THE MORPHOLOGY OF VEGETATIVE REGENERATION IN *CALLUNA VULGARIS*

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SUMMARY

Calluna vulgaris, in certain habitats, provides useful grazing for herbivores; management is generally by burning, with the aim of promoting vigorous production of young shoots by vegetative regeneration for the stem base. However, the capacity for such vegetative regeneration declines with age. The general morphology of the plant is described, with particular reference to the sequence of development in a single season's growth and to the stages in resumption of growth after overwintering. On this basis, an interpretation is given of the responses to grazing and burning, with evidence derived from detailed observation of treated plants and from transverse sections of stems. Light grazing at the periphery of the plant causes (i) the growth of a few of the uppermost short shoots into new long shoots, and (ii) the appearance of clusters of shoots from lower, woody, parts of the branches. Heavier or more sustained grazing emphasizes the second of these responses. Vegetative regeneration after burning is also of the second category, confined to undamaged positions near the base of the stem.

The clusters of shoots appear at the points of origin of existing or former branches. The conclusion, derived both from morphological observations and from evidence of the deep-seated origin of these new shoots, is that they are derived from persisting dormant buds on the close-packed nodes just below the base of each long shoot. These nodes belonged to the overwintering end-of-season short shoot from which the long shoot developed.

INTRODUCTION

Heathlands dominated by *Calluna vulgaris* have long provided grazing for sheep, cattle and game birds. Management of heaths is traditionally by burning, which serves the two-fold purpose of preventing tree colonization and promoting a vigorous new growth of young, relatively highly nutritious shoots of *Calluna*. The importance of *Calluna* in this context depends in part upon its ability to respond to grazing by the abundant production of new shoots at the periphery of the dwarf shrub (Fenton, 1937; Clouston, 1943; Thomas, 1956; Poore and McVean, 1957; Grant and Hunter, 1966) and in part to its capacity for regeneration after fire (Kayll and Gimingham, 1965). Regeneration may take the form of seedling establishment, but quicker re-development of cover and production of edible shoots results when vegetatative regeneration takes place from the stem bases of the plants of which the stand was composed before burning. The aim of burning management, therefore, is where possible to achieve maximum vegetative regeneration. It has been shown that this demands a carefully controlled fire, which clears the above-ground combustible material but does not inflict prolonged very high temperatures in the region of the stem-bases, causing death. Further, it appears that the capacity for vegetative regeneration declines with increasing age of the stem, especially

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over about 15 years (Lovat, 1911; Eliot, 1953; Nicholson and Robertson, 1958; Gimingham, 1960; Kayll and Gimingham, 1965). The desirability of a regular rotation of burning as a means of grouse-moor management was stressed by Lovat in 1911. Similar practice had been widespread among hill shepherds from at least as early as 1800, and continues at the present time as the generally accepted system of moorland management in Britain.

Explanation of the responses of *Calluna* to grazing and burning is therefore of importance not only in regard to the morphological behaviour of the plant itself, but also as a contribution to the ecology of production and management of heaths. Grant and Hunter (1966) have demonstrated increased production in response to cutting regimes in imitation of grazing: this has been confirmed in the present study (Mohamed, 1967). This result raises the question of the location of the dormant buds from which the new growth proceeds, when leading shoots are cropped. A similar question is posed by the development of clusters of new shoots from the woody stem base after burning, or cutting close to ground level. Hitherto there have been no facts available on which to answer these questions. Beijerinck (1940) suggested that the latter response might originate from 'adventitious shoots produced as a result of mechanical injury' and Whittaker (1960) states 'it is possible that accessory buds are involved'. However, no firm evidence has been available, nor, until the work of Miller and Miles (1970), has any reason been offered for the decline in vegetative regeneration with increasing age. The morphological and anatomical investigations reported in this paper were undertaken to resolve some of these problems.

General morphology

The normal annual cycle of events in the extension growth of the branch-system of *Calluna* has been described by Nordhagen (1937) and Beijerinck (1940), and is illustrated in Fig. 1.

A leading long shoot, which measures up to about 11 cm in north-east Scotland, represents the extension-growth of 1 year. Short shoots bearing closely imbricated leaves are produced laterally on the long shoot in two zones, separated by a zone of flowering branchlets. Those produced early in the season occupy a basal zone, reaching lengths of up to 3 cm, and are themselves sometimes branched. Others, produced later in the season after formation of the flowering laterals, occupy a zone around and a little below the apex. These normally measure between 1 and 3 mm. Short shoots and flowering laterals are borne in opposite, decussate pairs, in the axils of the leaves on the long shoots. Long-shoot leaves are considerably longer than those of the short shoots, and the nodes are relatively widely spaced.

