Mixed Grazing and Climatic Determinants of White Clover (Trifolium repens L.) Content in a Permanent Pasture

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The effects of grazing regime (cattle, sheep and mixed cattle + sheep) on white clover content (clover dry matter as a percentage of total dry matter) were measured in a permanent pasture over a 7 year period in the west of Ireland (53°17'N 8'47'E). Rotational grazing was simulated by grazing for short intense periods of 3-4 d at 3 to 5 week intervals. In general, cattle grazing resulted in higher clover content (13.5%) compared with mixed (9.5%) or sheep (4.9%) grazing. The ranking of clover contents (cattle > mixed > sheep) which developed rapidly in 1990 persisted until 1996. Clover contents under mixed grazing tracked those under cattle grazing during the first 4 years, and sheep grazing during the final 3 years. Within-year relativities in clover content among grazing regimes that existed at the start of the grazing season persisted throughout the year. There was an indication that differences in clover content between grazing regimes at the end of grazing persisted until the following spring. A regression analysis of clover content in each grazing period showed strong effects of grazing regime, generally positive relationships with mean air temperature in the period and clover content in the preceding period, and an interaction between air temperature and clover content in the previous period. Implications for pasture management and experimentation are discussed.

Key words: Mixed grazing, cattle, steers, sheep, temperature, precipitation, climate, community dynamics, competition, statistical modelling, white clover, Trifolium repens, clover content.

INTRODUCTION

In Ireland, about 80% of grazing land consists of permanent pastures with an estimated growing season clover content (average clover dry matter (DM) as a percentage of total DM) of 5%. About 3% of pastures are re-seeded annually.

Introduction/regeneration of white clover is motivated by its ability to substitute for fertilizer nitrogen (N) use and to improve pasture quality relative to grass-only swards (Thomson, 1984; Laidlaw and Teuber, 2001). Generally, white clover is grown in association with one or more grass varieties and, for meat production, is grazed by cattle and sheep separately or together. Low sward clover content and its variability among years, with time of year, and with management practices are the main problems encountered.

The success of establishment/regeneration varies with the method used (Naylor et al., 1983; Culleton et al., 1988; Tiley and Frame, 1988; Muto and Martin, 2000) and with the incidence of pests and disease (Boatman and Haggar, 1985; Ferguson et al., 1988; Martin, 1991; Rhodes et al., 1998; Goldson et al., 2000). A clear framework for predictable success has not yet emerged, perhaps due to the wide range of potential influences involved and the difficulty of researching more than a few of these within any one experiment.

The persistence of sward clover depends upon the effects of companion grass species (Chestnutt and Lowe, 1970; Frame, 1990; Woledge et al., 1992; Collins et al., 1996; Barthram, 1997), of pests and disease indicated above, and of changes in clover morphology (Curll et al., 1985a,b; Fothergill et al., 1996) and physiology (Orry et al., 1998). These factors are influenced by a range of management interventions (Nolan, 1975; Curll et al., 1985a,b; Hoglind and Frankow-Lindberg, 1998; Fothergill et al., 2000a,b) and climatic characteristics (Brougham, 1959; Wachendorf et al., 2001b). Physiological and simulation models suggest that legume dynamics in mixed pastures cannot be fully understood without combining ecological and physiological concepts of species interactions at three different scales: competitive interactions at the patch-scale, dispersal at the between-patch scale, and seasonality at the field-scale (Schwinning and Parsons, 1996a,b, 1999). The effects of grazing management, animal behaviour and climatic factors are reviewed briefly in the following sections.

Grazing management

Comparisons of different systems of sheep grazing management, and combinations of sheep grazing and resting for conservation, have indicated that resting early in the season (Sheldrick et al., 1993), in either mid or late season (Curll and Wilkins, 1985) or in late season only (Fothergill et al., 2000a), or exploitation of the rest period involved in rotational grazing (Brock et al., 1988), can help to maintain sward clover content. Other studies suggest that resting benefits clover by allowing it to attain a sufficiently
high position in the canopy from where it can intercept irradiation, and that resting for too long, or a wrongly timed rest period, can have deleterious effects due to shading by the grass component (Newton and Davies, 1987; Orr et al., 1990; Grant and Barthram, 1991; Sheldrick et al., 1993; Barthram and Grant, 1995). Curl and Wilkins (1985) found that timing of the rest period had no effect at low stocking rates, but at high stocking rates mid- or late-season rests were most beneficial.

