REGENERATION OF HEATHER (*CALLUNA VULGARIS* (L.) HULL) AT DIFFERENT AGES AND SEASONS IN NORTH-EAST SCOTLAND

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INTRODUCTION

On upland grazings in Britain gamekeepers and shepherds have traditionally burned old heather (*Calluna vulgaris*) to increase the amount of young growth available as food for red grouse (*Lagopus lagopus scoticus*), red deer (*Cervus elaphus*) and sheep. The aim is to burn patches in rotation so that all heather is renewed every 10–20 years. This is often difficult to achieve because of unfavourable weather, shortage of labour and a law that limits the length of the burning season (Miller 1964). Hence, as an alternative to burning, some landowners have recently begun to use rotary cutters.

Heather should be burned or cut so that cover is rapidly renewed. Apart from the loss of production, the longer the ground remains bare, the greater is the likelihood that undesirable plants will invade or that the soil will erode. Vegetative regeneration from buds at the base of the burnt stems gives the quickest recovery since there is a fully-developed root system containing food reserves immediately available to the young shoots. If heather should be killed by fire, regeneration depends on seed and it may be a long time before complete cover is restored.

Observations early this century suggested that vegetative regeneration declined with increasing age (Lovat 1911; Wallace 1917). More recently, Kayll & Gimingham (1965) concluded that heather stems older than about 15 years regenerated less readily from the base than younger ones; however, they studied only three ages of heather, and the youngest was already 12–13 years old. Grant (1968) observed that young heather regenerated more quickly than old, but that satisfactory regeneration could occur up to the age of 20–25 years.

This paper deals with the problem more fully. Regeneration was studied from heather stems aged from 2–3 to 34–37 years. There were three main aims. The first was to determine the age when vegetative regeneration was most rapid after burning or cutting. The second was to find if there was any difference between regeneration after burning or cutting in autumn (October and November), and in spring (March and April); many gamekeepers are reluctant to burn in autumn since they believe that heather does not regenerate as quickly after an autumn fire as after a spring fire. The third was to examine the relation between the age and density of heather stems; since vegetative regeneration is from buds at the base of the old stems, a decline in rate of regeneration with increasing age could be due to a decrease in the density of stems.

MATERIALS AND METHODS

Study area

All studies were at 120–220 m a.s.l. on a 65-ha block of Kerloch moor in Kincardine-

shire, north-east Scotland. The soils were peaty podsols. Heather was predominant, with an average cover of about 75%. *Erica cinerea* and *E. tetralix* were frequent, with about 5% cover each. Cover of other flowering plants was negligible, though a few (e.g. *Nardus stricta* and *Trichophorum caespitosum*) were locally abundant in small patches. The vegetation was grazed freely by rabbits (*Oryctolagus cuniculus*), mountain hares (*Lepus timidus*) and red grouse, but fences excluded cattle and sheep.

About one-third of the study area had been burned in patches between autumn 1961 and spring 1965. During this period seventy-seven patches, varying from a few square metres to 1·5 ha in size, were burned over an existing mosaic of heather stands of different ages.

Regeneration after fire

The age of the heather canopy at the time of burning was determined by counting annual rings of living stems at the edge, and of dead stems at the middle, of each burnt patch. In this way ninety-nine stands, aged 3–37 years before burning, were recognized. These were allotted to five age-classes, viz. 6–10, 11–15, 16–20, 21–25 and 26–30 years. From each age-class two stands of heather that had been burned in the spring of each of the years 1962–65, and in the autumn of 1964, were selected. In each stand the vegetation in ten random quadrats of 0·1 m^2 was clipped at ground level. Heather was separated from other species, dried to constant weight at 80° C, and the results examined by analysis of variance.

As a further check on regeneration after fire, the proportion of ground covered by heather was estimated by eye to the nearest 10% within ten random quadrats of 0·1 m^2 in each of thirty-five different stands burnt between autumn 1963 and spring 1965. The reliability of such estimates of heather cover has been discussed by Miller, Jenkins & Watson (1966). The data were placed in five age-classes as above. Since there were disproportionate numbers of observations in the different sub-classes, analysis of variance was by the method of fitting constants (Kempthorne 1952). Differences between autumn 1963 and 1964, and between spring 1964 and 1965, were first eliminated by calculating constants for each year and adjusting the data to represent the amount of cover in the third growing season after burning. The adjusted data were used to compare different seasons and age-classes in the analysis of variance.

