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# A QUANTITATIVE ANALYSIS OF SHOOT PHENOLOGY AND DOMINANCE IN HERBACEOUS VEGETATION

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## SUMMARY

(1) Variation in standing crop and in litter has been measured by seasonal sampling and sorting of the herbaceous vegetation at thirteen sites in the Sheffield region. The vegetation types examined comprised tall herb, woodland floor and grassland communities. At each site the living fraction in 4–10 replicated 0·25 m$^2$ quadrats was separated into its components, and graphs were plotted showing the shoot phenology of the more common species.

(2) At the sites in which herbaceous vegetation was growing under fertile, relatively undisturbed conditions, there was a large peak in standing crop during the summer ($>400$ g m$^{-2}$ dry weight), and the vegetation contained few species. The low species-densities at these sites appeared to be related to the ability of certain species to exercise competitive dominance, a phenomenon involving the rapid expansion of a dense leaf canopy during the period June–August, coupled with the production of a high density of persistent litter.

(3) In the woodland and grassland sites examined, the sum of the maximum standing crop and the litter did not exceed 800 g m$^{-2}$, and a variety of plant phenologies was encountered. At two of the woodland sites vernal species were prominent; these plants exhibited truncated periods of shoot growth, which preceded full expansion of the tree canopy and followed immediately the marked decline in density of tree litter in early spring.

(4) At the sites where the standing crop was severely restricted by low soil fertility, the commonest phenological pattern was that of the evergreen; in certain of these species, no seasonal peak of shoot expansion could be detected. In two of the limestone grasslands investigated, forbs with mid-summer peaks of shoot expansion were prominent; the majority of these plants had relatively deep root-systems, and appeared to exploit reserves of moisture during periods when many grasses were subjected to desiccation.

(5) A consistent feature of the results was the marked amplitude of seasonal variation in the abundance of bryophytes, expansion of which coincided with the moist, cool conditions of spring and autumn.

(6) A general conclusion drawn from this study relates to the control of species-density in herbaceous vegetation. The results suggest that the potential for high species-density corresponds approximately to the range of 350–750 g m$^{-2}$ in the sum of maximum standing crop and litter.

## INTRODUCTION

Although interspecific differences in the seasonal patterns of shoot expansion have long been recognized as a characteristic feature of many types of herbaceous vegetation in Europe (Salisbury 1916; Ellenberg 1939; Lieth 1970), few attempts have been made to measure these patterns quantitatively. This paper describes an investigation in which the shoot phenology of the constituent species of several types of herbaceous vegetation of common occurrence in the British Isles has been measured in terms of the seasonal changes in the dry weight per unit area of living shoot material. Thirteen sites were selected which covered a wide range of vegetation and soil characteristics, micro-climate and productivity, and the results have been used in an attempt to explore the significance of shoot phenology in relation to the processes which control vegetation structure and species-composition.

In this study no measurement has been made of characteristics such as leaf area or chlorophyll content, and the investigation has not included the underground parts of the vegetation. These restrictions were inevitable, given the scale of the investigation. However, the procedure which has been adopted is based upon the premise that phenological data referring exclusively to the above-ground component and expressed in terms of dry weight provide a valuable insight into the mechanism determining vegetation structure and species-composition. This assumption derives from theories which are summarized in the next section.

## THEORETICAL CONSIDERATIONS

The arguments which are relevant to this investigation refer to (a) the nature of competition between plants, (b) the interaction of competition with two other primary determinants of vegetation, here described as stress and disturbance, and (c) the nature of dominance. A detailed analysis of these phenomena has been attempted elsewhere (Grime 1977); here the main points will be summarized in the form of the following propositions.

(1) Competition between plants may be defined as the tendency of neighbours to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space (Grime 1973b).

(2) The intensity of competition between plants reaches a maximum in circumstances allowing the rapid development of a large biomass of plant material, i.e. where there is high productivity and minimal damage to the vegetation. Under these conditions, the species which prevail are those which are best equipped to capture resources and to maximize production. High competitive ability is represented, therefore, by a combination of genetic characteristics which, by maximizing production, facilitate the exclusive occupation of fertile, relatively undisturbed environments (see (8)). Competitive herbs are perennials, and possess in common such features as a high, dense canopy of leaves, the production of which coincides with an extended period when environmental conditions are conducive to high productivity.

(3) High competitive ability above-ground depends upon the development of a large mass of shoot material, which itself depends upon high rates of uptake of mineral nutrients and water. Hence, although the mechanism of competition may culminate in above-ground competition for space and light, the outcome may be influenced or even predetermined by earlier competition below ground (Donald 1958; Mahmoud & Grime

1976). It seems likely that the abilities to compete for light, mineral nutrients, water and space are related to such an extent that the effect of natural selection has been to cause them to be developed to a comparable extent in particular genotypes, i.e. various competitive abilities tend to be inter-dependent and co-variable.

(4) The factors which limit the plant biomass in any habitat and reduce the intensity of competition may be classified under two headings—stress and disturbance.

Stress consists of the phenomena which restrict production, e.g. shortages of light, water, mineral nutrients and suboptimal temperatures. These shortages may be an inherent characteristic of the environment, or they may be induced or intensified by the vegetation itself. The most widespread forms of plant-induced stress arise from shading and from reductions in the levels of mineral nutrients in the soil (as a result of their accumulation in the plant biomass). Disturbance arises from the partial or total destruction of living or dead components of the vegetation, by the activities of herbivores, pathogens and man (trampling, mowing, ploughing, etc.), and by phenomena such as wind-damage, frosting, desiccation, soil erosion and fire.

(5) The roles of both stress and disturbance change according to their severity. At low intensities, both processes function as modifiers of competition, whereas at high intensities each is capable of exercising a dominant and direct impact upon species-composition and vegetation structure.

This impact involves the elimination or debilitation of species of high competitive ability, and the selection of species which are of lower competitive ability but are capable of surviving under the prevailing forms of stress or disturbance.

(6) Stress and disturbance exercise different forms of natural selection, and at severe intensities each has evoked a distinct strategy in herbaceous plants (Grime 1974).

Stress-tolerant plants exhibit a range of features which are adaptations to continuously unproductive conditions. These features, reviewed by Grime (1977) in relation to particular forms of stress, include morphological reductions, inherently slow rates of growth, an evergreen habit, long-lived organs, sequestration and slow turnover of carbon, mineral nutrients and water, low phenotypic plasticity, infrequent flowering and the presence of mechanisms which allow the vegetative plant an opportunistic exploitation of temporarily favourable conditions.

The most consistent feature of species adapted to persistently and severely disturbed habitats is the tendency for the life-cycle to be that of the annual, a specialization clearly adapted to exploit environments intermittently favourable for rapid plant growth. A related characteristic of many ruderals is the capacity for high rates of dry matter production (Baker 1965; Grime & Hunt 1975), a feature which appears to facilitate rapid completion of the life-cycle and maximizes seed production.

(7) It is suggested, therefore, that in herbaceous plants there are three primary strategies, each of which may be identified by reference to a number of characteristics, including morphological features, resource allocation, phenology and response to stress. The competitive strategy prevails in productive, relatively undisturbed vegetation, whereas the stress-tolerant strategy is associated with continuously unproductive conditions, and the ruderal strategy is characteristic of severely disturbed but potentially productive habitats. These three strategies are, of course, extremes. The genotypes of the majority of plants appear to represent compromises between the conflicting selection pressures associated with particular equilibria between competition, stress and disturbance.

(8) In experiments and in studies of natural vegetation, examples of the impact of plant

size have been widespread (cf. Boysen-Jensen 1929; Watt 1955; Black 1958). A consistent feature of succession in vegetation is the incursion of plants of greater stature, and at each stage of succession the major components of the plant biomass are usually the species with the largest life-forms. It is necessary, therefore, as pointed out by Grubb (1976), to acknowledge the existence of another dimension—that of dominance—in the mechanism controlling the composition of plant communities and the differentiation of vegetation types. In attempting to analyse the nature of dominance it is helpful to recognize two components:

(a) the mechanisms whereby the dominant plant achieves a size larger than that of its associates; this mechanism will vary according to which strategy is favoured by the habitat conditions;

(b) the deleterious effects which large plants may exert upon the fitness of their smaller neighbours; the nature of these effects does not vary substantially according to habitat or strategy, and consists principally of the forms of stress which arise from shading, deposition of leaf litter and depletion of mineral nutrients and water in the soil.

It is suggested, first, that dominance depends upon a positive feed-back between (a) and (b), and, secondly, that because of the variable nature of (a), different types of dominance may be recognized. A distinction can be drawn between 'competitive', 'stress-tolerant' and 'ruderal' dominants. In 'competitive dominants' (usually perennial herbs, shrubs and trees of the early stages of succession in productive habitats) large stature depends upon a high rate of uptake of resources from the environment, whilst in 'stress-tolerant dominants' (usually perennial herbs, shrubs and trees of unproductive habitats, or of the late successional stages of productive habitats) large stature is related to the ability to sustain slow rates of growth under limiting conditions over comparatively long periods. Large stature in 'ruderal dominants' (usually annual herbs) depends upon such plant characteristics as large seed reserves and rapid rates of germination and growth.

Propositions (1)–(8) lead to a number of predictions, which in the Discussion will be examined in relation to the data collected in this investigation.

## MATERIALS AND METHODS

### *General procedure*

At each of the sites investigated, an area was selected which was fairly uniform with respect to topography and vegetation. The site was visited at intervals of approximately 5 weeks, and on each occasion samples of vegetation located at random within the area were collected, by removing all above-ground living and dead plant material in a number of 0·25 $m^2$ quadrats. At all the sites investigation covered the period April–October 1975, and in five cases samples were also collected throughout the preceding winter. The vegetation of certain sites recovered rapidly from clipping, and, where necessary, marker pegs were used to avoid the risk of sampling the same area more than once.

In the laboratory, the living material in each sample was sorted into its constituent species, and the litter was separated into herbaceous and woody components. The materials were then oven-dried and weighed, and graphs were plotted in order to examine

Table 1. *Some characteristics of the sites investigated, and details of the sampling procedure*

| Site number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nat. Grid ref. | 43/176655 | 43/179658 | 43/174688 | 43/163661 | 43/245754 | 43/324813 | 43/324813 | 43/324813 | 43/324813 | 43/324813 | 43/177656 | 43/177657 | 43/526836 |
| Sample size ($m^2$) | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·25 | 0·06 |
| Sampled area ($m^2$) | 25 | 100 | 20 | 100 | 100 | 36 | 200 | 900 | 400 | 400 | 100 | 100 | 50 |
| Number of replicates | 5 | 5 | 4 | 5 | 5 | 5 | 10 | 10 | 10 | 10 | 5 | 5 | 10 |
| Geological stratum* | CL | CL | CL | CL | MG | CM | CM | CM | CM | CM | CL | CL | ML |
| Slope (°) | 0 | 30 | 4 | 30 | 0 | 0 | 0 | 0 | 24 | 39 | 30 | 35 | 30 |
| Aspect (°) | – | 150 | 90 | 20 | – | – | – | – | 250 | 290 | 360 | 190 | 215 |
| Soil pH (0–3 cm) | 6·5 | 4·0 | 7·1 | 6·0 | 6·5 | 6·5 | 6·3 | 4·2 | 3·7 | 3·5 | 6·5 | 6·9 | 7·5 |
| Soil type† | A | LB | B | R | A | A | A | B | LB | P | MR | R | MR |
| Vegetation‡ | TH | TH | TH | TH | TH | TH | WF | WF | WF | WF | G | G | G |
| Species-density (number per 0·25 $m^2$) | 3·5 | 3 | 7·5 | 4 | 3 | 3 | 9 | 4 | 3·5 | 1 | 21 | 14 | 18 |
| Altitude (m) | 198 | 229 | 290 | 231 | 131 | 114 | 114 | 117 | 168 | 152 | 213 | 213 | 107 |
| Initial sampling date | 4.75 | 4.75 | 4.75 | 4.75 | 4.75 | 4.75 | 10.74 | 10.74 | 11.74 | 10.74 | 4.75 | 4.75 | 11.74 |
| Final sampling date | 11.75 | 11.75 | 11.75 | 11.75 | 1.76 | 11.75 | 11.75 | 9.75 | 11.75 | 10.75 | 2.76 | 1.76 | 11.75 |

* Geological stratum: CL, Carboniferous Limestone; MG, Millstone Grit; CM, Coal Measures; ML, Magnesian Limestone.

