GROWTH AND MAINTENANCE RESPIRATION OF PERENNIAL ROOT SYSTEMS IN A DRY GRASSLAND DOMINATED BY AGROPYRON DASYSTACHYUM (HOOK.) SCRIBN.

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SUMMARY

Respiration coefficients were determined for laboratory-grown root systems of Agropyron dasystachyum (Hook.) Scribn. (northern wheatgrass). The growth respiration coefficient (0.85 g g⁻¹) was similar to published rates for species from mesic sites. The maintenance coefficient (0.037 g g⁻¹ d⁻¹) was relatively low, suggesting that plants growing in semi-arid habitats have inherently low maintenance costs per unit of biomass. The proportion of total root biomass requiring maintenance (degradable fraction) was determined by measuring the non-structural root biomass. The degradable fraction (0.13) was substantially lower than published measurements of functional (or ‘live’) biomass, because the latter include structural biomass, which has no maintenance requirement. Respiration parameters, root growth, degradable root fraction, soil temperature and soil moisture were used to construct a model of root respiration in field-grown roots. The maintenance coefficient was adjusted downward during periods of water stress and low temperature when roots probably were dormant. Parameters in the model, particularly the degradable biomass fraction, explained much of the discrepancy between respiration rates of laboratory-grown and field-grown root systems. Maintenance respiration represents a substantial outlay in the carbon budgets of dry grasslands but is lower than expected considering the large root biomass in these systems.

Key words: Agropyron dasystachyum (Hook.) Scribn., carbon budget, grassland ecosystem, growth and maintenance respiration, roots.

INTRODUCTION

The production and maintenance of a relatively large below-ground biomass is characteristic of grassland ecosystems. From 56 to 96% of total plant biomass in natural North American grasslands is below ground (Marshall, 1977). Root biomass (0 to 60 cm depth) at the Pawnee (short grassland) and Cottonwood (mixed grassland) sites in the western USA averages 1368 and 1690 g m⁻², respectively; mixed grassland at the Matador site in western Canada has a biomass of 2026 g m⁻² (Sims & Coupland, 1979). The potential exists for root respiration to constitute a substantial carbon cost to plants with such large root systems (Caldwell, 1979).

Total respiration of plant tissue can be partitioned into that associated with growth and with maintenance using the approach of Thornley (1970):

\[ R = mW + g \frac{dW}{dt}, \]

where \( R \) is the respiration rate per plant (or root system), \( W \) is plant weight and \( \frac{dW}{dt} \) is the growth rate. The maintenance coefficient \( (m) \) is the amount of carbon
respired to maintain existing biomass, and the growth coefficient \((g)\) is the amount of carbon respired per unit of carbon used in growth.

The maintenance respiration of perennial grass root systems depends on the fraction of biomass which requires maintenance and on the variation in the root system's maintenance requirements. Thornley (1977) concludes that the fraction of plant tissue requiring maintenance decreases with size (and age) of the plant, since an increasingly larger fraction of the biomass is taken up by structural tissue, which has a low maintenance requirement. This has been confirmed for sorghum grown under constant environmental conditions (McCree, 1983). Techniques for estimating 'live' or 'functional' root biomass (Ueno, Yoshihara & Okada, 1967; Knievel, 1973; Singh & Coleman, 1977) overestimate degradable biomass because structural material is included in the biomass values.

The specific maintenance respiration rate depends on the proportion of degradable (non-structural) biomass. This may partly explain the large discrepancy between respiration rates of laboratory- and field-grown roots (Redmann & Abouguendia, 1978). There can be substantial errors in using laboratory-determined respiration rates to model respiration in field-grown roots. The controlled conditions which are possible in laboratory work are essential in experiments dealing with the effects of environment on root respiration and other aspects of root functioning. The problem is how to apply these results to the field situation.

The objective of this paper is to describe the root respiration of *Agropyron dasystachyum* (Hook.) Scribn. from a semi-arid, mixed grassland using the concept of growth and maintenance respiration and to examine the use of the non-structural carbon fraction as the basis for calculating and comparing the maintenance respiration rates of laboratory- and field-grown roots.

