Modelling Seedling Growth Rates of 18 Temperate Arable Weed Species as a Function of the Environment and Plant Traits

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INTRODUCTION

There has been a shift in recent years in the focus of UK agricultural policy (Curry, 2002). Whereas previously research was aimed at maximizing yields by optimizing inputs, there has now been a recognition that the over-reliance on pesticides is not sustainable. One area of particular concern has been the sharp reduction in the populations of farmland bird species, which is often attributed to intensive crop management (Chamberlain et al., 2000). Arable weeds occupy an important position in the agro-ecosystem as a food source for invertebrates and higher trophic groups, as well as having an intrinsic biodiversity value (Marshall et al., 2003). There is, therefore, a desire at the policy-making level to develop weed management strategies that, as well as maintaining yield, preserve ecologically significant populations of native species within the field by reducing herbicide inputs.

The potential for reducing current herbicide applications can be realized by tailoring doses to specific weed problems based on the long-term economic threshold of the weed. This threshold has been defined as ‘the density above which weeds should be controlled in order to optimise returns over a number of years’ (Cousens et al., 1986). Knowledge of the effect of specific weed populations on crop yield is, therefore, integral to any sustainable weed management decision. The relationship of yield loss to the level of weed infestation has been modelled from empirical observations using a variety of functions, but is usually best described by a rectangular hyperbola (Lundkvist, 1997). A model of this type has been developed based on relative weed dry weight (Lutman et al., 1996) or green area (Kropff et al., 1995):

\[ YL(\%) = \frac{q[L_w/(L_w + L_c)]}{1+(q/m-1)[L_w/(L_w + L_c)]} \times 100 \]  

where \( YL \) is yield loss, \( L_w \) is weed green area index, \( L_c \) is crop green area index, \( q \) is the relative damage coefficient (yield loss per unit relative weed green area at low weed densities) and \( m \) is the maximum yield loss expected at very high weed populations.

This relative green area model is a potentially useful tool in supporting weed management decisions. It avoids the time constraints of counting individual weeds (Sim, 1987) and could potentially be based on a visual assessment of crop and weed ground cover (Lutman and Cussans, 1995; Storkey et al., 2000). However, a problem arises when the crop and the weed have different growth rates during the early part of the season when assessments are made. When this occurs, the relative damage coefficient, \( q \), will be highly dependent on the time at which the weed population is assessed. A simple thermal time model based on the response of relative growth rate of leaf area (\( RGRL \)) to
temperature has been proposed to model the change in $q$ with time (Kroff and Spitters, 1991):
\[
q = q_0 \exp [(RGRL_c - RGRL_w) \, t]
\]
where $q_0$ is the value of $q$ at time of first assessment when $t = 0$, $RGRL_c$ and $RGRL_w$ are the relative growth rates of the leaf area of crop and weed, respectively (per growing day degree) and $t$ is the time period in growing day degrees from $t = 0$.

This dynamic simulation model is based on knowledge of weed eco-physiological parameters, specifically the response of seedling growth to the environment. Once this parameter is known for the species competing in a system, the parameter, $q$, can be calibrated to different growing seasons and assessment dates. Previously, when the aim of weed research was to maintain yield by achieving optimal weed control, efforts were focused on understanding the response of growth rate to the environment of a few economically important weed species. The additional objective of encouraging farmland biodiversity has highlighted the paucity of basic biological information, such as seedling growth rate, for a large number of common but less competitive species found in UK arable fields.

Seedling relative growth rate is also acknowledged to be central to understanding the functional ecology of species adapted to different environments (Grime and Hunt, 1975; Grime et al., 1997; Hunt and Cornelissen, 1997; Poorter and Garnier, 1999). The annual arable weed flora is generally made up of ruderal species that are adapted to fertile, disturbed environments. One of the characteristics of ruderals is a high potential relative growth rate in the seedling phase (Grime, 2001). However, within a weed flora there will be a range of growth rates (Seibert and Pearce, 1993). Variability in growth rate is a function of a number of plant traits with trade-offs with other plant functions. For example, specific leaf area ($SLA$, $m^2\, g^{-1}$ leaf) has been found to be positively correlated with relative growth rate but negatively correlated with leaf life-span (Poorter and Garnier, 1999). These trade-offs will have important implications for an individual species’ competitive ability and biodiversity value.

