Vegetational Dynamics in Calluna heaths

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Synopsis

1) Heath vegetation, widely dominated by *Calluna vulgaris* in western Europe, is subject to various processes of change in composition, which are reviewed in this paper.

2) Some heath communities, such as dwarf montane heaths and certain wet heaths, show evidence of being steady-state ecosystems (i.e. the absence of overall compositional change). Others, including the majority of lowland heaths on the more freely drained soils, unless they are managed, are dynamic or potentially so, tending to undergo successional change.

3) The question as to how both types can be dominated by the one species is answered by reference to some of its biological attributes. *Calluna* possesses some features of 'r-selected' organisms and in favourable habitats behaves as a seral dominant because its occupancy of the 'patch' is limited in time. Under more extreme conditions it may produce prostrate stems rooting in moist humus, propagating the plant vegetatively and maintaining occupancy indefinitely.

4) 'Patch dynamics' are therefore important in heath vegetation. Steady-state systems show cyclical changes. While such cycles may occur on some lowland heaths, they remain repetitive only so long as the gap phase remains free of other, more persistent species, such as certain grasses, bracken, shrubs or trees. Most lowland heaths are open to this type of successional change, given the presence in the neighbourhood of seed parents or, as appropriate, rhizomes of potential invaders.

5) Die-back of *Calluna* over larger areas, such as may be caused by climatic extremes or insect attack, may also promote successional change. Maintenance of *Calluna* dominance thus normally requires management by grazing, burning, cutting or turf stripping to arrest succession. Burning creates bare areas on which short post-fire secondary successions take place, in which the 'initial floristic composition' factor is of over-riding importance.

Heath communities, Calluna vulgaris, steady-state ecosystems, successional change, cyclical change, secondary successions

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Introduction

A recurrent theme among Professor Bornkamm's wide-ranging ecological researches has been the study of vegetation dynamics, and in particular the role of competition and other plant interactions in contributing to successional change. In a number of instances (e.g. BORNKAMM 1981, 1988) he examines these problems in the context of secondary successions. As the latter constitute one important aspect of the processes of change at work in heathland vegetation, it is appropriate to offer a brief review on this subject in appreciation of the importance of his contributions to vegetation science.

The word 'heathland' in ecological literature is taken to denote a vegetation type characterised by evergreen, woody low shrubs, seldom more than 1 m high, of ericoid form and appearance. In Europe, the leading (though not the only) dominant of this formation is heather, *Calluna vulgaris*, which is the chief species both of lowland heaths in the more oceanic western parts (the 'Atlantic region') and of montane heaths more widely within the limits of its geographical distribution.

Much has been written on the subject of vegetation dynamics in heathland, some of it conflicting. There has been little attempt, however, to take an overview of the processes at work, and it is therefore the purpose of this paper to make some progress in this direction. The terms 'vegetation dynamics' or 'processes of change' can be applied on various spatial scales: here, 'processes of change' are taken to refer to overall changes in community composition (both changes in the complement of species and changes in the quantitative representation of species present). Patch dynamics on a smaller scale will also receive mention, for example with reference to cyclical changes.

Long term studies of heath vegetation (e.g. LIPPE et al. 1985; WATT, 1955) raise a problem of immediate and fundamental importance. While certain types of *Calluna* heath appear to have the characteristics of steady-state ecosystems, others are clearly dynamic and undergo vegetational change as defined above, or at least seem to be potentially dynamic. Yet both types are dominated by the same species. In view of the fact that in stable environments change *versus* stability is in many cases attributable to biological characteristics of the dominant species, the question

arises here as to how it comes about that both steady-state and dynamic systems can be dominated by one and the same species.

Certain facts about steady-state and dynamic heath systems and about the biology of *Calluna* will first be reviewed, and some explanations suggested. Various types of observed change will then be discussed in more detail, followed by brief consideration of the role of past and present management in controlling change and achieving heathland conservation.

Steady-state heath systems

Heath ecosystems for which there is evidence of long-term stability (i.e. lack of overall compositional change, even if there is flux on the scale of the 'patch'), without any intervention of management, appear to fall into two categories.

1) Montane *Calluna* heaths; normally those above the potential tree-limit. These are dwarf-heaths in which the dominant *Calluna* forms a low, prostrate mat of often intertwined stems, the height being restricted by wind-pruning usually to less than 10 cm (BAYFIELD, 1984).

