Germination and establishment of seedlings in different phases of the Calluna life cycle in a Scottish heathland*

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Abstract

Previous authors have suggested that cyclical succession takes place in Calluna-dominated heathland, and is determined by the different growth phases of the dominant. Characteristic species are said to invade at different stages of the life cycle of Calluna, particularly in the initial and pioneer phases and in the degenerate phase. In the last phase, gaps are formed due to separation and dying of the oldest frame branches.

This paper aims to analyze in which microhabitat and in which phase of the Calluna life cycle seedling emergence and establishment is possible.

More seedlings appear in pioneer Calluna than in mature Calluna stands in experimentally manipulated micro-sites. In pioneer Calluna establishment is affected only by application of litter, in mature Calluna by increased illumination. The differences between treatments disappeared after three years, but not the difference in establishment between stands.

Seedling emergence from species sown experimentally was different in the successive phases of Calluna. Highest emergence was in the pioneer stand.

In a seedling survey also most seedlings appeared and established in the pioneer phase. The number of recently germinated seeds was high in all phases. However, seedling survival was very low, except in the pioneer stands. This study does not of itself show evidence for cyclical succession in Calluna-dominated heath vegetation. Colonization of gaps by seedlings of Calluna in mature or degenerate phases is possible, but must be an infrequent occurrence.

Introduction

In 1947 A. S. Watt put forward an explanation of the patchy nature of certain types of vegetation, on the basis of cyclical changes in the occupancy of the patch. Examples were drawn from woods, bogs, grasslands, heaths and mountain communities. In heath vegetation dominated by Calluna vulgaris it was suggested that the cycle might be determined by changes in the morphology of Calluna individuals as, with increasing age, they passed through successive growth phases: pioneer, building, mature and degenerate (Watt, 1947, 1955; Barclay-Estrup, 1971; Gimingham, 1972).

During the late mature and building phases, a gap begins to appear in the center of a Calluna bush as the oldest frame-branches separate and die. The diameter of this gap expands with the progression of branch death from the center towards the margin of the bush. Other species then have the opportunity to colonize within the gap (e.g. bryophytes, lichens, grasses, Arctostaphylos uva-ursi, etc.). However, it was suggested by Watt that in time

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Calluna would return to occupy its original situation, thus completing the cycle.

While observations (at least in some British heaths) of young Calluna plants occupying the center of gaps provide some evidence for this cycle, the origin of these young individuals has not been investigated. It has often been stated that in vigorous heath stands Calluna seedlings may be lacking or present only in very low densities (Tamm, 1956; Cook, 1979; Grime, 1979; Miles, 1979). However, gaps created by animals, or perhaps by dying plants, may offer, locally, safe sites for seed germination and seedling establishment (Grubb, 1977; Harper, 1977), while in some cases young plants may become established by a form of layering.

Miles (1973, 1974a) showed that seedlings may become established in experimentally bared areas in heathlands, but that seedling density depended upon the soil type and the size of the gap created. Similarly, the number of different species colonizing gaps depends both upon soil type (especially nutrient availability) and upon the species present in the surrounding vegetation (Mallik & Gimingham, 1983). However, it is not known how the capacity of various species to germinate and establish may be affected by undisturbed stands of Calluna in its various growth phases. Nor is there much information as to the exact positions in which different species will germinate. The experiments described in this paper were designed to answer some of these questions by investigating germination and early establishment in stands in each of the main growth phases and in gaps of varying size, and thus to contribute some evidence as to how cyclical changes might come about.

Study site

The Muir of Dinnet is a National Reserve in NE Scotland (grid reference n. 436984). The soil is a freely drained brown podsolic soil with a fairly deep (30–35 cm) layer of sandy loam and very little surface accumulation of humus (1.5–2 cm). The pH of the soil is about 5. The vegetation can be assigned to the Arctostaphyleto–Callunetum (McVean & Ratcliffe, 1962) which is in this area very herb-rich. Major species are Campanula rotundifolia, Carex pilulifera, Deschampsia flexuosa, Festuca ovina, Galium saxatile, Lathyrus montanus, Potentilla erecta, Pyrola media, Sieglingia decumbens, Trientalis europaea, Vaccinium vitis-idaea.

The moor is managed by burning small patches in successive years. As a result there are stands of heather of all ages from 1 to 30 years. In Table 1 the division into different types of vegetation structure is shown, based upon a separation of the different stages of the Calluna life cycle. The initial and pioneer Calluna stages are the most herb-rich stages. An ‘initial’ phase is included, to distinguish the immediate post-fire period (one or two years only) before the development of a pioneer Calluna stand.

In the building phase Calluna vulgaris and Erica cinerea are the dominant species. In the mature phase Calluna vulgaris is completely dominant, and in the degenerate phase Calluna vulgaris and Arctostaphylos uva-ursi are the dominant species.

Materials and methods

Experiment I

Bared areas were created in pioneer and mature Calluna stands. Two ‘gap sizes’ were adopted: 200 cm² and 25 cm², these being created by clipping the vegetation and removing regrowth every 10 days during the first year. Loose litter was removed, but reintroduced to half the plots to a depth of 0.5 cm. Half of the plots received a dressing of fertilizer (as

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<tr>
<th>Table 1. Percentage cover of different micro-habitat types in the different successional phases of the Calluna life cycle.</th>
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<tbody>
<tr>
<td>Bare ground</td>
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<tr>
<td>Initial/pioneer</td>
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<td>Pioneer/building</td>
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<td>Mature</td>
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<td>Degenerate</td>
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<td>Arctostaphylos</td>
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