This study parameterized the response of early relative growth rate to the environment of a cross-section of annual weed species from the UK along with two contrasting crop species. The main objective was to test the hypothesis that a simple thermal time model eqn (2) is adequate for describing the change in the relative green area of two competing species during the exponential growth phase. This was compared with an alternative model that included a term for accumulated radiation. In addition the variation in seedling relative growth rate and its components between species was used to investigate the possible existence of contrasting strategies for establishment within the species investigated.

**MATERIALS AND METHODS**

**Experimental procedure**

Seeds for 18 weed species representing a cross-section of the common flora found in arable fields were obtained from Herbiseed Ltd (Berkshire, UK). Germination tests were carried out on the weed seeds and seed of two contrasting crop species, *Brassica napus* ‘Apex’ and *Triticum aestivum* ‘Consort’ to enable germination of all the species to be synchronized. Seeds were then germinated on filter paper moistened with 0-01 mol KNO₃ in Petri dishes in a range of conditions appropriate to the individual species (Table 1). The exception was *Galium aparine*, which was germinated in a layer of damp peat and sand to help break dormancy. Germinated seeds were sown into 25 9-cm square pots for each species containing a mix of 80 % sterilized screened loam, 20 % lime-free grit and 2 kg m⁻³ of a slow-release fertilizer. Two seeds were sown into each pot and thinned down after emergence to standardize initial seedling size. As far as possible all species were sown within a few days of each other. Pots were arranged in an outdoor sand bed in five replicate blocks, each block containing five pots of each species. Air temperature and daily accumulated radiation were recorded at a nearby meteorological station. The experiment was repeated twice in the autumn and twice in the spring. The sowing dates were 12 October 2001, 8 March 2002, 27 September 2002 and 24 April 2003. The spring sowing date in 2003 was later than intended because of a failure of some species to germinate when the experiment was first established in March. However, the results from this later experiment provided a useful test of the robustness of the growth models.

At approx. 7-d intervals for the autumn sowings and 4-d intervals for the spring sowings, five seedlings (one from each block) were sampled from each species. Shorter sampling intervals in the spring experiment were used to

<table>
<thead>
<tr>
<th>Species</th>
<th>Daytime temperature (°C)</th>
<th>Night-time temperature (°C)</th>
<th>Days to maximum germination rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alopecurus mysurosoides</td>
<td>20</td>
<td>15</td>
<td>6</td>
</tr>
<tr>
<td>Avena fatua</td>
<td>20</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Brassica napus</td>
<td>15</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>Bromus sterilis</td>
<td>15</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>Capsella bursa-pastoris</td>
<td>20</td>
<td>15</td>
<td>No</td>
</tr>
<tr>
<td>Chenopodium album</td>
<td>20</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Fallopia convolvulus</td>
<td>20</td>
<td>15</td>
<td>6</td>
</tr>
<tr>
<td>Galium aparine</td>
<td>15</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Geranium molle</td>
<td>20</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>Lolium multiflorum</td>
<td>15</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>Matricaria perforata</td>
<td>15</td>
<td>10</td>
<td>Yes</td>
</tr>
<tr>
<td>Myosotis arvensis</td>
<td>15</td>
<td>10</td>
<td>Yes</td>
</tr>
<tr>
<td>Papaver rhoeas</td>
<td>15</td>
<td>10</td>
<td>Yes</td>
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<tr>
<td>Poa annua</td>
<td>15</td>
<td>10</td>
<td>Yes</td>
</tr>
<tr>
<td>Polygonum aviculare*</td>
<td>15</td>
<td>10</td>
<td>Yes</td>
</tr>
<tr>
<td>Senecio vulgaris</td>
<td>20</td>
<td>15</td>
<td>No</td>
</tr>
<tr>
<td>Sinapis arvensis</td>
<td>15</td>
<td>10</td>
<td>No</td>
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<tr>
<td>Stellaria media</td>
<td>20</td>
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<td>No</td>
</tr>
<tr>
<td>Trifolium aestivum</td>
<td>15</td>
<td>10</td>
<td>Yes</td>
</tr>
<tr>
<td>Veronica persica</td>
<td>20</td>
<td>15</td>
<td>No</td>
</tr>
</tbody>
</table>