† Soil type: A, alluvium; B, brown earth; LB, leached brown earth; R, rendzina; MR, mull-rendzina.

‡ Vegetation: TH, tall herb community; WF, woodland floor community; G, grassland.

the pattern of variation occurring in the dry weight of each vegetation component over the period investigated.

### *Sites*

The thirteen sites examined are listed in Table 1; all were situated within a radius of 29 km from the centre of Sheffield, south Yorkshire. In selecting the sites, vegetation of recent origin was excluded. Each site was situated in an area of landscape containing a diversity of long-established vegetation types, and it is considered unlikely that the reservoir of species in the vicinity of the site was a major limiting factor upon the species-densities recorded in Table 1. Figure 1 shows the location of the sites in relation to the major geological boundaries and to the stations from which the climatic data used in the investigation were collected. The vegetation types investigated may be classified into tall herb communities, woodland floor communities and grasslands.

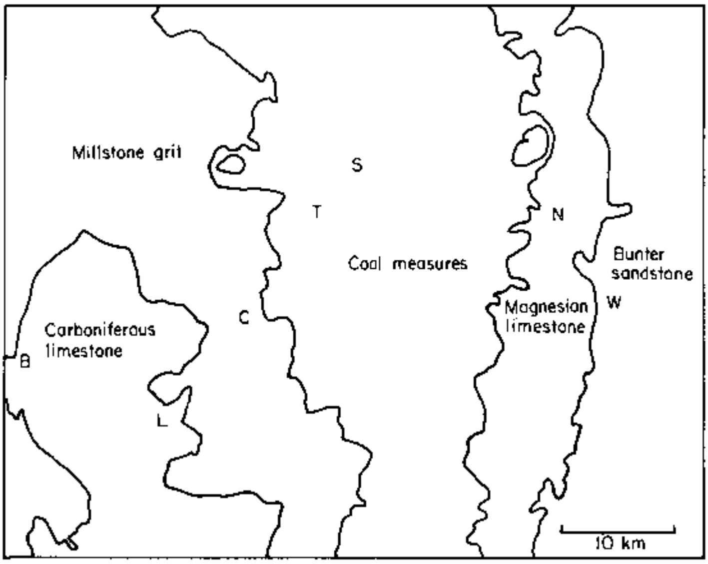

FIG. 1. Map showing the location of the sites investigated (L,C,T,N) in relation to the meteorological stations (B,S,W) and to major geological boundaries. L, Lathkilldale (Sites 1–4, 11, 12); C, Calver (Site 5); T, Totley Wood (Sites 6–10); N, North Anston (Site 13); B, Buxton; S, Sheffield; W, Warsop.

#### *Tall herb communities* (*Sites* 1–6)

Four of the tall herb communities were situated on derelict land in the general vicinity of Lathkilldale, on the Carboniferous Limestone of north Derbyshire. Site 1 was a bed of stinging nettle (*Urtica dioica*)*, occupying an area of dale-floor on the site of a disused sheep-pen approximately 2 m above the summer level of the adjacent River Lathkill. Site 2 was located within an extensive stand of bracken (*Pteridium aquilinum*), colonizing an area of south-facing dale-side in which the limestone was overlain by a deep acidic mineral soil. The patch of *Chamaenerion angustifolium* forming Site 3 occurred in a

* Nomenclature follows that of Clapham, Tutin & Warburg (1962).

small roadside hollow with a deep mineral soil. Site 4 was situated at Ricklow in Upper Lathkilldale, and consisted of a uniform stand of *Filipendula ulmaria* on a steeply-sloping north-facing terrace with rendzina soil.

The two remaining tall herb communities both occurred on deep, continuously-moist, alluvial soils. Site 5 was approximately 40 m from the bank of the River Derwent at Calver Bridge, north Derbyshire, and consisted of a stand of *Petasites hybridus* subjected to lateral shade, on one side by a high wall and on the other by a plantation of *Populus* × *canadensis*. Site 6 was at Totley Wood, which is on the Coal Measures and lies within the north-west boundary of the city of Sheffield. The vegetation at this site consisted of a stand of *Urtica dioica* in a small clearing (25 m diameter) in mixed deciduous woodland and scrub, some 50 m from a small stream. Although Site 6 was surrounded by a fringing tree-canopy (see Site 7 for list of tree species), sampling was confined to the centre of the clearing where there was no overhead shade.

### *Woodland floor communities (Sites* 7–10)

The sites in this category were all located in Totley Wood, and were selected to represent four types of woodland ground-cover of widespread occurrence in the southern Pennines (Woodhead 1906). From our own observations and those of Scurfield (1953), it would appear that, despite sporadic felling and coppicing, woodland has been present at Totley for a considerable period. Site 7 was immediately adjacent to the clearing (Site 6), which it resembled closely in terms of topography and soil type. The tree canopy (of *Acer pseudoplatanus*, *Alnus glutinosa*, *Crataegus monogyna*, *Fraxinus excelsior* and *Sambucus nigra*), although continuous, was rather sparse, and when fully expanded (about 1 June–30 September) caused the level of visible radiation reaching the woodland floor to fall by an average value of *c.* 11% below that measured simultaneously at the centre of the clearing; measurements were made at random positions using the technique of Evans (1956).

Site 8 occurred in mature woodland situated on a terrace elevated *c.* 5 m above the stream. In the ground flora, four species (*Endymion non-scriptus*, *Holcus mollis*, *Galeobdolon luteum* and *Milium effusum*) were prominent, and the soil was a rather acidic locally-gleyed brown earth. The dense tree canopy included tall specimens of *Quercus petraea*, *Fraxinus excelsior* and *Acer pseudoplatanus* (up to 28 m in height), and over the period 1 June–30 September the mean value for visible radiation at the ground surface was *c.* 8% of that measured at an unshaded site outside the wood.

In Totley Wood sampling was also carried out at two sites (9 and 10) on a steeply-sloping hillside overlooking Site 8. At Site 9 the soil was a degenerate brown earth, supporting a thin but continuous canopy of stunted *Quercus petraea* (up to 20 m in height), with occasional *Betula pubescens*, and a ground flora consisting mainly of *Pteridium aquilinum*, *Holcus mollis*, *Deschampsia flexuosa*, *Endymion non-scriptus* and *Milium effusum*. The average value for visible radiation at the ground surface during the summer was *c.* 19% of that measured outside the wood. At site 10 the soil was a shallow podzol, supporting a pure stand of *Deschampsia flexuosa* beneath a sparse canopy of very stunted *Quercus petraea* (up to 14 m in height); the amount of radiation reaching the herb layer was reduced on average to *c.* 14% of that outside the wood.

### *Grasslands (Sites* 11–13)

Two of the grassland sites were in areas of derelict pasture in Lathkilldale. Each had

Table 2. *Monthly means at three meteorological stations for daily minimum and maximum temperatures (°C) during the period of the investigations (October* 1974 *to December* 1975), *and their deviations (°C) from the long-term averages* (1931–60, 1943–65 *and* 1961–70 *for Buxton, Sheffield and Warsop respectively*)

| | Buxton (300 m altitude) | | | | Sheffield (135 m altitude) | | | | Warsop (46 m altitude) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Temperature (°C) | | Deviation (°C) | | Temperature (°C) | | Deviation (°C) | | Temperature (°C) | | Deviation (°C) | |
| | Max. | Min. | Max. | Min. | Max. | Min. | Max. | Min. | Max. | Min. | Max. | Min. |
| October | 8·1 | 3·3 | −3·2 | −2·2 | 10·0 | 5·2 | −3·6 | −2·2 | 10·6 | 5·2 | −3·8 | −1·0 |
| November | 7·5 | 2·5 | −0·1 | −0·7 | 8·7 | 3·7 | −0·5 | −0·7 | 8·9 | 2·8 | +0·2 | +0·6 |
| December | 8·3 | 3·8 | +2·9 | +2·7 | 9·9 | 5·1 | +3·1 | +2·9 | 10·2 | 4·9 | +4·3 | +5·4 |
| January | 7·2 | 2·8 | +3·0 | +3·3 | 8·9 | 3·8 | +3·1 | +2·5 | 9·1 | 3·1 | +3·5 | +3·5 |
| February | 5·1 | 0·6 | +0·6 | +1·1 | 8·4 | 1·7 | +2·1 | +0·4 | 6·5 | 0·8 | +0·4 | +0·9 |
| March | 5·6 | 0·4 | −1·6 | −0·8 | 6·8 | 1·7 | −2·2 | −0·7 | 7·6 | 1·4 | −0·9 | +0·5 |
| April | 9·8 | 3·2 | −0·3 | +0·4 | 12·2 | 5·1 | −0·3 | +0·2 | 12·3 | 4·2 | +0·5 | +1·0 |
| May | 11·7 | 4·2 | −1·8 | −1·2 | 13·8 | 5·6 | −1·9 | −0·7 | 14·0 | 4·4 | −1·4 | −1·2 |
| June | 17·4 | 7·9 | +0·7 | −0·5 | 20·1 | 9·7 | +1·5 | −0·5 | 20·9 | 6·0 | +1·4 | −2·2 |
| July | 19·3 | 11·3 | +1·4 | −0·7 | 21·7 | 14·3 | +1·9 | +2·1 | 22·2 | 10·6 | +2·3 | +0·9 |
| August | 21·4 | 12·3 | +3·7 | +2·0 | 24·6 | 14·0 | +5·2 | +2·2 | 24·8 | 11·2 | +5·1 | +1·7 |
| September | 14·8 | 7·6 | −0·4 | −0·9 | 17·3 | 9·5 | +0·1 | −0·7 | 18·0 | 6·7 | +0·1 | −2·2 |
| October | 11·3 | 4·7 | +0·0 | −0·8 | 13·3 | 6·5 | −0·3 | −0·9 | 13·5 | 5·2 | −0·9 | −1·0 |
| November | 7·3 | 2·3 | −0·3 | −0·9 | 8·8 | 3·3 | −0·4 | −1·1 | 9·1 | 1·6 | +0·4 | −0·6 |
| December | 6·3 | 2·4 | +0·9 | +1·3 | 8·2 | 3·5 | +1·4 | +1·3 | 8·2 | 1·0 | +2·3 | +0·5 |

not been grazed for a period of at least 20 years. Fires occur periodically in Lathkilldale (Lloyd 1968, 1972), but neither of the sites had been subject to burning over the 5 years prior to the investigation. The two sites were situated in close proximity, on directly opposed north-facing and south-facing dale-sides on unleached shallow calcareous soils (Sites 11 and 12 respectively). Although both supported a mixture of grasses and forbs, they differed markedly in species-composition.

Site 13 provided a contrast with the Lathkilldale grasslands in that it was located in an area of rough grassland at North Anston, on the Magnesian Limestone of south Yorkshire. The samples were taken from a small area of *Brachypodium pinnatum* grassland. Although subjected neither to grazing nor burning, the turf at this site was quite sparse, a feature probably related to the steep slope and to the shallow depth of the mull-rendzina soil.