Regeneration after cutting

Six almost pure stands of heather, aged 2–3, 6–8, 12–14, 16–18, 21–24 and 34–37 years, were chosen for the experiment and fenced against rabbits and hares. Replication was impracticable. In October 1964 the vegetation was cropped from nine random plots of 0·25 m^2 in each stand; a second set of nine plots was cropped in April 1965. Loose litter was raked off after cropping, and the surrounding vegetation cut back to prevent shading of the plots. In October 1965 regeneration was assessed by two methods. First, the number of sprouting centres, i.e. loci from which groups of heather shoots arose on the cut stems, was counted in each plot. Second, the heather which had regenerated was harvested from all plots, dried at 80° C and weighed.

The density of old stems was estimated from counts in ten random quadrats of 0·1 m^2 within each stand. A comparative measure of soil water content, expressed as per cent oven-dry weight of soil, was obtained from three cores, 10 cm deep, taken from each plot. The thickness of the surface layer of organic matter in the soil (L + F + H horizons) was

measured at the centre of each plot. The relation between these three variables and the dry weight of the heather which had regenerated was examined by multiple regression analysis.

Age and density of heather stems

Thirty heather stands, aged from 2 to 28 years, were sampled to determine the relation between age of heather and density of stems. Ten quadrats of 0·1 m^2 were placed at random in each stand, the heather cropped to ground level, and the stems counted. The regression of stem density on age of stand was calculated.

RESULTS

Regeneration after fire

There were significant ($P<0·05$) differences between age-classes in the standing crop (Table 1) and percentage cover (Table 2) of heather which had regenerated after burning. Regeneration was most rapid from heather 6–10 years old, the youngest age-class sampled. It decreased progressively the older the heather had been at the time of burning, and was least rapid from heather 26–30 years old.

Regeneration was more rapid after burning in autumn. At the end of two growing seasons, the standing crop in stands burned in autumn 1964 was nearly twice ($P<0·05$) as large as that of stands burned in spring 1965 (Table 1). Similarly, the proportion of ground covered by new growth three growing seasons after an autumn fire was 38% more ($P<0·001$) than after a spring fire (Table 2).

Regeneration after cutting

The pattern of regeneration from heather of different ages after experimental cutting was the same as that after burning. Thus the standing crop after one growing season was greatest from heather 6–8 years old (Table 3), equivalent to the 6–10 year age-class in Tables 1 and 2. It progressively decreased the older the heather had been at the time of cutting. The standing crop from heather 2–3 years old, for which no comparable age-class was sampled in the survey of regeneration after fire, was similar to that from the stand 16–18 years old.

The amount of heather which regenerates is the product of the number and weight of the sprouts which originate from the base of the old stems. The density of sprouting centres was greatest in heather 6–8 and 12–14 years old, whereas the growth from the sprouting centres was greatest in heather 2–3 and 6–8 years old (Table 3). Hence most regeneration occurred in the stand 6–8 years old which had a large number of highly productive sprouts.

At the end of one growing season, there was more regeneration on areas cut in spring than on areas cut in autumn (Table 3). This was because there were more sprouting centres and the sprouts had grown more rapidly after cutting in spring. This result is opposite to that obtained after burning; possible explanations are given in the Discussion.

The ranking of the mean densities of old stems in the six stands (Table 4) closely resembles that for the mean yields of regenerated heather (Table 3). Using individual plot values, the correlation coefficient for the relation between these two measurements is 0·356 ($P<0·001$), indicating that stem density before cutting may have had some

influence on the amount of regeneration. Spatial variation in regeneration may also have been influenced slightly by the depth of surface organic matter ($r = 0{\cdot}245$, $P<0{\cdot}05$), but probably not by soil moisture ($r = 0{\cdot}135$).

Age and density of heather stems

Data from plots sampled in the cutting experiment suggested that the density of heather stems decreased in stands older than 6–8 years (Table 4). Since these values were obtained from one example only of each age-class, a wider survey was made. This confirmed that stem density progressively decreased with increasing age of heather (Fig. 1). The best fit to these data is obtained by a straight line, and there is no statistical evidence of a steepening decline in stem density beyond 15 years.