2) Certain wet-heaths on peaty substrata. Here *Calluna*, while still being the physiognomic dominant, may share prominence with species such as *Eriophorum vaginatum* and *Sphagnum* spp. While in many cases it may be difficult to discount the possible effects of past management practices such as grazing or burning, studies such as that by FORREST (1971) at an altitude of 550 m in the Pennine Range of central north England indicate that here the criteria for steady-state ecosystems are met. This is to say that the dominants are in balance, there is no overall change in composition, quantitative representation (cover, biomass), or age-structure. In this case the age-structure curve of the *Calluna* stand showed no break in the general trend and the mortality rate of mature *Calluna* stems was shown to be constant with time. The population of stems had a modal age of 8 years and a mean age of 11.5 years.

Dynamic or potentially dynamic heath systems

Most of the lowland heaths on the more freely-drained soils in the west European heath region either show evidence of change (changes in the age-structure of the *Calluna* population, or increases in the quantitative representation of other species such as grasses, bracken, tall shrubs and trees), or are ma-

naged in such a way as to arrest successional changes (e.g. by grazing, cutting, burning, turbary, plaggen or other traditional management). Except in the case of grazing, the effect of these practices is usually to remove most of the above-ground vegetation and to replace the 'normal' successional processes with repeated secondary successions. Most of these heaths have, in fact been derived from former forest, generally as a result of direct or indirect human interference. If management is withdrawn, and if suitable seed-sources are available, they usually undergo change towards the re-establishment of woodland (GIMINGHAM, 1972).

Calluna is therefore in some instances the dominant species of steady-state systems while in others it is a temporary dominant of seral, or potentially seral, communities.

Some explanations based on biological features of *Calluna*

Calluna shows many of the biological features of 'r-selected' plants. According to GRIME (1979) the 'r-selected' type is made up of organisms with a short life-expectancy and large reproductive effort. *Calluna* certainly meets the latter criterion, having a very high reproductive capacity, producing 200,000 or more seeds m^{-2} which are small and light, effectively dispersed and show high germinability. In addition, germination tends to be intermittent and, under suitable conditions of storage, viability may be retained for many years, often resulting in large soil seed-banks (up to 40,000 m^{-2}).

The criterion of a short life-cycle is scarcely met if by 'short' is meant a life-span of just one or two years. But in normal optimal habitats (such as those of lowland heaths on freely-drained soils in temperate, sub-oceanic climates), the life-span of a *Calluna* bush is generally limited to little more than 30 years, often less. Thus, although a perennial, in comparison with tall shrubs and trees its life cycle is relatively short, and is geared to behaviour as a seral and not a 'climax' dominant. It is capable of rapid colonisation of open habitats, but is unable to retain occupancy of its patch indefinitely. In the normal course of events it opens up the spot to the possibility of colonisation by other species and consequent vegetational change.

If some of the biological characteristics of *Calluna* tend to be those of a seral dominant, how then can its dominance of certain steady-state ecosystems be explained? Both the examples described above are communities occurring in environmental conditions which may be regarded as sub-optimal for *Calluna* (wet peaty-soils, and the higher altitudes). Here certain other morphological attributes come into play.

These are (i) the capacity to produce large numbers of new green-shoots if the main long-shoot apices are killed off (MOHAMMED AND GIMINGHAM, 1970) and (ii) the capacity to produce adventitious roots from prostrate stems if these are buried in moist humus or peat or sometimes in a bed of moss (SCANDRETT AND GIMINGHAM, 1989). Both of these responses tend to delay or prevent the physiological ageing process in the stems and to keep the plant in a juvenile or 'building phase', producing new shoots, almost indefinitely.

In the dwarf, montane *Calluna* heaths, vertical long-shoots are continually pruned back by exposure to high winds. New short-shoots are produced prolifically, while extension growth takes place only in creeping branches, which produce adventitious roots in the moist surface humus. The result is a low-growing, prostrate mat of inter-twined woody stems, which may persist for many years.

WATT (1947) showed that in these dwarf heaths the shoot growth of *Calluna* is inclined to be centrifugal. On the older parts of the prostrate stems the foliage-bearing shoots die and are stripped by the wind. Lichens (*Cladonia* spp.) may establish among the bare stems for a time, to be followed by lateral spread of species present in the area, such as *Arctostaphylos uva-ursi*. In time, *Calluna* may replace the *Arctostaphylos* by vegetative spread from the margin. Thus, on any one spot the vegetation follows a process of cyclical change, but overall the community is in a steady state. This applies even in more exposed situations where growth is unidirectional (METCALFE, 1950; BAYFIELD, 1984). The *Calluna* stems extend only into the wind-shadow of the cushion of living shoots, and are eroded away behind. Belts or stripes of vegetation move slowly across exposed plateaux or gentle slopes in the direction of the prevailing wind, such that occupancy of any one spot follows a cycle (Fig. 1).