Table 3. *Monthly totals at three meteorological stations for rainfall (mm) during the period of the investigations (October* 1974 *to December* 1975), *and their deviations (mm) from the long-term averages* (1943–65, 1943–65 *and* 1941–70 *for Buxton, Sheffield and Warsop respectively)*

| | Buxton (300 m altitude) | | Sheffield (135 m altitude) | | Warsop (46 m altitude) | |
|---|---|---|---|---|---|---|
| | Rainfall (mm) | Deviation (mm) | Rainfall (mm) | Deviation (mm) | Rainfall (mm) | Deviation (mm) |
| October | 151·0 | +48·0 | 55·9 | − 6·1 | 61·1 | +13·1 |
| November | 157·6 | +26·6 | 121·1 | +36·1 | 70·9 | +18·0 |
| December | 138·1 | +14·9 | 71·1 | −10·9 | 33·8 | −15·2 |
| January | 179·9 | +39·9 | 73·2 | − 8·8 | 48·8 | − 5·2 |
| February | 37·8 | −58·2 | 15·8 | −46·2 | 18·7 | −26·3 |
| March | 83·4 | + 7·4 | 58·8 | + 6·8 | 60·2 | +17·2 |
| April | 102·3 | +16·3 | 46·9 | − 3·1 | 38·2 | − 3·8 |
| May | 62·7 | −16·3 | 86·2 | +30·2 | 34·4 | −16·6 |
| June | 19·0 | −69·0 | 47·7 | −11·3 | 5·2 | −40·8 |
| July | 33·9 | −70·1 | 69·9 | +10·9 | 59·3 | + 6·3 |
| August | 53·5 | −62·5 | 46·7 | −26·3 | 27·5 | −38·5 |
| September | 91·2 | −23·8 | 34·6 | −31·4 | 34·2 | −15·8 |
| October | 46·5 | −56·5 | 27·2 | −34·8 | 16·9 | −31·1 |
| November | 88·0 | −41·0 | 28·6 | −56·4 | 34·7 | −31·3 |
| December | 120·3 | −32·7 | 43·0 | −39·0 | 44·5 | − 4·5 |

### *Climate*

In Tables 2 and 3 climatic data for three sites representative of the altitudinal range encompassed by the sampled areas are presented, in the form of monthly means of the daily maximum and minimum air temperatures (measured within Stevenson screens 1·5 m above the ground) and of monthly totals of rainfall. The data from Buxton (300 m altitude) indicate that, over the period covered by the investigation, temperatures were marginally but consistently lower in each month and rainfall rather greater at the higher altitudes to the west of Sheffield.

Weather conditions during the period investigated were abnormal in several respects. Comparison with the monthly long-term averages for the same stations in Tables 2 and 3 reveals that rainfall was exceptionally low, particularly at Buxton, over the period May–December 1975. It is quite clear, also, that temperatures were unusually high in the winter period (December 1974 to February 1975), and again in June, July and August 1975.

### *Sampling and sorting*

Some ecological and topographical features of the thirteen sites are presented in Table 1, together with information concerning the sampling procedure. With the exception of Site 13, where the quantity of vegetation available for sampling was exceptionally small, the area of each sample was 0·25 $m^2$, and at all sites estimations of species-density (number of herbaceous species per unit area) were also based upon samples of this size. Species-density is a function of sample-size, and the values given in Table 1 are significant only in a comparative sense. The choice of 0·25 $m^2$ for the measurement of species-density was governed by the need to make replicated estimations within rather small stands of vegetation, and by a concern that the samples should fall within the range found previously (Grime 1973a, c) to be sensitive to effects of dominance upon the species-density of herbaceous vegetation.

At a number of sites initial difficulty was experienced in deciding where the boundary occurred between litter and soil. This was resolved by regarding as litter all the material above the zone exploited by roots. At the open sites with tall herbs and in woodland the sampling procedure involved clipping the vegetation at the soil surface. In certain of the grassland communities turves were cut, so that the separation of litter and soil could be completed in the laboratory.

The samples were stored at 5 °C until they could be sorted into their constituent species. Bryophytes were not separated into species, and, with the exception of *Pteridium aquilinum* at Site 9, no attempt was made to measure the contribution of individual species to the herbaceous litter. After sorting, all the materials were dried in an oven at 80 °C for 48 h prior to weighing.

### *Presentation of the results*

For each site graphs have been drawn, showing the change in mean dry weight per unit area of living herbaceous shoot material and litter over the sampling period; for the woodland sites data for the tree litter (leaf material only) has also been plotted. Additional graphs have been drawn for the main species at each site. The data obtained for minor contributors to the vegetation, and for those showing a scattered but contagious distribution within the sampling area, could not be analysed satisfactorily; these species are listed in Appendix 1.

## RESULTS

### *Tall herb communities**

*Site* 1 (Urtica *stand, Lathkilldale*)

Figure 2(a) shows the changes in dry weight of living shoot material and litter in the Lathkilldale nettle-patch over the period April–November 1975. There was a clearly defined seasonal increase in standing crop, reaching a pleateau of 550–650 g $m^{-2}$ from June to September. Herbaceous litter, composed almost exclusively of the remains of the stems of *Urtica dioica*, was present in abundance, and showed little variation throughout the period over which samples were collected.

From Fig. 2(a) it is apparent that a considerable amount of green material was

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* For the purposes of this paper the usual definition of tall herb communities has been expanded to include vegetation dominated by *Pteridium aquilinum* and *Petasites hybridus*.

present in the early spring. Reference to Fig. 3 (b) and (c), in which graphs are given for the main components of the standing crop, indicates that at this time the living material was made up of *U. dioica*, the annual species *Galium aparine* and bryophytes. In the early spring, *Urtica dioica* was represented by the apices of unexpanded shoots situated close to the ground surface, and *Galium aparine* by a large number of seedlings which had germinated during the preceding winter. A high proportion of the bryophytes was found to be attached to the herbaceous litter, and appeared to have effectively colonized the new litter deposited in the previous autumn.

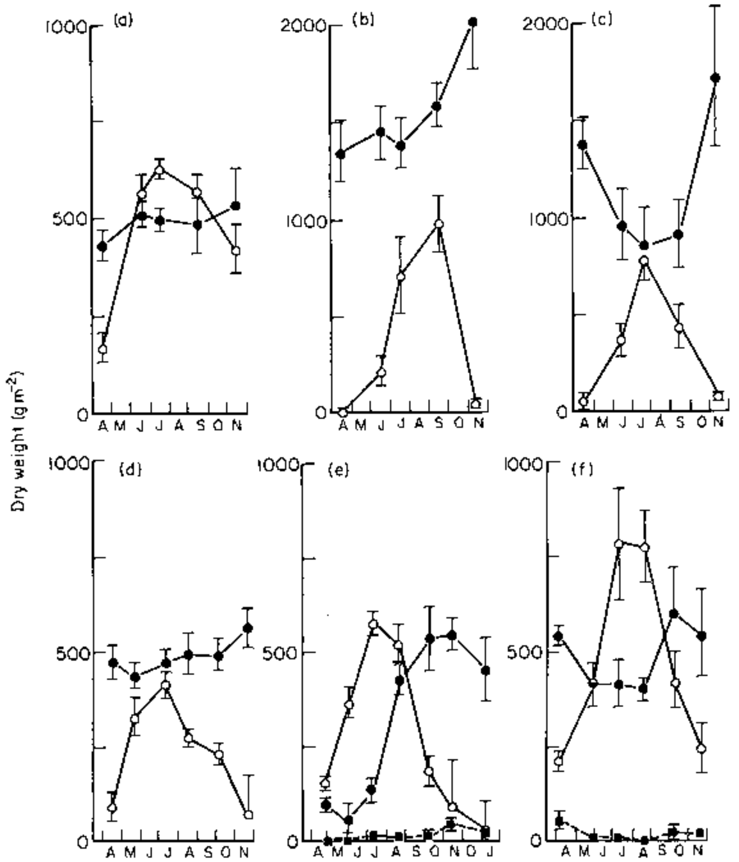

FIG. 2. Seasonal changes in total living shoot material (○), herbaceous litter (●) and tree litter (■) in six tall herb communities. Standard errors are indicated by the vertical lines. (a), Site 1 (*Urtica* stand, Lathkilldale); (b), Site 2 (*Pteridium* patch, Lathkilldale); (c), Site 3 (*Chamaenerion* stand, Lathkilldale); (d), Site 4 (*Filipendula* stand, Lathkilldale); (e), Site 5 (*Petasites* stand, Calver Bridge); (f), Site 6 (woodland clearing, Totley Wood).

In the spring and early summer the shoots of *Urtica dioica* expanded to become the dominant component, reaching a peak in dry matter in September. In the autumn the leaf canopy of *U. dioica* deteriorated rapidly, and by November only the stems remained.

The main period of shoot expansion in *Galium aparine* occurred during the spring. After a short period of growth, seed production and senescence occurred in July and

August. Expansion of the bryophyte component to a peak in July was followed by a catastrophic decline in August and September, with a recovery apparent in November.

The remaining contribution to the standing crop consisted of rather scattered shoots of *Agropyron repens*, some of which tended to be overgrown by the canopy of *Urtica dioica*, the expansion of which was closely matched by that of *Agropyron repens*.

*Site* 2 (Pteridium *stand, Lathkilldale*)

The area of bracken examined in Lathkilldale achieved the highest standing crop recorded in the investigation. The total amount of living shoot matter continued to rise throughout the summer (Fig. 2 (b)), to a peak value of *c.* 1000 g m$^{-2}$ dry weight in September; this was followed by a steep autumnal decline. The vegetation at Site 2 consisted of an almost pure stand of *Pteridium aquilinum*, and the pattern shown in Fig. 2 (b) is clearly a function of the phenology of this species. Examination of the seasonal changes in shoot weight of *P. aquilinum* (Fig. 3 (a)) confirms this fact, and establishes that shoot growth in bracken was delayed in comparison with the other tall herbs (*Urtica dioica, Chamaenerion angustifolium* and *Filipendula ulmaria*) examined in Lathkilldale.

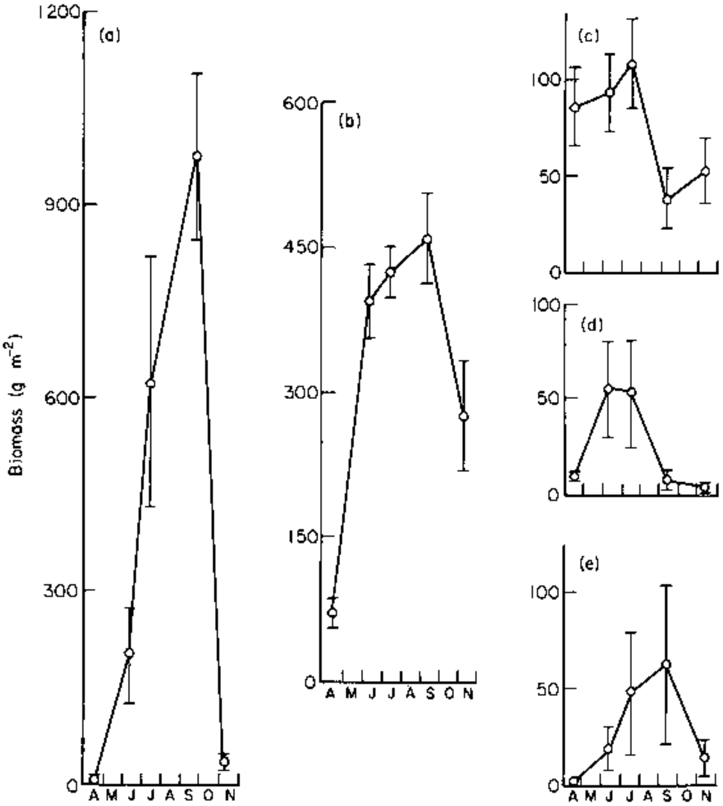

FIG. 3. Seasonal changes in the amounts of living shoot material of the main vegetation components at Sites 1 and 2. Standard errors are indicated by the vertical lines. (a), *Pteridium aquilinum* (Site 2); (b), *Urtica dioica* (Site 1); (c), bryophytes (Site 1); (d), *Galium aparine* (Site 1); (e), *Agropyron repens* (Site 1).

A striking feature of Site 2 was the amount of herbaceous litter, which exceeded that of the living component by a considerable margin, even during the summer peak in standing crop. The herbaceous litter was composed almost exclusively of the debris from *Pteridium aquilinum*. A distinct rise in litter occurred in the autumn, and corresponded with the onset of senescence and frost-damage in the bracken fronds.

An additional feature of this site was the absence, except in trace quantities, of vernal herbs and bryophytes.

*Site* 3 (Chamaenerion *stand, Lathkilldale*)

Both standing crop and herbaceous litter at Site 3 exhibited clearly-defined symmetrical patterns over the period May–October (Fig. 2(c)). The dry weight of the living herbaceous component was close to zero in April, but then rose to a maximum of *c*. 800 g m$^{-2}$ at the end of July. This was followed by a continuous decline to a value of approximately 180 g m$^{-2}$ in November. Concurrently, the dry weight of herbaceous litter remained above that of the standing crop, but showed a wide amplitude of seasonal variation, with the minimum occurring at midsummer.