The importance of within-sward variability in cattle-grazed grass/clover swards, associated with dung soiling, has been emphasized in many reports (Nolan and Connolly, 1977, 1988; de Rancourt et al., 1980; Gibb and Baker, 1989; Murphy et al., 1995a). Gibb et al. (1989) found that continuous grazing by beef cattle of perennial ryegrass/white clover swards, of differing initial clover contents at three heights, resulted in similar clover contents at a given height after 3 years. Johnson and Morrison (1997) found that the proportion of clover in a sward grazed by beef cattle varied seasonally but was not affected by grazing height or N application (0 and 50 kg ha\(^{-1}\)).

Many studies attest to the plasticity of clover response and its ability to recover within a relatively short period under different managements and N fertilizer application (Laidlaw, 1984; Curl et al., 1985b; Brock et al., 1988; Fothergill et al., 1996; Elgersma et al., 1998; Hoglind and Frankow-Lindberg, 1998; Muto and Martin, 2000). Several experiments have shown that the variability of clover contribution is related to the fragmentation of plants in winter, resulting in an increase in simply-structured, lighter plants (Brock et al., 1988; Fothergill et al., 1996, 2000b; Hoglind and Frankow-Lindberg, 1998; Muto and Martin, 2000).

Results on defoliation management and under controlled laboratory conditions are perhaps most relevant in elucidating mechanisms such as interspecific competition (Boatman and Haggar, 1985) and physiological responses (e.g. Orry et al., 1998; Grant and Barthram, 1991; Barthram and Grant, 1995). They shed little light on grazing responses, primarily due to differential and preferential grazing patterns among animal species (Bjarnason, 1984; Nolan and Connolly, 1989), and the spatially complex nature of the animal contribution to nutrient cycling (Murphy et al., 1995b).

Grazing animal diet selection

Generally sheep have a higher preference for clover than cattle. Many studies have shown how preferential selection among plant species and, under mixed grazing, differential selection between animal types, greatly modifies sward state and can modify the sward to the benefit of another species (Curl et al., 1985a,b; Collins, 1989; Nolan and Connolly, 1989; Wright et al., 1992; Parsons et al., 1994; Murphy et al., 1995a; Del Pozo and Osoro, 1997; Del Pozo et al., 1997; Nolan and Nastis, 1997; Nolan et al., 1999; Soegaard et al., 2000). Sheep grazing, in producing relatively uniform swards, and cattle grazing, in creating patchy swards consisting of up to 40% refused cattle dung-soiled areas (de Rancourt et al., 1980; Gibb and Baker, 1989; Nolan and Connolly, 1989; Murphy et al., 1995a), greatly modify the environment for clover development. These effects may vary with sward management, pasture availability and time (Concha and Niclo, 2000).

Climate/weather

Temperature requirements for clover are higher than those for perennial ryegrass (Mitchell, 1956; Davies, 1992). The effects of temperature on clover growth (Jelmini and Nösberger, 1978), and on increasing sward clover content under laboratory and field conditions (Brought, 1959; Newton et al., 1994), are well documented. Temperature, radiation and precipitation were intimately involved in determining sward clover content throughout the annual cycle in a comparison of two cultivars under cutting management across 12 sites over several years (Wachendorf et al., 2001a,b).

Irradiance influences clover performance both by its intensity (Benhart, 1963) and quality (Thompson and Harper, 1988; Thompson, 1993, 1995). Its impact can be modified by grazing/cutting management (Grant and Barthram, 1991; Barthram and Grant, 1995). However, there is evidence (Faurie et al., 1996) that trade-offs between the greater ability of clover to capture light than its associated grass species (Lantinga et al., 1999), and its poorer use of captured light, may reduce the impact of light as a determinent of compositional change in clover-grass mixtures.

Although clover can extract water from deeper soil layers than ryegrass (Guckert et al., 1993), it is more sensitive to drought than the agriculturally important grasses (Low and Armitage, 1959; Stiles, 1966; Guckert et al., 1993; Lucero et al., 1999). The relationship between clover content over the growing season and precipitation is complex (Kleter, 1968; Bircham and Gillingham, 1986; Wachendorf et al., 2001b). It is likely that grazing managements that alter the sward state also change the microclimate within the vegetation canopy and can be expected to modify these climatic effects.

That clover-grass associations form a complex, dynamic system with great flexibility and plasticity, which respond to many different factors, is clear from this review. The degree to which the variability of the clover contribution for a particular system can be reliably controlled by management interventions is less easy to discern. This paper sets out to address two questions: (1) what are the effects of grazing by sheep and cattle on clover content in a permanent grassland sward and to what extent are these modulated by mixed grazing; and (2) to what extent is variability in clover content during the grazing season affected by climate under a particular grazing regime?