* Chilled at 3 °C for 10 d before being placed in incubator.
avoid the plants become too large and self-shading becoming a growth-limiting factor. The soil was washed off the roots and the plants divided into leaves, stems and roots. The green area of leaves and stems was measured using a leaf area meter (Delta-T Devices Ltd, Cambridgeshire, UK) and subsequently the dry weights of the separate plant parts was determined. Green stem area was included when modelling the relative growth rate of total green area (RGR) as this is the variable used in the empirical models of crop/weed competition. However, when calculating specific leaf area (m^2 leaf g^-1 leaf), net assimilation rate (g total dry matter m^-2 leaf) and leaf area ratio (m^2 leaf g^-1 total dry matter) only the green area of the leaves was used.

Seed dry weight (minus the seed coat and other non-investing structures) was determined for each species. One hundred seeds were calculated for each species as described above. The seed coat and any other non-investing structures could then be removed easily. The dry weight of the non-investing structures from 100 seeds was measured and taken away from the dry weight of 100 whole seeds.

Analysis

When plotted against thermal time, it was found that relative growth rate remained constant. Therefore, the classical approach to calculating RGR was used (Evans, 1971), fitting a simple function based on thermal time to the combined data for each species from all four experiments:

\[
\ln (L) = \ln (L_0) + RGR \Sigma T - T_b
\]

where \(L\) is green area, \(L_0\) is initial green area at emergence, \(RGR\) is the relative growth rate of total green area, \(T\) is daily mean temperature and \(T_b\) is the base temperature.

The equation relating the parameter, \(q\), in empirical yield loss model to accumulated thermal time eqn (2) assumes that the two competing species share the same base temperature. Equation 3 was, therefore, fitted to the data for each species using a base temperature of 0 °C.

Two methods were used to attempt to improve the performance of the simple thermal time model. Firstly, base temperature was allowed to vary. The optimal base temperature for the increase in green area for each species was derived using a program written in C++ which fitted the equation to thermal time using 40 different base temperatures between -10 and 10 °C with intervals of 0.5 °C. The optimal base temperature was chosen as the one which gave the best fit to a linear regression for the data from all four experiments for each species (Scaife et al., 1987; Cousins et al., 1992). Secondly, the model was extended further by including a term for accumulated radiation. This was achieved by adopting the effective day degrees (EDD) method (Scaife et al., 1987), eqn (4). Units of EDD take account of both accumulated temperature and radiation, using a parameter, \(f\), to measure the relative importance of the two variables in accounting for variability in \(\ln (L)\) (eqn 5). Adding the reciprocals of the two limiting factors to growth, light and temperature, is analogous to quantifying the resistances in an electrical circuit. The equivalent conductance of the combination cannot exceed the smaller of the two components and, therefore, combines the effect of both limiting factors (Aikman and Scaife, 1993).

\[
\ln (L) = \ln (L_0) + RGR \Sigma EDD
\]

\[
EDD_{i}^{-1} = DD_{i}^{-1} + f PAR_{i}^{-1}
\]

where \(DD\) is day degrees (°Cd) and \(PAR\) is accumulated photosynthetically active radiation (MJ), all on day \(i\).

The program written to optimize base temperature was modified to find the combination of the base temperature (between -10 and 10 °C with intervals of 0.5 °C) and the parameter, \(f\) (between 0 and 2 with intervals of 0.01) which gave the best fit to a linear regression for each species. RGR (d^-1), of total dry weight, is a product of a physiological component, net assimilation rate (NAR, g m^-2 d^-1), and a morphological component, leaf area ratio (LAR, m^2 leaf g^-1 total dry weight); LAR is a product of specific leaf area (SLA, m^2 g^-1 leaf), and leaf weight ratio (LWR, leaf dry weight divided by total dry weight). These variables were calculated for each species and experiment using the mean values for SLA, LAR and LWR from all five harvests. It was assumed that over the early period of growth being studied in this experiment, the increase of leaf area remained exponential and that dry weight was linearly related to green area. The method for calculating NAR proposed by Evans (1971) was therefore used, eqn (4); \(\frac{W_2 - W_1}{T_2 - T_1}\) and \(\frac{L_2 - L_1}{T_2 - T_1}\) were calculated from linear regressions fitted to the increase in the natural logarithms of total dry weight and leaf area against time.