**MATERIALS AND METHODS**

**Measurement of root respiration and root growth**

Plants of *A. dasystachyum* were grown from seed in solution culture in a growth chamber with constant air temperature (20 °C), relative humidity (76%) and a 12 h photoperiod. Irradiance at the base of the shoots was 1300 to 1560 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). Plants were rooted in full-strength Hoagland's solution (Salisbury & Ross, 1978) with iron supplied in the chelated form.

Root respiration was measured by sealing the roots of entire individual plants into Hoagland's solution (pH c. 6.5) and measuring the increase in total \(\text{CO}_2\) concentration \((\text{CO}_2 + \text{HCO}_3^- + \text{CO}_3^{2-})\) of the solution with an Orion model 95–02 \(\text{CO}_2\) electrode. Initial \(\text{CO}_2\) concentration was adjusted to a standard level using sodium bicarbonate. Respiration was measured over the change in concentration of 4.5 to 8.5 \(\mu\)l l\(^{-1}\) \(\text{CO}_2\). Preliminary measurements indicated that respiration rate was unaffected by this concentration range. Each of 20 plants was sampled one to eight times during a period of 61 to 113 d after seed germination. As there may be diel variations in root respiration (Hansen, 1977), respiration of each plant was measured in both the light and dark period at each sampling interval, and averaged to give an estimate of the respiration rate for that day. All measurements were made at 20 °C.

Root growth rates were estimated by fitting polynomial equations to the data for root dry weight as a function of time for the individual plants on which
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Respiration measurements were made. The equations were fitted to the logarithmically-transformed data for root dry weight using the techniques of Hughes & Freeman (1967). Root dry weights of living plants were estimated from a regression of dry weight against whole plant fresh weight determined on parallel samples ($r^2 = 0.989$, $n = 18$). Logarithmic transformations of fresh and dry weights were used in the analysis.

A line was fitted to the data relating specific respiration with relative growth rate using Bartlett's three-group method (Sokal & Rolf, 1969). Respiration and growth data for all individual plants were combined for determination of $g$ and $m$ using Eqn (2).

Dividing Eqn (1) by $W$ results in:

$$\frac{R}{W} = m + g \frac{dW/dt}{W},$$

which describes a linear relationship between specific respiration rate ($R/W$) and relative growth rate ($[(dW/dt)/W]$). The slope of this relationship is $g$ and the $y$ intercept is $m$ (Thornley, 1970). The growth conversion efficiency ($Yg$), which is the increase in mass of plant material per unit mass of substrate used (Thornley, 1970), is calculated as:

$$Yg = \frac{1}{1+g}.$$  

**Determination of non-structural biomass**

Chemical determinations were made on roots harvested at the end of the laboratory experiments and on field-grown roots. The latter were separated from cores removed from the upper 20 cm on 20 July, 1982. The soil cores were soaked overnight in a 10% solution of Calgon (sodium hexametaphosphate and sodium carbonate) to disperse the clay colloids. After soaking, the roots were separated using a mechanical root washer (Coupland, 1974). This procedure collects all the root fragments except those small enough to pass through a no. 60 sieve (0.25 mm opening). Roots were dried at 80°C, and ground to pass through a 1 mm mesh screen.

The total carbon content of laboratory-grown roots was calculated using protein, carbohydrate, lipid, lignin and organic acid content, along with conversion values in Hesketh & Jones (1980). Total carbon in field-grown roots was measured by combustion and CO$_2$ collection (Tiessen, Bettany & Stewart, 1981). Total nitrogen was estimated by the Kjeldahl method and converted to protein by multiplying by 6.25 (Penning de Vries & Van Laar, 1976). Lipid content was estimated by extraction with petroleum ether. Lignin and cellulose determinations were made using the potassium permanganate method (Van Soest & Wine, 1968). Hemicellulose content was determined as the difference between neutral-detergent fibre and acid-detergent fibre (Barnes, 1973). Where hemicellulose was not analyzed, it was assumed to be equal to cellulose content (Penning de Vries, 1975). Mineral content was determined by ashing at 600°C for 3 h. Organic acid content was assumed to be 5% of total dry weight (Penning de Vries, Brusting & Van Laar, 1974). Total carbohydrate was obtained by subtraction. All determinations were made on duplicate samples. Non-structural carbon was calculated as total carbon in biomass minus the sum of cellulose-, hemicellulose- and lignin-carbon.
Root respiration in the field