MATERIALS AND METHODS

Experimental location and layout

The experiment was conducted at Teagasc Research Centre, Athenry, Ireland (53°17’N 8°47’E) on a loam/rendzina soil
Grazing and vegetation

Three grazing regimes were used: cattle (eight 1-year-old steers); sheep (22 1-year-old dry sheep); and mixed (four steers + 11 sheep), chosen on the basis of previous experience and results (Connolly and Nolan, 1976; Nolan and Connolly, 1989) as similar; this was subsequently verified (see below) by the approximate equivalence of pre-grazing DM over the experiment. All grazings were standardized for periods of 3-4 d, at about 3 to 5 week intervals for the years 1990–1994 (Table 1). For 1995 and 1996, the protocol was changed: blocks 1 and 5 were grazed at 3 week (Short) intervals and blocks 2 and 4 at 4 week (Long) intervals, and these were respectively increased to about 4 and 5 weeks from July to simulate different rotational grazing speeds. Block 4 was omitted from 1994 onwards. The mean pre-grazing total DM (kg ha\(^{-1}\)) for cattle-grazed plots over the 7 years was 4.1 and 5.9% greater than for sheep- and mixed-grazed plots, respectively. N fertilizer was applied to all plots at a rate of 51 kg ha\(^{-1}\) in spring.

Five randomly selected areas (each 10 cm × 100 cm) within each plot were clipped to 1–2 cm above ground level with electric hand-held Gardina shears before each grazing. All material was weighed fresh and, generally, two 100 g samples were separated into grass and clover components, which were dried in a hot air oven for 16 h at 90 °C and weighed. Clover content and total DM (kg ha\(^{-1}\)) were then calculated.

Statistical methods

Clover contents are presented on both percentage and logarithmic scales. They were converted to the logarithmic scale for analysis to correct for non-normality and heteroscedasticity, and the standard errors of differences (s.e.d.) and tests of significance are presented for that scale only. Twenty out of a total of 683 clover content values were zero and these were replaced by 0.386, the lowest non-zero clover content in the data, before transforming to the logarithmic scale. For each year, log(clover content) was analysed as a randomized block design with grazing regime as the treatment factor. Within years, a repeated measures analysis was performed to assess the effect of grazing date. A split-plot analysis was used, the validity of which was satisfactory for the repeated measures data.

While the analysis above provided considerable insight into the effects of grazing regime and its interaction with grazing period, it left unexplained variations in the pattern of clover content across periods from year to year. It is argued that clover content in a particular plot and period is the resultant of the sward status entering the period, the treatments (grazing regime) applied during the period, and other factors affecting the system during the period and perhaps during the preceding period. A regression model was developed that related log(clover content) for each plot in each grazing period in each year to: grazing regime; climatic variables measured during the present and, perhaps during the preceding period; and to a set of independent variables defining sward state in the preceding period. The climatic variables examined (not available for 1994) were mean and accumulated air temperature (°C), mean and total radiation (J cm\(^{-2}\)) and mean and total precipitation (mm) during the period and the preceding period. These were correlated at the Birr meteorological station (53°05'N 7°54'E, 57 m above sea level) located about 80 km from the research site, in a region of uniform topography and climate. The variables characterizing sward status during the previous period were clover content and total DM, both on the logarithmic scale. The first period of the grazing

Table 1. Dates of grazing for 1990 to 1996 (January 1st = day 1)

<table>
<thead>
<tr>
<th>Year</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Grazing period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>185</td>
<td>204</td>
<td>232</td>
<td>253</td>
</tr>
<tr>
<td>1991</td>
<td>84</td>
<td>112</td>
<td>140</td>
<td>168</td>
</tr>
<tr>
<td>1992</td>
<td>100</td>
<td>132</td>
<td>160</td>
<td>199</td>
</tr>
<tr>
<td>1993</td>
<td>96</td>
<td>140</td>
<td>172</td>
<td>207</td>
</tr>
<tr>
<td>1994</td>
<td>101</td>
<td>122</td>
<td>143</td>
<td>172</td>
</tr>
<tr>
<td>1995</td>
<td>96</td>
<td>117</td>
<td>138</td>
<td>159</td>
</tr>
<tr>
<td>1996</td>
<td>96</td>
<td>124</td>
<td>152</td>
<td>180</td>
</tr>
</tbody>
</table>

1 and 2 refer to Short and Long rest periods between grazings.
In 1995 and 1996, rotations in blocks 1, 3 and 5 had a shorter duration (Short) and those in blocks 2 and 4 had a longer duration (Long).
season was excluded owing to a lack of measurements of clover content for the preceding winter period. The error structure included year-to-year and within-year (across grazing period) components. Sphericity of within-year error structure was tested and there was no evidence of a more complex error structure. Block was tested and omitted from the final model as not significant. REML (Restricted Maximum Likelihood) as implemented in Genstat (Payne et al., 1993) was used to fit the models and allow for the complex error structure.