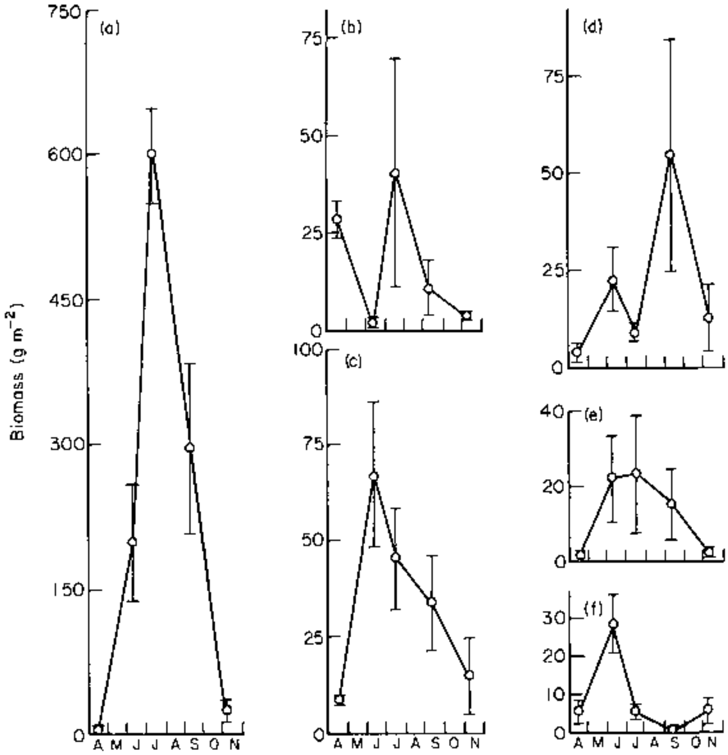

FIG. 4. Seasonal changes in the amounts of living shoot material of the main vegetation components at Site 3. Standard errors are indicated by the vertical lines. (a), *Chamaenerion angustifolium*; (b), bryophytes; (c), *Urtica dioica*; (d), *Agropyron repens*; (e), *Arrhenatherum elatius*; (f), *Galium aparine*.

In Fig. 4 (a)–(f) graphs are presented for the main constituents of the standing crop.

The dominant component, *Chamaenerion angustifolium*, was scarcely detected in April, but then expanded its shoots extremely rapidly to achieve a maximum in July. At this time the shoots of *C. angustifolium* were about 1·5 m in height, and there was widespread senescence in the older shaded part of its leaf canopy. Shoots of *Urtica dioica* were interspersed throughout the site, and in early spring the amount of shoot dry matter of this species exceeded that of *Chamaenerion angustifolium*. By the beginning of July, however, most of the *Urtica dioica* was submerged by the canopy of *Chamaenerion angustifolium*, and this was reflected in a premature decline in shoot dry weight (cf. the graphs for sites 1 and 6 (Figs 3(b) and 5(h)), in which *Urtica dioica* retained a dominant position in the leaf canopy). Minor contributors to the standing crop at Site 3 were the annual species *Galium aparine* and the grass *Arrhenatherum elatius*. The latter was represented mainly by seedlings and small plants, and reached a maximum standing crop in July. Bryophytes and scattered shoots of *Agropyron repens* were recorded locally within the site, but their occurrence in the samples was too erratic to permit graphs to be drawn.

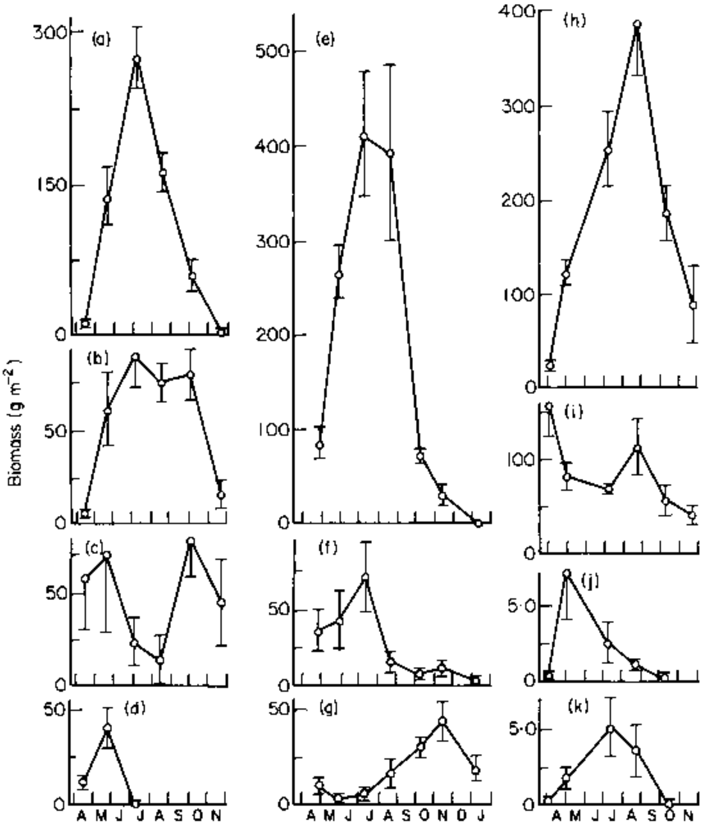

FIG. 5. Seasonal changes in the amounts of living shoot material of the main vegetation components at Sites 4, 5 and 6. Standard errors are indicated by the vertical lines. (a), *Filipendula ulmaria* (Site 4); (b), *Mercurialis perennis* (Site 4); (c), bryophytes (Site 4); (d), *Anemone nemorosa* (Site 4); (e), *Petasites hybridus* (Site 5); (f), *Poa trivialis* (Site 5); (g), bryophytes (Site 5); (h), *Urtica dioica* (Site 6); (i), bryophytes (Site 6); (j), *Poa trivialis* (Site 6); (k), *Galium aparine* (Site 6).

*Site* 4 (Filipendula *stand, Lathkilldale*)

At Site 4 the peak in standing crop of *c*. 400 g $m^{-2}$ attained in July (Fig. 2(d)) was small in comparison with other tall-herb communities, and fell below the weight of herbaceous litter (which tended to increase over the period examined).

In April bryophytes were present in abundance on the herbaceous litter (Fig. 5 (c)), and at this stage vascular plants were represented mainly in the form of unexpanded shoots of *Anemone nemorosa*, *Mercurialis perennis* and *Filipendula ulmaria*. By the middle of May the leaves and flowers of *Anemone nemorosa* were fully expanded (Fig. 5 (d)), and there was a peak in the dry weight of the bryophytes. In the following month the composition of the standing crop changed considerably, and by the beginning of July the area was covered by a rather homogeneous leaf canopy in which the upper layers were composed of *Filipendula ulmaria* (Fig. 5 (a)), whilst the lower, shaded stratum included the shoots of *Mercurialis perennis* (Fig. 5 (b)). This closure of the leaf canopy coincided with the disappearance of *Anemone nemorosa*, and simultaneously there was a marked decline in the frequency of bryophytes.

The phenology of the two most prominent herbs, *Filipendula ulmaria* and *Mercurialis perennis* (Fig. 5 (a) and (b)), differed in that the former exhibited a rather narrow peak in dry matter, with a rapid decline after flowering, whereas the latter maintained a fairly constant biomass of living shoot material until mid-October. Deterioration of the herbaceous canopy in autumn coincided with a recovery in the frequency of bryophytes. The seedlings and small plants of *Arrhenatherum elatius*, which were of common occurrence at Site 4, showed a peak in dry weight of living shoot material in August.

*Site* 5 (Petasites *stand, Calver Bridge*)

Among the tall herb communities, the one examined at Calver was unusual in that both the standing crop *and* the herbaceous litter showed a very strong seasonal fluctuation (Fig. 2 (e)). The amplitude of fluctuation in the litter was from 60 g $m^{-2}$ in May to 550 g $m^{-2}$ in November.

Reference to Fig. 5 (e) confirms that seasonal patterns in living and dead shoot material were largely determined by the phenology of *Petasites hybridus*, the dominant species at the site. In April *P. hybridus* was represented exclusively by flowering shoots, massive non-photosynthetic structures which collapsed after seed release at the end of May; by this time expansion of the vegetative shoots had commenced. The canopy of *P. hybridus* was composed of a relatively small number per unit area of large radical leaves (to 2 m tall), and attained a maximum biomass of just over 400 g $m^{-2}$ in August. From July onwards, the laminae of *P. hybridus* were subject to predation by slugs, and damage was particularly severe in senescent leaves at lower levels in the canopy. A rapid deterioration of *P. hybridus* occurred in September, and by January 1976 no living above-ground shoot material of this species remained.

*Poa trivialis* was also recorded at the site, and showed a peak of shoot dry matter in July (Fig. 5 (f)). The pattern of the bryophyte component was unusual, in that although a maximum was attained in November no expansion was detected in the preceding spring (Fig. 5 (g)).

*Site* 6 (*woodland clearing, Totley Wood*)

In the clearing at Totley Wood (Fig. 2(f)) a well-defined peak in the standing crop occurred in August. The dry weight of herbaceous litter, most of which was composed of the stems of *Urtica dioica*, remained above 500 g m$^{-2}$ throughout the period of study, and a maximum was observed in October. A variety of herbaceous plants occurred in the samples (Fig. 5 (i)–(k) and Appendix 1), but all except *U. dioica* (Fig. 5(h)) were either confined to small localized patches or were recorded in trace quantities. In particular, *Galium aparine* and *Poa trivialis*, both of which were abundant in adjacent areas, were extremely scarce. In contrast, the frequency of bryophytes was the highest encountered in the investigation. As at Site 1, most of the bryophytes were found to be attached to the decaying stems of *Urtica dioica*.

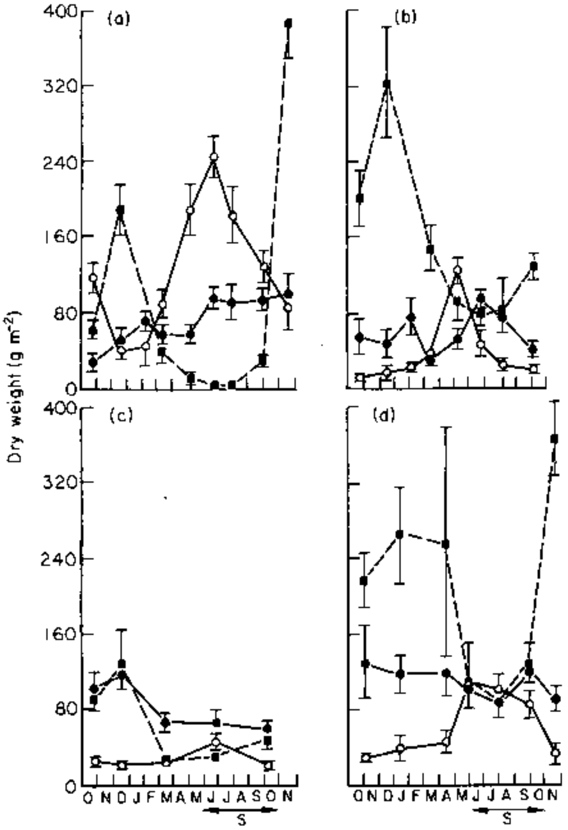

FIG. 6. Seasonal changes in total living shoot material (○), herbaceous litter (●) and tree litter (■) in the ground flora at four shaded sites in Totley Wood. Standard errors are indicated by the vertical lines. S denotes the period of maximum shading by the tree canopy. (a), Site 7 (*Poa trivialis–Ranunculus ficaria–Urtica dioica* stand); (b), Site 8 (*Holcus–Endymion* stand); (c), Site 10 (*Deschampsia flexuosa* stand); (d), Site 9 (*Holcus–Pteridium* stand).

## *Woodland floor communities*

### *Site* 7 (Poa trivialis–Ranunculus ficaria–Urtica dioica *stand, Totley Wood*)

As in all the woodland sites, data collection at Site 7 extended over a period of 1 year, and this allowed a description of phenological events during the unshaded phase, and also provided an estimate of the annual variation in density of tree litter.

