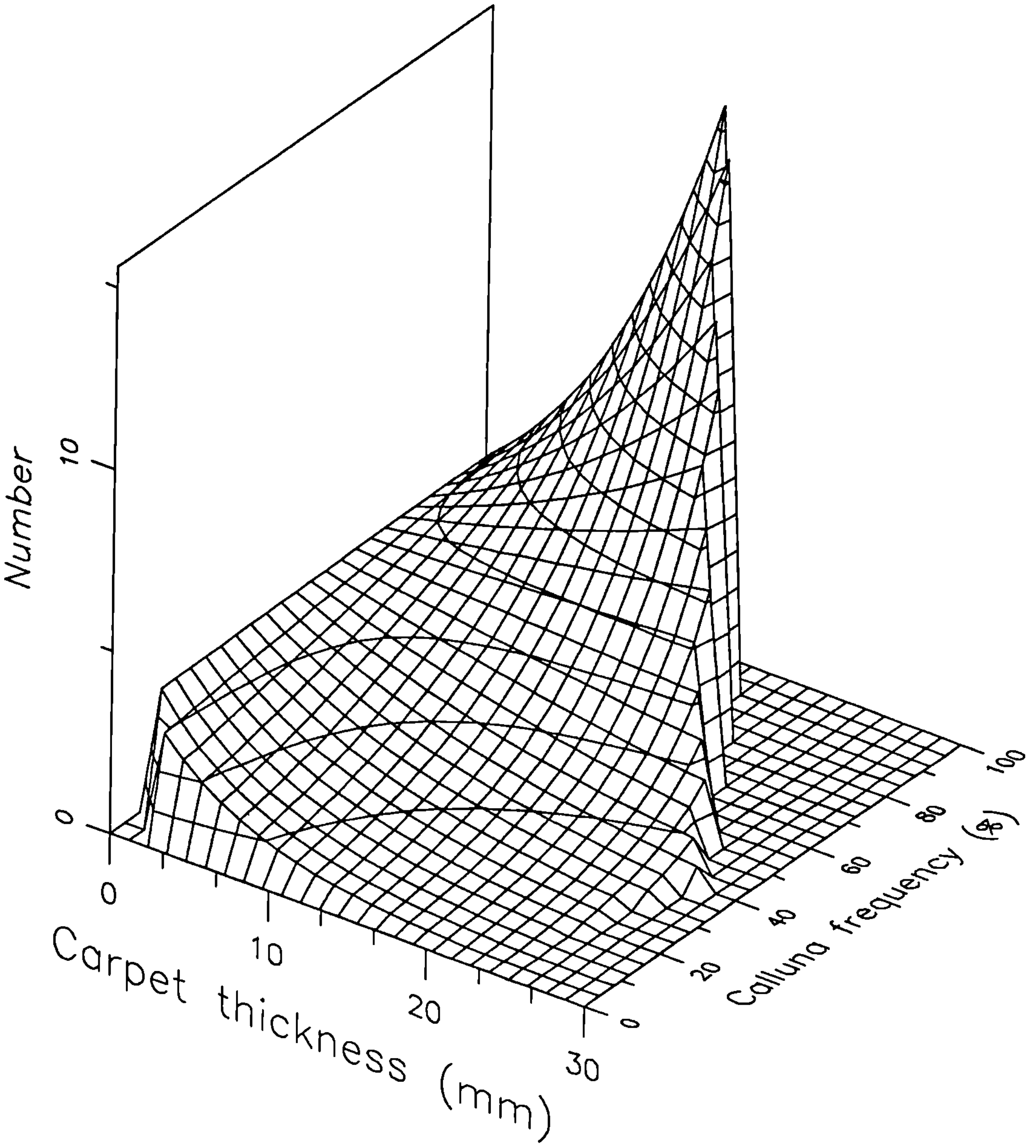
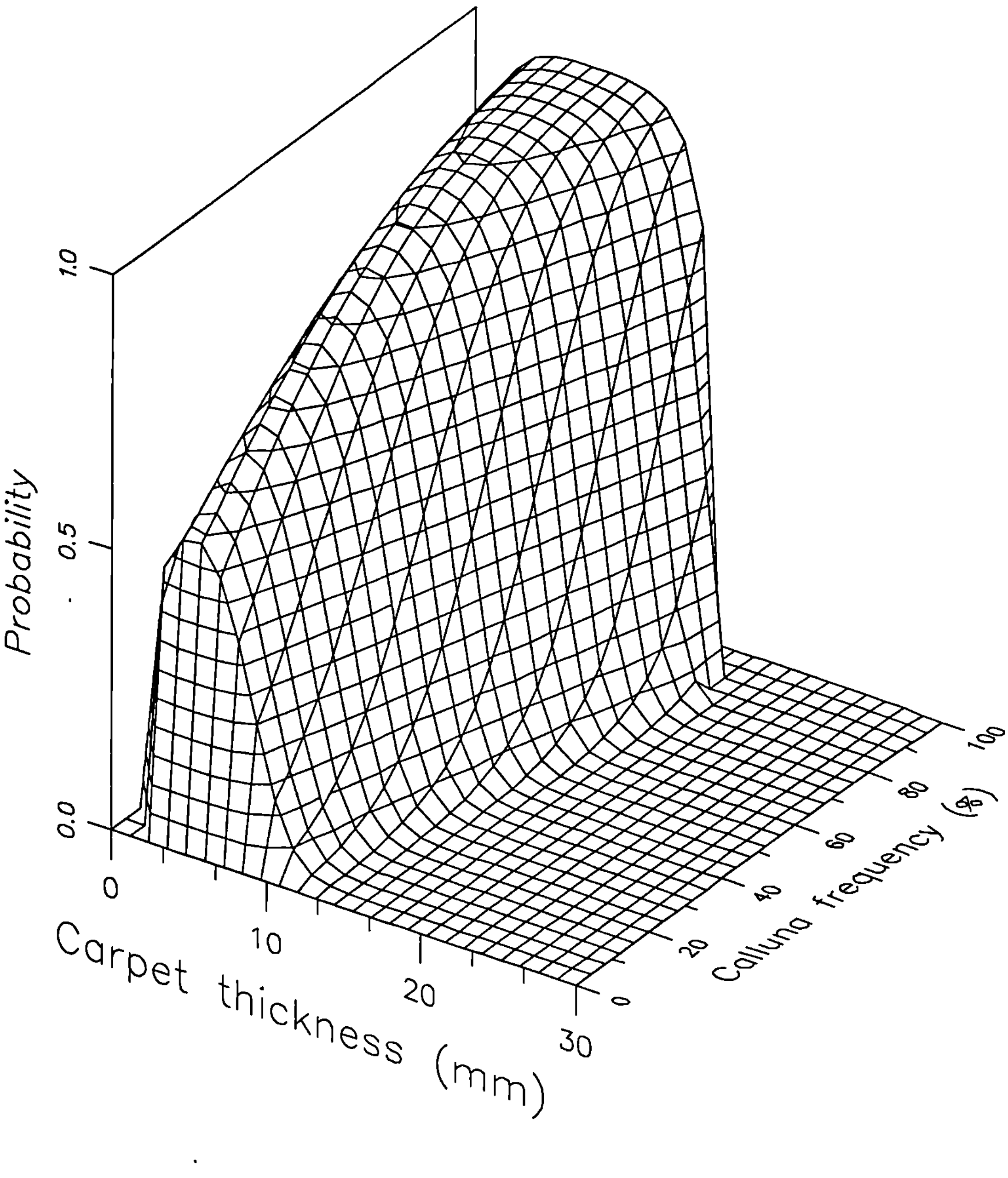


Figure 6.4. Fitted probability of occurrence of *Calluna* seedlings as a function of the frequency of adult heather and the thickness of the carpet of *C. introflexus*. The function is only ilustrated within the convex hull of the sampled space. The contour lines are ilustrated at intervals of 0.05 probability.



(Gimingham 1972) and also because the speed of regeneration of a full heather cover, from seed, will very much depend on the establishment of new plants in the gaps. On the other hand, the fact that the seedlings can be establishing under the protection of adult plants, irrespective of the presence of the moss, suggests that it is unlikely that *C. introflexus* can completely prevent the regeneration of the Callunetum.

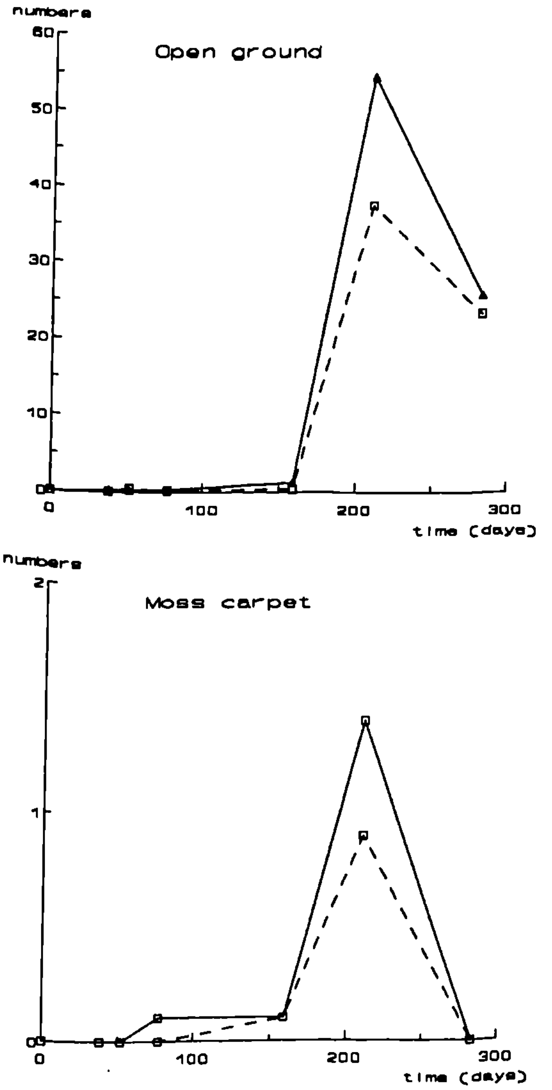
The results of the experiment to assess the impact of the carpets of *C. introflexus* on the establishment of *Calluna* are summarised in Table 6.4. The baseline germination was substantial, averaging 785 in the field plates and 930 in the greenhouse ones (at the end of two months approximately). The field plates were germinating very slowly because it was difficult to maintain an adequate moisture supply. However, one of them had its lid accidental fractured and then water infiltrated into the plate providing a continuous source of moisture; the seeds germinated quickly afterwards to a total of 1018. The outcome of the experiment is very conclusive (Figure 6.5), although some germination took place in the plots with moss carpets (which were over 1 cm thick), all of the seedlings died by the end of the experiment. Establishment of *Calluna* only took place on plots where *C. introflexus* carpet was removed.

It is also clear that there was very little effect of the addition of seed to the plots, which suggests that natural sources were readily providing active seeds (either from the seed bank or from new production), as could be expected because of the abundant production and efficient dispersion of seeds characteristic of *Calluna* (specially at a building stage). It is, however, also evident that a substantial amount of the seeds that were available for germination failed to do so. It is assumed that many of them were incorporated into the seed bank, which is known to be massive, even after long periods under afforestation (G. Benítez pers. comm.).

Table 6.4. Summary of results of the germination experiment. The germination averages are seedling counts per 100 cm^2. The moss treatment is the presence of 100% cover of *C. introflexus* carpet versus open ground. The seed condition refers to the artificial addition of 25 mg of heather seed.

		Germination averages			
		No moss		Moss	
Date	Days	No seeds	Seeds	No seeds	Seeds
Oct-90	0	0.0	0.0	0.0	0.0
Nov-90	38	0.1	0.3	0.0	0.0
Nov-90	52	0.5	0.2	0.0	0.0
Dec-90	77	0.2	0.3	0.0	0.1
Mar-91	159	0.4	1.3	0.1	0.1
May-91	210	37.5	54.5	0.9	1.4
Jul-91	283	23.4	25.8	0.0	0.0
Final average dimensions (mm)					
Seedling length		7.7	7.0	-	-
Carpet thickness		-	-	20.7	18.9

Figure 6.5. Average amounts of germination of *Calluna* on open ground and on carpets of *C. introflexus*. Values are for 100 cm^2. The maximum germination corresponded to that observed on May-1991. In the two graphics a continuous line represents the plots where 25 mg of seed were added to supplement natural sources, the dashed lines depict the plots where no extra seeds were added.



6.4 Discussion

The results are consistent with the findings of the greenhouse experiment (chapter 5) and with the suggestion made there that the strong reduction in germination would seriously limit the establishment of *Calluna* seedlings under field conditions. Also, the finding that, provided that there is adequately moisture supply, heather seedlings can develop on carpets of *C. introflexus* is consistent with the observation that they were positively associated with the carpet when desiccation protection was provided by the cover of adult *Calluna* individuals.

The results of the survey seem to contradict the observation that, in general, *Calluna* regeneration from seed under its own canopy and on its own litter is restricted (Gimingham 1972). As Gimingham (1972) pointed out, it is clear that *Calluna* is an apt colonist of open habitats, because of its high reproductive capacity and relatively effective and rapid dispersal. Nevertheless, it has to be considered that the community examined was not in an advanced building stage and therefore neither the canopy was too close nor the accumulation of litter under the heather was too big. At the same time it has to be pondered that, although the availability of light at ground level is of paramount importance, protection from desiccation is also essential. These two conflicting requirements can be fulfilled to a degree under the cover of intermediate size individuals of *Calluna* (especially near its periphery), which provides an explanation for the positive association between *Calluna* cover and the occurrence of seedlings. It can further be proposed that, if the seedlings succeed in becoming established, they would contribute to the radial expansion of the area initially acquired by the fostering heather individual (evidently in combination with some vegetative growth). However, this process is not expected to be sufficient to regenerate a full *Calluna* canopy quickly enough; some establishment of new nuclei should take place in the gaps existing in the regenerating community. At this point the impact of *C. introflexus* may be determinantal, because it will hinder the formation of these new heather development nuclei. Therefore, although it does not seem likely that *C. introflexus* can completely supress the regeneration of *Calluna*, it is quite possible for the moss to slow down the development of a full *Calluna* cover.