The methodology used here is based on that described in Connolly and Wachendorf (2001), where many statistical and other issues relevant to the modelling are discussed. In particular, the use of initial biotic conditions in modelling growth in mixed species communities is not widespread, with much of the literature using the initial densities of species (Suehiro and Ogawa, 1980; Spitters, 1983; Firbank and Watkinson, 1985; Connolly et al., 1990; Menchaca and Connolly, 1990; Gibson et al., 1999). Connolly and Wayne (1996) used initial seedling biomass of two species as independent variables in a model of the growth of two competing weed species immediately following establishment. The ratio of species leaf area early in the growth of a crop-weed community was used in Kropf and Spitters (1991) in modelling crop yield loss from weed competition. Wachendorf et al. (2001b) employed this strategy extensively in modelling growth dynamics of clover in grass/clover swards at 12 sites in Europe. Connolly et al. (2001) stressed the need to allow for initial biotic conditions in modelling competitive effects in community development to avoid the possibility of bias due to differences in the initial sizes of the competing species. This approach prevents the confounding of starting differences among species with aspects of interspecific interaction that occur during the period of study, a problem that is present in virtually all current approaches to the analysis of mixed species communities (Gibson et al., 1999; Connolly et al., 2001). In communities of perennial species, the use of species densities at the start of a growth period can present difficulties. Density may not be a meaningful measure and may be very difficult to determine for a species such as white clover once it has spread by clonal reproduction, whereas its contribution to swards can be determined by sampling at any stage. When interest centres on a particular phase of growth, long after sward establishment, it may be more sensible to use the community status at the start of the period of interest rather than at the start of the experiment as a reference point for what happens during the period. The observed sward state variables at the start of the period of interest are taken largely to integrate the previous history of the sward.

**RESULTS**

*Mean growing season clover content*

In each year, the mean growing season clover content was highest for cattle grazing, intermediate for mixed, and lowest for sheep grazing (Table 2). Averaged over all years, the clover contents were 13.5, 9.3 and 4.8 % for cattle, mixed and sheep grazing, respectively. For cattle grazing, the 1995 clover content (7.8 %) was comparatively very low. Clover contents for the sheep and mixed regimes were low during the final 3 years. In all years, cattle grazing resulted in higher ($P < 0.05$) mean clover contents than sheep grazing. Mixed grazing generally led to lower annual clover content than cattle grazing, significantly so in 1993, 1994 and 1995. The overall clover content for mixed grazing was higher than for sheep grazing, significantly so ($P < 0.05$) in 1990 to 1993. Clover content under mixed grazing was closer to that under cattle grazing in the first 4 years and to sheep grazing in the final 3 years.

**Within-year patterns**

F-values and their significant for the effects of grazing regime, dates of grazing and the interaction between these two factors on log(clover content) for each year are shown in Table 3. Generally, the effects of grazing regime and grazing period were significant but their interaction was not. Clover content was generally at a maximum in July and August (days 180–250) for all years, although the pattern differed widely among years (Fig. 1). On the percentage scale (Fig. 1A–F), there was a clear change in the differences among treatments with advancing grazing date but with grazing regimes generally preserving their relative order of clover content. The non-significance of the grazing regime x period interaction in most years for log(clover content) suggests that the proportional difference between treatments in clover content remained broadly constant with grazing period and this is reflected in the patterns shown in Fig. 1. On the logarithmic scale (Fig. 1H–N) the mean response lines are roughly parallel across grazing dates for all years. Thus, if clover content for cattle grazing was twice as high as for mixed grazing early in the season it tended to remain so

<table>
<thead>
<tr>
<th>Year</th>
<th>Cattle</th>
<th>Mixed</th>
<th>Sheep</th>
<th>s.e.d.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>14.3</td>
<td>13.3</td>
<td>6.7</td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td>15.1</td>
<td>12.5</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>1992</td>
<td>18.4</td>
<td>14.9</td>
<td>7.3</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>13.5</td>
<td>9.8</td>
<td>4.4</td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>14.0</td>
<td>5.3</td>
<td>2.4</td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>7.8</td>
<td>3.1</td>
<td>3.3</td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>11.5</td>
<td>6.5</td>
<td>5.2</td>
<td></td>
</tr>
</tbody>
</table>

The analysis was carried out on the logarithmic scale and the s.e.d. values and tests of significance are presented for that scale only. Means with different superscripts are significantly different at the 5 % level or less.