On the wet heaths with peaty substrata, but in less extreme climatic conditions, vertical growth may not be inhibited to the same extent, but the main woody branches tend to be less rigidly erect and to spread sideways at an early stage, rooting abundantly where they become buried in the surface peat. The plant is in effect propagating vegetatively by a process of 'layering', which may result in a clonal ring of satellite clumps of shoots around the site once occupied by the original plant (KEATINGE, 1975). There is flux in the occupancy of patches, but an overall steady state.
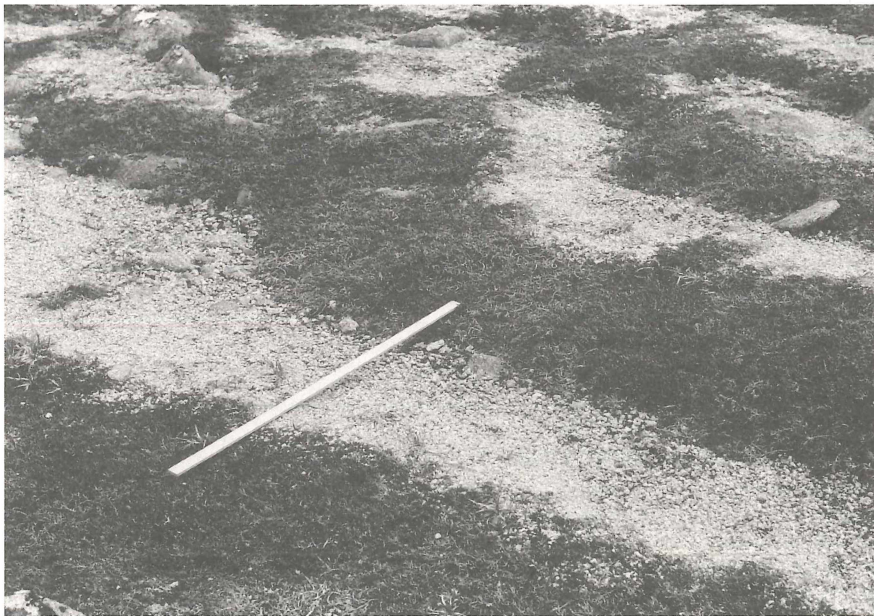

Fig. 1
High altitude dwarf montane heath in the Cairngorm Mountains, Scotland (ca. 790 m). The stripes or 'waves' are composed mainly of *Calluna vulgaris* and move slowly in the direction from upper right to lower left of the picture, under the influence of strong winds. Prostrate *Calluna* shoots grow over the bare gravel into shelter provided by the cushions.
At the back of the cushions dead foliage and branches are stripped by the wind, leaving bare creeping stems anchored well behind the stripe. Lichens colonise amongst these twisted stems. Thus, while the vegetation as a whole is in a 'steady-state', on any particular spot there is a process of cyclical change.

In the example investigated by FORREST (1971), a blanket bog at relatively high altitude, both processes were at work. He states "The maintenance of a steady state is probably the result of a complex set of factors including restriction in canopy height, upward growth of the bog surface, the trailing growth form, and the gradual dying off of old buried stems". (Restriction in canopy height was attributed to the action of high winds in killing shoots that project well above the mean height.)

It is along these lines that the participation of *Calluna* in steady-state ecosystems, in habitats which are sub-optimal for the species, may be explained, whereas in more favourable habitats it behaves as a seral dominant.

Patch dynamics

It was A.S. WATT (1947, 1955) who first described the life history of individual *Calluna* bushes in favourable habitats, dividing it up into phases: pioneer (the colonizing phase); building (the main phase of vegetative growth); mature (the phase of reduced vigour, with incipient gap formation in the centre); degenerate (the phase of death of central branches and expansion of the canopy-gap). He ascribed the patchy nature of uneven-aged stands of *Calluna* to this process, and suggested that it was responsible for patch dynamics. Furthermore, he indicated that in his study-area in S.E. England (Breckland, East Anglia), which had not been subject to burning for many years, the canopy gaps forming in the centre of old *Calluna* bushes were initially colonized by lichens and bryophytes. Eventually, however, the mor humus slowly decayed, leaving humus-stained mineral soil on which seedling *Calluna* could become established. (A few other vascular plant species could take part in this cycle, but in this area the number of individuals was small.) Watt also noted that new cycles could be initiated by vegetative lateral spread of *Calluna* from neighbouring bushes.