Figure 6(a) shows the seasonal variation at Site 7 in the dry weights of herbaceous shoots, herbaceous litter and tree litter. In 1976 the peak in standing crop occurred in August, and in this respect there was a similarity with Site 6. However, the maximum value (*c.* 250 g m$^{-2}$) was only 20% of that attained in the clearing. A further point of difference from Site 6 was the scarcity of herbaceous litter, which varied between 30 and 100 g m$^{-2}$. At Site 7 there was a very pronounced seasonal fluctuation in tree litter—the mass per unit area remained high (*c.* 200 g m$^{-2}$) during the winter of 1976, but fell extremely sharply in the early spring to a minimum of about 10 g m$^{-2}$.

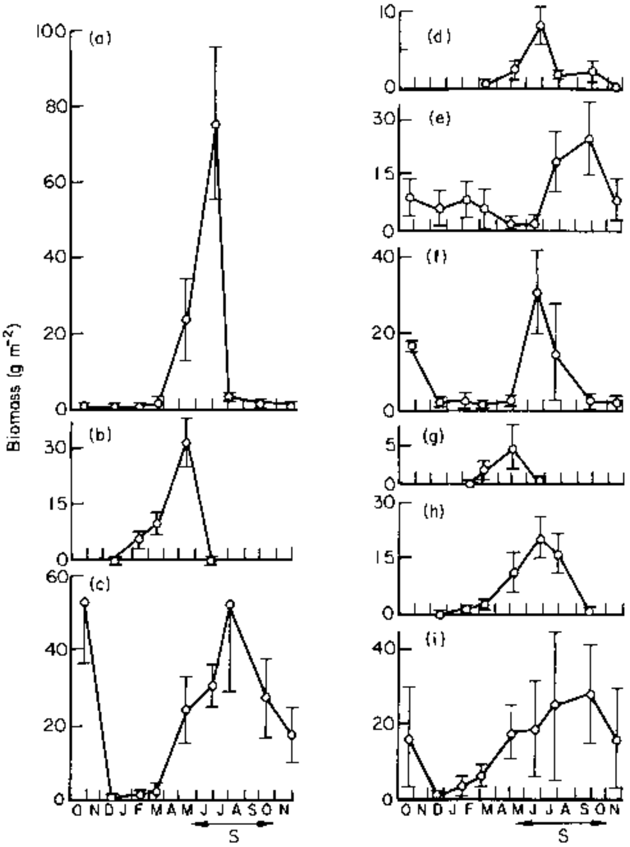

FIG. 7. Seasonal changes in the amounts of living shoot material of the main vegetation components at Site 7. Standard errors are indicated by the vertical lines. S, tree canopy fully expanded. (a), *Poa trivialis*; (b), *Ranunculus ficaria*; (c), *Urtica dioica*; (d), *Circaea lutetiana*; (e), *Veronica montana*; (f), *Festuca gigantea*; (g), *Anemone nemorosa*; (h), *Galium aparine*; (i), *Mercurialis perennis*.

In contrast with Site 6, the vegetation at Site 7 was not dominated by a single species. Seven herbaceous plants were significant contributors to the standing crop, and among the nine species for which graphs could be drawn (Fig. 7(a)–(i)), a range of different phenologies was apparent. One rather heterogeneous type was made up of *Poa trivialis, Ranunculus ficaria, Galium aparine* and *Anemone nemorosa*. Of these, *Ranunculus ficaria* (Fig. 7(b)) was the most extreme vernal type, in that leaf expansion was well-advanced by

February and all trace of the shoots of the species had disappeared by the beginning of June. *Poa trivialis* (Fig. 7(a)), which expanded much later, reached a higher mass per unit area of shoot material than any other plant recorded at the site. In this species the peak value preceded full expansion of the tree canopy, coincided with flowering and was followed by a catastrophic decline in July.

Although *Urtica dioica* was frequent within the site, the plants showed low vegetative vigour and many shoots failed to produce flowers. The peak in shoot dry weight in *U. dioica* (Fig. 7(c)), although much reduced, coincided with that exhibited by the same species growing in the clearing (Site 6).

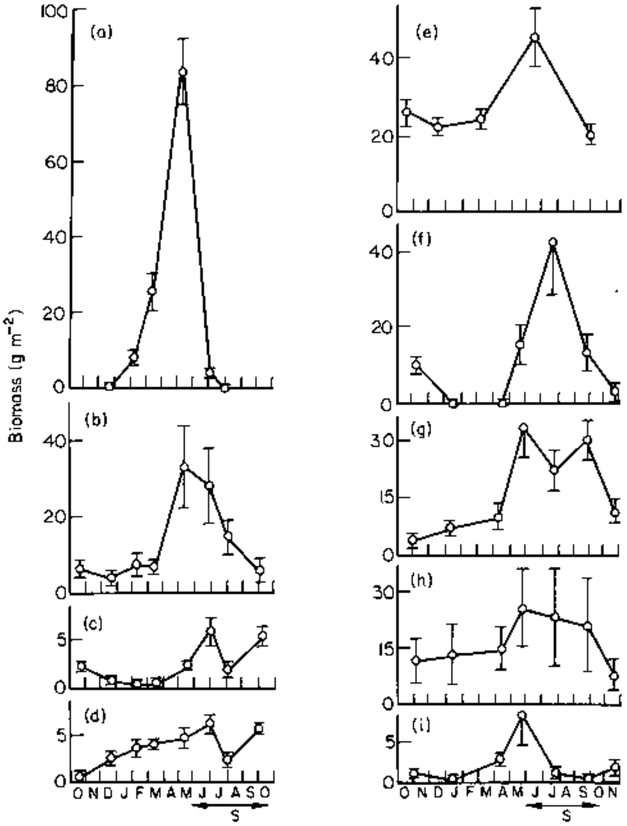

FIG. 8. Seasonal changes in the amounts of living shoot material of the main vegetation components at Sites 8, 9 and 10. Standard errors are indicated by the vertical lines. S, tree canopy fully expanded. (a), *Endymion non-scriptus* (Site 8); (b), *Holcus mollis* (Site 8); (c), *Milium effusum* (Site 8); (d), *Galeobdolon luteum* (Site 8); (e), *Deschampsia flexuosa* (Site 10); (f), *Pteridium aquilinum* (Site 9); (g), *Holcus mollis* (Site 9); (h), *Deschampsia flexuosa* (Site 9); (i), *Milium effusum* (Site 9).

Shoots of two species, *Mercurialis perennis* and *Veronica montana*, were recorded at all times of the year, but the outstanding feature of their phenologies (Fig. 7(i) and (e)) was a broad peak in shoot dry weights occurring during the period of maximum shade from the tree canopy. In another evergreen species, *Festuca gigantea*, a different pattern was obtained; here a narrow peak in shoot dry weight was associated with the production of culms in June (Fig. 7(f)).

An outstanding feature of Site 7 was the extreme scarcity of bryophytes.

*Site* 8 (Holcus–Endymion *stand, Totley Wood*)

From Fig. 6 (b) it is evident that a small amount ($<30$ g m$^{-2}$) of living herbaceous shoot material was present for most of the year at Site 8, although this rose to a peak of *c.* 130 g m$^{-2}$ in May, immediately before full expansion of the tree canopy. Herbaceous litter remained rather sparse (*c.* 100 g m$^{-2}$), and showed two peaks: the first, in February, may have been the result of frost damage to overwintering shoots of species such as *Milium effusum*, whilst the second, in June, was associated with senescence of *Endymion non-scriptus* and *Holcus mollis*. The pattern in the amount of tree litter resembled closely that observed at Site 7, but larger amounts persisted during both the winter (*c.* 320 g m$^{-2}$) and the summer (*c.* 80 g m$^{-2}$).

When the standing crop is separated into its constituent species (Fig. 8 (a)–(d)), four main components may be recognized. As in Site 7, the largest contribution was from a vernal species, in this case *Endymion non-scriptus*. Full development of the tree canopy coincided with senescence and seed production in *E. non-scriptus*, and with a gradual decline in the density of *Holcus mollis*, which showed a peak slightly later than *Endymion*. As the summer progressed, the shoots of *Holcus mollis* became etiolated, and many were subject to mildew attack. In comparison with stands of *H. mollis* growing in nearby clearings, the species showed extremely low vegetative vigour, and flowering was almost completely suppressed. Foliage of *Galeobdolon luteum* and *Milium effusum* persisted in Site 8 throughout the year, and both species, moreover, flowered under the tree canopy in June.

*Site* 9 (Holcus–Pteridium *stand, Totley Wood*)

The gross phenological characteristics of Site 9 are presented in Fig. 6(d). The standing crop showed two distinct phases: during the winter the dry weight of living shoots remained constant at *c.* 30 g m$^{-2}$, but in April there was a rapid expansion to a value of *c.* 100 g m$^{-2}$, which was maintained for most of the shaded period and then returned to 30 g m$^{-2}$ in October. The amount of herbaceous litter remained fairly constant at about 125 g m$^{-2}$ throughout the year. A substantial proportion of the herbaecous litter was derived from *Pteridium*, the shoot biomass of which varied from a minimum of *c.* 20 g m$^{-2}$ in July to values exceeding 50 g m$^{-2}$ in the autumn. As in Sites 7 and 8, a marked discontinuity in the amount of tree litter was observed in the early spring, at which time the values fell from *c.* 260 g m$^{-2}$ to a summer minimum of *c.* 80 g m$^{-2}$.

Four herbaceous plants contributed significantly to the standing crop in Site 9, and graphs for these species are shown in Fig. 8(f)–(i). The shoots of *Pteridium aquilinum* expanded during the period in which shade was cast by the tree canopy and, although numerous, the majority of the fronds were very stunted. The maximum in dry weight of shoot material of *P. aquilinum* occurred in July, and was 41 g m$^{-2}$. In comparison with *P. aquilinum* growing in the open at Lathkilldale (Site 2), the peak occurred 2 months earlier and was reduced by about 96%. During the summer a high proportion of the standing crop at Site 9 was attributable to *Holcus mollis* and *Deschampsia flexuosa*, but in contrast to *Pteridium aquilinum* both these species (especially the latter) were major contributors to the herbaceous canopy during the winter. *Milium effusum* was a minor component of the vegetation, but showed a peak of 5 g m$^{-2}$ shoot dry matter in the early summer. Vernal species were represented by scattered individuals of *Endymion non-scriptus*, and bryophytes were virtually absent.

*Site* 10 (Deschampsia flexuosa *stand, Totley Wood*)

The results for this site are shown in Fig. 6(c). The standing crop, consisting entirely of the evergreen species *Deschampsia flexuosa* (Fig. 8(e)), remained low throughout the year, and varied between a winter minimum of *c.* 22 g m$^{-2}$ and a midsummer maximum of about 45 g m$^{-2}$. The tussocks of *D. flexuosa* were conspicuously stunted in comparison with those growing on colluvial brown earth soils at lower levels on the slope, and inflorescences were extremely scarce. Bryophytes were very restricted in occurrence.

The dry weight of litter from *D. flexuosa* exceeded that of the living shoots throughout the year, and showed a marked increase during the winter. In contrast with the results obtained from Sites 7–9, tree litter showed a more gradual decline, commencing during the winter. This effect was probably due to the fact that tree leaves falling on to Site 10 were not effectively trapped by the *D. flexuosa* tussocks, and tended to be blown away down the steep slopes.