\[
NAR = \frac{\frac{W_2 - W_1}{T_2 - T_1}}{\frac{L_2 - L_1}{T_2 - T_1}}
\]

A correlation matrix was calculated using Genstat (Payne et al., 1987) to investigate the relationships between RGR and its components, pooling the data for the two autumn seasons and the two spring seasons together. The relative contribution of NAR and LAR in determining the variation in RGR between the species was further analysed by investigating alternative strategies for seedling growth in different environments. The pathway analysis proposed by Poorter and Remkes (1990) was used. In this analysis, the values for RGR, LAR and NAR were converted to zero mean and unit standard deviation and regressed onto one another, giving an estimate of how a change of one standard deviation of one variable affects another (also measured in units of standard deviation).

RESULTS

Modelling RGR

Sowing seedlings in the autumn and the spring exposed them to contrasting environmental conditions that would typically be experienced in the field in crops sown in the UK. For the first season, the mean temperatures over the autumn and spring experimental periods were 9.1 and 9.5 °C.
respectively and the mean daily total radiation values were 4.3 and 13.7 MJ m\(^{-2}\). For the second season, the respective temperature values were 8.7 and 13.6 °C and the total radiation values were 3.9 and 13.7 MJ m\(^{-2}\). Averaged over the two seasons, spring temperatures were 2.6 °C higher than in the autumn and 10.7 MJ m\(^{-2} \text{d}^{-1}\) more total radiation was accumulated.

The simple thermal time model (eqn 2) was found to be inadequate for modelling the growth of weed seedlings over the autumn and the spring. Using a common base temperature of 0 °C, the model fitted to the data from all four experiments for each species only accounted for an average of 70% of the variance in green area. The fitted model optimized for the best base temperature for each species slightly improved the performance of the model. However, it still only accounted for an average for all the species of 74% of the variance in green area.

The effective day-degree model accounted for more of the variation in green area against time for the four experiments combined. Including radiation as a variable in the model increased the mean variance accounted for of all the species to 95% for green area. The optimized parameter values for \(T_b\), \(f\), and RGRL are presented in Table 2. Of particular note are the large values for the parameter, \(f\), that were estimated for the predominantly spring-germinating species, Polygonum aviculare, Chenopodium album and Fallopia convolvulus. This indicates that the growth of these species is being limited most by the lower light intensity in the autumn. Finally, it is important to note that the base temperatures estimated by the model are extrapolations of the data and may not represent a true biological limit (Cousens et al., 1991). The improvement of the model is illustrated using the example of Chenopodium album in Fig. 1.

**Components of RGR**

The difference between the growing seasons resulted in a shift in the balance of the physiological and morphological components of RGR (Tables 3 and 4; Fig. 2). In the autumn, variability in NAR contributed more to the observed differences in RGR between the species than did LAR when all the species were analysed together. There was a significant correlation of RGR with NAR but not with LAR (Table 5). The values from the pathway analysis were NAR = 0.81 and LAR = 0.49. Species with a high autumn RGR had relatively more efficient photosynthesis at the lower light and temperatures. In the spring, variation in LAR played a greater role in determining RGR. There was a significant correlation of RGR with both LAR and NAR (Table 5). The results of the pathway analysis were NAR = 0.67 and LAR = 0.69. The positive correlation between LAR and RGR in the spring was due to variation in SLA rather than LWR (Fig. 2).