This hypothesis of cyclical change (which implies a steady-state ecosystem) was for a time widely accepted as the norm (e.g. BARCLAY-ESTRUP AND GIMINGHAM, 1969). However, more recently questions have been raised as to whether there is any firm evidence for repetitive cycles in lowland heaths, outside the rather dry sub-continental conditions of the East Anglian Breckland (MILES, 1981). It is, indeed, difficult, or impossible, to find evidence of *Calluna* re-establishing from seed in canopy-gaps in moister habitats, largely because the gaps are normally immediately occupied by bryophytes, lichens or other vascular plant species (e.g. *Vaccinium myrtillus* or *Empetrum nigrum*). However, observational evidence

for the return of *Calluna* in such gaps can be found quite readily in undisturbed stands, but only as a result of vegetative layering of stems from surrounding bushes. In such instances there is no accelerated decay or dispersal of humus, and the *Calluna* stems become buried in the surface peaty material or moss, in which they can root (GIMINGHAM, 1988; SCANDRETT AND GIMINGHAM, 1989).

If such cycling is a reality, it might suggest that where it does occur the heath communities should be in a steady-state, whereas it has been claimed above that in the lowlands (except on very wet substrata) they are not. The reason is that these systems continue cycling only so long as no other species capable of occupying the habitat more permanently gains entry in the gaps. Examples of such species include tall shrubs and trees, (e.g. *Betula* spp. *Pinus sylvestris*, *Quercus* sp.), tussock grasses such as *Deschampsia flexuosa* in relatively dry sites and *Molinia caerulea* in wetter ones, or bracken (*Pteridium aquilinum*) in those areas in which it is vigorous. Wherever these species are present as potential 'invaders' the vegetation may not be in a steady-state, because *Calluna* is liable to yield occupancy to them when canopy-gaps appear (GONG AND GIMINGHAM, 1984) and thus to behave as a seral dominant. While much of the well-documented decline in the extent of lowland heathland is the result of afforestation, agriculture or development, a considerable proportion is due to these natural successional processes which proceed unless halted by management. Exceptions may be found in areas far removed from seed sources or beyond the reach of rhizomes of potential colonists, or where for climatic or edaphic reasons their entry may be inhibited. Under these conditions the community may continue to undergo cyclical change and may remain in a steady-state for prolonged periods.

Die-back of *Calluna* over larger areas

The entry of competitors in canopy gaps is not, however, the only way in which vegetation change may occur in heaths. *Calluna* may sometimes die back over extensive areas, if for example a relatively old stand is subject to severe late frost and desiccation, or to an attack of heather beetle (*Lochmaea suturalis*), or winter moth (*Operophtera brumata* – infestation by which is a relatively new event seen in recent years in Scotland). There is evidence that these outbreaks of pests (at least of heather beetle) are more severe where N enrichment has occurred. These large die-back areas are not quickly re-colonized by *Calluna* and may provide opportunities for trees, bracken or grasses to take over (MARRS, 1986).

Managed *Calluna* stands

For many generations the potentially dynamic trends in *Calluna* heathlands have been held back by management, such as grazing, cutting, burning or turf-stripping. Grazing has an effect similar to that of wind-pruning, maintaining the stand in a relatively juvenile condition and a steady state. The other treatments remove the greater part of the above-ground biomass, prevent further succession, and create bare areas on which short secondary successions take place. In these the "initial floristic composition" factor is of major importance, and the community is usually quickly reconstituted, largely from the species present before the treatment (HOBBS AND GIMINGHAM, 1984).

Conservation of heathland ecosystems

In conclusion, research on vegetation dynamics in *Calluna* communities reinforces the view that, apart from those examples which are clearly in a steady state, conservation of heathland demands management. Without it, successional processes will lead to replacement of heath by other types of vegetation. Any of the traditional forms of management may be employed, but there are two important considerations:

1) *Calluna* communities belong to acidic soils, low in calcium and other plant nutrients. The competitive balance between *Calluna* and potential invaders is a delicate one, which can easily be altered, for example in favour of grass species, by nutrient accumulation (HEIL AND DIEMONT, 1983). Most traditional management practices tend at least at intervals to deplete the fund of nutrients in the ecosystem and thus help to maintain heath vegetation. On the other hand, modern inputs of nitrogen and other nutrients in polluted rainfall operate in the opposite direction, and management directed towards counteracting their effects may be required.

2) Management in the past has generally been aimed at the maintenance of uniform, dominant stands of *Calluna* suitable for herbivore production. For purposes of nature conservation, however, an uneven patchy stand containing *Calluna* in all its growth phases, with other components of the community occupying canopy gaps, is more conducive to biodiversity. Management calculated to produce conditions in which cyclical change can be perpetuated, although difficult to achieve, is probably the ideal.

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