A similar process of moss inhibition on the regeneration from seed of *Calluna* has been proposed as an explanation of the events taking place at the degenerate phase of the *Calluna* cycle (Watt 1955, Gimingham 1972). The substantial development of pleurocarpous mosses together with the accumulation of litter from the heather itself interfere with the establishment of the seedlings of *Calluna*, and thus it may take some time before *Calluna* can re-establish itself. Thus if *C. introflexus* produces an extensive carpet in a stand it will bring about, within a few years of development (probably less than 10 years), conditions similar to those that would otherwise be produced after more than 25 years (in a degenerate stand of *Calluna*). In spite of the interference by the moss being possible, it seems to be the case that *C. introflexus* is not always able to colonize to such an extent as to produce a full carpet in the gaps of a regenerating moorland, especially if the community is developing vigorously from vegetative sprouts. This would be generally the case when burning early in the *Calluna* cycle, *i.e.* at about the early mature stage. It can be conceived that under such circumstances, because a cooler fire would be produced and vigorous vegetative regrowth would take place, there will be suitable conditions for heather germination and seedling establishment which, simultaneously, will depress the formation and development of a carpet of *C. introflexus* because of the rapid reduction of open space. Within this management setting, only when burning later in the *Calluna* cycle (towards the end of the mature stage or early in the degenerate stage) is it likely that suitable condition for the formation of moss carpets may arise, because then it can be expected less vegetative regrowth and the dependence on seedlings to provide the future *Calluna* stand will make the regeneration to proceed at a slower rate. Less vegetative regrowth and larger open patches might favour the development of carpets of *C. introflexus*. However, it also has to be recalled that small carpets of *C. introflexus* seemed to be favourable to the occurrence of the seedlings of *Calluna*. Therefore, it is likely that strong inhibition of the development of the community will take place only occasionally, when conditions are suitable for the development of a full and thick carpet of the moss. This would explain the fact that the colonization by *C. introflexus* has not generally been perceived as posing a serious threat, probably with the exception of some coastal dunes in the Netherlands (Meulen, Hagen & Kruijsen 1987). At the same time, further study of *C. introflexus* seems well justified, specially in relation to the formation, spread and dynamics of the carpets, which would provide the information required to more fully understand the development pattern and likely impact of the invasion by this southern moss.

7. Impact of *Campylopus introflexus* on the regeneration of a Callunetum

7.1 Introduction

In the last 50 years, since its introduction into Europe, the distribution of *Campylopus introflexus* has expanded greatly, mainly in dunes, heathlands and moorlands; sometimes the colonization has been in such an aggressive way that the exclusion of vascular plants has resulted. It has been suggested that the colonization by *C. introflexus* is favoured by disturbance, especially fire, and that it may take place quickly (Richards 1963, Gradstein & Sipman 1977, Verdus 1979). However, Clément & Touffet (1988) found, in Brittany, that *C. introflexus* was not a very early colonizer of burnt sites, since it only appeared after two years from the initial fire. Nonetheless, they also found that the moss was able to produce very dense carpets especially in dry, oligotrophic habitats where erosion was taking place. Dense carpets have also been observed in The Netherlands (Meulen, Hagen & Kruijsen 1987), Ireland (Richards 1963) and England (in the North York Moors National Park, see chapter 4).

The investigation of the behaviour of the moss in colonizing burnt habitats is particularly important in the case of heather moorland because of the widespread use of fire in the management of the community. The purpose of burning the heather is to stimulate the vigorous production of young heather shoots, to feed sheep and red grouse (*Lagopus lagopus scoticus*), and also to maintain a mosaic of heather in different stages of development, which gives support to denser populations of red grouse (Gimingham 1972, Usher & Gardner 1988). Therefore, the management of the heather moorland is dependent on a rapid regeneration of *Calluna* cover.

Because of the potential of the moss to produce thick carpets that can prevent the establishment of vascular plants, it is important to evaluate the dynamics of the regeneration process of the moorland community after fire, in the presence of *C. introflexus*. It is especially important to consider the effect that the moss may have on the establishment of *Calluna*, commonly the monopolistic dominant of the heathlands. When *Calluna* is burned in suitable conditions (*i.e.* at 10-15 years old in its building or mature phase), post-burnt vegetation develops mainly by vegetative means. However, if there is a catastrophic wildfire, or if the *Calluna* is burned at its degenerate phase, revegetation depends mainly on seedlings establishment (Mallik 1986).

Considering the succession models of Connell & Slatyer (1977) it is hypothesised that *C. introflexus* may be able to produce an inhibition on the development of the moorland community. Therefore, a quick colonization by *C. introflexus* that would prevent the establishment of other species, specially *Calluna*, should be expected. The mechanism of interference that is proposed (chapter 1) assumes that the presence of the moss may modify substantially the regeneration niche (Grubb 1977) of *Calluna* and probably other species. The seeds of *Calluna* are very small (approximately 0.5 mm in diameter), which suggests they are of suitable size for its germination to be affected by the moss shoots of *C. introflexus* (which usually are between 0.5 and 5 cm tall and grow forming dense carpets). *Calluna* germination is better on organic than on mineral soils but a consolidated substrate is better than a loose one and a sustained supply of moisture is essential (Gimingham 1972). Light availability is important but probably not limiting (Gimingham 1972, Pons 1989). The conditions required for seedling establishment are more restricted than those for seed germination. Again the water supply is critical and good availability of light is important. The seedlings of *Calluna* will fail to establish if the surface of the substrate dries out (Gimingham 1972); this would limit establishment on moss carpets because the carpets of *C. introflexus* tend to dry out during late spring and the summer period, when germination of *Calluna* is most active. The burning of the vegetation creates specific environmental conditions in the post-fire period resulting in a limiting kind of regeneration niche that influences vegetation redevelopment (Mallik 1986). Mallik concluded that burning leads to a significant decrease in the moisture contents in the top 2 cm of the soil and to a considerable fluctuation in temperature and moisture conditions in the atmosphere just above the ground, which explain the massive seedling mortality that is normally observed soon after germination. Mallik, Hobbs & Rahman (1988) found that the presence of charred organic matter, mat moss and lichen patches can inhibit seedling establishment. These conditions of the regeneration niche may be not so limiting for *C. introlfexus* because of its wide tolerance to soil constraints (Clément & Touffet 1988), therefore, if *C. introflexus* develops quickly enough it may produce a carpet of enough size (extent and depth) to interfere with the germination and establishment of the seedlings of *Calluna*.

The aim of this chapter is to asses the effect that *C. introflexus* may have on the recuperation of *Calluna* moorland after burning. Because strong inhibition is believed to be possible only if the moss develops quickly after a fire, the interest centred in the short period after burning (18 months).

7.2 Methods

The research was carried out in a permanent site on Kildale Moor (national grid: NZ612113) in the North York Moors National Park at approximately 270 m altitude. A plot 15 by 25 m was fenced to exclude sheep. The area is in the neighbourhood of Lonsdale plantation (a forest of *Pinus sylvestris*), which lies to the southwest of the study area (Figure 7.1). The dominant soils in the area are loamy stagnopodzols and podzols over sandstone (Carrol & Bendelow 1981). The area is a moorland dominated by *Calluna* in a building stage (approximated cover was 43.4% and nearly 20 cm tall at the beginning of the experiment). A large amount of *C. introflexus* was present (approximately 48.9% cover and an average carpet thickness of 7 mm). Other important components were *Juncus squarrosus*, *J. effusus*, *Agrostis cannina*, *Rumex acetocella*, *Carex pilulifera*, *Polytrichum commune* and *P. juniperinum*. *Erica tetralix* was present but it was very rare.

The field experiment was designed as follows. A set of 12 square plots, each 1 m × 1 m, were burnt using a metal shield to prevent surrounding vegetation from being damaged. Because the existing vegetation was not in an advanced building stage, to simulate the conditions of a normal fire the square was filled with fresh *Calluna* material harvested from neighbouring areas (and thus, the resulting fire was probably slightly on the hot side). Another factor included in the experiment was the effect of sheep grazing. Therefore, six 1 m plots were chosen randomly within the fenced area and another 6 in the adjacent unfenced ground (Figure 7.2). The experiment can be described as a randomized design with sub-sampling. Because of the restriction to randomization that was imposed by the fencing, there is no appropriate way of testing the effect of sheep exclusion (the plots are only pseudo-replicates). However, the whole experimental area was chosen to be fairly homogeneous, which can reduce the importance of the randomization restriction making it possible, at least approximately, to test for the effect of fencing. The experiment was initiated on 10 November 1989 and the plots were marked by

Figure 7.1. Location of the regeneration experiment at Kildale Moor (National Grid Reference NZ612113).

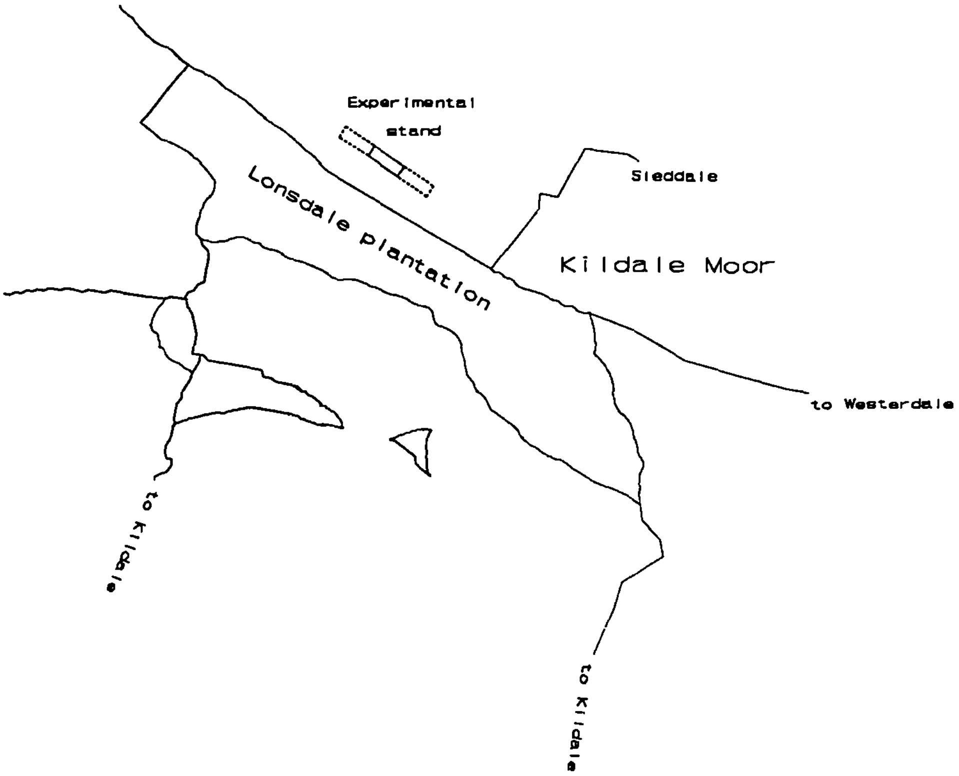
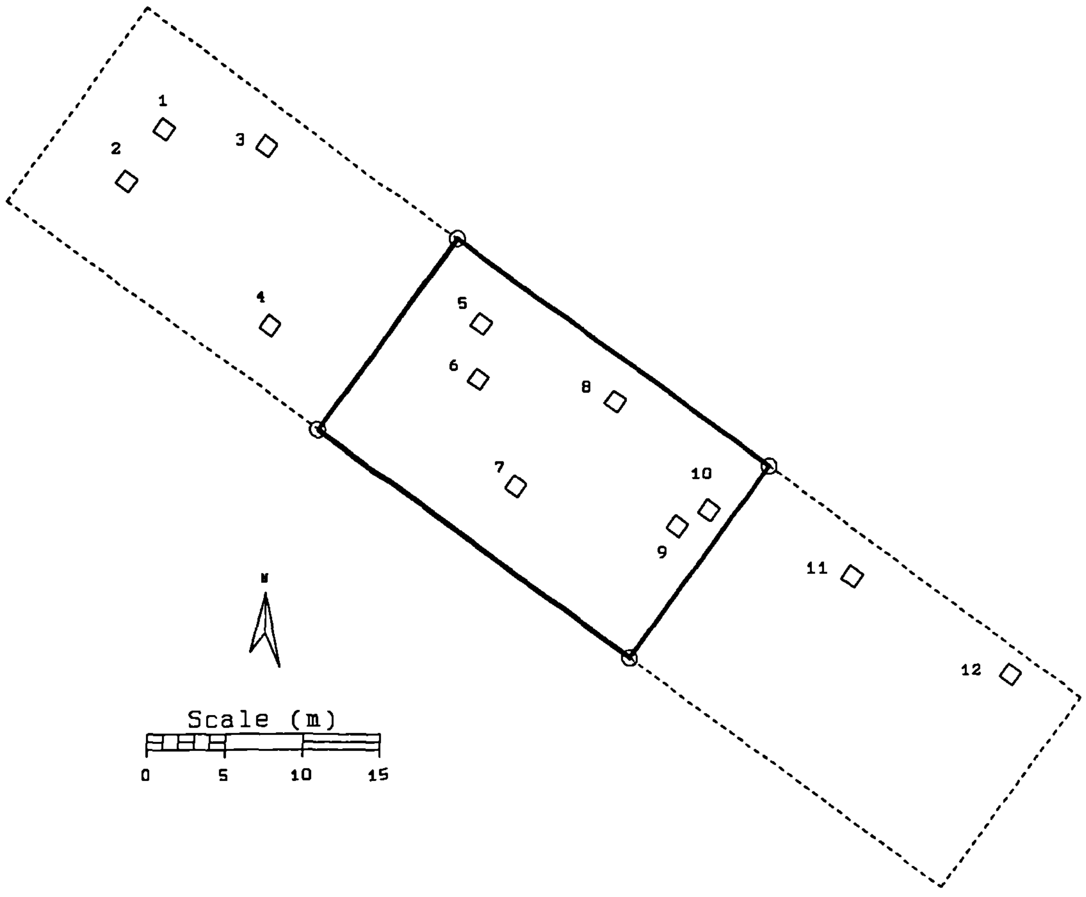


Figure 7.2. Layout of the experimental plots at Kildale Moor. The central stand was fenced to exclude sheep grazing. The plots were placed randomly, in the case of the unfenced condition randomisation was achieved considering the two stands together. The cover of *C. introflexus* and *Calluna* as well as species composition was similar in all the three stand.



plunging wooden pegs into each corner. The regeneration process was monitored by sampling the central 0.5 m square within each plot. The sampling was conducted placing a grid of 400 squares, each 2.5 cm by side, on the plot and recording the species present in each grid square. For *Calluna* a distinction was drawn between presence of seedlings and growth (branches extending from neighbouring grid squares). The number of seedlings occurring in each square was also counted as well as the maximum size of growing seedlings. For *C. introflexus* both the occurrence of establishing propagules (recognized as those fixed to the substrate) and the growth of carpet was recorded. Moss carpet growth was identified because either the propagule protonema started to produce new shoots and therefore to expand laterally or because of the presence of an area showing relatively uniform cover by the moss, probably the result of spore germination).