**Table 2. Mean white clover content under cattle, mixed cattle + sheep and sheep grazing for 1990 to 1996**

Table 3. F-values and significance of grazing regime, grazing period and their interaction for log(clover content) in 1990 to 1996

<table>
<thead>
<tr>
<th>Year</th>
<th>Grazing regime</th>
<th>F</th>
<th>P</th>
<th>Grazing period</th>
<th>F</th>
<th>P</th>
<th>Regime x period</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td></td>
<td>8-36</td>
<td>0.011</td>
<td>16-27</td>
<td>&lt;0.001</td>
<td>1.51</td>
<td>0.178</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td></td>
<td>21-02</td>
<td>&lt;0.001</td>
<td>30-82</td>
<td>&lt;0.001</td>
<td>2.17</td>
<td>0.016</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1992</td>
<td></td>
<td>13-65</td>
<td>&lt;0.001</td>
<td>31-48</td>
<td>&lt;0.001</td>
<td>1.18</td>
<td>0.324</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td></td>
<td>16-75</td>
<td>&lt;0.001</td>
<td>7-03</td>
<td>&lt;0.001</td>
<td>1.68</td>
<td>0.107</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td>9-84</td>
<td>0.013</td>
<td>12-27</td>
<td>&lt;0.001</td>
<td>1.62</td>
<td>0.099</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td></td>
<td>8-57</td>
<td>0.017</td>
<td>39-71</td>
<td>&lt;0.001</td>
<td>1.31</td>
<td>0.238</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td></td>
<td>3-82</td>
<td>0.085</td>
<td>8-58</td>
<td>&lt;0.001</td>
<td>0.31</td>
<td>0.985</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Model of log(clover content) in each grazing period related to log(clover content) and log(total herbage DM) in the preceding period, grazing regime and mean temperature and precipitation sum for the period

<table>
<thead>
<tr>
<th>Source</th>
<th>Estimate</th>
<th>s.e. (s.e.d.)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1-45</td>
<td>0-446</td>
<td>0.001</td>
</tr>
<tr>
<td>Cattle (C)</td>
<td>0</td>
<td>0-0859</td>
<td>S vs. M &lt;0.001</td>
</tr>
<tr>
<td>Mixed (M)</td>
<td>-0-929</td>
<td>0-0859</td>
<td>C vs. M 0.001</td>
</tr>
<tr>
<td>Sheep (S)</td>
<td>-0-989</td>
<td>0-0859</td>
<td>C vs. S &lt;0.001</td>
</tr>
<tr>
<td>Log(preceding clover content)</td>
<td>0-83</td>
<td>0-174</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Log(preceding clover content) squared</td>
<td>0-062</td>
<td>0-0238</td>
<td>0.009</td>
</tr>
<tr>
<td>Mean temperature</td>
<td>0-266</td>
<td>0-0312</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature x log(preceding clover content)</td>
<td>-0-062</td>
<td>0-0129</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

1 The mean s.e.d. for comparisons among the effects of cattle, mixed cattle + sheep and sheep grazing.

Table 5. Mean air temperature (°C) for late winter and for the grazing periods in the model

<table>
<thead>
<tr>
<th>Year</th>
<th>Jan 1 to Mar 31</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>7-26</td>
<td>16-1</td>
<td>16-1</td>
<td>15-6</td>
<td>11-5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td>5-07</td>
<td>8-0</td>
<td>9-5</td>
<td>12-2</td>
<td>14-5</td>
<td>15-5</td>
<td>14-5</td>
<td>8-3</td>
</tr>
<tr>
<td>1992</td>
<td>6-39</td>
<td>8-7</td>
<td>14-1</td>
<td>15-5</td>
<td>14-2</td>
<td>11-3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>6-43</td>
<td>9-5</td>
<td>12-7</td>
<td>14-1</td>
<td>13-6</td>
<td>10-9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>5-64</td>
<td>8-9</td>
<td>10-4</td>
<td>12-0</td>
<td>15-4</td>
<td>17-9</td>
<td>17-6</td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>5-64</td>
<td>9-9</td>
<td>10-7</td>
<td>14-4</td>
<td>17-6</td>
<td>16-8</td>
<td>12-8</td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>5-26</td>
<td>7-8</td>
<td>10-9</td>
<td>13-5</td>
<td>15-9</td>
<td>15-1</td>
<td>12-1</td>
<td></td>
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<td>1996</td>
<td>5-26</td>
<td>7-8</td>
<td>12-1</td>
<td>14-4</td>
<td>15-6</td>
<td>14-4</td>
<td>11-4</td>
<td></td>
</tr>
</tbody>
</table>

1 and 2 refer to Short and Long rest periods between grazings.
In 1995 and 1996 separate data are shown for Short and Long periods.

through the remainder of the grazing season. For all years, the relativity in the early grazing season was broadly maintained through the grazing season. In addition, relative differences among grazing regimes at the end of the grazing season were broadly reflected in differences in clover content in spring of the following year (Fig. 1).