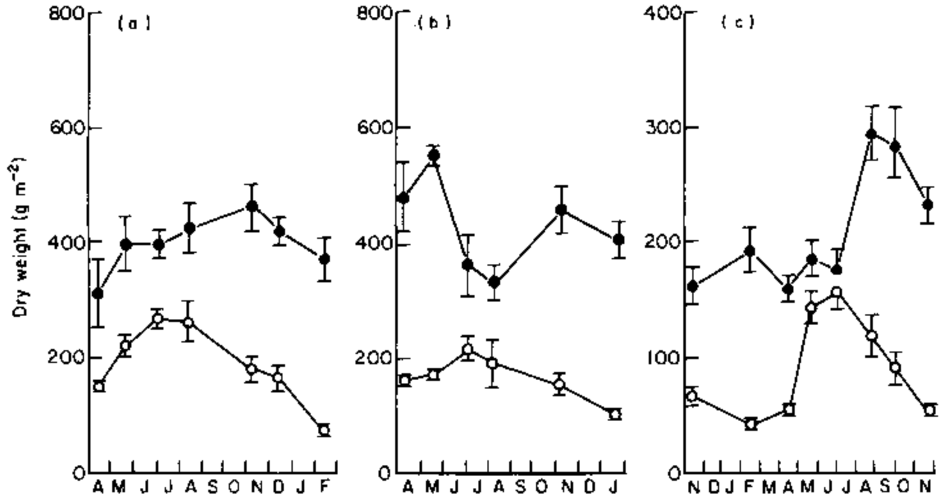

FIG. 9. Seasonal changes in total living shoot material (○) and herbaceous litter (●) in three grasslands. Standard errors are indicated by the vertical lines. (a), Site 11 (north-facing slope, Lathkilldale); (b), Site 12 (south-facing slope, Lathkilldale); (c), Site 13 (North Anston).

## *Grasslands*

*Site* 11 (*north-facing slope, Lathkilldale*)

Figure 9(a) illustrates the seasonal variations in dry weight of living shoot material and herbaceous litter in the north-facing grassland in Lathkilldale. In comparison with the tall-herb communities in the vicinity (Sites 1–4), the standing crop (*c.* 260 g m$^{-2}$) was low, showed a less pronounced seasonal variation, and reached the maximum rather earlier in the summer. Through the period examined the standing crop was exceeded by the amount of herbaceous litter, which reached a maximum of *c.* 450 g $m^{-2}$ in October.

The graphs in Fig. 10(a)–(l) show the seasonal patterns in the various components of the standing crop. The most striking feature of these results is the fact that the total contribution of bryophytes was greater than that of any single herbaceous plant. A strongly bi-modal pattern was apparent for the bryophytes, with peaks each of *c.* 65 g $m^{-2}$ in May and December, and a minimum of *c.* 30 g $m^{-2}$ at the beginning of September. None of the herbaceous plants at the site appeared to exercise a dominant role, and a range of different phenologies was apparent among the eleven species for which data were obtained. Differences occurred with respect to both the magnitude and the timing of peaks in shoot dry matter. In certain species, e.g. *Carex flacca* and *Koeleria cristata*, comparatively little fluctuation was detected, whereas in others there was a well-defined summer peak. Among the latter, a distinction may be drawn between species such as *Poterium sanguisorba* and *Centaurea nigra*, in which the curves rise and fall from the baseline (i.e. there are no over-wintering shoots), and those such as *Festuca* spp. and

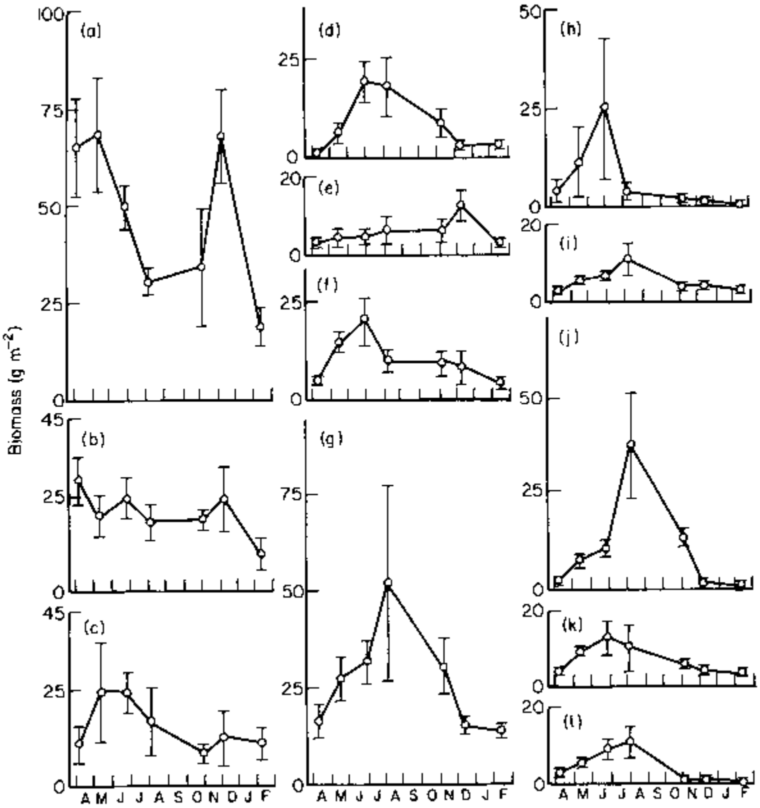

FIG. 10. Seasonal changes in the amounts of living shoot material of the main vegetation components at Site 11. Standard errors are indicated by the vertical lines. (a), Bryophytes; (b), *Carex flacca*; (c), *Festuca ovina*; (d), *Helictotrichon pubescens*; (e), *Koeleria cristata*; (f), *Anthoxanthum odoratum*; (g), *Festuca rubra*; (h), *Helictotrichon pratense*; (i), *Holcus lanatus*; (j), *Poterium sanguisorba*; (k), *Succisa pratensis*; (l), *Centaurea nigra*.

*Succisa pratensis*, which continued to make a major contribution to the standing crop throughout the year.

It is interesting to note that in Fig. 10 only four species exhibit peaks in shoot development coinciding with the mid-summer (July–August) maximum in radiation and temperature. These are *Poterium sanguisorba* and *Centaurea nigra*, forbs with long tap-root systems, and *Festuca rubra* and *Holcus lanatus*, grasses more familiar as dominants of productive vegetation. Most of the remaining species at Site 11 flowered and produced a peak in shoot dry weight in the early spring. In three species (*Carex flacca, Festuca ovina* and *Koeleria cristata*) the data suggest a small autumnal peak, corresponding to that recorded for the bryophytes. However, because of variability in the data the occurrence of this phenomenon could not be established statistically.

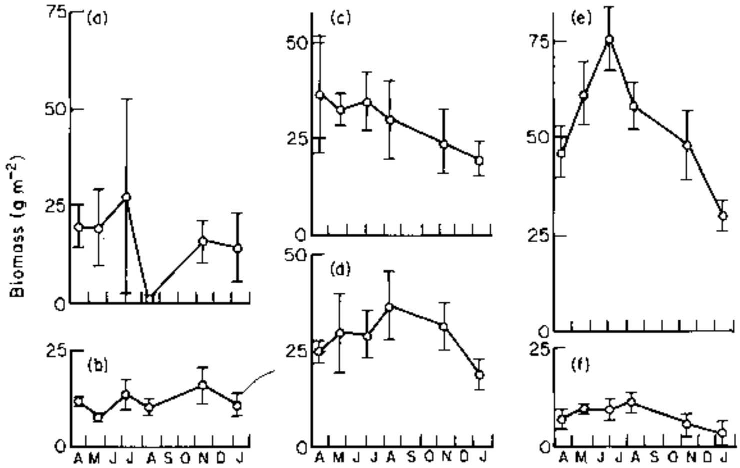

FIG. 11. Seasonal changes in the amounts of living shoot material of the main vegetation components at Site 12. Standard errors are indicated by the vertical lines. (a), Bryophytes; (b), *Koeleria cristata*; (c), *Helianthemum chamaecistus*; (d), *Helictotrichon pratense*; (e), *Festuca ovina*; (f), *Carex flacca*.

### *Site* 12 (*south-facing slope, Lathkilldale*)

The standing crop in the south-facing grassland at Lathkilldale (Fig. 9(b)) was lower, and showed a smaller amplitude of seasonal fluctuation than its counterpart on the opposite slope (Site 11), although the maximum again occurred in July. Herbaceous litter was more abundant than on the north-facing slope, and appeared to decline in quantity during the summer. Although bryophytes were less frequent than on the north-facing slope, a bimodal curve was obtained again (Fig. 11(a)), and by mid-August living bryophytes virtually disappeared from the turf at Site 12. There were major contributions to the standing crop from five vascular plants (Fig. 11 (b)–(f)), all of which retained a leafy canopy during the winter. In *Koeleria cristata* and *Carex flacca*, and in the xeromorphic sub-shrub *Helianthemum chamaecistus*, no significant increase in shoot dry weight was detected during the summer. In *Festuca ovina* an expansion occurred at the time of flowering in June, and in *Helictotrichon pratense* a maximum was observed in August. However, in both of these species a considerable residue of living shoot material remained in the winter.

*Site* 13 (*North Anston*)

In terms of both living material and herbaceous litter, the site at North Anston (Fig. 9(c)) proved to be the least productive of the three grasslands examined. The standing crop appeared to remain constant over the winter of 1975 (*c.* 60 g m$^{-2}$), then rose during the spring to achieve a maximum of *c.* 160 g m$^{-2}$ in July. Over the same period the standing crop of litter remained at *c.* 170 g m$^{-2}$, rising to *c.* 300 g m$^{-2}$ by the beginning of September.

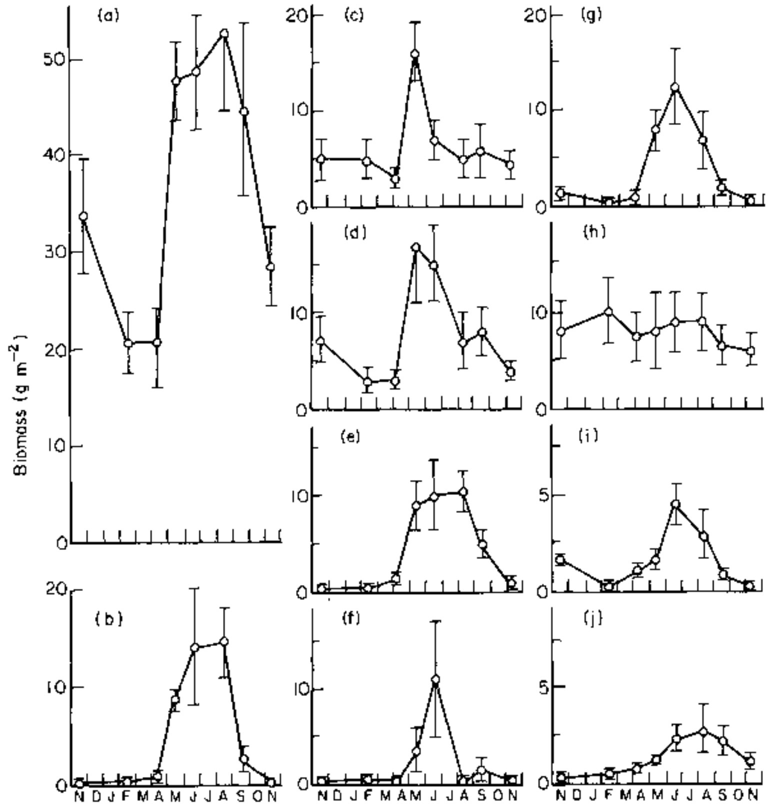

FIG. 12. Seasonal changes in the amounts of living shoot material of the main vegetation components at Site 13. Standard errors are indicated by the vertical lines. (a), *Brachypodium pinnatum*; (b), *Trifolium medium*; (c), *Carex caryophyllea*; (d), *Briza media*; (e), *Centaurea nigra*; (f), *Lotus corniculatus*; (g), *Leontodon hispidus*; (h), *Carex flacca*; (i), *Hieracium lachenalii*; (j), *Campanula rotundifolia*.

One species, *Brachypodium pinnatum*, remained the major contributor to the standing crop throughout the year (Fig. 12(a)), and produced a broad peak of *c.* 50 g m$^{-2}$ over the summer period. Among the remaining species, a spectrum of phenologies similar to that observed on the north-facing slope of Lathkilldale (Site 11) was obtained. At one extreme *Carex flacca* showed no marked fluctuation in shoot weight (cf. Sites 11 and 12), whilst at the other, several relatively deep-rooting forbs (*Campanula rotundifolia*, *Centaurea nigra*, *Leontodon hispidus*, *Lotus corniculatus*, *Trifolium medium*) developed peaks during the summer, but were scarcely detectable in the winter. The weight of shoot material in *Briza media* and *Carex caryophyllea* remained fairly constant throughout the year, but showed a temporary increase at the time of flower production in the spring.