Data on growth and maintenance respiration, along with the non-structural (degradable) root biomass fraction were used to predict root respiration in a mixed grassland dominated by *A. dasystachyum* located at the Matador Field Station, 45 km north of Swift Current, Saskatchewan, Canada (50° 36' N, 107° 45' W). Respiration rates, calculated using Eqn (1), were adjusted to daily mean soil temperatures measured at 20 cm depth at the Matador Site (Ripley, 1972) assuming that the maintenance respiration coefficient had a $Q_{10}$ of 2-0 (Ryle et al., 1976). There is no information on how $m$ is influenced by water stress in *Agropyron*-dominated dry grasslands. It was therefore assumed that roots became 'dormant' when soil water potential dropped below −1·5 MPa, and that $m$ for dormant roots was 0·0005 g g$^{-1}$ d$^{-1}$. Data on root carbon content, root growth and soil water status were obtained from Coupland (1974), Warembourg & Paul (1977) and de Jong (1973), respectively. Root respiration of laboratory- and field-grown roots was expressed on the basis of their non-structural carbon contents.

RESULTS AND DISCUSSION

Root respiration in laboratory-grown plants

The mean respiration rate of laboratory-grown roots of *A. dasystachyum* was 5·03 mg CO$_2$ g$^{-1}$ h$^{-1}$. This rate is similar to values reported for other non-cultivated perennial grass species grown under similar conditions (Williams & Kemp, 1978). Values for cultivated species tend to be slightly higher. Hansen (1977), for example, found that the respiration rate of *Lolium multiflorum* roots varied between 10·6 and 20·7 mg CO$_2$ g$^{-1}$ h$^{-1}$ depending upon growing conditions.

Based on the regression of specific respiration on relative growth rate (Fig. 1), the $g$ of *A. dasystachyum* roots was 0·85 g g$^{-1}$ ($Y_g = 0·54$ g g$^{-1}$). The $m$ was 0·037 g g$^{-1}$ d$^{-1}$. The $Y_g$ was within the range of values reported for roots of several non-grass species (Table 1). The $m$ was substantially lower than most of the values reported for roots, although it was similar to whole plants or shoots (Hesketh, Alberte & Jones, 1980). The cost of root growth in *A. dasystachyum* is similar to a number of other (mostly mesic) species, but the cost of maintaining these roots is lower.

Non-structural root biomass

The non-structural carbon content of laboratory-grown roots was 54% of total biomass carbon (Table 2), slightly higher than young, whole plants of *Zea mays* (45%), as reported by Penning de Vries et al. (1974). Non-structural carbon made up 13% of total carbon in field-grown roots. There were differences in the methods of determining non-structural carbon in field- and laboratory-grown roots in the present study, but it is unlikely that this can account for the differences observed. Even when using the same procedure as that used for field-grown roots, laboratory-grown roots had a relatively high non-structural carbon content (28 to 67%), which varied depending on root age and growing conditions (R. E. Redmann, unpublished data). Results agree with values of non-structural carbon contents in roots of other native perennial grasses including *Festuca scabrella* (15%), *Stipa spartea* (5%) and *Stipa comata* (7%), calculated using data in Herman, McGill & Dormaar (1977).

The long axes of vascular tissue connecting the root tips with the shoot in grassland root systems consist primarily of metabolically-inactive tissue requiring
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Fig. 1. Relationship between specific respiration rate and relative growth rate for laboratory-grown *Agropyron dasystachyum* plants. The line was fitted by Bartlett's three-group method. The slope and intercept were 0.85 and 0.037 g g\(^{-1}\) d\(^{-1}\), respectively.