The apex of a long shoot may continue growth in a subsequent year, producing a new long shoot. More frequently, however, growth is resumed not in this apex but by the development of usually two, three or four of the end-of-season short shoots positioned just below the apex, giving rise to new long shoots. All the other short shoots may simply undergo further growth as short shoots in a second or even a third season, but their functional life is limited and after this time they die and later drop off.

The result of these growth sequences is a system of branching in which annually each stem axis is generally replaced by two or three new axes of growth. Lignification in these begins at their bases even in the first year, and eventually they may become part of the system of frame branches which, in an undamaged bush, maintains the hemispherical

form. At the periphery, behind the current year's growth, the previous season's production shows a pattern of zones of short shoots separated by bare portions of stem marking the zones from which flowers have fallen (Fig. 1a).

In addition to the leading long shoots, some of the short shoots (including, sometimes, those in the basal zone) may produce weaker long shoots. These, here referred to as lateral long shoots, are more divergent in their direction of growth, seldom exceed 8 cm, do not survive as frame branches, and are eventually shed.
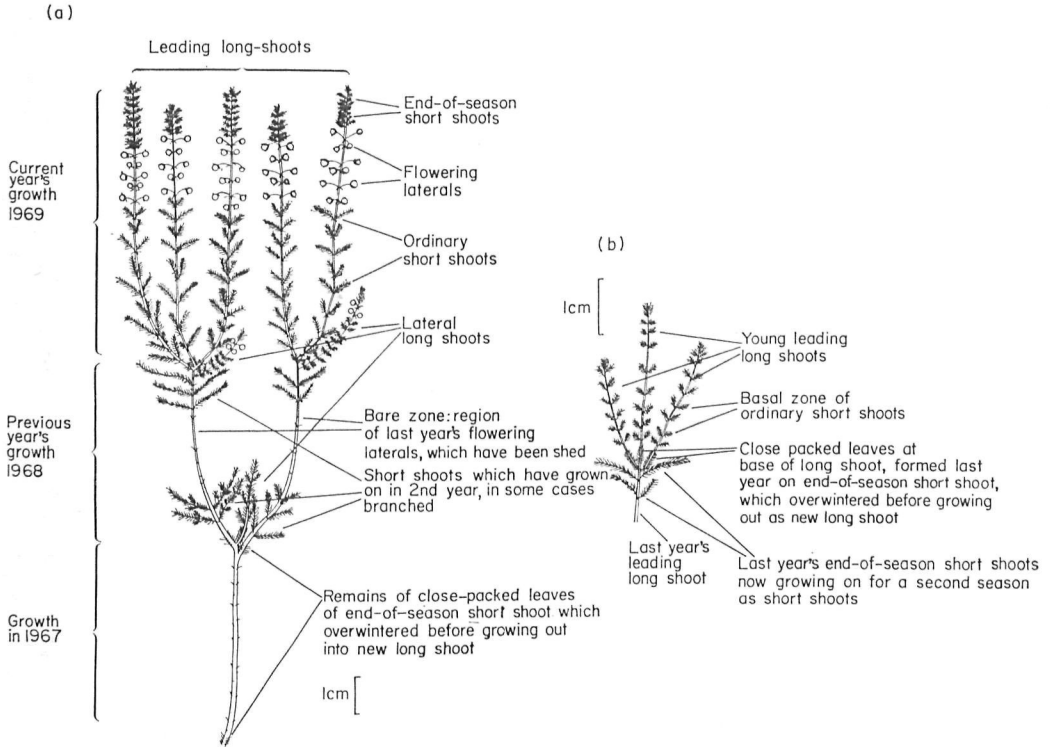

Fig. 1. Diagrams to illustrate annual growth and branching in *Calluna vulgaris*. (a) Condition at the end of the growing season (early October); (b) shoot tip early in the growing season (June) to show new long shoots developing from overwintered end-of-season short shoots.

It follows that, as growth proceeds during the season, many of the axillary buds on a long shoot develop into short shoots or flowering shoots. Some may remain dormant, to develop later (p. 746). However, it is always the case that there are some dormant buds just below the base of a long shoot. These are the axillary buds of the close-packed leaves on the very short end-of-season short shoot from which, in the following year, the long shoot was derived (Fig. 1b). Alternatively, if the new long shoot was derived by resumption of growth in the apex of a previous year's long shoot, there is a similar group of dormant axillary buds formed at closely spaced nodes in the overwintering terminal bud. Thus at the base of every branching-point, or at the junctions between 1 year's growth and the next, there is a set of dormant buds.