The analysis of frequency and count data was conducted using generalized linear models (GLM). These models alow the analysis of the data using a suitable random distribution, pertinent to the kind of data, within a familiar regression framework (Aitkin, *et al.* 1989). When the random distribution used is not the normal, the tests of significance are carried out using maximum likelihood ratio statistics that are asymptotically χ^2 distributed; these will be denoted here by G^2 (*cf.* Bishop, Fienberg & Holland 1975). All model fits, including the analysis of normal data, were carried out with the GLIM package (Baker 1985). The general modelling strategy was initially, to build a model considering time and the fencing factor and then, to test the effect of the moss within the resulting model.

7.3 Results

There was a total of 13 species recorded in the squares. Their average frequencies in the unfenced and fenced plots are shown in Table 7.1. The mosses start to colonize the plots soon after the fire, specially the two species of *Polytrichum.* They were the only mosses that apparently managed to survived the fire in some plots; they started to grow in areas occupied by the same species before the fire. The success of *Polytrichum* spp. as pioneers has been recognized on other occasions (Clément & Touffet 1988, Maltby, Legg & Proctor 1990). *Polytrichum* has underground rhizome-like stems from which aerial shoots arise (Smith 1978) and it is quite likely that these 'rhizomes' may have been able to survive a vegetation fire. A large amount of propagules of *C. introflexus* arrived in the plots but with very little success in establishing themselvs. It is not until after approximately seven months that some evidence of *C. introflexus* establishment and spread started to show. By this time it was also apparent that the main components of the community were all participating in the colonization process. Some species appeared later in the sequence, like *Erica tetralix*; however, it is believed that this is a consequence of the low probability of arrival of seeds from this species rather than of the post-fire conditions being unsuitable for the germination of *E. tetralix.* Another late arrival was *Aira praecox*, but being an annual, it is not clear if the plant was just missed out in the initial samplings beacuse of the normal time of seed germination and its short life cycle. A few seedlings of *Pinus sylvestris* were found in some of the fenced plots, but they did not survive (they probably were predated).

In the colonization of the plots there is a clear predominance of *Calluna, C. introflexus, Polytrichum commune* and *P. juniperinum.* The development of the

Table 7.1. Average number of grid-squares per plot where each species was recorded in the experimental plots (the total number of grid-squares per plot is 400). In the row 'days' the number of days since the initial fire is indicated.

	Unfenced plots						Fenced plots					
Year	1990					1991	1990					1991
Sample	Mar1	Mar2	May	Jun	Aug	Apr	Mar1	Mar2	May	Jun	Aug	Apr
Species / **Days**	117	130	193	229	277	531	118	130	213	229	277	546
C. introflexus												
Carpet	1.3	1.3	2.2	12.8	24.8	231.8	0.0	0.0	11.5	51.8	79.5	322.0
Propagules	51.0	30.3	0.3	23.7	3.2	50.0	116.2	85.0	47.5	54.2	11.3	27.3
Calluna												
Growth	0.0	0.0	0.2	0.5	5.2	14.3	0.0	0.0	0.0	0.0	0.8	5.0
Seedlings	0.0	0.2	3.7	6.8	17.3	172.7	0.2	0.0	1.2	1.3	7.0	151.7
Erica tetralix	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Aira praecox	0.0	0.0	0.0	0.0	0.0	9.3	0.0	0.0	0.0	0.0	0.0	6.5
Agrostis canina	0.0	0.2	1.0	2.8	4.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0
Juncus effusus	0.0	0.0	0.0	0.7	0.7	1.5	0.0	0.0	0.0	0.0	0.0	0.0
Juncus squarrosus	0.0	0.0	0.2	0.2	2.2	2.7	0.0	0.0	0.0	0.0	0.0	1.2
Polytrichum commune	24.2	42.3	45.3	62.2	54.5	71.0	35.0	50.2	57.8	63.7	55.3	80.7
Polytrichum juniperinum	11.2	15.0	11.5	19.0	20.7	42.3	5.3	8.8	11.5	11.7	15.8	33.7
Pohlia nutans	0.0	0.0	0.0	0.7	0.0	9.0	0.5	0.2	0.0	1.7	2.2	7.3
Pinus sylvestris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.0
Rumex acetosella	1.5	2.5	2.8	0.3	0.7	13.5	3.8	4.7	2.0	1.5	0.0	4.7
Carex pilulifera	0.0	0.0	0.3	0.5	0.8	1.5	0.0	0.0	0.0	0.0	0.0	0.0

frequency of these species in time is illustrated in Figures. 7.3, 7.4 and 7.5. Their pattern of colonization is very similar in both the unfenced and the fenced plots. Although there is more contrast in the final frequency values in the fenced ones, the ranking is the same in both fenced and unfenced plots. Another feature apparent in the plots is that the initial colonization, immediately after the initial fire, is rather poor, particularly in regards to *Calluna* seedling frequency. In some other studies it has been found that the initial production of *Calluna* seedlings is rather scant. Hobbs & Gimingham (1984) found no seedlings, in burnt sites of building heath (in quadrats 1 m^2), within the first year after the initial fire. However, other observations from burnt sites have shown that abundant seedling production can take place in newly burnt sites (Mallik, Hoobs & Legg 1984). It is known that there is a large amount of *Calluna* seedling mortality but, despite the low amount of initial *Calluna* germination, there was a steady increase in the amount of space taken up by growing seedlings, as suggested by the increase of frequency of growth shoots of *Calluna*. This growth was completely due to development of newly established seedlings. No vegetative regeneration of *Calluna* was observed in any plot (probably corroborating the suggestion that the fires were on the hot side).

Amount of Calluna *seedlings*

The number of seedlings found in each plot on the different occasions is presented in Figure 7.6. The counts of *Calluna* seedlings were analyzed using a GLM assuming a Poisson random component and log link function. In this case the initial model included a fence term and a second order polynomial on the number of days since the initial fire as explanatory variables (the large amount of seedlings recorded in the last sampling date requires a non-linear representation), but the fit was very poor (residual G^2=1467.1 with 39 degrees of freedom) and it was found that

Figure 7.3. Frequency of occurrence of *Calluna* in 2.5 cm squares within a plot 50 cm by side. Unfenced plots are represented by the solid line, fenced ones by the broken line. Growth refers to frequency of squares where lateral seedling extension have entered.

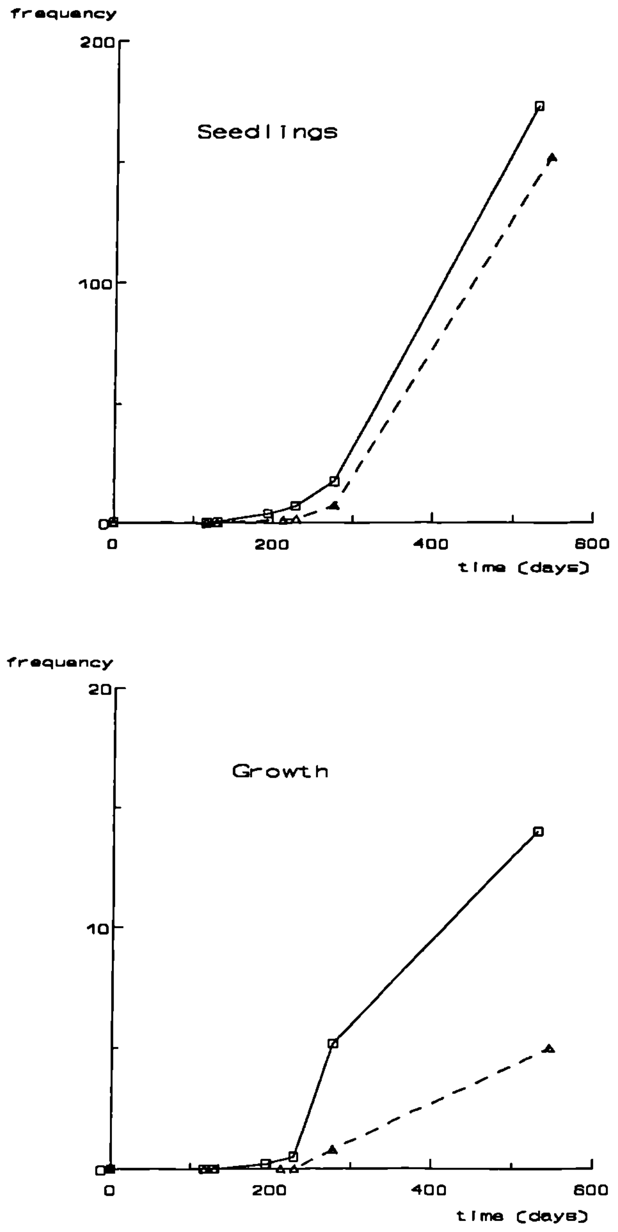


Figure 7.4. Frequency of occurrence of *C. introflexus* in 2.5 cm squares within a plot 50 cm by side. Unfenced plots are represented by the solid line, fenced ones by the broken line.

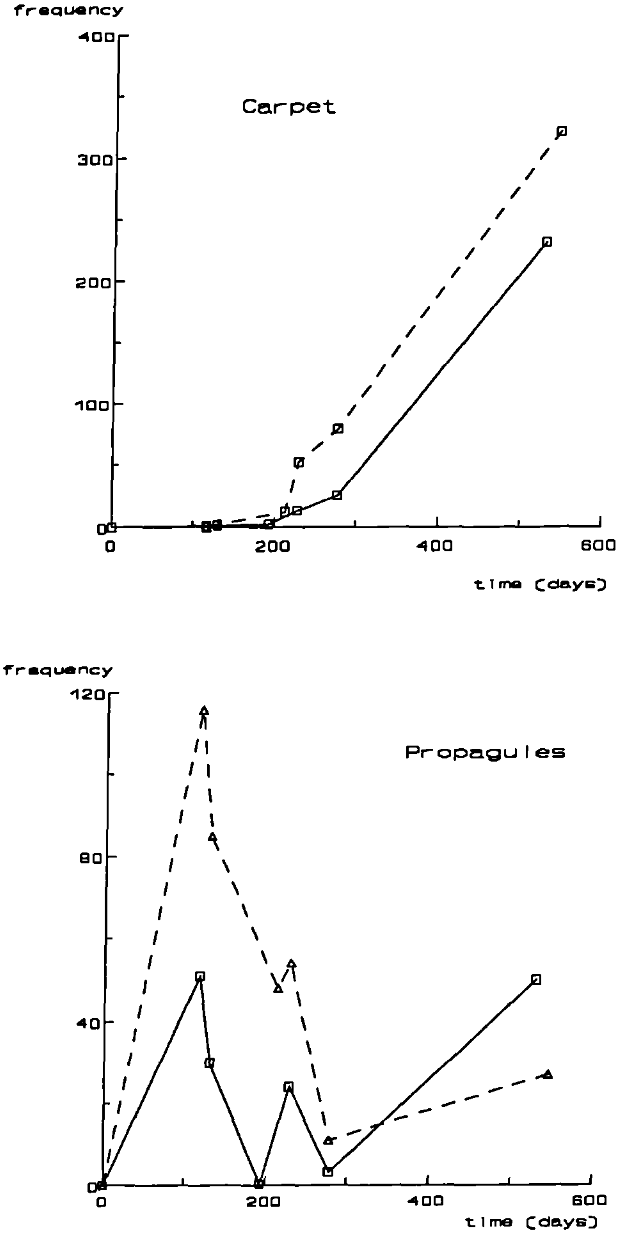
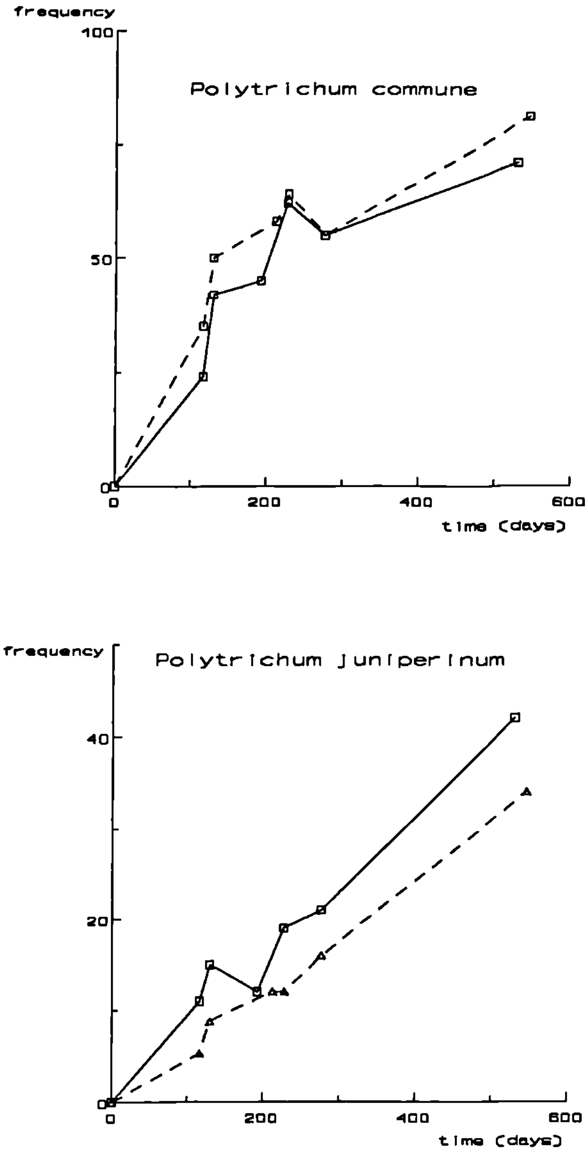


Figure 7.5. Frequency of occurrence of *Polytrichum commune* and *P. juniperinum* in 2.5 cm squares within a plot 50 cm by side. Unfenced plots are represented by the solid line, fenced ones by the broken line.