Model of clover dynamics over the grazing season

Despite the consistency of response to grazing regime within each year, the pattern of seasonal clover content varied widely across years; it was in an attempt to understand these changes that the model was developed. The final model selected included effects of grazing regime, clover content in the preceding period, and mean temperature in the period being modelled (Table 4). Mean temperature interacted with clover content in the preceding period. Mean temperatures for each period for each year are shown in Table 5 (data missing for 1994).

Clover content for a grazing period was predicted from the model for cattle, mixed and sheep grazing for a range of preceding period clover contents and three mean temperatures lying within the range of mean temperatures experienced (Fig. 2). The range of preceding period clover contents for each grazing regime used in the predictions was based on the first and third quartile of preceding period...
FIG. 1. Clover content for each grazing period and grazing regime for 1990–1996: cattle (●), mixed (▲) and sheep (■) as % (A–G) and log (clover content) (H–N). In 1995 and 1996 the days on the horizontal axis are those for the short system, but the values plotted are means over both systems.
The interpretation of effects in this series of models should take into account the conditional nature of coefficients in multiple regression, and potential confounding. Biotic independent variables e.g. clover content in the preceding period, may themselves contain effects of plot, climate and grazing regime, but these effects are discounted in assessing the effects of grazing regime and climate in the period being modelled. Thus, the estimated grazing regime effects are those that occurred in the current period at a common value of clover content in the preceding period. Both radiation sum and mean temperature are important explanatory variables if included separately, but radiation sum is no longer important when fitted in association with mean temperature; their effects may be partly confounded, suggesting that mean temperature is a partial surrogate for radiation sum.

In summary, the analysis shows that grazing regime is a very strong determinant of sward clover content and that these effects occur rapidly and are broadly consistent both within and between years, with proportional differences established early in the grazing season being maintained throughout the season. Mean temperature in a period is a strong, positive determinant of clover content within a period, helping to explain the different patterns of seasonal clover contents observed over the 7 years of the experiment. Neither DM in the preceding period, nor any other climatic variable in the current or preceding period, merited inclusion in the final model of clover content.

DISCUSSION

This study aimed to identify the relative influences on sward clover dynamics of grazing by cattle, sheep, or sheep and cattle together, which are under management control, and climate, which is not. The results in respect of climate and
ment of grass-clover swards. These issues are discussed and some aspects of the design and analysis used are considered.

Community dynamics are affected by grazing regime, climate and sward state

White clover can respond rapidly to management. Overall, cattle grazing gave the highest (13-5 %) mean sward white clover content over the grazing season and sheep grazing the lowest (4-8 %) with mixed grazing giving intermediate values (9-3 %). These differences were established very rapidly, from an initial clover content of about 5 % (Fig. 1A) and persisted throughout the 7 years. The clover content under mixed grazing drifted from being close to cattle grazing levels at the start of the experiment to close to sheep grazing levels at the end, suggesting that dilution of the sheep influence in mixed grazing delayed the effects recorded for sheep-only grazing. These effects are probably partially due to differential and preferential dietary selection between animal types (Nolan and Connolly, 1977, 1989; Forbes and Hodgson, 1985; Murphy et al., 1995a; Del Pozo et al., 1996, 1997). Within the grazing season, the strong and consistent proportional difference between grazing regimes indicated the radically different sward states produced by the grazing regimes which can be attributed to differential utilization of vegetation and preferential selection for clover by sheep. Schwinning and Parsons (1996b) claimed that selective grazing does not essentially alter the grass-legume interaction. Perhaps the conflict between that position and the results presented here is because, in their analysis, selection is for the whole plant vis-à-vis that of another species. This does not allow for the effect that removing part of a plant has on its interaction with associated species.

While the analysis of clover content across grazing periods shows a simple relationship among the different grazing regimes, it does nothing to explain the great variation in clover content over grazing periods (Fig. 1). It is here that the model plays its role, indicating that the dynamics of clover content over successive grazing periods are largely determined by grazing management, climatic variation and sward state in the preceding period.