Resumption of growth in spring

The normal sequence of development of overwintering buds was followed in a large number of shoots taken from a random sample of thirty plants from different stands in Aberdeenshire, in 1967. Where apical buds of leading long shoots have escaped damage during the winter, these are usually the first to break dormancy; alternatively, if these are dead the first to grow are the hibernating terminal buds of a small number of the end-of-season short shoots just below the apex. From these buds, young long shoots extend bearing bright green foliage on widely spaced nodes, contrasting strongly with the closely packed dull green overwintered foliage of the end of the previous season's growth.

The terminal buds of the previous year's lateral long shoots and of the ordinary short shoots below the flowering zone generally tend to sprout late in the spring, after those of the end-of-season short shoots. At about the same time, any dormant axillary buds remaining on the widely spaced nodes of the vegetative zones of the previous year's long shoots may sprout, starting with those nearest the apices and then in order downwards. This sprouting commences earlier in the spring if the apical bud of the long shoot is dead or destroyed, and the new shoots produced tend to be more vigorous than those formed later in the season in the presence of an active apex.

The arrangement of leaves on the long shoots is in opposite pairs; usually their axillary buds develop simultaneously, producing paired shoots, but sometimes only one of the paired buds may sprout. It appears that by the second (or possibly third) season all these axillary buds on the vegetative zones of the long shoots have sprouted, unless dead or destroyed.

In addition to the developments hitherto described, a certain number of plants produce clusters of sprouts from positions on the otherwise bare, woody, perennial frame branches of the plant, considerably below the main canopy. A single cluster may consist of up to fourteen new shoots, presumably originating from closely aggregated buds (Plate 1, No. 1). Observations indicated that the extent to which this type of sprouting occurs depends upon the proportion of the terminal buds of the previous year's long shoots which fail to grow on. These clusters of new shoots are of the greatest importance in accounting for vegetative regeneration after burning, and to some extent after grazing.

Responses to grazing, cutting and burning

Light grazing at the periphery of the plant tends to remove the tips of the long shoots and some or all of the current year's increment on short shoots situated lower down. The result is to cause: (i) the growth of a few of the uppermost undamaged short shoots or lateral long shoots into new leading long shoots (Plate 1, No. 2), (ii) the appearance of clusters of new shoots from lower parts of the branches. Again, the extent to which the latter happens depends upon the amount of damage at the periphery. The effect is always to increase the number of leading long shoots, and hence in time the number of new short shoots, with a consequent increase in production of edible material and an increase in the density of the canopy. Heavier or repeated grazing, however, causing removal of a substantial proportion of the foliage-bearing shoots, tends to confine the response to (ii), above, and to increase the number of clusters produced per plant.

The effect of burning is to destroy the whole of the upper part of the plant, but if potential sites remain for the production of the clusters of shoots on the woody branches the plant is capable of vegetative regeneration. Upon the capacity to develop such

No. 1 Development of a cluster of new shoots after cutting away the branch system above, or burning.

No. 2. Stimulation of growth in lateral long shoots after cutting; no new shoots have developed in former flowering zone.

No. 3. Clusters of young shoots produced at branching points on woody frame branches, after removal of canopy and upper parts of branches.

No. 4. Cut base of a 26-year old stem, at the point of departure of the main frame branches.

(Photographs bs E. Middleton.)

B. F. MOHAMED AND C. H. GIMINGHAM—*REGENERATION IN* CALLUNA

clusters from the stem base, particularly where it has been protected from the full effects of the fire by burial under soil, humus or a layer of moss or lichen, rests the suitability of *Calluna* for management by burning. The problem becomes one of further investigation of this response.