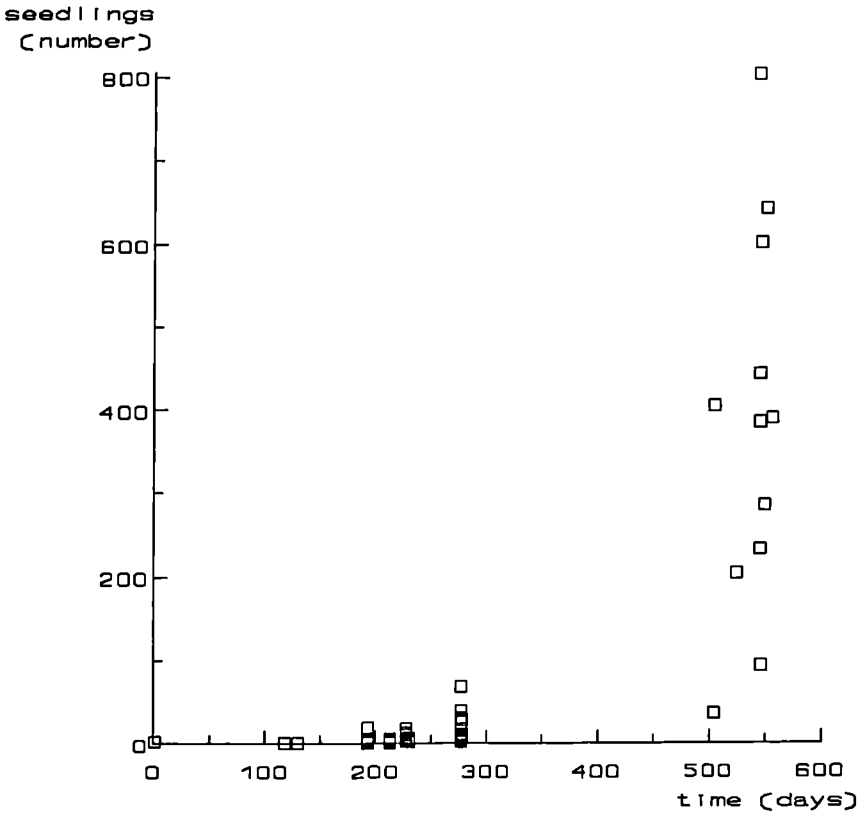


a term to identify the individual plots was required. The new basic model included the plot term and the second order polynomial on days. The fit of this model was much better than the fence one but still not completely satisfactory (residual G^2=279.54 with 31 degrees of freedom, still suggesting a substantial lack of fit). A further improvement was obtained adding the interaction terms of the polynomial with plot, to account for a heterogeneous time response of the plots. The improvement was substantial and the residual deviance of this model showed no evidence of lack of fit (G^2=17.19 with 12 degrees of freedom). The effect of the mosses on the number of heather seedlings was tested adding the total frequency of each moss species to this basic model. None of the moss species showed any evidence of association with the number of seedlings of *Calluna.*

Length of heather seedlings

Considering the length of established seedlings in the experimental plots it was found that the plants of *Calluna* in the unfenced plots were significatively larger than those in the fenced plots (approximately twice as large, F=13.95 with 1/10 degrees of freedom). This is a surprising result, because it is the opposite of what it can be expected. The result parallels the fact that seedlings failed to establish for longer time on the fenced plots (Table 7.1 and Figure 7.6). No definite explanation can be provided for these facts. As mentioned in the methods section, this contrast can be tested only approximately, which implies that the significant effect can not be attributed definitely to the fence factor. To test the idea that there were differences in the time that the seedlings had for development, a covariate indicating the number of sampling dates between the first record of growth in the plot and the date of the data was included in the model together with its interaction with sampling date. As could be expected these two terms were found to be significant F=5.60

Figure 7.6. Density of seedlings found in each experimental plot 0.5 m × 0.5 m.



with 2/10 degrees of freedom). The significant interaction was interpreted to be due to the fact that, although in the two cases there was a positive effect of developing time, in the May 1991 sample the growth was smaller because it mostly spanned the season when *Calluna* is dormant. The effect of *C. introflexus* on this result was tested including in the model the frequency of carpet occurring in the plots. A significant effect of the interaction between carpet and date was apparent (F=6.91 with 1/7 degrees of freedom) suggesting an association between moss carpet and size of the seedlings. The interaction is explained because the association was negative in Aug 1990 but nil in May 1991 (Figure 7.7), which suggests that the association is only a consequence of the different speeds of colonization and not an initial inhibition of *Calluna* growth by *C. introflexus*.

Growth of Calluna *seedlings*

Table 7.2 shows the frequency of grid-squares into which *Calluna* seedlings grew, the maximum size of the plants and the corresponding size of the developing carpet of *C. introflexus*, for the dates on which the growth of *Calluna* seedlings started to be more evident. The thickness of the *C. introflexus* carpets was very small in the August 1990 sample and because of that were not recorded. Considering the sample from May 1991 only, it is clear that the size of the carpet is fairly homogeneous; an ANOVA (considering the plots nested within the fence factor) showed no fence effect (F=1.11 with 1/10 degrees of freedom). The maximum size of the *Calluna* young plants seemed to decrease in the unfenced plots contrasting with an increase in the fenced ones. However, a similar ANOVA demonstrated no significant differences in the amount of change in size between the fenced and unfenced plots (interaction term <date.fence>, F=3.42 with 1/10 degrees of freedom).

Figure 7.7. Size of *Calluna* seedlings versus frequency of *C. introflexus* carpet. The squares represent samples from August-90 and triangles are samples from May-91.

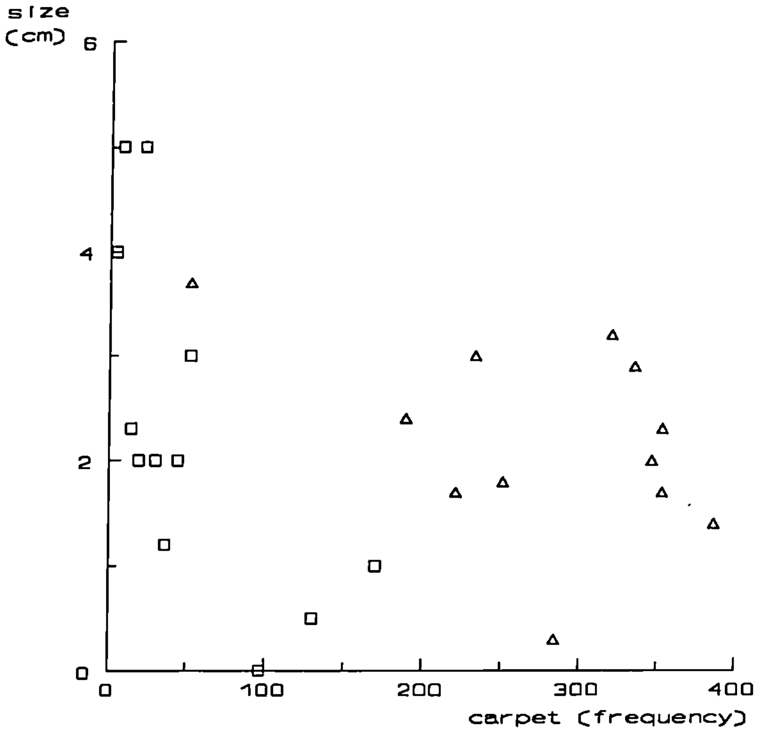


Table 7.2. Growth of *Calluna* and *C. introflexus* after fire. *Calluna* growth refers to the proportion of grid-squares, out of 400 within a plot, where branches of heather seedlings were present. The dates August-1990 and May-1991 correspond, respectively, to 277 and 546 days after the initial fire.

	Calluna vulgaris				*C. introflexus*
	Size (cm)		Growth (%)		carpet thickness (mm)
Plot	Aug 1990	May 1991	Aug 1990	May 1991	May 1991
Unfenced plots					
1	4.0	3.7	6	8	4
2	5.0	2.0	21	13	2
3	2.0	1.8	0	9	3
4	5.0	2.4	1	16	2
11	3.0	3.0	3	25	5
12	2.0	3.2	0	15	5
Fenced plots					
5	2.3	2.3	2	8	4
6	0.5	1.4	0	1	5
7	2.0	1.7	1	11	3
8	1.2	1.7	0	3	4
9	0.0	0.3	0	0	3
10	1.0	2.9	2	7	8
			Averages		
Unfenced	3.5	2.7	5	15	4
Fenced	1.2	1.7	1	5	5

Neither was an effect of dates found (*F*=0.13 with 1/10 degrees of freedom), which is what could be expected because the interval between observations covers mainly the time of the year when *Calluna* is inactive.

The frequency of growing shoots of *Calluna* seedlings is an indication of the amount of space the population is securing (without implying the exclusion of other species). There is a clear increase on the amount of space taken up by the heather. These results were tested using the number of grid-squares where shoots of growing *Calluna* seedlings were observed (out of the total 400). These proportions were assumed to follow a binomial distribution and, thus the dataset was analyzed as a binomial GLM with logit link function. The model that fitted best included a plot identification term (which accounted for each plot individually), and, similarly to the previous analysis, the developing time term in interaction with date. The need to include an individual plot term instead of a general fence factor was due to the large heterogeneity of the plot responses. The fit was very close, as was clear from the residual deviance G^2=4.06 (with 9 degrees of freedom); also, an examination of the residuals showed no indication of lack of fit. The interpretation of the interaction is the same as that provided for the size of *Calluna* seedlings. There is a positive effect of the developing time, but this is much smaller in the May 1991 sample because it mainly covered the inactive period of *Calluna*. Contrasting the effect of *C. introflexus* with this model showed no significant effect of the moss (G^2=1.47 with 2 degree of freedom simultaneously for the interaction with time and the main effect). Neither did the two *Polytrichum* species (G^2=1.56 with 4 degrees of freedom simultaneously for the two species and their interaction with time) show any effect.

Association analysis at the grid-square level

The approach used above has concentrated on the total values of the variates per plot, however, it is possible that a closer inspection may provide a better understanding of the relationships between *Calluna* and the main moss species. Towards this end, the individual 2.5 cm squares from each plot can be used to carry out an analysis of the association, at the lowest grid size, between the mosses and *Calluna*. Only the last sampling date was used because it is then that the frequencies are large enough to make this kind of analysis worthwhile. The approach followed is based on the use of multiway contingency tables (Greig-Smith 1983), but the analysis was carried out using GLM (Aitkin *et al.* 1989). Because not all the mosses occurred in all of the plots, and also considering the large heterogeneity of plot response demonstrated above, it was decided to apply the analysis to each group of plots defined according to the species of *Polytrichum* present and, failing this, each plot was analyzed independently. The grid-squares were classified according with the mosses present in them (among *C. introflexus*, *P. commune* and *P. juniperinum*). Taking as response the presence of *Calluna* seedlings the random component of the GLMs used was the binomial taking the total number of grid-squares in the plot as sample size. The link functions used was the logit. The results of these analyses can be summarised in a table of the probabilities of occurrence of *Calluna* seedlings under the different possible combinations of the mosses as estimated by the fitted models (Table 7.3). The association of the occurrence of *Calluna* seedlings with the carpet of *C. introflexus* was usually strongly positive, except in the case of plot 2, where there was no association, and plot 5, where there was an interaction with *P. juniperinum* because, when present, it reversed the association. As in the previous case, *P. commune* was mostly positively associated with the incidence of *Calluna*

Table 7.3. Probability (%) of occurrence of *Calluna* seedlings in association with the presence of the three main mosses within individual grid-squares (400 per experimental plot). For the analyses the plots were grouped according to the species of *Polytrichum* that were present in them. If plot responses were too heterogeneous within a group then the analysis was applied to the individual plots. The residual deviances are those associated with the final model once non-significant terms were eliminated (deviances are approximately χ^2 distributed with the degrees of freedom indicated within brackets in the corresponding column). Under the 'stand' heading it is indicated whether the plot was located within a fenced (F) or an unfenced (U) area.

			Moss presence within grid-squares								
		P. commune	No				Yes				
		P. juniperinum	No		Yes		No		Yes		Residual deviance (df)
Stand	Plot	*C. introflexus*	No	Yes	No	Yes	No	Yes	No	Yes	
Both *P. commune and P. juniperinum present in the whole plot*											
U	1		4	16	4	16	9	30	9	30	5.96 (3)
U	3		26	42	26	42	10	18	10	18	7.68 (4)
F	10		6	42	6	42	6	42	6	42	3.27 (5)
U	4		45	78	45	78	-†	-	-	-	4.76 (3)
P. juniperinum present in the whole plot											
F	5		31	53	70	63	-	-	-	-	8.90 (3)
F	6‡		-	31	-	29	-	-	-	-	
F	9		1	21	19	57	-	-	-	-	
U	12		18	66	31	52	-	-	-	-	
P. commune present in the whole plot											
F	7		9	50	-	-	19	56	-	-	4.90 (6)
F	8		13	61	-	-	26	66	-	-	
U	11		17	68	-	-	33	74	-	-	
Neither *P. commune nor P. juniperinum present in the whole plot*											
U	2		53	53	-	-	-	-	-	-	0.03 (1)

† There were only 2 grid-squares with this combination and the rest of the *P. commune* sub-table was empty.

‡ All the seedlings in the plot were observed together with *C. introflexus* a no otherwise.

seedlings except for plot 3 where it was strongly negatively associated and plot 10 that was not associated at all. In the whole experiment there were 8 plots where *P. juniperinum* was present. In half of these cases, it showed no association with heather seedlings and, for the rest, two were positively associated, one negatively so and another one showed a mixed response (plot 12): a positive association when the carpet of *C. introflexus* was absent and a mildly negative one otherwise.

These same association patterns can be analyzed considering the actual number of seedlings occurring under the different moss combinations. This approach would provide stronger evidence on the strength of the associations (Greig-Smith 1983). There were 2,158 grid-squares where *Calluna* seedlings occurred out of a total of 4,800. Clearly, there are too many empty squares; in order to avoid them it was decided to conduct the analysis on the sub-set of the grid-squares where *Calluna* seedlings were present. In this way, the analysis carried out is conditional on the occurrence of *Calluna* seedlings; occurrence which, from the previous results, is known to be mostly positively associated with the presence of the mosses. The results of these analyses are summarised in Table 7.4. The general pattern is one of lack of association between the occurrence of the mosses and the number of seedlings of *Calluna.* There were three exceptions, in two of them a positive association with the presence of *C. introflexus* was demonstrated (although mildly so), and in the third one it was found that there was a positive association with *C. introflexus* and at the same time that there was negative association with *P. commune*. These results suggest that, although the seedlings of *Calluna* do occur more frequently where there are mosses, the moss presence does not encourage the appearance of a larger amount of seedlings.

Table 7.4. Association of the number of *Calluna* seedlings with the presence of the three main mosses within individual grid-squares in the experimental plots. Therefore, abundance values are number of seedlings in $6.25cm^2$. The analysis was carried out using only the grid-squares where seedlings were present. Expected density values are given as a basic figure under the 'no moss' heading; the moss effect can be obtained adding the amount indicated under the headings of the respective moss species (*Polytrichum juniperinum* was never found to have a significatn effect and thus it was omited). CI=*C. introflexus* carpet, PC=*P. commune* and PJ=*P. juniperinum.* The analysis of the overall occurrence of seedlings was realised separately (see Table 7.3).