Climatic effects are large and immediate in their impact on sward composition. The effects of air temperature were evident within a few weeks of growth (Fig. 2) and were comparable in magnitude to those of grazing regime. Having included biotic measures of sward status in the preceding period, climate in the preceding period was unimportant. Effects of air temperature on sward clover content, similar to those observed here, have been reported under laboratory conditions (Newton et al., 1994), in the field (Brougham, 1959; Wachendorf et al., 2001b) and in a model of ryegrass-clover swards under changing temperature conditions (Topp and Doyle, 1996). Sensitivity of clover to drought has been reported by Low and Armitage (1959) and Stiles (1966) but soil moisture deficit is rarely encountered in these soils, perhaps explaining the absence of precipitation from the model. Despite the considerable evidence for the importance of irradiance in the development of clover, radiation did not appear in the model once temperature was included. Its effects were possibly confounded with those of temperature, with which it was positively correlated across the periods and years studied ($r = 0.39$, $P = 0.008$). The ambiguous results in relation to irradiance may be due to the trade-offs between the greater ability of clover to capture light compared with its associated grass species, and its poorer use of it (Faurie et al., 1996).

The importance of sward state in the preceding period, particularly at low temperature, was reflected in a generally strong positive effect of preceding period clover content (Fig. 2). The consequences of a poor sward clover content in spring may persist throughout the following summer as reduced proportions and yields (Eagles and Othman, 1988; Collins et al., 1991), as predicted precisely by the current model at lower temperatures. The reliance on previous sward state means that the system has a memory and can accumulate the effects of early season growing conditions, which may largely influence summer clover contents. The low clover contents in 1995 relative to other years may be due to the very low spring clover contents (Fig. 1F and M) and the lower than average temperatures in late winter and the first half of the 1995 grazing season (Table 5). This agrees with the results of a 7 year defoliation study of Elgersma et al. (1998) in which reductions in clover content occurred only in severely cold winters. A decline in clover content followed by recovery was also noted in Brock et al. (1988), Hoglund and Frankow-Lindberg (1998), Fothergill et al. (2000a) and Muto and Martin (2000). The periodic 'clover crash' described in Fothergill et al. (1996) associated with coeval clover plants may explain declines but since, in a permanent pasture, individual clover plants are less likely to be synchronous in age, a crash theory could only partially account for the observed pattern.

While the ranking of mean clover contents across grazing regimes tended to be the same in autumn and spring, the clover levels in both seasons fluctuated from year to year (Fig. 1A–G). Elgersma et al. (1998) suggested that the tendency is to return to a 'normal level' for a particular treatment by the end of the growing season. Perhaps the system does, on average, display this stability and the observed fluctuations are due to climatic variation over years (Table 5).

The very clear effects of temperature on clover content under grazing (Fig. 2) raise the question as to whether the effects on clover content reported in the literature of resting in spring, mid-season or late season, or their combinations, apply equally at low and high temperatures. Indeed, the importance of climate in this study and its absence from consideration in most published work raises the same question in respect of the results cited for many management practices. These results suggest that systems based on grass and clover genotypes should be tested over a range of climatic and grazing regimes. Replication of experiments across sites differing in climatic conditions, or long-term experimentation at a site, allows the effects of climatic variables to be better estimated. Long-term experiments are also valuable in testing the persistence of
clover and grass genotypes and in investigating system features such as clover crashes and the conditions associated with them.

Management implications

The results suggest a very plastic dynamic system, which responds rapidly to controlled and uncontrolled pressures and builds on existing sward state so that its path through any growing season is subject to unpredictable climatic variation once the grazing regime has been selected and spring clover content established. The inherent unpredictability of sward content makes the use of clover an uncertain tool in grassland management. However, since the response to management practices such as grazing practice and fertilizer N under grazing, which are under human control, can also be very variable (Gateley et al., 1984; Ryan et al., 1984; D. Collins, pers. comm.), the argument as to which is better is not simple. These results, and those in Wachendorf et al. (2001a,b), suggest that attempts to control clover content should concentrate in the short term on grazing management and establishing a desirable level of clover in spring and, in the longer term, on the continuation of breeding programmes to produce clover cultivars which are better adapted to lower temperatures and growth with grass companions. Recently, there has been increased emphasis on developing white clover with adequate cold tolerance for northern European environments (Collins et al., 1991; Caradus, 2000; Wilkins and Vidrigh, 2000).

Wachendorf et al. (2001b) reported that sward state in spring was affected by sward conditions of both clover (clover leaf area) and the associated ryegrass (tiller density) in the previous autumn, and radiation, precipitation and temperature conditions in winter and spring. Of these influences, only sward conditions in autumn are partly under management control. While spring and summer management have consequential effects on sward state in the autumn, appropriate integration of resting and grazing managements, and the use of mixed and alternate grazing by different animal types at the end of the grazing season, are likely to produce high levels of clover leaf area in autumn. The weight of evidence suggests that a graze-rest-graze management over the season or an early autumn rest (Curll and Wilkins, 1985; Fothergill et al., 2000a), lax grazing (Curll, 1982; Woledge et al., 1992, but see Dennis and Woledge, 1982) or grazing by cattle, mixed or alternate grazing rather than by sheep only (Garwood et al., 1982; Gibb et al., 1989; Evans et al., 1992) all promote higher autumn clover content. Continuous sheep grazing, particularly at high stocking rates, militates against white clover persistence and production, compared with rotational-grazing (Widdup and Turner, 1983; Curll et al., 1985a,b). Uninterrupted continuous grazing by cattle also has adverse effects on white clover persistence (Gibb et al., 1989). White clover is favoured by switching from high to low stocking rates (Curll, 1982) or by inserting a rest interval and subsequent silage cut. However, the effect of climate during summer and autumn on these practices has not been examined.