## DISCUSSION

### '*Representativeness*' *of the data*

A factor to be considered before attempting to generalize from the data obtained in this study is the unusual weather conditions which occurred during the period of the investigation. Particularly to the west of Sheffield, the summer of 1975 was unusually hot and dry (Tables 2 and 3), and it seems possible that this may have had some impact on the results. However, with the exception of Site 4, at which wilting of *Filipendula ulmaria* was observed in July 1975, no signs of moisture stress were observed at the sites dominated by tall herbs or at the woodland sites, the majority of which are situated on alluvial terraces with a high water-table. Signs of desiccation were observed in grasses growing on the south-facing slope of Lathkilldale (Site 12), but this appears to be a recurrent feature of the vegetation at this site.

It seems reasonable to conclude, therefore, that although the unusual climatic conditions may have caused minor effects on the size of the standing crop and in the timing of shoot growth and leaf senescence, there is no evidence to suggest that major modifications of shoot phenology occurred.

Further evidence of the representativeness of the data is the close agreement of the information collected in this study with the phenological observations of Salisbury (1916), Ellenberg (1939), Lieth (1970) and Williamson (1976), which refer to several of the species encountered in this investigation, e.g. *Anemone nemorosa*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Festuca rubra*, *Poa trivialis* and *Ranunculus ficaria*.

### *Interpretation of the results*

#### *Competitive exclusion*

From propositions (2), (3) and (8) on pp. 760–1 it is to be expected that competitive exclusion will be detectable at sites in which herbaceous vegetation is growing under fertile conditions and is subject to little disturbance.

Six of the sites examined in this study (Sites 1–6) conformed to this pattern, and all contained relatively few species. At each there was a high peak in standing crop during the summer ($>400$ g $m^{-2}$), and at this peak most of the living shoot material was accounted for by a single species. The dominant species were *Urtica dioica* (Sites 1 and 6), *Pteridium aquilinum* (Site 2), *Chamaenerion angustifolium* (Site 3), *Filipendula ulmaria* (Site 4) and *Petasites hybridus* (Site 5). It is immediately obvious that these plants have a number of morphological and phenological characteristics in common. Each produces a tall, dense leaf canopy, and is capable of lateral spread by means of rhizomes. In all five species there is no leaf canopy during the winter, and the shoots (or radical leaves, in the case of *P. hybridus*) are relatively massive structures which depend for their initial expansion upon mobilization of underground reserves of photosynthate. An additional characteristic shared by all five species is the coincidence of full leaf expansion with the period June–August, when daylength, irradiance and temperature are conducive to high productivity.

Although it seems likely that, to a large extent, the low species-densities in Sites 1–6 are due to the ability of a single species to monopolize the aerial environment during the late spring and summer, further analysis is required in order adequately to account for the scarcity of associated herbs at these sites. In particular, it is necessary to explain why species with shoot phenologies complementary to the dominants, i.e. vernal or evergreen plants, tend to be excluded. From the results of this investigation there is strong evidence suggesting that the exclusion mechanism depends upon the presence throughout the year of a high density of herbaceous litter. Three features of the results support this conclusion.

First, in the site which most nearly approximates to a single-species stand (Site 2) the dominant plant, *Pteridium aquilinum*, is a frost-sensitive species with a short-lived canopy, and the most constant feature of the aerial environment is the presence of a very dense accumulation of litter, which shows comparatively little variation with season. This situation contrasts strikingly with that at Site 5, in which the abundant litter deposited by *Petasites hybridus* decays rapidly to a minimum in the spring, at which time *Poa trivialis* and *Galium aparine* make a major contribution to the standing crop.

A second observation which suggests the importance of litter in the mechanism of competitive exclusion concerns the morphology and vernation of the herbaceous plants frequent at Sites 1–6. Without exception, the shoots of these plants are robust structures capable of penetrating a thick layer of litter and expanding the leaf laminae above it. These features occur not only in the dominants but in the small number of associated species [*Agropyron repens* (Sites 1, 2 and 3), *Arrhenatherum elatius* (Site 3), *Anemone nemorosa* (Site 4) and *Mercurialis perennis* (Site 4)]. It is also interesting to note that the large-seeded annual *Galium aparine* was recorded at several sites with copious litter (Sites 1, 3, 5 and 6), and that during the sorting of samples collected in the spring numerous seedlings of this species with extended hypocotyls penetrating the litter were observed.

The third source of evidence concerning the role of litter arises from the abundance of bryophytes at Sites 1, 3, 5 and 6. At each of these sites, bryophytes expanded rapidly during the moist cooler periods in the year to form a discontinuous layer *above* and in intimate association with the herbaceous litter. In another paper the implications of this phenomenon will be discussed; here it is relevant merely to comment that both the luxuriance of the bryophyte cover and its specific location indicate that in these sites litter, either as a source of shade or as a physical barrier to the extension of the shoots, appears to have been the only factor excluding vernal or evergreen herbs.

It is concluded, therefore, that the low species-densities at Sites 1–6 are due to competitive exclusion, a process arising from vigorous growth by 'competitive dominants' (see p. 762)—species which are strongly competitive, attain a large size, and subject smaller species to forms of stress by shading, depletion of soil mineral nutrients and through the deposition of litter.

### *Debilitation of competitive species*

According to the arguments advanced under points (3) and (5) on pp. 760–1, at sites in which the density of herbaceous shoot material and litter is restricted by stress and/or disturbance, it is to be expected that potentially competitive species will be reduced in vigour, and that species of lower competitive ability will be able to co-exist with them. Confirmation of this prediction may be obtained by examining the data for Sites 7–13, at each of which the sum of the standing crop and the herbaceous litter (both values taken at the time when the former is at its maximum) fell below 800 g $m^{-2}$. The most conspicuous of the 'debilitated competitors' were *Pteridium aquilinum* (Site 9), *Urtica dioica*

(Site 7), *Holcus mollis* (Site 8) and *Brachypodium pinnatum* (Site 13). For each of these species an attempt can be made to recognize the symptoms and causes of reduced vigour.

Comparison of the performance of *Pteridium aquilinum* at Sites 2 and 9 shows that in the woodland conditions at the latter site the species was extremely stunted in growth, a phenomenon which was almost certainly due, in part, to the infertile acidic soil and to absorption of mineral nutrients by tree roots. However, perhaps of greater significance was the effect of shade from the trees. This conclusion is suggested by the premature decline in shoot dry weight of *P. aquilinum* at Site 9, a process which coincided with full expansion of the tree canopy.

Similar effects of the tree canopy appear to have operated with respect to *Urtica dioica* (Site 7) and *Holcus mollis* (Site 8). In both cases, comparison with neighbouring unshaded sites (for *Urtica dioica* cf. Site 6) revealed several symptoms associated with reduced vigour. In both species the peak in dry matter occurred prior to full expansion of the tree canopy, and there was a marked reduction in flowering. During the shaded summer phase *Holcus mollis* at Site 8 became extremely etiolated, and premature senescence of the shoots was associated with widespread infection by mildew.

In comparison with its performance on deeper soils in nearby hollows, *Brachypodium pinnatum* at Site 13 showed a marked reduction in vegetative vigour, litter accumulation and inflorescence production. Site 13 was situated on a steep slope with a shallow calcareous soil, and it seems likely that the vigour of *B. pinnatum* was held in check by limitations in supply of mineral nutrients.

Two further examples of the persistence of suppressed specimens of species of potentially high competitive ability occurred in the derelict grassland on the north-facing slopes of Lathkilldale (Site 11). The species concerned, *Holcus lanatus* and *Festuca rubra*, resembled the other plants noted under this heading in that a peak in shoot dry weight occurred during the summer. Evidence of the moderately high potential of these plants for competitive dominance is available from separate investigations (Thurston 1969; Smith, Elston & Bunting 1971), in which marked expansions in these species coinciding with the disappearance of smaller associated species were recorded following the application of mineral fertilizers to unproductive base-rich and calcareous grasslands.

### *Selection of species of lower competitive ability*

From the arguments advanced under points (5) and (6) on p. 761, it is predictable, first, that at sites in which the standing crop and amount of litter remains low, species of lower competitive ability will predominate; and, secondly, that the phenologies of these plants will reflect the relative importance of stress and disturbance in the mechanisms limiting the shoot biomass. Where stress is the major determinant the dominant phenology is likely to be that of the evergreen, whereas at sites subjected to disturbance the prevailing phenologies will be short and adapted to exploit the intervals between successive disturbances, or between disturbance and the re-establishment of a closed canopy of competitive species. In some situations moderate intensities of both stress and disturbance occur, and here it is to be expected that the phenologies will be intermediate between those of extreme stress-tolerant and ruderal species.

Within the spectrum of phenologies displayed by plants of lower competitive ability in this study, three particular types may be recognized:

(1) *Evergreens.* The group of plants here described as evergreens includes species such

as *Carex flacca* in which no significant seasonal fluctuation in living shoot material was detected, and also species such as *Festuca ovina* in which, although green material was present throughout the year, there was a well-defined summer peak.

In the present study, evergreens were excluded from the six most productive sites (Sites 1–6). However, it is interesting to observe that the least productive of these (Site 5) contained *Mercurialis perennis*, a species in which only a brief interval separates the senescence of overwintering leaves and the expansion of new shoots in the spring.

All of the woodland and grassland sites examined contained evergreen species, and with the exception of two of the woodland sites (7 and 8) these plants formed a major component of the vegetation. In the woodlands, the most prominent evergreens were *Deschampsia flexuosa* (Sites 9 and 10), *Galeobdolon luteum* (Site 8), *Milium effusum* (Site 8) and *Veronica montana* (Site 7). The grassland evergreens included *Carex flacca* (Sites 11, 12 and 13), *Koeleria cristata* (Sites 11 and 12), *Carex caryophyllea* (Sites 11 and 13), *Anthoxanthum odoratum* (Site 11), *Briza media* (Site 13), *Helianthemum chamaecistus* (Site 12), *Festuca ovina* (Site 12), *Helictotrichon pratense* (Site 12) and *Plantago lanceolata* (Site 13).

(2) *Vernals*. A general feature of the vegetation examined in this study was the scarcity of ruderal plants. With the exception of *Galium aparine* (Sites 1, 3 and 7), no annual species contributed significantly to the standing crop at any of the sites investigated. This may be related to the fact that none of the habitats was subject to severe forms of disturbance. However, one particular ruderal characteristic—a brief shoot phenology—was apparent in four perennial plants, which, together with *G. aparine*, formed a rather heterogeneous group of plants, here described as 'the vernals'. In the early spring these species exhibited a rapid expansion of the shoot, and this was followed by an equally rapid decline in the late spring and early summer. The earliest and most truncated shoot growth periods occurred in three geophytes, *Ranunculus ficaria* (Site 7), *Endymion non-scriptus* (Site 8) and *Anemone nemorosa* (Sites 4 and 7); in each of these species expansion of the shoot was initiated by mobilization of reserves from underground storage organs. In *Poa trivialis* (Sites 5, 6 and 7), which, like *Galium aparine*, was characterized by a longer phase of shoot expansion extending into the early summer, there are no such underground reserves, and here shoot growth appeared to be a function of photosynthetic activity.

All of the perennial vernal species, and, in particular, the three geophytes, have characteristics (low stature, limited capacity for lateral spread) previously associated with low competitive ability (Grime 1973a, c; Mahmoud & Grime 1976), and in this respect they resemble ruderal plants such as the summer annuals of arable fields. An additional feature of the vernals is their intolerance of deep shade, a characteristic first noted by Blackman & Rutter (1950) in experiments with *Endymion non-scriptus*. It would appear, therefore, that the most important characteristic of the vernals is their ability to exploit the existence during the spring, in certain types of herbaceous vegetation, of temporary periods in which there are opportunities for the growth of species of low competitive ability.*

Evidence in support of this hypothesis is available from the present investigation. It has been noted earlier in this discussion (p. 783) that herbaceous litter appears to play a major role in competitive exclusion, and examination of the results reveals that at each

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* In this respect they conform to the 'perennial ephemeroids' of Noy-Meir (1973) and the 'stress-tolerant ruderals' of Grime (1977).

of the three sites in which vernals were prominent the quantity of herbaceous and tree litter was low during the spring. These sites consisted of a tall-herb community (Site 5), in which the low density of litter was caused by the rapid decay of the leaves of *Petasites hybridus*, and two woodland sites (Sites 7 and 8), where the small quantity of herbaceous litter could be related to the fact that the growth and litter production of the potentially productive components of the herb layer was severely reduced by shade and/or depletion of soil mineral nutrients by the trees. It is interesting to note that in these two woodland sites full expansion of the vernal element also coincided with the seasonal minimum in the density of tree litter.