Plot	*Polytrichum* Mixture	Model	Residual deviance (df)	Expected number of seedlings		
				No moss	CI	PC
1	PC & PJ	Null	7.22 (27)	1.3	-	-
2	None	Null	148.28 (211)	1.9	-	-
3	PC & PJ	Null	55.07 (130)	1.6	-	-
4	None	Null	422.98 (240)	3.3	-	-
5	None	CA*	192.86 (202)	1.5	+0.7	-
6	PJ	Null	93.10 (117)	2.0	-	-
7	PC	CA**	176.46 (138)	2.0	+0.9	-
8	PC	Null	291.74 (233)	2.6	-	-
9	PJ	Null	22.00 (67)	1.4	-	-
10	PC & PJ	Null	105.27 (145)	2.0	-	-
11	PC	CA***+PC*	303.15 (208)	2.0	+0.7	-0.5
12	PJ	Null	122.80 (212)	1.8	-	-

* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$

7.4 Discussion

It is evident that the hypothesis that *C. introflexus* may conform to the inhibition model of Connell & Slatyer (1977) is not supported by the results of this study. The successional process found seems better described by the tolerance model proposed by these authors. There is evidence that the colonization of burnt sites by *C. introflexus* can proceed quickly, but, at least in the initial stages, its presence does not prevent the immigration and establishment of other species. On the contrary, a strong positive association was demonstrated with *Calluna.* Gimingham (1972) pointed out that *Calluna* cannot establish if a high saturation deficit develops in the air-layer close to the ground during the early phases of growth and development of the seedlings. The presence of a moss cover may reduce the likelihood of this happening, which may explain the positive association between the mosses and the occurrence of *Calluna* seedlings. Nevertheless, in this case the association is not interpreted as an indication of a facilitation by the mosses on the colonization of the plots by *Calluna* seedlings. It seems more likely that what is taking place is the co-occurrence of these species in the best places available for establishment, which would explain the fact that, in general, the number of *Calluna* seedlings was not affected by the presence of the mosses. Of course this would not prevent there being some competitive interaction later on.

Although it does not seem to be the general situation, it may still be suggested that *C. introflexus* can produce an inhibition on the development of the moorland if the establishment of other components is severely limited giving more time for a thick carpet of the moss to develop. This seems to be the case in some other examples where the inhibition model has been found to be in operation

(Niering & Goodwin 1974). It is probably also the case of some moorlands themselves where, because of the management practices, the development of heather has been encouraged at the same time that trees and tall shrubs have been checked to such an extent that the resulting community 'resists' the establishment of forest vegetation, leading to the so called *Calluna* cycle (Watt 1955, Gimingham 1972, Gimingham 1988). In the management of the moorland it is also known that delaying the reestablishment of *Calluna* may result in the development of a different dominance structure of the community, some times with bryophytes being dominant, that resists the establishment of *Calluna.* Because of the speed of development and the cover produced by the mosses in the experimental plots, the results of this study suggest that the two species of *Polytrichum* and *C. introflexus* are good candidates to produce this effect, which corresponds with what has been observed in the field.

Another possible interpretation can be provided by considering that the colonization process seems to correspond to a lottery system where stochastic processes have a dominant role. This is indicated by the fact that all the possible association outcomes (*cf.* Fagerström 1988) were observed between *Calluna* and the mosses, and because of the wide heterogeneity of the magnitude of the association between *Calluna* and *C. introflexus* that was found. It can also be argued that the moss and the heather are engaged in a competition for space rather than in a consumptive competition. Yodzis (1986) has pointed out that competition for space is distinct because this resource can be repeatedly recovered and used by different consumers and because this recovery is linked with (if not identical to) mortality in the consumer population. It has been suggested that within a lottery competition process succession can take place without a need to invoke, as necessary successional mechanism, systematic changes in the physical environment or differences in competitive ability for any resources other than space. Given time, certain combinations of annual seed (propagule) production and longevity of the adult plant can produce a successional sequence (Liljelund, Ågren & Fagerström 1988). These authors found that a model incorporating these features will produce successional sequences in an environment that fluctuates randomly around some mean (i.e. it is stationary in the statistical sense). These two attributes are enough to determine the rate of invasion and the ability of the species to persist in later stages. The assumptions of this model are that there is a fixed number of sites where each site can support only one adult individual and that the winner is chosen at random. Replacement can only occur when a plant individual dies or is removed (say by herbivory or disease) so that an empty site is made available for colonization (this makes space the critical limiting resource). More than one propagule can arrive in an empty site, but only one will retain it through a process of random selection (lottery) among the candidates at the site. Liljelund, Ågren & Fagerström (1988) found that the general pattern predicted by such a model is one of consistent non-repeating change in community composition over time where species with a high annual production of propagules and short life span are gradually replaced by species with the reverse characteristics. If the species are contrasting in the values of these two attributes then the species with the shorter lifespan will eventually be eliminated from the community. However, this exclusion may require a very long time to happen (the longer the more similar the species are!). Because of this slow rate of competitive exclusion, the process would make possible the coexistence of the early species together with the later dominant ones (assuming that perturbations, that would reset the process, have a large probability of occurrence in such a long period). Even if one of the species is an inferior competitor for sites, in a lottery driven system, it can coexist in the community if the competitive inferiority is compensated by a larger production of propagules or by a greater longevity (Fagerström & Ågren 1979, Fagerström 1988).

It could be argued that a similar lottery situation could approximate what is taking place in the moorland-*C. introflexus* system. This would explain the fact that, even when *C. introflexus* cannot outcompete an established *Calluna* individual, the moss manages successfully to remain in the community because of its longevity (probably of about the same span as that of *Calluna*), and high reproductive output (both by propagules and by spores). Similarly, in those cases where the moss has a boosted output of propagules (spores, propagules and even carpet fragments) relative to that of *Calluna* (probably reduced by grazing or other disturbance factors) the resulting overcompensation of competitive handicap (*cf.* Liljelund, Ågren & Fagerström 1988) would explain the occasional occurrence of *C. introflexus* dominated stands. These conceptis can be linked to the alternative notions emerging from the challenge to the view that *Calluna* heathlands go through an ordered cyclical process. Although criticisms have been made on various grounds (Miles 1981, Hobbs & Legg 1983, Prentice, van Tongeren & de Smidt 1987, Marrs 1986, Gimingham 1988), the realization that heathland communities are much more variable than was once thought and that the species replacement sequence is not an ordered one, has induced a belief that stochastic events are very important in the dynamics of the heath communities.

8. General discussion and conclusions

8.1 Discussion

The literature on invasive plant species has been concerned almost completely with higher plants, especially angiosperms and gymnosperms, although a number of ferns (notably *Pteridium aquilinum*) and some species of horsetail (*Equisetum* spp.) are also included (Heywood 1989). The only example of bryophytes mentioned by Heywood is that of *Campylopus introflexus.* In an account on plant invasions in the Netherlands, Weeda (1987) mentions only 3 mosses (together with about 200 species of vascular plants). Of these three mosses only *C. introflexus* is recognized as the an invasive species that, in the Netherlands, is spreading aggressively independent of human interference (Weeda 1987). In general, among the paucity of examples worldwide of invasive bryophytes, *C. introflexus* has an outstanding place. Probably because of its recent introduction into Europe, the development of the invasion has been more or less well documented (chapter 1). It is also important because it is one of the very few examples of invasive bryophytes that has shown the capability of spreading aggressively within newly colonized habitats.

The presence of *C. introflexus* in the North York Moors National Park provided the opportunity to evaluate the role and impact of this invasive moss in *Calluna* dominated communities. Throughout this thesis it has been the purpose to gather information along two main lines of enquiry: (1) to determine the factors controlling the distribution of *C. introflexus* in the area and (2) to evaluate the potential impact of the moss on the dynamics of the moorland communities, specifically on *Calluna*, its dominant component.

In chapter 4 it was demonstrated that *C. introflexus* has a wide distribution among the different *Calluna* dominated communities in the North York Moors National Park. It was also shown that it is clearly more abundant where *Calluna* has lower cover, as might be expected because of the preference of the moss for open conditions (and the general pattern shown by plant invaders). This suggests that the moss is establishing itself successfully in stands in the pioneer or early building development stages. However, it was recognised that the moss tends to decline in cover as the heather communities develops. *C. introflexus* may survive under the canopy of mature heather, but in any case it will be largely excluded from the community.

In chapter 4 it was also argued that the loose blocks that *C. introflexus* tend to form when its carpets are thick enough may provide an additional form of propagation that contributes to the moss's ability to retain colonised territory. Because of the potential importance of this behaviour, the dynamics of the carpets of *C. introflexus* and their impact on other species seems an interesting issue for further investigation.

In chapter 5 it was demonstrated that *C. introflexus* has an inhibitory effect on the development of *Calluna*, under optimum growing conditions, other than a strong reduction in germination potential. No allelopathic effect on the germination of heather seeds was found and, it was demonstrated that the plants growing on moss carpets had a better performance than those growing on open ground. This implies that, as expected, the moss's impact is confined to its potential interference with the physical characteristics of the regeneration conditions where the seeds of heather germinate and its seedlings develop. The potential inhibition of *C. introflexus* on *Calluna* should then take the form of modifications produced by the moss on the regeneration niche of the heather. On the bases of this results it can be expected that when the carpets are thick enough (approximately 1 cm thick) the resulting seed bed might allow seed germination, but it will be almost impossible the establishment of *Calluna* seedlings, because of the proneness of the carpets to dry out. This idea was explored with a field experiment under field conditions (chapter 6). Because the possible inhibition is mediated by interference with the regeneration niche of *Calluna,* it is suggested that the main form of interaction between the moss and heather should be competition for space (*sensu* Yodzis 1986).

In chapter 6 it was further shown that, although *Calluna* is able to germinate on top of carpets of *C. introflexus*, under field conditions, the seedlings failed completely to establish themselves. It was detected that some 'fostering' of heather seedlings by adult *Calluna* individuals is possible (under the conditions of the sampled stand, which was an early building stage Callunetum). However, the ability of the heather to expand its cover may be hindered by the moss if a carpet of *C. introflexus* more than 1 cm thick develops in the gaps of the developing community. Therefore, a delay in the development of the moorland could be expected under these conditions. This also corroborates the conjecture that the interaction between these two species is taking place in the form of competition for space. Along this same line of reasoning, the results of chapter 6 seemed to suggest that it will be difficult for either species to replace each other once they have become established.

In chapter 7 it was shown that *C. introflexus* starts to establish after a fire practically at the same time as the other main components of the moorland. The presence of the moss, during the observation period, showed mostly a positive association with the occurrence of *Calluna* seedlings. However, this positive association was very variable in magnitude (and in some cases even absent); because of this, the positive association was interpreted to be a consequence of the moss and *Calluna* sharing the best places for establishment (with *C. introflexus* showing a wider colonization ability). This suggests that the sort of conditions described in chapter 6 potentially leading to a delay in the development of the community are likely to arise when *C. introflexus* is abundant in the surroundings of a regenerating heathland (and heather cover is being produced initially by seed recruits rather than vegetatively).

Despite it being considered possible for the moss to delay the development of the Callunetum, it is believed that eventually *Calluna* will outcompete the moss. As discussed in chapter 7, it is therefore interesting to ponder how an obviously inferior competitor manages to remain in the community. Although the part played by the disturbance is obviously paramount in this regard, it is believed that, as argued in chapter 7, a non-equilibrium rationale to understand the dynamics of the community is useful in this case. First, it has to be accepted that the colonization process corresponds to a lottery system (where stochastic processes have a dominant role). Second, as proposed above, it has to be accepted that the moss and the heather are engaged in a competition for space rather than in a consumptive competition (Yodzis 1986). With these two assumptions the suggestion made in chapter 7 can be accepted. This is that the regeneration of the moorland can take place without the need to invoke, as a necessary successional mechanism, systematic changes in the physical environment or differences in competitive ability for any resources other than space (which anyway may take place). The successional sequence in the moorland would then be mostly a consequence of different combinations of annual seed (or propagule) production and longevity of the adult plants involved (*cf.* Liljelund, Ågren & Fagerström 1988). Within this setting, the exclusion of a species will take longer the more similar the species are. This seems to provide an interesting prediction in relation to the invading potential of a species: if a neophyte species has similar environmental requirements, reproductive output and longevity, to a native (dominant?) species, its successful introduction and naturalization is more likely. This conjecture is in flagrant opposition to another common explanation for successful invasion, namely that of invoking the occupation of an 'empty niche'. This latter idea (although it may be legitimate in some cases) has the drawback that it is always possible, *a posteriori*, to postulate a suitable niche axis along which there is an 'empty niche' (*cf.* Silvertown & Law 1987). However, coexistence in the lottery model requires a specific kind of niche differentiation because the permanence of a species in the community depends on the factors (Chesson 1986), namely (1) that there should be overlap of generations and, (2) that there should be a separation at the recruitment stage on the preferred environmental conditions for establishment, at least in such a way that variation in the ratios of recruitment rates in time are produced. These situation is referred to as the 'storage effect' (Warner and Chesson 1985). The idea is that recruitment from different breeding periods become added together in the adult population (or propagule bank of some kind), where they are stored (with some losses by mortality). This reserve is used every breeding season, but principally during favourable periods (Chesson 1986).

It seems interesting to mention that one thing that seems to contribute to the invasive success of *C. introflexus* in the moorlands, is its similarity in ecological preferences to *Calluna*. This would suggest that the two species should be competing strongly, considering the traditional Lotka-Volterra rationale. However, this will only apply at equilibrium, which is unlikely to be the case in a regenerating community. If this setting were the case in the moorland system, it would mean that the presence of the moss is transient in the community and therefore, that it should be eventually eliminated by the stronger competitors in the community, unless perturbations are frequent enough to keep the community away from the point of equilibrium where exclusion takes place (which indeed may be the case). One consequence of this idea is that reducing the amount of perturbation would control the expansion of the moss (but this may be equally deleterious to *Calluna*, an early successional element itself!).

The alternative non-equilibrium setting described above seems more useful to gain a better understanding of the role of the moss (although it will suggest that the exclusion of the moss from the community, through competition, would be very unlikely). Considering this approach, the large overlap in ecological preferences would mean that the dynamics of occupation of the empty space available, as well as the production of these empty spaces (which is assumed to be a function of adult mortality), will firstly, facilitate the successful colonization by *C. introflexus* of the moorland habitat and, secondly, it will make possible its permanence in the community. Considering that the moss is an inferior competitor to *Calluna*, the process would require differentiation on the regeneration niche (assuming that the two species are more or less of the same longevity), because the moss would require, to compensate for its competitive inferiority by having an increased propagation output. Therefore, the coexistence should be mediated by the storage effect.