Table 1. *Mean yield (g dry matter m^{-2}) of heather in October* 1966 *in heather stands burned in* 1962–65

Age (years)	No. of stands	Time of burning: Spring 1962	Spring 1963	Spring 1964	Autumn 1964	Spring 1965	Mean	95% confidence limits
(A) Effect of age of heather at time of burning								
6–10	10	625	309	111	241	168	291	237–344
11–15	10	419	315	185	208	44	235	181–288
16–20	10	506	290	187	75	9	213	160–267
21–25	10	339	263	70	19	45	147	84–201
26–30	10	405	195	70	7	15	138	85–192
(B) Effect of season of burning								
Autumn 1964	10						110	86–134
Spring 1965	10						56	32– 80

Table 2. *Mean proportion of ground (cover percentage) covered by heather which had regenerated by the end of the third growing season after burning*

Age (years)	No. of stands	Mean cover	95% confidence limits
(A) Effect of age of heather at time of burning			
6–10	11	52	47–57
11–15	4	48	39–57
16–20	10	37	31–43
21–25	4	44	35–53
25–30	6	37	30–44
(B) Effect of season of burning			
Autumn	19	51	47–55
Spring	16	37	33–41

If the density of stems decreases, there must be a decrease in the number of potential sprouting centres and this will decrease the rate of regeneration. In fact there is a close correlation ($r = 0{\cdot}922$, $P<0{\cdot}001$) between the mean yield of heather that had regenerated two growing seasons after burning (from Table 1) and the mean density of stems in five different age-classes (Fig. 2).

Table 3. *Number of sprouting centres and mean yield per sprouting centre of heather in October* 1965 *in heather stands of different ages cut to ground level in October* 1964 *and April* 1965

Age (years)	No. of plots	Cut October 1964	Cut April 1965	Mean	95% confidence limits
(A) Mean yield (g dry matter m^{-2})					
2–3	18	5	14	10	4–15
6–8	18	37	47	41	31–52
12–14	18	25	34	30	20–40
16–18	18	4	10	7	4–10
21–24	18	12	21	16	4–29
34–37	18	1	4	3	1–4
Mean		14	22	18	
No. of plots		54	54		
95% confidence limits		9–19	15–28		
(B) No. of sprouting centres (m^{-2})					
2–3	18	59	84	71	36–106
6–8	18	216	278	247	193–302
12–14	18	280	374	327	240–414
16–18	18	80	137	109	72–146
21–24	18	132	180	156	93–220
34–37	18	16	47	32	15–48
Mean		131	183		
No. of plots		54	54		
95% confidence limits		95–167	140–226		
(C) Mean yield (mg sprouting centre $^{-1}$)					
2–3	18	111	152	132	82–183
6–8	18	163	196	179	138–220
12–14	18	90	89	89	76–103
16–18	18	43	74	59	39–79
21–24	18	70	86	78	53–103
34–37	18	46	86	69	48–89
Mean		89	114		
No. of plots		54	54		
95% confidence limits		69–110	64–164		

Table 4. *Mean density of stems before cutting, soil water content to* 10 *cm and depth of organic matter at the soil surface in single plots of heather stands of different ages, which had been cut to ground level in October* 1964 *and in April* 1965

Age (years)	Density (stems m^{-2})	Soil water (% dry weight)	Depth of surface organic matter (cm)
2–3	580	134	4·6
6–8	1108	98	6·0
12–14	914	76	2·9
16–18	284	152	5·5
21–24	276	146	5·7
34–37	184	102	4·4

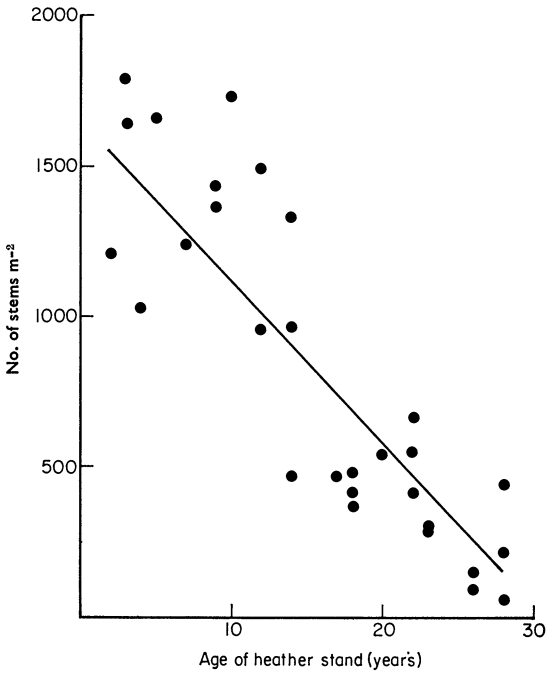

FIG. 1. Relation between the age (A) and density of stems (S) of heather. $S=1656-5{\cdot}32A$.