Field and glasshouse experiments were designed to examine vegetative regeneration in *Calluna* at various ages after subjection to several clipping and burning treatments to resemble mild and severe grazing, and normal and intense fire. These are not reported in full here, but they demonstrated: (a) that in control plants few clusters of new shoots are produced on the woody parts of the plants, (b) that light clipping, removing the apical buds of the leading and lateral long shoots, stimulates the production of a somewhat larger number of these clusters, (c) that cutting away the whole canopy caused the production of a series of clusters at several levels on the woody frame-branches (Plate 1, No. 3), (d) that burning of plants less than about 14 years of age resulted in the development of clusters from protected positions at the base of the stems, as observed in the field, (e) that the vigour of these responses, measured in terms of number of clusters produced per individual, decreases with increasing age from about 15 years.
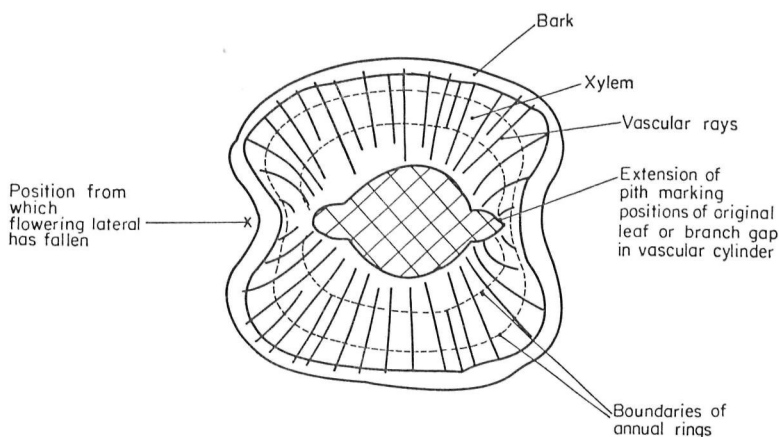

Fig. 2. Transverse section through a node on the bare portion (formerly the flowering zone) of the 3-year old sector of a stem. (Diagram from tracing of a photomicrograph.)

On plants from which the canopy had been removed, leaving only the bare woody branches, observations indicated that the position of the developing clusters of shoots was related to the points of origin of existing or former main branches, i.e. opposite the 'leaf-gaps' in the vascular cylinder associated with former leaves on the main long shoot. As explained earlier, these branching points are situated where each successive leading long shoot produced its hibernating end-of-season short shoots (Plate 1, No. 3). These parts of the stems are normally somewhat thicker than the regions between them. (The 'storeyed' arrangement of the developing clusters may be obscured by distortion of the branching pattern in dense stands).

ANATOMICAL EVIDENCE

The origin of these shoots was further investigated by transverse sections in different parts of the plant. Fig. 2 shows a section cut at a node in the former flowering zone of the

3-year old portion of a branch. The section shows no sign of buds, merely a pair of opposite indentations representing the positions from which the short flower shoots have been shed, together with their subtending leaves. As a result, after the first season the part of the long shoot which produced flowers becomes bare (as described above), while for a further year or two the green foliage shoots are retained on the vegetative parts. The flowering zone, therefore, is incapable of producing any further shoots or branches (Plate 1, Nos. 2 and 3).
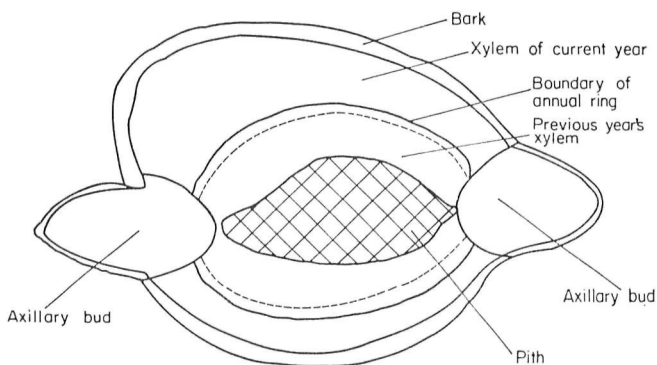

Fig. 3. Transverse section through a node in the vegetative portion of a 2-year old long shoot, showing the start of development of a pair of axillary buds. (Diagram from tracing of a photomicrograph.)
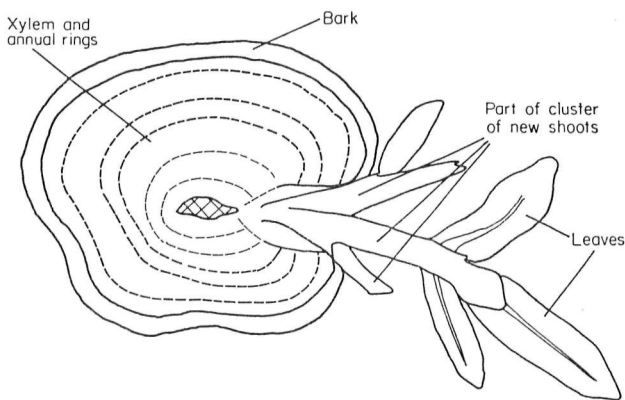

Fig. 4. Transverse section near a branching point in the 6-year old sector of a stem, after cutting higher up to remove peripheral branches and foliage. Development of a cluster of new shoots has begun, and their deep-seated origin is shown. (Diagram from tracing of a photomicrograph.)