Warner & Chesson (1985) suggested that the environment that appears most conducive to the development of life history features that encourage coexistence by the storage effect is one that is relatively benign and permanent for established adults, but where young individuals encounter and secure a new site by chance rather than direct competition with other young. Contrary to this opinion, it is believed that the early stages of development of a community in a unfavourable environment may be equally suitable. In limiting environments, like the moorlands, colonizers are typically long-lived (Grubb 1989), which suggests that the species are pressed to rely heavily on the storage effect. A large disseminule output causes the propagules to be typically small and, therefore, their performance will very much depend on environmental conditions. This implies that there will be strong fluctuation in recruitment between reproductive seasons. Finally, the process of colonization will be of a lottery kind, as suggested by the results of the regeneration experiment (chapter 7). The loose block behaviour of *C. introflexus* indeed can be understood in this way, because it will represent an efficient exploitation of the storage effect.

8.2 Conclusions

The moss is currently widespread in the North York Moors National Park. It shows its maximum cover in young heather stands, where on average *Calluna* cover is 43% and 9 cm in height. Although there are cases of stands where large carpets of *C. introflexus* occur it is not a common event.

The habit of *C. introflexus* of forming 'loose blocks' provides an additional form of propagation that should help the moss to retain colonized habitat at the same time as making it difficult for other species to establish themselves. However, the overall effect of the invasion by *C. introflexus* on the moorlands of the North York Moors National Park is not clear cut. The development of *Calluna* can benefit from the presence of a moss carpet but, at the same time, the carpets of *C. introflexus* can severely limit the establishment of *Calluna* from seed.

Occasionally the moss should be able to interfere the development of the Callunetum, but this is expected to happen only when the growth of *Calluna* is reduced by some other factors, like grazing. Alternatively when the regeneration of the moorland depends exclusively on the contribution of plants developing from seed, as happens after a severe fire, the moss may have a good opportunity to interfere with the regeneration of a full *Calluna* cover.

Because the permanence of the moss in *Calluna* dominated communities is believed to be due to the operation of a lottery system in the moorland, the moss is expected to occur in irregularly distributed patches across the area. It is also anticipated that these patches will shift location in time (not necessarily in the short term). The lottery system could thus be used to predict that the invasion of the Callunetum by *C. introflexus* will increase the variance of *Calluna* cover both spatially and temporally.

9. References

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10. Appendix

During my first year at the University of York I undertook the MSc Biological Computation. The final project of that course was an application of fuzzy set clustering to the analysis of ecological data. Subsequently I prepared, during the development of my D.Phil. project on *Campylopus introflexus*, the paper on fuzzy set clustering included here and which was published in the volume 78 of the *Journal of Ecology*.

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FUZZY CLUSTERING OF ECOLOGICAL DATA

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SUMMARY

(1) Many concepts in ecology are imprecise because ecosystems are large, loosely organized objects. Fuzzy-set theory provides a mathematical approach that is able to cope with imprecision. The aim of this paper is to demonstrate that fuzzy sets are a suitable description of ecological communities, using *Calluna vulgaris* moorland data from the North York Moors National Park as an example.

(2) The clustering approach used, the fuzzy *c*-means algorithm (or fuzzy ISODATA), requires a starting classification that is refined by a least-squares criterion. The starting strategy used in the example was based on the division of one ordination axis. Ordination axes were also used to reduce the high level of noise present in the ecological data. Fuzzy clustering was compared with the classification produced by TWINSPAN.

(3) The first division of TWINSPAN contrasted species of wet environments (*Agrostis canina*, *Sphagnum recurvum*, *Polytrichum commune* and *Eriophorum angustifolium*) with *Pohlia nutans*, a moss which grows on peaty or sandy banks and often under mature *Calluna vulgaris*.

(4) Fuzzy *c*-means show a strong clustering into two groups, although there were indications of a substructure at three or perhaps five groups. The two groups contrasted sites from wet habitats and those from drier habitats, in close agreement with TWINSPAN results. When clustering into three or more groups, it is hypothesized that the clusters of drier habitats are associated with the *C. vulgaris* development cycle.

(5) As an exploratory approach to vegetation classification, fuzzy clustering may be more appropriate than classification into 'hard' bounded groups. In comparison with TWINSPAN, fuzzy clustering produces clusters which are more strongly correlated with relevant external environmental variables. This may reflect the fact that ecological communities are more similar to fuzzy sets than to ordinary sets with sharp boundaries.

INTRODUCTION

Fuzzy-set theory was introduced by Zadeh (1965) as a way to represent and manipulate non-probabilistic uncertainty (Bezdek 1987). The theory has been applied widely, for example in pattern analysis, decision-making and artificial intelligence. One well-developed application is in cluster analysis, which has been applied in ecology (McBratney & Moore 1985; Dale 1988; Dayong 1988). It has also been applied in ordination (Roberts 1986) and natural-resource management (Ayyub & McCuen 1987; Wenger & Rong 1987). For a general introduction to the subject see Bosserman & Ragade (1982) and Kauffmann (1975).

In ordinary set theory an element either does or does not belong to a particular set. An indicator variable can be associated with each element to signal its membership status, taking a value of 1 if the element is a member and 0 otherwise. In fuzzy-set theory this idea is extended to allow the indicator variable to have any real value within the interval [0, 1]. In this way, the elements have degrees of membership and the set, whose boundaries are no longer well defined, is termed 'fuzzy'. Sometimes it can be considered that the indicator variable is equivalent to a probability, but this is not always true despite the fact that both are constrained to lie within the interval [0, 1]. The indicator variables for a single element do not necessarily sum to 1 over all of the sets, as would be the case for probabilities

(Kauffmann 1975; Bezdek 1981). Probabilities are related to the uncertainty of observing a particular result. Indicator variables or membership values measure the similarity between an element and the 'semantic' description of the set (Bezdek 1987). Fuzzy-set theory therefore makes it possible to cope with uncertainty derived from vague definitions of the sets to which an object might belong.

Bosserman & Ragade (1982) argued that, according to systems theory, the precision with which a set of variables is measured decreases as the size of the system increases. These authors also pointed out that the number of state variables that can be measured when modelling the dynamics of a system usually grows with its size. In consequence, because ecosystems are large and loosely organized systems, many concepts and definitions in ecology are bound to be imprecise. It therefore seems attractive to use a theoretical approach in ecology that is able to cope with objects which are imprecisely defined.

Community classification is equivalent to the concept of set partition. In ordinary set theory, a partition is a division of an original set into two or more subsets which are mutually exclusive and non-empty (these are termed 'hard' or 'crisp' partitions). In fuzzy-set theory, a partition does not necessarily consist of mutually exclusive subsets; in fact, there must be some overlap in at least one pair of fuzzy subsets in every truly fuzzy partition (Bezdek 1981). In order to make the fuzzy partition of a set possible, the following restriction has to be introduced: all the membership values of any element must sum to 1 (Bezdek 1981).

Despite the fact that species composition varies more or less continuously along environmental gradients (Whittaker 1975; Austin 1985), some groups of species can often be recognized. This duality is important in explaining many ecological phenomena; fuzzy-set theory can be used to approach both the concept of communities as recognizable entities, and the concept of species composition changing along a continuum. The precise species composition of a community is uncertain because of the influence of stochastic processes, and also because the concept of community itself is vague. Another important feature of the fuzzy-set approach is that, even if the communities are assumed to be discrete units, it is impossible to sample the units before they are identified, hence any sample will be affected by some degree of mixing.

The aim of this paper is to demonstrate that fuzzy sets are a suitable representation of ecological communities, but also that their use requires a philosophical view of the data that is different from the usual approach adopted by ecologists. It can be argued that the human mind tends to filter out fuzziness, which results in a perception of discrete objects, discrete classes of things and discrete events. Nevertheless, it is interesting to delay this filtering in such a way that the extent of the fuzziness can be better perceived and then more objectively dealt with.

METHODS

There are several possible approaches that can be used to produce fuzzy-set clustering, but it is important to be aware that one of those reported in the ecological literature (e.g. Dayong 1988), although based on a fuzzy-set argument, was shown by Dunn (1974a) to be equivalent to a single-linkage clustering (which is not fuzzy at all unless $\mathbf{B}_k$ clustering is used). Another clustering approach based on fuzzy-set theory was developed by Dunn (1974b), Bezdek (1974, 1981, 1987) and Bezdek *et al.* (1981a, b). The method, which produces true fuzzy clusters, is known as the 'fuzzy *c*-means algorithm' (or fuzzy

ISODATA). This method has not previously been used for clustering ecological community data, apart from an informal example in Bezdek (1987) and Dale (1988).

The fuzzy c*-means algorithm*

The fuzzy c-means algorithm is based on minimizing the within group sum of squares, J_m (U, V, A), which is given by

$$J_m(\mathbf{U}, \mathbf{V}, \mathbf{A}) = \sum_{i=1}^{n} \sum_{j=1}^{c} (u_{ij})^m (d_{ij\mathbf{A}})^2 \qquad (1)$$

where

$$(d_{ijA})^2 = \| \mathbf{x}_i - \mathbf{v}_j \|_{\mathbf{A}}^2 = (\mathbf{x}_i - \mathbf{v}_j)^{\mathrm{T}} \mathbf{A} (\mathbf{x}_i - \mathbf{v}_j)$$

is a distance measure calculated as a norm-induced metric, **A** is the norm-inducing matrix (any matrix of dimension p, where p is the number of attributes considered), m is the 'fuzziness parameter' ($1 \leqslant m < \infty$), $\mathbf{x}_i$ is the vector of attribute measurements made on individual i ($i = 1, 2, \ldots, n$), the vector $\mathbf{v}_j$ is the 'centre of cluster' j ($j = 1, 2, \ldots, c$), u_{ij} is the membership value of the individual i on cluster j, **U** is the membership matrix, **V** is the matrix of cluster centers ($\mathbf{U} = \{\mathbf{u}_{ij}\}$ and $\mathbf{V} = \{\mathbf{v}_j\}$).

Equation 1 defines the clustering techniques ISODATA and k-means (Seber 1984) when $m = 1$. The partition is hard when $m = 1$ and becomes fuzzier as m approaches ∞ (Bezdek 1981). Although m may have a wide range of values, it has been found, purely on the basis of empirical results, that values around 2 produce satisfactory results (Dunn 1974b; Bezdek 1981; Granath 1984; McBratney & Moore 1985). This is also supported because, as was argued in the introduction, a hard partition is not appropriate for representing ecological communities; but at the same time a completely fuzzy partition (where all the memberships are $1/c$) is clearly not desirable. Thus, what is required is a balance between 'hardness' and 'fuzzyness', which is usually achieved when m takes values around 2. In consequence $m = 2$ is used throughout this paper. To minimize eqn 1 the following two conditions must be satisfied

$$\mathbf{v}_j = \frac{\sum_{i=1}^{n} (u_{ij})^m \mathbf{x}_i}{\sum_{i=1}^{n} (u_{ij})^m} \qquad (2)$$

$$u_{ij} = \left\{ \sum_{k=1}^{c} \left[\frac{(d_{ij\mathbf{A}})^2}{(d_{ik\mathbf{A}})^2} \right]^{1/(m-1)} \right\}^{-1}. \qquad (3)$$

The fuzzy c-means algorithm (Bezdek 1974, 1981) consists of solving these equations iteratively, given a number of clusters, c, and a norm-inducing matrix, **A**. The classification produced is non-hierarchical.

Equations 2 and 3 are the necessary conditions for **U** and **V** to be associated with a *local* minimum or saddle point of eqn 1. When $\mathbf{x}_i = \mathbf{v}_j$, which implies $d_{ij} = 0$, u_{ij} cannot be calculated using eqn 3. This condition is called a 'singularity' (Bezdek 1981). Whenever a singularity occurs, the corresponding individual must have no membership value in any cluster where $d_{ij\mathbf{A}} > 0$. The membership in the clusters where $d_{ij\mathbf{A}} = 0$ is arbitrary (up to the constraint of the algorithm that the membership values must add up to 1 for each individual). Given the local convergence proprieties of this clustering approach, it is clear that different starting membership configurations may converge to different minimizers. It is therefore important to specify the starting strategy.

The norm-inducing matrices that are most commonly used are the identity matrix (which induces an Euclidean norm), the diagonal matrix formed with the inverses of the variances of each attribute (induces a diagonal norm), and the inverse of the matrix of variances (which induces the Mahalanobis norm). Any norm used is related to different geometric and statistical properties of the data (Bezdek 1981). The Euclidean norm is suitable when the attributes are statistically independent and approximately equally variable; the shape of the clusters is therefore approximately hyperspherical. The diagonal norm is useful when the attributes are statistically independent but markedly unequally variable; the cluster shape is then hyperellipsoidal. The Mahalanobis norm is similar to the diagonal norm, the only difference being that is useful when the features are statistically dependent. Usually the norm is fixed initially, but it is also possible to allow it to vary during the analysis (Gustafson & Kessel 1979).

Ordination as a basis for clustering

A frequent problem in community ecology is the fact that, despite the lack of any marked environmental difference, replicate samples are almost never 100% similar. Instead they often have similarities of only 50–90% (Gauch 1982) owing to random variation of dispersal and establishment, and to sampling restrictions. It is assumed that ordination selectively recovers patterns where several species are involved simultaneously in the dominant axes and selectively defers noise to axes associated with the smaller eigenvalues (Gauch 1982). Ordination therefore reduces noise. Reciprocal averaging axes (Hill 1973), or indeed any other ordination axes, can be used as the variables on which to perform the clustering to reduce noise problems. Reciprocal averaging was chosen in this case because, according to ter Braak (1985), this ordination technique approximates a maximum likelihood Gaussian ordination which was regarded as more sensible than the linear assumption implicit in principal component or principal coordinates analyses. TWINSPAN (Hill 1979) also uses reciprocal averaging ordination axes as the basis of the clustering.

Using the fuzzy *c*-means algorithm, the clustering process can be based on ordination axes, and the centroid vectors can be expressed in the original coordinates (usually species). This is a great advantage because the results can be interpreted in terms of the species abundances themselves (or proportions if the data are in a presence/absence format). The centroids are computed as weighted averages and hence, once the final membership values (which are the weights) are computed, the same weights can be applied to the original coordinates to express the centroids of this partition in the original dimensionality. The same procedure can be applied to any other external variables which are associated with the sample. It should be noticed, however, that these centroids are not necessarily the same as those which would be computed from the original data.

How many clusters are there?