### Table 2. Estimates of parameters of the model of green area (L) fitted to effective day-degrees; \(\ln (L) = \ln (L_o) + (\text{RGRL} \times \text{EDD})\)

<table>
<thead>
<tr>
<th>Species</th>
<th>(T_b) (°C)</th>
<th>(f)</th>
<th>(\ln (L_o)) (cm(^2))</th>
<th>RGRL (EDD(^{-1}))</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alopecurus myosuroides</td>
<td>2.5</td>
<td>0.16</td>
<td>-2.31</td>
<td>0.025</td>
<td>0.97</td>
</tr>
<tr>
<td>Avena fatua</td>
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<td>0.14</td>
<td>0.09</td>
<td>0.015</td>
<td>0.95</td>
</tr>
<tr>
<td>Brassica napus</td>
<td>-0.5</td>
<td>0.08</td>
<td>0.43</td>
<td>0.012</td>
<td>0.97</td>
</tr>
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<td>0.98</td>
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<tr>
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<td>-2.68</td>
<td>0.016</td>
<td>0.76</td>
</tr>
<tr>
<td>Chenopodium album</td>
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<td>0.028</td>
<td>0.98</td>
</tr>
<tr>
<td>Fallopia convolvulus</td>
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<td>-1.37</td>
<td>0.034</td>
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<td>0.95</td>
</tr>
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<td>0.020</td>
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<td>0.024</td>
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<td>Myosotis arvensis</td>
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<td>-2.01</td>
<td>0.018</td>
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<td>Papaver rhoeas</td>
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<td>0.99</td>
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<tr>
<td>Poa annua</td>
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<td>-3.10</td>
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<td>0.98</td>
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<tr>
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<td>-2.11</td>
<td>0.022</td>
<td>0.95</td>
</tr>
</tbody>
</table>

**Fig. 1.** Modelling the early relative growth rate of Chenopodium album sown in the autumn of 2001 (closed circles) and 2002 (open circles) and the spring of 2002 (closed squares) and 2003 (open squares) using (A) day degrees or (B) effective day-degrees.
There were clear differences between the grass and the broadleaf weeds in the relative contribution of the components of \( RGR \). In both the autumn and the spring, \( NAR \) made a greater contribution to any given \( RGR \) in the grasses than it does in the broadleaf species (Fig. 2). This appeared to be a consequence of alternative solutions to the trade-off between \( LWR \) and \( NAR \) (Fig. 3). The plasticity of seedlings growing in different environments was also demonstrated; \( SLA \) decreased in the spring when light intensities were higher. This effect appeared to be greater for the broadleaf species.

The differential physiological and morphological response of the species to variation in the light and temperature regimes resulted in non-significant correlations...
of the growth parameter values between the two autumn seasons and between the mean values for the autumn and the spring. However, the values of $RGR$, $NAR$ and $LAR$ measured in the spring, when conditions were closer to the optimal for growth, were significantly correlated ($P < 0.001$) between the two experiments.

Finally, there was a strong negative correlation between growth in the spring (when $RGR$ will be approaching its potential maximum) and initial seedling size (Fig. 4), which in turn was largely determined by seed reserves; the $R^2$ of initial seedling size plotted against seed weight (minus non-investing structures) was 0.93 ($P < 0.001$).

**DISCUSSION**

**Modelling RGR**

The empirical model of yield loss based on relative weed green area (eqn 1) relies on underpinning from a dynamic simulation model. The dramatic change in the parameter, $q$, with time due to the differences in the relative growth rates of the crop and the weed has been demonstrated in a collaborative study validating the relative green area model using different assessment dates (Lotz et al., 1996). It has been proposed that a simple function based on thermal time is adequate for predicting this change in $q$ (eqn 2). In using this function two assumptions are made. Firstly, that temperature is the only environmental factor limiting growth, and secondly that both species are growing exponentially.

This study has shown that the simple thermal time model is not robust enough to be applied to plants emerging at different times in the year due to the large differences in incident radiation. Many of the species used in this study, such as *Stellaria media*, *Sinapis arvensis* and *Poa annua*, are common in both autumn- and spring-sown crops in the UK. The use of effective day-degrees, combining accumulated day-degrees and radiation, provided a more robust model which could also be applied to weeds growing at different latitudes. Because the effective day-degree model uses two commonly available meteorological inputs (mean temperature and daily radiation), the parameters obtained in this study could easily be incorporated in a weed management support system to complement the empirical model.