Throughout the grazing season the negative effect of low temperature on clover content can also be ameliorated by grazing management. Grazing by cattle produced an immediate improvement in clover content in comparison with sheep grazing. This strong effect suggests that the presence of two or more animal types on the same farm creates the possibility of grazing them together, separately or consecutively, even for periods of relatively short duration within a given grazing season, to modify sward clover content. Variation in the relative grazing and conservation requirements of cattle and sheep (Nolan et al., 1999) also creates flexibility that may be exploited to manipulate sward composition. The various management strategies mentioned in Curll et al. (1985a,b) are also available for improving clover content. The resilience of the clover-ryegrass system is further indicated by the ability of white clover to recover from hard grazing, or N applications or reversal of such managements (Laidlaw, 1984; Curll et al., 1985b; Brock et al., 1988; Hoglind and Frankow-Lindberg, 1998; Elgersma et al., 1998; Muto and Martin, 2000).

Under Irish conditions, over 80 % of pastures are permanent, and conventional ploughing and reseeding is not a widespread practical option due to cost, topography, rock outcrops, wetness etc. New clover must therefore be introduced by techniques such as surface seeding or sod drilling. However, the immediacy and predictability of the response of clover content to grazing regimes suggest that in mixed livestock farming systems management may offer alternatives to reseeding as a method for improving clover content of swards. Whether this would occur at levels of clover higher than those observed in these swards is an open question.

Other issues

This study focused on clover content because of a primary interest in the determinants of sward composition. While changes in total mass of components could potentially be confounded with compositional changes, this does not appear to be the case with these data. One can analyse the two components, grass DM and clover DM or, alternatively, create the two variables grass (or clover) content and total DM. Total DM pre-grazing is not affected greatly by grazing regime, with DM in sheep and mixed grazed pastures being about 4 and 6 % lower, on average, than that in pastures grazed by cattle over the 7 years, although this varied for particular grazing regimes and years. Since white clover content is strongly affected by grazing regime, the perspective chosen seems to be a useful way to reduce the dimensionality of the problem, to concentrate on clover content rather than on an examination of the two separate components of DM. Also, the inclusion of DM in the preceding period in the model was not significant, which is further evidence of its unimportance as an additional determinant of clover content. Finally, the clover difference among grazing regimes is not an artefact of the greater patchiness of cattle-grazed swards (de Rancourt et al., 1980; Forbes and Hodgson, 1985; Gibb and Baker, 1989; Murphy et al., 1995a), a result of a higher
clover content in the higher, less utilized, DM areas. DM per unit area pre-grazing in these high-grass (dung-soiled) areas is in the order of three-times that in low-grass areas (de Rancourt et al., 1980). However, in the years 1994 to 1996, the association between clover content and DM appeared to be negative, with clover contents about 50% greater in low- than in high-grass areas in the cattle-grazed plots in the current study.

Several issues arise in respect of the experimental design. As a replacement series, it is open to the possibility of giving biased information in respect of comparisons among the three grazing regimes (Connolly, 1986, 1987, 1997; Connolly et al., 2001). However, the mean pre-grazing total DM values were very close and, although there were significant differences among grazing regimes in pre-grazing total DM in some years, any consequential bias introduced would be very minor relative to the very large effects of grazing regime. The pastures were not standardized with respect to post-grazing pasture height or common animal metabolic weight. Standardization to a common height ignores the very different utilization of pastures by sheep and cattle which results in relatively even swards for the former and very patchy swards for the latter. Mixed grazed swards are intermediate, but vary with the relative proportions of sheep and cattle in the mix. This renders pasture height a very poor tool for standardization (Gibb and Baker, 1989; Nolan and Connolly, 1989; Murphy et al., 1995a,b). Standardizing animal metabolic weights across treatments implies that this provides a basis for substitution between species that would ensure standardized pasture grazing. This was discussed by Connolly and Nolan (1976), who proposed quite a different methodology for computing interspecific substitution rates that depend on the experimental results rather than being the starting point of experimentation.

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