It is unlikely that a satisfactory answer to this question exists. According to McBratney & Moore (1985), it could be particularly difficult to answer for environmental data. Some clustering approaches, including fuzzy *c*-means, often have multiple local stationary points for a given value of *c*. At the same time, it can be shown that a global optimization (the best one mathematically) is not necessarily the best practical *c*-partition of the data

(Bezdek 1981). A measure of the 'strength' of the clustering is therefore helpful in finding an appropriate number of groups in the sample.

To help in identifying a suitable number of clusters, the partition coefficient (Bezdek 1974, 1981) has been used. This is

$$F_c = \sum_{i=1}^{n} \sum_{j=1}^{c} (u_{ij})^2/n, \qquad c' \leqslant F_c \leqslant 1. \tag{4}$$

where $c' = 1/c$. F_c will reach a relative maximum when the 'best' number of clusters is fitted (provided that $m \neq 1$). This should be taken as a gross indication of the number of clusters because F_c does not involve explicitly either the data or the algorithm used in making the partition (Bezdek 1981). Nevertheless, it has been used with satisfactory results in several applications (Bezdek 1974; McBratney & Moore 1985). One minor inconvenience of F_c is its range from $1/c$ to 1, which makes it difficult to compare values between different c values. An appropriate normalization is

$$F'_c = \frac{cF_c - 1}{c - 1} \tag{5}$$

where F'_c lies within the interval [0, 1].

Comparison of TWINSPAN *and fuzzy* c*-means*

It is interesting to compare a fuzzy clustering approach with an established hard partition method. TWINSPAN (Hill 1979), now widely used in community ecology, produces a hard partition of one ordination axis as a basis of a hierarchical dichotomous classification.

The groups of species associated with the clusters from both TWINSPAN and fuzzy c-means algorithms may be compared to evaluate the similarities between the two methods. In fuzzy c-means those species which have a stronger contrast between the largest and the smallest centroid values are better discriminators, and can therefore be considered to be more 'typical' of the group in which they are best represented. This is particularly clear with presence/absence data, because the centroids are expressed as proportions of each species within the corresponding clusters. Bezdek (1981) used this criterion for 'feature selection'. In TWINSPAN the indicator species have a similar role in cluster characterization.

Fuzzy clustering allocates sites to groups on the bases of membership values. Although this makes it difficult to compare fuzzy c-means with TWINSPAN, it is precisely this feature that is one of the greatest advantages of fuzzy clustering. However, to compare site allocation between the two methods the following rule can be used to convert the fuzzy partition into a hard partition: assign each individual to the cluster in which it has the highest membership value (if there is a tie, the individual is arbitrarily assigned to the first cluster in the tie). This hard partition may then be used to compare site allocation between TWINSPAN and fuzzy c-means, although it should be kept in mind that to construct a hard partition from a fuzzy one introduces precisely the same problems which fuzzy sets were invented to avoid. The comparison is based on a contingency table where the columns are the groups from fuzzy clustering, the rows are the groups from TWINSPAN, the arrangement of groups maximizing the entries along the main diagonal. The entries themselves are the counts of sites allocated to each combination of TWINSPAN and fuzzy groups. If there is a perfect agreement between the two methods, the off-diagonal elements will all be zero. A measure of overall agreement is the K statistic (Bishop, Fienberg &

TABLE 1. List of localities sampled in North York Moors National Park.

Locality	National Grid reference	Number of samples	Sample identity number
Kildale Moor	NZ6111 and 6408	6	1–6
Westerdale Moor	NZ6506	2	7–8
Castleton Rigg	NZ6804 and 6805	4	9–12
Spaunton Moor	SE7095	6	13–18
Rosedale Moor	SE7199 and NZ7100	6	19–24
Glaisdale Moor	NZ7300 and 7301	5	25–29
Lealholm Moor	NZ7509 and 7510	4	30–33
Egton Moor	NZ7501, 7602 and 7901	13	34–46
Levisham Moor	SE8494	5	47–51
Fylingdales Moor	SE8897	4	52–55

Holland 1975). The groups produced by any method of clustering are labelled in an arbitrary way. Hence, to compare the results of different analyses the equivalent groups must be matched. The maximum value of the K statistic for different orderings of the groups can therefore be used as a criterion to select matching groups, although this approach may be cumbersome if there are many groups to compare.

DATA DESCRIPTION

There are four broad types of land use in the North York Moors National Park (North York Moors National Park Department 1984): moorland dominated by *Calluna vulgaris* (L.) Hull (which covers 35% of the Park), coniferous plantations (20%), broadleaved and mixed woodland (5%), and farmland (40%). The moorlands have developed over Jurassic rocks and under low-rainfall conditions, contrasting with the general rule that moorlands develop in uplands over geologically old rocks, with high rainfall. The moors of the park are the result of human activities during prehistoric and historic times. All samples were in *C. vulgaris* moorland, as detailed in Table 1. Sampling was conducted on fifty-five subjectively selected sites. At each site, four posts at 4-m intervals marked the location of a sampling line. At each post, two samples were taken, on each side of the line, 0·5 m from the post. The sample was a square quadrat, 0·5 m on side, divided into a grid of twenty-five squares. The number of squares where a species was present was recorded, summed for eight quadrats, and the result was expressed as a percentage occurrence of each species in 200 squares, rounded to the nearest integer.

RESULTS

The data were arranged into six different data-sets for the analyses (Table 2). These data-sets were chosen to avoid the clustering being influenced either by the rare or the very common species.

TWINSPAN analysis

The first division was very similar for the six data-sets; it was associated with the species of wet environments (*Agrostis canina, Sphagnum recurvum, Polytrichum commune* and *Eriophorum angustifolium*) on one side and, on the other side, with *Pohlia nutans*, a moss which grows on peaty or sandy banks and under *Calluna vulgaris* (Watson 1968). The second level of division produced four groups. The first two (A and B) corresponding to

TABLE 2. Data-sets considered for the analyses. The labels are used subsequently to refer to the data-sets in the text.

Species included	Number of species included	Label
All	80	ALL-SPP
Those occurring on at least five sites	27	ST5
Those occurring on at least ten sites	18	ST10
Those with a total frequency of at least 10%	47	FQ10
All except *C. vulgaris* and those present on only one site	53	CAL-ST1
All except *C. vulgaris* and those present on less than ten sites	17	CAL-ST10

the wet group in the primary division, were very unstable with different indicator species in the six datasets (the most constant indicator, in three analyses, was *Erica tetralix* for group B). The other two groups (C and D) correspond to the drier primary division. The indicator for group C, in all six analyses, was *P. commune*, which grows on acid moorlands and is frequent on wetter parts of acid 'white' moor (Watson 1968). Group D has two indicators in all six analyses, *Dicranum scoparium* and *Hypnum jutlandicum*, the latter commonly found beneath the *C. vulgaris* canopy in its mature and degenerate phases (Gimingham 1972). Comparison of these six analyses indicates that the rare species may be distorting the clusters, and also that the presence of the almost ubiquitous *C. vulgaris* is having a distorting effect, especially on the side of the dichotomy corresponding to the wetter habitats. Thus, the results of analysis of data-set CAL-ST10 (Table 2) were considered to be the most satisfactory TWINSPAN grouping (Table 3).

Fuzzy c-*means clustering*

The analyses were conducted on both the percentage frequency data matrix and the presence/absence equivalent, using normalized (unit-length) reciprocal averaging axes (one to three axes were considered). The starting strategy of the clustering consisted of two stages. First, the largest reciprocal averaging axis was divided into segments of equal length, the number of segments corresponding to the number of clusters that were to be fitted. Secondly, the observations found in each segment were given an arbitrary membership of 0·9 in the cluster corresponding to that segment and a membership value of $0{\cdot}1/(c-1)$ for each of the remaining clusters.

The values of the partition coefficient, without normalization, suggested two clusters in most of the analyses, although there were indications of a substructure at three or perhaps five groups. In all the cases, the first two groups were related with the division between sites from wet habitats and those from drier habitats, in close agreement with TWINSPAN results. Indicators of wet habitats were *Agrostis canina*, *Erica tetralix*, *Juncus effusus*, *Nardus stricta*, *Polytrichum commune* and *Sphagnum recurvum*. Indicators of drier habitats were *Calluna vulgaris*, *Erica cinerea*, *Vaccinium myrtillus*, *Campylopus introflexus*, *C. paradoxus*, *Dicranum scoparium*, *Hypnum jutlandicum* and *Pohlia nutans*.

TABLE 3. The classification produced by TWINSPAN with the moorlands data-set CAL-ST10 (see Table 2). Only the first two levels of divisions of the data-set are shown. Site numbers are given in Table 1.

			Groups	
	A	B	C	D
			Site numbers	
Species	22334455	2335	111111222223334445	1111223334444455
	12812053545	4569232	3012679035781461263	793458467890478901
Agrostis canina L.	5555455-512	43-1124	-------------- - --	--4----- ---------
Juncus effusus L.	5555555-52-	3------	----2-4----- ------	------------2-----
Sphagnum recurvum P. Beauv.	55545552555	-------	-- - ---- - 5 -23-	----- --- --------
Erica tetralix L.	535------55	-245555	----- - 54---3	4 --- -1- 22------
Eriophorum angustifolium Honckeny	5342-313-55	----5 -	- -3 21 - - 52 2	--- -- -- -----
Juncus squarrosus L.	2--5-------	1324-4-	----2-41- 2--------	------------1-----
Polytrichum commune Hedw.	55455555554	534-4 3	2-- 512 52 1255554-	-2-- ---- -2---1-
Deschampsia flexuosa (L.) Trin.	---54-3-1--	-------	1--- -- -- 13----	21-2---------2-434
Empetrum nigrum L.	32-4-------	-------	-3143--31-43 3--3--	-1----------4-----
Vaccinium myrtillus L.	--214---23-	-1-3--2	---2--52 325-55-352	13455-5-----51--11
Campylopus introflexus (Hedw.) Brid.	-----------	5- 1--4	-42-413-4--44 2----	--3 -2--1---------
Campylopus paradoxus Wils.	-------2---	4144--3	553 434 21 543 22-2	4 4 251-551--455-2
Cephaloziella sp.	-------2---	---43--	----2-----3115-5---	----22-1---1-1---1
Gymnocolea inflata (Huds.) Dum.	----1------	14-----	---132---23 215342	----11--------1---
Dicranum scoparium Hedw.	2---------1	1----2-	----123---1- 1--1--	225544 1-343422252
Hypnum jutlandicum Holmen & Warncke	1--------42	-----5-	-----------1---1-2-	45-32-2----5551322
Pohlia nutans (Hedw.) Lindb.	---1--21---	2--1-14	-243422-23553244544	134 4325-2-3343341

TABLE 4. Agreement between TWINSPAN classification of moorlands data and fuzzy clusters. K is defined in eqn 6 and the data-sets are introduced in Table 2. The lowest normal deviate value was $z=2{\cdot}61$, which is statistically significant.

Data-set	Number of reciprocal averaging axes	Agreement (K)	
		Frequency data	Presence/absence
ALL-SPP	1	0·404	0·376
ALL-SPP	2	0·373	0·261
ALL-SPP	3	0·373	0·341
ST5	1	0·252	0·364
ST5	2	0·381	0·453
ST5	3	0·399	0·352
CALL-ST10	1	0·553	0·465
CALL-ST10	2	0·427	0·501
CALL-ST10	3	0·414	0·656

To compare in detail the fuzzy clustering results with the TWINSPAN results, four fuzzy groups were produced and compared with TWINSPAN results with data-set CAL-ST10. There was always a significant agreement in site allocation between the two methods (Table 4), the closest agreement ($K=0{\cdot}656$) being for data-set CAL-ST10 with three reciprocal averaging axes, and using presence/absence data. The centroids and membership values for the fuzzy clustering of this analysis are shown in Tables 5 and 6. There is

TABLE 5. Centroids generated by the fuzzy clustering of data-set CAL-ST10. Only presence/absence information was used and hence the centroid values are proportions of presence of the species in the four fuzzy groups. The clustering was performed using three reciprocal averaging axes and the partition coefficient, F_c', was 0·342

	Fuzzy groups			
	A	B	C	D
Flowering plants				
Agrostis canina	0·826	0·451	0·172	0·019
Deschampsia flexuosa	0·456	0·020	0·114	0·659
Empetrum nigrum	0·384	0·049	0·353	0·100
Erica tetralix	0·328	0·816	0·094	0·151
Eriophorum angustifolium	0·709	0·352	0·180	0·019
Juncus effusus	0·825	0·040	0·188	0·018
Juncus squarrosus	0·262	0·397	0·233	0·021
Vaccinium myrtillus	0·570	0·483	0·488	0·763
Mosses				
Campylopus introflexus	0·027	0·204	0·679	0·021
Campylopus paradoxus	0·068	0·715	0·851	0·747
Dicranum scoparium	0·155	0·299	0·470	0·826
Hypnum jutlandicum	0·208	0·206	0·107	0·917
Pohlia nutans	0·371	0·611	0·893	0·931
Polytrichum commune	0·908	0·487	0·793	0·148
Sphagnum recurvum	0·862	0·102	0·055	0·046
Liverworts				
Cephaloziella sp.	0·031	0·351	0·321	0·355
Gymnocolea inflata	0·157	0·379	0·468	0·161

Table 6. Membership values for the fifty-five sites obtained with fuzzy *c*-means clustering of the moorlands data-set CAL-ST10. Presence/absence information was used and the clustering was performed using three reciprocal averaging axes. Site numbers are given in Table 1.