Using the effective day-degree model to describe the change in the relative green area of the crop and the weed still assumes that the two species are growing exponentially and competition for resources has not begun. If the window of opportunity for weed management extends into a period when plants are competing for resources, a more comprehensive simulation model is required. A number of models of this type have been developed (Spitters and Aerts, 1983; Kropff et al., 1984; Wilkerson et al., 1990; Kropff and Spitters, 1992; Weaver et al., 1993; Cavero et al., 1999). However, although the model describing the exponential growth phase may only be applicable to a limited period (Lotz et al., 1996; Storkey et al., 2003), the early relative growth rate remains an important parameter in these more complex simulation models of crop/weed competition (Kropff et al., 1992).
Components of RGR

Rapid seedling growth is a characteristic of weeds adapted to the frequently disturbed, highly fertile environment of an arable field (Grime et al., 1988). However, there were large interspecific differences in the RGR of the arable weeds selected for this study. The trade-off between seed size and seedling growth rate is well established in the literature (Fenner, 1983; Shipley and Peters, 1990; Westoby et al., 1992; Seibert and Pearce, 1993) and was demonstrated in this study for spring growth. It is likely that this trade-off has been the driving evolutionary factor in determining the contrasting strategies for seedling establishment of the weeds studied here. Species with a small seed size and high fecundity, for example Stellaria media and Senecio vulgaris, are adapted for widespread dispersal to take advantage of ephemeral open spaces. However, these species must also have a high seedling RGR in order to gain a foothold in a rapidly expanding canopy in the spring. This appears to be achieved largely through developing leaves with a high SLA. This may involve trade-offs with other plant functions, such as leaf lifespan and the mean residency time of nutrients in the plant (Poorter and Garnier, 1999). However, it is difficult to draw any firm conclusions regarding the implications of a high seedling SLA for other plant functions because of the plasticity of this trait within a species in different environments (Smith, 1982; Wilson et al., 1999).

There was no difference in the response of spring RGR to SLA between the grasses and broad leaf species. However, in both the autumn and the spring, for any given RGR the grasses had a higher NAR and a lower LAR. This appears to be a consequence of alternative solutions to the trade-off between NAR and LWR. The grasses that tend to be the larger-seeded, later-maturing species, invest relatively more resources into roots early in the season. As a consequence, it is likely that the leaves will have a higher nitrogen concentration per unit leaf area, increasing NAR. The

![FIG. 3. Correlation between NAR and LWR (P < 0.01) for grass weeds growing in the autumn (open squares) and the spring (open circles) and broadleaf species growing in the autumn (closed squares) and the spring (closed circles).](https://academic.oup.com/aob/article-abstract/93/6/681/256083)

![FIG. 4. Correlation between RGR and initial seedling dry weight (P < 0.001) estimated by the effective day-degree model for all species measured in the spring of 2002 (open circles) and 2003 (closed circles).](https://academic.oup.com/aob/article-abstract/93/6/681/256083)
early investment in roots may be an adaptation to competition for resources later in the season when water and nutrients become limiting. All the grass weeds studied here were characterized by a low LWR when compared with the broadleaf species and, with the exception of *Poa annua*, are also considered to be among the priority weeds for control in winter cereals in the UK because of their high competitive ability (Blair *et al*., 1999).

Previous authors have attempted to identify general trends in the relative contributions of NAR and LAR in determining variation in RGR in different groups of higher plants (Poorter and Remkes, 1990; Hunt and Cornelissen, 1997; Poorter and Garnier, 1999). However, these studies have generally been done in controlled environments under near-optimal conditions for growth. It is, therefore, difficult to interpret the data presented here (measured in outdoor, non-optimal conditions) in the same context. While large comparative studies carried out under standard environmental conditions are underway to measure a range of eco-physiological traits with contrasting strategies for growth and reproduction.

Seedling growth rate is an important plant trait in determining plant strategy and relative competitiveness of weeds and crops. This study has demonstrated the importance of studying this trait in the context of the response of the wider eco-physiology of contrasting weed species to changing environmental conditions. Further experiments are underway to measure a range of eco-physiological traits throughout the growing seasons of the species used in this study. It may then be possible to combine information on these traits with the data presented in this study in a multivariate analysis that would identify groups of species with contrasting strategies for growth and reproduction.

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**LITERATURE CITED**


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