Fig. 3 shows a section through a node in the vegetative portion of a 2-year old long shoot. In this instance, the pair of axillary buds remained dormant in the first year of growth, and are here shown sprouting in the second year. The origin of these buds in the 1-year old tissues is demonstrated, the second ring of xylem having been added around them. However, examination of many stems gave no evidence of this type of shoot production after an age of about 2 (or perhaps 3) years.

In regard to regeneration, the most important illustration is that in Fig. 4. The section was taken very close to a branching point in the 6-year old portion of a stem, at the position where a cluster of new shoots was beginning to form following removal of the upper parts of the branch system by cutting higher up. The point of origin of these shoots is shown to lie at a considerable depth in the stem. The subsequent development of such a cluster is shown in Plate 1, No. 1.

The conclusion, derived from observation of the positions of the clusters and the depth of origin of the stem bases in the parent twig, is that the shoots are derived from the persisting dormant buds of the closed-packed nodes just below the base of each long shoot (described on p. 745) or from meristematic tissue associated with the original leaf and bud traces. Despite the fact that these are clearly surrounded by a considerable thickness of secondary xylem during subsequent years' growth and lignification, it appears that for a time at least they retain the capacity to produce sprouts.

Here, too, may be part of the explanation of the declining ability of *Calluna* to regenerate after fire, from about the age of 15 years. The continued addition of secondary xylem may in time engulf the buds or eliminate the leaf gap, so that development becomes impossible. Plate 1, No. 4, shows the base of a stem about 26 years old which failed to respond to cutting just above the position of the separation of the main woody branches. The deep invaginations in the outline represent the departure of these main branches, the age of which varied from about 17 to 19 years. An impression is gained of the extent to which buds originally present at the very base of these branches would be buried by subsequent growth.

DISCUSSION

The interpretation here presented rests on normal morphological developments and does not require the postulation of 'new' buds formed, for example, at the site of an injury. Detailed consideration of the morphology of *Calluna* is sufficient to explain its importance as a producer of food for grazing animals, and the success with which it has for gernerations been managed by burning. The findings indicate that there is no intrinsic advantage in burning as a method of management: it is merely a means of removing the canopy and promoting the production of the clusters of new shoots. Indeed, should practicable systems of cutting be available for all kinds of heathlands they might be expected to produce better results (if sprouting is the only consideration), because a greater number of potential sprouting centres is retained. This is borne out by examination of the stem bases after a fairly severe fire, where it is apparent that regeneration may be confined to places which have been protected from heat by burial, or the presence of other vegetation, etc. On occasion sprouts are produced only from the lower side of a procumbent stem base, curving round the stem before emerging and growing upwards. Presumably other buds which could have developed from the upper side were killed.

Miller and Miles (1970) have accounted for the poorer performance of old stands of heather as regards vegetative regeneration by showing that as stands age the number of 'tillers' or stems emerging from the ground declines. Hence there are fewer stem-bases on which regeneration can take place. Doubtless this is the main factor, but the present account shows that it will be reinforced by a decline in the capacity for old stems to produce sprouts, with the progress of addition to the secondary wood.

It follows from these findings that the structure of *Calluna* stands will vary not only according to whether the stand has developed without interference or has been managed,

but also according to the type of management and, in the case of fire, the age of the preceding stand before burning. Where vegetative regeneration is vigorous and numerous clusters of shoots develop, a dense stand of erect stems results and the identity of the original clusters soon becomes obscured by the production of second order branches. Alternatively, where old *Calluna* has been burnt poor initial sprouting results in sparse uneven clusters composed of few sprouts, producing groups of somewhat divergent stems interspersed with young plants derived from seedlings. Such a stand is slow to re-establish continuous cover and may give rise to an uneven canopy, in contrast to the smooth even-aged stucture in the former case.

In the light of this, there is reason to suggest that where it is desired to maintain good productive stands of *Calluna* (a) severe and continuous grazing, involving widespread elimination of both apical and axillary shoots and buds in the canopy, should be avoided; (b) very intense fires producing high temperatures at ground level should be avoided; (c) stands should be burnt before reaching an age of about 15 years. The declining capacity for vegetative regeneration from about 15 years of age may be partly explained by the continuing addition of xylem, so engulfing the buds that development may become impossible.

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