Site	Fuzzy groups			
number	A	B	C	D
1	0·608	0·198	0·110	0·084
2	0·704	0·127	0·106	0·063
3	0·072	0·151	0·727	0·051
4	0·102	0·168	0·677	0·053
5	0·060	0·813	0·091	0·036
6	0·102	0·662	0·157	0·079
7	0·042	0·063	0·049	0·845
8	0·626	0·179	0·113	0·083
9	0·152	0·096	0·144	0·608
10	0·186	0·138	0·469	0·207
11	0·156	0·161	0·537	0·147
12	0·189	0·117	0·490	0·204
13	0·021	0·041	0·919	0·019
14	0·163	0·124	0·134	0·579
15	0·069	0·177	0·145	0·610
16	0·053	0·078	0·837	0·032
17	0·043	0·090	0·816	0·051
18	0·077	0·257	0·533	0·133
19	0·129	0·137	0·677	0·057
20	0·507	0·115	0·294	0·084
21	0·826	0·047	0·076	0·051
22	0·762	0·063	0·091	0·085
23	0·143	0·142	0·599	0·116
24	0·019	0·024	0·033	0·925
25	0·020	0·028	0·927	0·024
26	0·122	0·500	0·166	0·212
27	0·081	0·170	0·580	0·169
28	0·046	0·062	0·819	0·072
29	0·050	0·757	0·147	0·046
30	0·671	0·127	0·119	0·083
31	0·045	0·062	0·824	0·069
32	0·176	0·566	0·147	0·111
33	0·122	0·590	0·121	0·167
34	0·177	0·197	0·315	0·311
35	0·865	0·041	0·050	0·044
36	0·065	0·247	0·633	0·056
37	0·167	0·231	0·442	0·160
38	0·085	0·267	0·301	0·347
39	0·116	0·547	0·166	0·171
40	0·133	0·396	0·160	0·311
41	0·089	0·516	0·244	0·152
42	0·296	0·126	0·451	0·127
43	0·225	0·420	0·266	0·089
44	0·358	0·131	0·257	0·255
45	0·690	0·085	0·110	0·116
46	0·333	0·126	0·185	0·356
47	0·010	0·013	0·014	0·964
48	0·063	0·144	0·142	0·651
49	0·043	0·043	0·051	0·863
50	0·092	0·064	0·079	0·766
51	0·010	0·013	0·014	0·964
52	0·090	0·477	0·372	0·061
53	0·023	0·901	0·054	0·022
54	0·617	0·179	0·103	0·102
55	0·302	0·400	0·135	0·164

particularly close agreement between TWINSPAN and fuzzy *c*-means in the analysis of CAL-ST10 data-set for the wettest sites; the nine wettest sites (sites 2, 8, 21, 22, 30, 32, 35, 45 and 54) were allocated to group A in both analyses, except site 32. This site was unusual because of the small frequency of *Agrostis canina* and the absence of *Sphagnum recurvum*, which was replaced by *S. magellanicum* Brid., with a frequency of 60%. However, this was the only site where *S. magellanicum* was recorded, and this species was therefore not included in the analysis. Some disagreements are interesting: for instance site 44, which was allocated to group D by TWINSPAN but to group A by the hard equivalent of fuzzy *c*-means. Table 6 shows that the membership value for group A is not much larger than those for groups C and D. The site had a mixture of species from both dry (*V. myrtillus*, *D. scoparium*, *H. jutlandicum* and *P. nutans*) and wet habitats (*Juncus squarrosus*, *J. effusus* and *P. commune*). This demonstrates that membership values can be used to indicate sites with mixed vegetation or sites which are intermediate on a gradient.

The centroids (Table 5) show that *A. canina*, *J. effusus* and *S. recurvum* are good indicator species of group A, because the values are large for group A and small for the other groups. *E. tetralix* is the best indicator of group B, *C. introflexus* is the best indicator of group C, and *D. scoparium* together with *H. jutlandicum* are the best for group D. Some species may show bimodal behaviour; one example is *Empetrum nigrum*, which has its largest values both in groups A and C (although this is not immediately obvious in the TWINSPAN results, bimodality is suggested in Table 3 for this species). According to Gimingham (1972) and Hobbs & Gimingham (1987), *E. nigrum* may have two distinct ecotypes adapted to wet and dry conditions, respectively. The absence of some species can also be an important indicator, as, for example, the relative scarcity of *P. commune* from group D.

Using the clustering for data exploration

One interesting aspect of the fuzzy *c*-means clustering approach is the facility to explore the behaviour of other variables, based on the fuzzy classification. An example is the distribution, among the fuzzy clusters, of *Calluna vulgaris*, *Cladonia* spp., the amount of bare soil, the height of the vegetation, overall plant diversity, and the diversity of the bryophytes (using the Shannon–Weaver index in both these latter cases). For TWINSPAN, group means were computed for these variables. For fuzzy clustering eqn 2 was used to calculate the means. The magnitude of the differences between group means was evaluated for TWINSPAN using a one-way analysis of variance. The approach followed for fuzzy clustering was an extension of the idea of the analysis of variance, using its equivalence to a regression model where the groups are represented by dummy variables that have the value one if the observation corresponds to the group and zero otherwise (Draper & Smith 1981). Instead of using these dummy variables, the membership values were used directly as 'group variables' and, as they are constrained to sum to 1, only $(c-1)$ variables are required (c is the number of groups). The value of the F statistic can be regarded as a measure of the overall performance of the clustering technique in producing differences in the variable among the fuzzy sets (B. McArdle, personal communication). Given that the number of degrees of freedom are the same in this case ($n_1 = 3$, $n_2 = 51$), it is possible to compare the F values directly (Table 7), but in other cases it would be appropriate to use R^2.

The greatest contrast among the clusters is shown for vegetation height, overall plant diversity and frequency of *C. vulgaris*. The height differences are due mainly to group A, the tallest due to the height of the rushes. The fact that the taxon *Cladonia* spp. (with the

TABLE 7. Groups means for six variables not included in the TWINSPAN or fuzzy *c*-means clustering of data-set CAL-ST10. These group means are compared with an *F*-statistic, as discussed in the text (for $P=0{\cdot}05$, $F=2{\cdot}76$).

Variable and clustering method	Groups				Variance ratio (*F*)
	A	B	C	D	
Calluna vulgaris (%)					
TWINSPAN	36	76	93	93	20·08
Fuzzy *c*-means	41	84	91	94	16·49
Cladonia spp. (%)					
TWINSPAN	0	10	15	15	2·69
Fuzzy *c*-means	1	9	23	5	8·13
Vegetation height (cm)					
TWINSPAN	38	18	25	27	3·51
Fuzzy *c*-means	41	26	21	26	7·36
Bare soil (%)					
TWINSPAN	9	17	13	11	0·19
Fuzzy *c*-means	2	14	18	5	2·09
Plant diversity					
TWINSPAN	2·04	1·67	1·35	1·19	11·77
Fuzzy *c*-means	1·94	1·38	1·37	1·24	7·30
Bryophyte diversity					
TWINSPAN	1·01	1·11	1·22	1·01	0·91
Fuzzy *c*-means	0·95	0·98	1·25	1·23	2·16

fuzzy clustering) is also well contrasted suggests that it is associated at the drier groups with the dynamics of *Calluna vulgaris*, i.e. with the heather cycle described by Watt (1955) and Gimingham (1972, 1987). The mean values of *Cladonia* in the fuzzy clustering agree with the interpretation that group D is either the mature or building phase and group C is associated with the pioneer or declining phases of the Callunetum. Group B may also be part of this cycle, perhaps the degenerate phase; this is suggested by the presence of *J. squarrosus*, *E. angustifolium* and *A. canina* (Table 5). Both Gramineae and Juncaceae are well represented in this stage of the cycle, which is also the most diverse phase (Table 7) in the heather-dominated moorlands (Watt 1955; Gimingham 1972). These results suggest that fuzzy clustering may be revealing more of the *Calluna* cycle than TWINSPAN. As a basis of an exploratory approach to vegetation classification, fuzzy clustering may be more appropriate than classification with a hard partition.

The four clusters have been used because they could be compared with TWINSPAN. Without this constraint, it was found that five groups on data-set CAL-ST10, using the original frequency data and three reciprocal averaging axes, yield a better partition, considering the association with the external variables (Table 8). The clustering is associated with the same patterns discussed above. The new clustering comprises approximately the same previous four groups except that group B (Table 7) is divided into groups B1 and B2. The new group B1 can now be interpreted as pioneer phase, and the group B2 as degenerate phase (Table 8).

Seven new observations, all from Westerdale, were subsequently added to the data-set, and it was desired to see how they fitted into the classification already produced. Two of these observations were from burnt sites and another two from cut sites. Their classification into the fuzzy clustering was achieved by calculating their membership values according to their scores in the three ordination axes, using eqn 3. It should be remembered that this classification is related mainly to the understorey composition,

TABLE 8. Centroids and mean values of the external variables on the five groups fuzzy clustering of data-set CAL-ST10 with the original frequency data. Three reciprocal averaging axes were the basis of the clustering (critical value of $F=2{\cdot}57$ for $P=0{\cdot}05$, with $n_1=4$ and $n_2=50$ degrees of freedom).

	Fuzzy group					Variance ratio
Plant species	A	B1	B2	C	D	(F)
Agrostis canina	47	3	2	0	0	—
Deschampsia flexuosa	5	0	1	2	1	—
Empetrum nigrum	2	0	2	1	3	—
Erica tetralix	4	30	5	0	1	—
Eriophorum angustifolium	5	25	3	0	0	—
Juncus effusus	64	0	3	0	0	—
Juncus squarrosus	3	3	2	0	0	—
Vaccinium myrtillus	3	4	9	0	25	—
Campylopus introflexus	1	2	4	3	1	—
Campylopus paradoxus	1	5	6	39	2	—
Dicranum scoparium	0	0	3	3	7	—
Hypnum jutlandicum	0	4	2	1	7	—
Pohlia nutans	1	5	11	4	13	—
Polytrichum commune	51	19	29	1	2	—
Sphagnum recurvum	56	11	3	0	1	—
Cephaloziella sp.	0	11	1	0	1	—
Gymnocolea inflata	0	9	3	0	2	—
External variable						
Calluna vulgaris (%)	26	80	89	92	95	20·13
Cladonia spp. (%)	1	6	10	35	7	11·97
Vegetation height (cm)	44	24	25	18	31	6·62
Bare soil (%)	2	7	12	34	2	5·23
Plant diversity	1·99	1·75	1·60	1·11	1·20	10·43
Bryophyte diversity	0·85	1·29	1·33	0·98	1·03	2·62

TABLE 9. Membership values of seven site samples not included in the fuzzy clustering. The memberships were calculated with eqn 3 according to the scores on the three reciprocal averaging axes used in the fuzzy clustering of the frequency data of CAL-ST10.

	Groups				
Treatment	A	B1	B2	C	D
Untreated	0·039	0·045	0·105	0·028	0·783
Untreated	0·035	0·062	0·103	0·023	0·778
Untreated	0·024	0·029	0·058	0·012	0·878
Burnt	0·103	0·101	0·166	0·052	0·578
Burnt	0·079	0·422	0·212	0·048	0·239
Cut	0·059	0·120	0·154	0·040	0·626
Cut	0·028	0·045	0·082	0·019	0·826

because *Calluna vulgaris* was not used to produce the classification. The results show that there is a strong effect of the vegetation structure, before the treatment, on the community response to either fire or cutting (Table 9); this is in agreement with Hobbs & Gimingham (1987). The results also suggest that burning has a stronger effect than cutting, as could be expected.

DISCUSSION

Both the TWINSPAN and fuzzy clustering groups correspond well with other moorland studies. Gimingham (1972), quoting W. G. Smith's descriptions, characterized the 'dry heather moor' by the presence of *Calluna vulgaris* and *Erica cinerea*, and the 'heather moor' dominated by *C. vulgaris* but associated with *E. tetralix* on deep peat and in moister conditions. Gimingham pointed out that the main direction of variation in floristic composition is a gradient of organic content of the substratum, from podzol to peat, whilst at the same time there is a gradient of soil moisture. Tansley (1949) indicated that the drier moor is associated with *C. vulgaris* and *Vaccinium myrtillus* and the wetter moor with *Sphagnum* spp., which is also an agreement with the grouping produced by both TWINSPAN and fuzzy *c*-means.

The two groups of dry sites correspond with Gimingham's (1972) description of heath communities where species other than *C. vulgaris* are very poorly represented. One of the few associated dwarf-shrubs is *E. cinerea*, but it is more common to have extensive pure stands of *Calluna*. The constant elements are mosses such as *Dicranum scoparium*, *Hylocomium splendens*, *Hypnum cupressiforme* Hedw. (possibly a synonym of *H. jutlandicum*, according to Smith 1978) and *Pleurozium schreberi* (Brid.) Mitt. Gimingham pointed out that these communities occur generally where burning for sheep grazing or grouse rearing is regular, thus tending towards the production of a monoculture of *Calluna*. This type of vegetation has been termed: 'dry *Calluna* moor', '*Calluna–Erica cinerea* heath with reduced oceanic floristic element' and 'Callunetum vulgaris'.

Is the fuzzy *c*-means algorithm suitable for the analysis of ecological data? In comparison with TWINSPAN, it seems able to produce clusters which are more strongly correlated with relevant external variables (Tables 7 and 8). This may be a consequence of the fact that ecological communities are more similar to fuzzy sets than to sets based on hard partitions. In some instances the maximum fuzzy clustering membership values were large (above 0·9), but it is more common for them to be lower (between 0·5 and 0·7), which agrees with the fact that communities are formed along gradients, without sharp boundaries.

The partition coefficient as a means of evaluating the 'cluster validity' (Bezdek 1981), although helpful, seems rather crude. With coefficients which were not normalized there seemed to be a bias toward a small number of groups, whilst with normalized coefficients the bias appeared to be in the opposite direction. Although in principle all the fuzzy *c*-means family are non-hierarchical clustering procedures, they can be applied in a hierarchical way (Bezdek 1974, Bharati-Devi & Sarma 1986) to yield a polythetic, divisive clustering method. In general the great majority of systems proposed for vegetation classification have been hierarchical (Greig-Smith 1983), because such systems are usually less cumbersome and also more readily interpreted ecologically. The fuzzy *c*-means non-hierarchical approach is ecologically convenient for three reasons. First, the means and ranges of environmental variables can be explored, as in Table 7, in a similar way to that used in hierarchical systems. Secondly, clusters can be characterized in terms of 'typical' species composition (centroids in Table 5), which is very helpful in the ecological interpretation of the clusters produced. Thirdly, the membership values, as in Table 6, may be investigated to identify patterns of correlation with environmental factors or to locate intermediate samples. Observations with high maximum membership values can be regarded as typical of the pattern found in the data. Observations with roughly equal membership values for all clusters suggest that these observations do not follow that pattern very well. For instance, some sites in the clustering of moorland data, which had a mixture of species from wet and relatively dry conditions, were identified in this way. This is a main feature of fuzzy clustering that makes it superior to hard partition methods.

Once a description of ecological communities is obtained in terms of fuzzy sets, there are many possibilities for further analysis. For example, in modelling it is feasible to incorporate 'environmental heterogeneity' information in the form of membership functions, instead of random variation as in stochastic models (Kandel 1982). Another example is species interaction, which could be weighted according with degrees of membership to defined ecological communities. Such concepts lend support to the idea that fuzzy sets are a suitable tool for describing ecological communities. Species are not ubiquitous, because they are limited to particular assemblages of loosely structured ecological systems. As Roughgarden & Diamond (1986) considered, understanding the factors responsible for this 'limited membership' has a central role in explaining ecological phenomena. They also posed the question of which 'data structure' could be the most suitable for the study of ecological communities; fuzzy sets are obviously a good candidate.

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