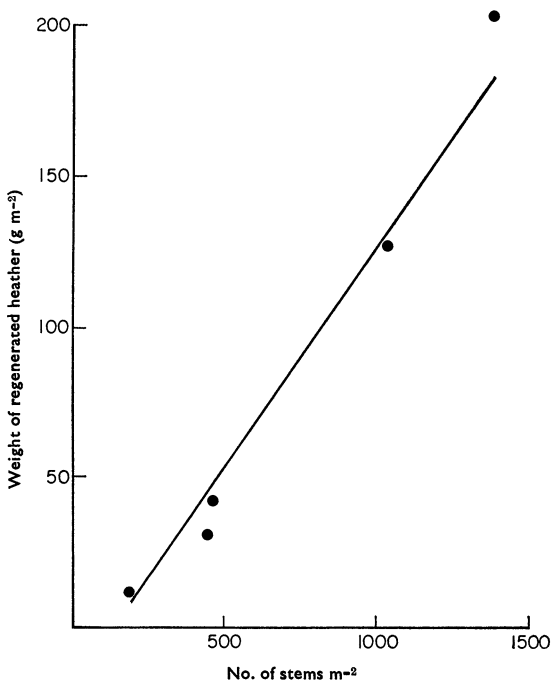

FIG. 2. Relation between the density of stems before burning (S) and the dry weight of heather which had regenerated two growing seasons after burning (W). $W=0{\cdot}16S-30{\cdot}1$.

DISCUSSION

Change in regeneration of heather with age

The data confirm that young heather regenerates more readily than old. Fenton (1951), Elliott (1953) and Kayll & Gimingham (1965) suggested that heather regenerates less readily as it ages, particularly after about 15 years. However, in the present study the rate of regeneration decreased progressively from the age of 6–10 years, without any sign of a sudden steep decline beyond 15 years.

The differences between young and old heather in the amount of new growth were greatest in the first year or two after burning or cutting, and thereafter became much less (Tables 1 and 3). This was probably because the older heather regenerated mainly from seed; when this happens there is sometimes a period with little or no growth, followed by a rapid development of cover (Grant 1968). Presumably many seedlings became fully established in gaps in the old stands by the end of the second growing season. These may have contributed significantly to total growth in the third season, and partially obscured initial differences caused by different rates of vegetative regeneration.

There are several possible reasons for the decline in vegetative regeneration with age. For example, Kenworthy (1963) found that fire temperature increased with the age of the heather burned; hot temperatures during burning may kill many plants, so decreasing the rate of vegetative regeneration. However, this cannot be the main reason since regeneration declined with increasing age in the cutting experiment also. The number of sprouting centres per 100 stems varies little with age (Tables 3 and 4): in heather 6–8 years old there were twenty-two sprouting centres per 100 stems in the original stand, and in heather 34–37 years old there were seventeen. Furthermore, although growth from the sprouting centres was most rapid in the two youngest stands (Table 3), the differences between stands were too small to account entirely for the progressive decline in rate of regeneration with increasing age. Hence there is no firm evidence of a decrease in the inherent capacity of heather plants to regenerate as they age.

The most likely explanation for the change in regeneration with age is that competition leads to 'self-thinning' in heather stands from an early age. If the density of stems decreases, the number of potential sprouting centres will also decrease. The close correlation between the density of stems before burning and the standing crop of new heather (Fig. 2) indicates that this may indeed be important in determining the success of regeneration.

Effect of the season of burning or cutting on regeneration

Regeneration was more prolific after autumn than after spring burning, whereas the effect of cutting in spring was superior to that of cutting in autumn. The treatments were given in the same season, 1964–65, so these inconsistent results cannot be attributed to differences in weather.

In March and early April, when most spring burning is done, the heather is beginning its seasonal cycle of growth. On the other hand, in October and November it is more or less dormant. Thus fire may injure the plant more in spring than in autumn and so delay regeneration or even kill the plants. Furthermore, the weather is often dry in early spring, when radiation influx may be large, evaporation rapid and rainfall small (Green 1964). In such weather, burning dry vegetation and litter may generate hotter temperatures

than at other times (Kayll 1966); and if the bases of the stems are exposed to excessive heat, the buds from which regeneration occurs are destroyed (Whittaker 1960).