(3) *Deep-rooted forbs.* A third group of species of relatively low competitive ability may be recognized, composed of five forbs (*Campanula rotundifolia*, *Centaurea nigra*, *Leontodon hispidus*, *Lotus corniculatus*, *Poterium sanguisorba*), the phenology of which resembled the competitive species in that there was a well-defined summer peak in shoot production. However, in certain other respects these plants differed considerably from the competitive species. In each the shoot was composed of one or more rosettes of leaves, a morphology which severely restricts both the height of the leaf canopy and the capacity for lateral spread above and below ground. An additional characteristic of these species is the presence in the majority of individuals of a tap-root system. As Walter (1973) has pointed out, such roots often penetrate deep fissures and allow the species to exploit reserves of moisture which are inaccessible to grasses and other shallow-rooted plants, many of which may become severely desiccated during the summer.

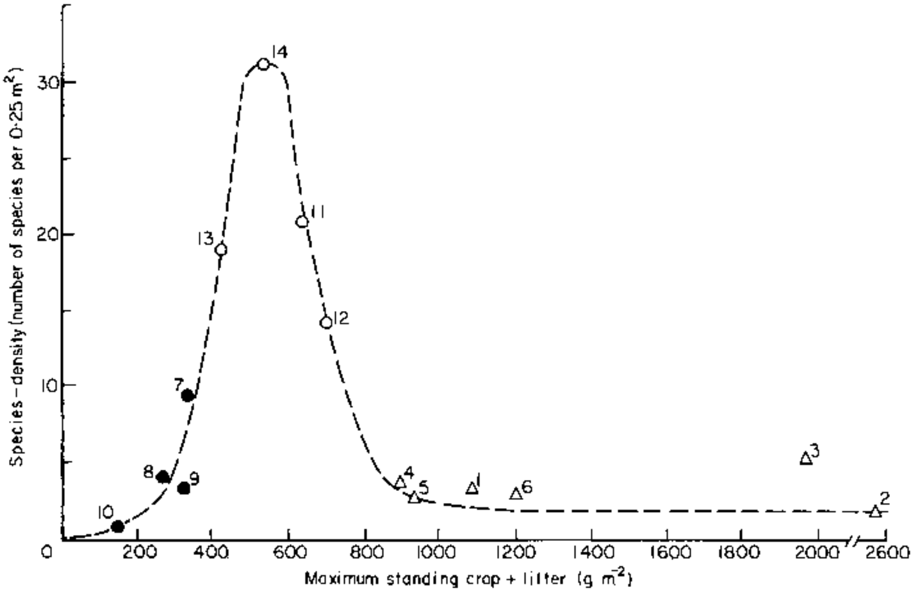

FIG. 13. The relationship between maximum standing crop plus litter and species-density of herbs at fourteen sites. ○, Grasslands; ●, woodlands; △, tall herbs. The curve is fitted by eye.

*Control of species density*

Earlier in this discussion it was concluded that measurements of the dry weights per unit area of shoot material and litter allow predictions to be made with regard to the intensity of phenomena such as competitive exclusion, the debilitation of competitive species and the incursion of species of lower competitive ability. The possibility arises, therefore, that the same measurements may be used to delimit components of the mechanism controlling species-density.

In Fig. 13 species-densities, recorded as the number of herbaceous species per 0·25 $m^2$, have been plotted against the sum of the dry weights of standing crop and litter (herbs plus trees), both taken at the time of the maximum in the standing crop. Figure 13 includes data for the thirteen sites involved in this study, together with comparable data collected simultaneously (S. B. Furness and J. P. Grime, unpublished) at an additional site (Site 14) located in an area of ancient species-rich limestone grassland, subjected to grazing by sheep and cattle, on a north-facing slope in Cressbrookdale.

The hump-backed curve in Fig. 13, depicting the change in species-density with increase in total weight of standing crop and litter, is consistent with the model proposed by Grime (1973c), and suggests that high species-densities are characteristic of a corridor of values for standing crop plus litter extending between about 350 and 750 g $m^{-2}$. Above this range (Sites 1–6), competitive exclusion occurs, whilst below it (Sites 7–10), the low species-densities are due to the small number of species adapted to withstand the combinations of the various forms of stress and disturbance occurring in these environments.

The precise form of the relationship described in Fig. 13 is clearly a function of sample size, and will be affected also by factors peculiar to the sites and to the period of the investigation. Further investigation on a wider variety of vegetation types, and collation of evidence from existing published sources will be necessary, in order, first, to define more accurately the range in total weight of standing crop and litter corresponding to the potential for high species-density; and, secondly, to recognize the additional factors which determine the species-densities realized at specific sites falling within this critical range.

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## APPENDIX

Lists of the species of flowering plants present within each of the sampled sites. Species appearing in Figs 5–12 are marked with asterisks.

Site 1
*Agropyron repens**
*Cirsium arvense*
*Galium aparine**
*Heracleum sphondylium*
*Poa trivialis*
*Ranunculus ficaria*
*Urtica dioica**

Site 2
*Arrhenatherum elatius*
*Chamaenerion angustifolium*
*Galium aparine*
*Holcus lanatus*
*Moehringia trinervia*
*Poa trivialis*

*Pteridium aquilinum**
*Rubus fruticosus*
*Urtica dioica*

Site 3

*Agropyron repens**
*Agrostis tenuis*
*Arrhenatherum elatius**
*Chamaenerion angustifolium**
*Dactylis glomerata*
*Festuca rubra*
*Galium aparine**
*Heracleum sphondylium*
*Lathyrus montanus*
*Pimpinella major*
*Poa pratensis*
*P. trivialis*
*Poterium sanguisorba*
*Rumex acetosa*
*Urtica dioica**
*Vicia sepium*

Site 4

*Anemone nemorosa**
*Anthoxanthum odoratum*
*Arrhenatherum elatius*
*Centaurea nigra*
*Festuca rubra*
*Filipendula ulmaria**
*Galium aparine*
*Geum rivale*
*Heracleum sphondylium*
*Holcus lanatus*
*Lathyrus pratensis*
*Mercurialis perennis**
*Poterium sanguisorba*
*Ranunculus ficaria*

Site 5

*Agropyron repens*
*Cardamine flexuosa*
*Epilobium hirsutum*
*Filipendula ulmaria*
*Galium aparine*
*Petasites hybridus**
*Poa trivialis**
*Urtica dioica*

Site 6

*Allium ursinum*
*Anthriscus sylvestris*
*Cardamine flexuosa*
*Chamaenerion angustifolium*
*Convolvulus arvensis*
*Cirsium arvense*
*Epilobium hirsutum*
*Equisetum arvense*
*Galium aparine**
*Heracleum sphondylium*
*Mercurialis perennis*
*Myosotis sylvatica*
*Poa trivialis**
*Ranunculus ficaria*
*Rubus fruticosus*
*Silene dioica*
*Stellaria holostea*
*Urtica dioica**

Site 7

*Alliaria petiolata*
*Allium ursinum*
*Anemone nemorosa**
*Arum maculatum*
*Cardamine flexuosa*
*Chrysosplenium oppositifolium*
*Circaea lutetiana**
*Festuca gigantea**
*Galium aparine**
*Hedera helix*
*Heracleum sphondylium*
*Mercurialis perennis**
*Myosotis sylvatica*
*Myrrhis odorata*
*Poa trivialis**
*Polygonum cuspidatum*
*Ranunculus ficaria**
*R. repens*
*Rubus fruticosus*
*Rumex obtusifolius*
*Silene dioica*
*Stachys sylvatica*
*Urtica dioica**
*Veronica montana**

Site 8

*Circaea lutetiana*
*Endymion non-scriptus**
*Galeobdolon luteum**
*Holcus mollis**
*Milium effusum**
*Oxalis acetosella*
*Rubus fruticosus*
*Silene dioica*
*Stellaria holostea*
*Veronica montana*

Site 9

*Deschampsia flexuosa**
*Endymion non-scriptus*
*Hedera helix*
*Holcus mollis**
*Milium effusum**
*Pteridium aquilinum**

Site 10

*Deschampsia flexuosa**
*Luzula sylvatica*
*Pteridium aquilinum*

Site 11

*Achillea millefolium*
*Agrostis tenuis*
*Angelica sylvestris*
*Anthoxanthum odoratum**
*Brachypodium sylvaticum*
*Briza media*
*Campanula rotundifolia*
*Carex caryophyllea*
*C. flacca**
*C. pulicaris*
*Centaurea nigra**
*Cerastium holosteoides*
*Cirsium palustre*
*Corylus avellana*
*Dactylis glomerata*
*Deschampsia cespitosa*
*Epilobium montanum*
*Festuca ovina**
*F. rubra**
*Fragaria vesca*
*Galium mollugo*
*G. sterneri*
*G. verum*
*Geum rivale*
*Helictotrichon pratense**
*H. pubescens**
*Heracleum sphondylium*
*Hieracium pilosella*
*Holcus lanatus**
*Hypericum perforatum*
*Koeleria cristata**
*Lathyrus montanus*
*Leontodon hispidus*
*Lotus corniculatus*
*Luzula campestris*
*Pimpinella saxifraga*
*Plantago lanceolata*
*Poa pratensis*
*Potentillo erecta*
*P. sterilis*
*Poterium sanguisorba**
*Ranunculus bulbosus*
*Rumex acetosa*
*Succisa pratensis**
*Taraxacum officinale*
*Valeriana officinalis*
*Veronica chamaedrys*
*V. montana*
*Viola riviniana*

Site 12

*Allium ursinum*
*Arabis hirsuta*
*Arrhenatherum elatius*
*Briza media*
*Campanula rotundifolia*
*Carex caryophyllea*
*C. flacca**
*C. pulicaris*
*Centaurea nigra*
*C. scabiosa*
*Cirsium vulgare*
*Crepis capillaris*
*Festuca ovina**
*F. rubra*
*Fragaria vesca*
*Galium sterneri*
*Helianthemum chamaecistus**
*Helictotrichon pratense**
*H. pubescens*
*Heracleum sphondylium*
*Hieracium pilosella*
*Hieracium* sp.
*Inula conyza*
*Koeleria cristata**
*Linum catharticum*
*Lotus corniculatus*
*Medicago lupulina*
*Pimpinella saxifraga*
*Plantago lanceolata*
*Polygala vulgaris*
*Poterium sanguisorba*
*Senecio jacobaea*
*Teucrium scorodonia*
*Thymus drucei*
*Veronica montana*
*Viola hirta*

Site 13

*Agrostis tenuis*
*Anthoxanthum odoratum*
*Arrhenatherum elatius*
*Betonica officinalis*
*Brachypodium pinnatum**
*Briza media**
*Bromus erectus*
*Campanula rotundifolia**
*Carex caryophyllea**
*C. flacca**
*Centaurea nigra**
*Cirsium arvense*
*Crataegus monogyna*
*Dactylis glomerata*
*Festuca ovina*
*F. rubra*

_Helictotrichon pubescens_
_Hieracium pilosella_
_H. lachenalii*_
_Holcus lanatus_
_Hypericum pulchrum_
_Lathyrus montanus_
_Lathyrus pratensis_
_Leontodon hispidus*_
_Linum catharticum_
_Lotus corniculatus*_
_Luzula campestris_
_Plantago lanceolata_
_Poa annua_
_P. pratensis_
_Polygala vulgaris_
_Potentilla erecta_
_Sieglingia decumbens_
_Taraxacum officinale_
_Trifolium medium*_
_Trisetum flavescens_
_Viola hirta_
_V. riviniana_