Fire kills the outer tissues of heather stems whereas cutting does not. Hence stems cut in autumn are exposed to desiccation, damage by frost and infection by pathogens during winter. Bannister (1964) found that there is internal water stress in heather in winter; and mechanical damage causes extensive necrosis, presumably as a result of desiccation (Watson, Miller & Green 1966). Therefore cutting, but not burning, in autumn might injure heather plants indirectly but nevertheless severely and so inhibit regeneration.

Comparative effects of burning and cutting

Less vegetative regeneration might be expected after burning than after cutting because hot temperatures will kill many buds. Kayll & Gimingham (1965) found that sprouting centres were more sparse and appeared later on burnt plots than on cut plots. In another experiment (G. R. Miller, unpublished data) plots of heather 13–15 years old were burned, or cut and raked clear of litter in spring; regeneration was measured after one growing season. The yield of heather which regenerated on the cut plots was 19·7 g m^{-2} with a cover of about 25%, and on the burnt plots, 2·5 g m^{-2} with a cover of less than 10%. The standard error of the difference between mean yields was 3·7 g m^{-2} ($P<0{\cdot}001$). Thus cutting and raking was more effective than burning in inducing rapid regeneration.

Practical considerations

Although regeneration was greatest from heather 6–10 years old, this may not be a desirable rotation for burning or cutting. At this age heather may not have achieved maximum cover, and repeated burning or cutting then might lessen its dominance and allow other plants to invade. Much of the heather has disappeared from moorland in parts of Wales, northern England, and south and west Scotland, and this has been ascribed to frequent burning coupled with heavy grazing (McVean & Ratcliffe 1962). Maximum cover is usually attained by about 10 years and therefore a rotation of 11–15 years might be a suitable compromise. Each piece of land should be treated strictly according to the status of the heather and the prevailing circumstances of climate, soil and grazing. For example, ungrazed heather at a sheltered site might have to be burned more frequently than exposed or closely grazed heather which is maintained as a short, vigorous and highly nutritious sward because it is constantly pruned by wind or animals (Grant & Hunter 1966, 1968).

In routine management, cutting has disadvantages. It takes much longer to cut than to burn, especially where it is difficult to use tractors. Further, cutting alone does not remove the layer, often deep, of bryophytes and loose litter at the soil surface; and indeed, unless the cut heather is collected and removed elsewhere, it will greatly augment the accumulation of debris. This would render the habitat unsuitable for germination and seedling establishment of heather (Gimingham 1960; Whittaker & Gimingham 1962); and the growth of vegetative shoots would be impeded by physical restriction and shading. On the other hand, careful burning can improve the habitat for seed germination without precluding all vegetative growth.

Cutting is perhaps a useful supplement to burning on areas where there is not much litter, particularly during wet weather when burning is impossible. If both techniques are to be used, the results of this study indicate that it might be best to burn in autumn and cut in spring.

ACKNOWLEDGMENTS

We are grateful to Miss P. Berry, Mr M. Chambers and Mr G. M. Dier for field assistance, to Mr P. Holgate for statistical help, and to Dr C. H. Gimingham, Miss S. A. Grant and several colleagues in the Nature Conservancy for reading and discussing this paper in draft.

SUMMARY

(1) The regeneration of heather (*Calluna vulgaris*) on peaty podsols at 120–220 m a.s.l. was studied by surveying patches burned during routine moor management and by cutting small plots experimentally.

(2) This was done to define the influence of the age of the canopy and the season of burning or cutting on the rate and amount of regeneration.

(3) Survey and experiment both showed that regeneration was most satisfactory from heather 6–10 years old and declined progressively with increasing age in older stands. This was probably due to a decrease in the number of centres from which regeneration could occur.

(4) Regeneration was more prolific after burning in autumn than after burning in spring. By contrast, it was more prolific after cutting in spring than after cutting in autumn.

(5) There are practical considerations which make it difficult to use cutting to encourage regeneration, but on suitable sites a combination of cutting and burning may be useful. Too frequent or too infrequent cutting or burning may have adverse long-term effects. In general it may be best to burn or cut every 11–15 years, but this will depend on the status of the heather, and on the local climate, soil and grazing pressure.

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(*Received* 27 *February* 1969)