Table 1. *Growth conversion efficiency* (Y\(_g\)) and *maintenance coefficient* (m) in roots (m corrected to 20 °C assuming a Q\(_{10}\) of 2.0)

<table>
<thead>
<tr>
<th>Y(_g) (g g(^{-1}))</th>
<th>m (mg g(^{-1}) d(^{-1}))</th>
<th>Species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.54</td>
<td>37</td>
<td><em>Agropyron dasystachyum</em></td>
<td>This study</td>
</tr>
<tr>
<td>0.59</td>
<td>140</td>
<td><em>Lolium multiflorum</em></td>
<td>Hansen &amp; Jensen (1977)</td>
</tr>
<tr>
<td>0.65</td>
<td>97</td>
<td><em>Pisum sativum</em></td>
<td>Mahon (1977)</td>
</tr>
<tr>
<td>0.44–0.65</td>
<td>117–302</td>
<td><em>Senecio viscosus</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.50</td>
<td>263</td>
<td><em>S. vulgaris</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.55–0.57</td>
<td>196–232</td>
<td><em>Hypochaeris radicata</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.49</td>
<td>110</td>
<td><em>Urtica dioica</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.60</td>
<td>194</td>
<td><em>Plantago coronopus</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.48–0.68</td>
<td>64–126</td>
<td><em>P. lanceolata</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.63–0.76</td>
<td>70–80</td>
<td><em>P. major</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.68</td>
<td>86</td>
<td><em>P. maritima</em></td>
<td>Lambers (1979)</td>
</tr>
<tr>
<td>0.69</td>
<td>37</td>
<td><em>Helianthus annuus</em></td>
<td>Szaniawski &amp; Kielkiewicz (1982)</td>
</tr>
</tbody>
</table>

* No fixation of N\(_2\).*

little maintenance. The tips of field-grown roots, being primarily juvenile tissue, probably resemble laboratory-grown root systems in having high specific respiration rates. Root tips, however, make up a small proportion of the total field-grown root system. Field-grown roots may also have a higher structural carbon content because of the relatively rapid decomposition of non-structural compounds and persistence of structural carbon after root death. By expressing respiration rates on the basis of non-structural tissue, it becomes possible to compare root systems of different form, such as those grown in the field vs in the laboratory.

This view of root systems in grasslands reconciles estimates of metabolically active roots obtained in the present study using chemical determinations (13%)
Table 2. Chemical composition of laboratory- and field-grown roots of Agropyron dasystachyum

<table>
<thead>
<tr>
<th>Chemical fraction</th>
<th>Type of roots</th>
<th>Laboratory-grown</th>
<th>Field-grown</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Carbon content</td>
<td>(% d. wt) (% total C)</td>
<td>(% d. wt) (% total C)</td>
</tr>
<tr>
<td>Nitrogenous compounds</td>
<td>53.16</td>
<td>22.4</td>
<td>27.6</td>
</tr>
<tr>
<td>Cellulose</td>
<td>45.16</td>
<td>17.7</td>
<td>18.5</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>45.16</td>
<td>17.7</td>
<td>18.5</td>
</tr>
<tr>
<td>Non-structural carbohydrates</td>
<td>45.16</td>
<td>19.2</td>
<td>20.1</td>
</tr>
<tr>
<td>Lipids</td>
<td>77.55</td>
<td>1.5</td>
<td>2.7</td>
</tr>
<tr>
<td>Lignin</td>
<td>61.96</td>
<td>5.9</td>
<td>8.5</td>
</tr>
<tr>
<td>Organic acids</td>
<td>35.18</td>
<td>5.0</td>
<td>4.1</td>
</tr>
<tr>
<td>Ash</td>
<td>—</td>
<td>10.6</td>
<td>0.0</td>
</tr>
<tr>
<td>Total carbon</td>
<td>—</td>
<td>43.2</td>
<td>100.0</td>
</tr>
<tr>
<td>Structural carbon</td>
<td>—</td>
<td>45.6</td>
<td>—</td>
</tr>
<tr>
<td>Non-structural carbon</td>
<td>—</td>
<td>54.4</td>
<td>—</td>
</tr>
</tbody>
</table>

Table 3. Respiration in mixed grassland (g C m\(^{-2}\) 127 d\(^{-1}\)) calculated using growth and maintenance coefficients determined in this study

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Respiration component</th>
<th>Growth</th>
<th>Maintenance</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>A*</td>
<td>66</td>
<td>2263</td>
<td>2329</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>66</td>
<td>556</td>
<td>622</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>66</td>
<td>261</td>
<td>327</td>
<td></td>
</tr>
</tbody>
</table>

* A, calculated using the published root biomass (660 g C m\(^{-2}\)) and root growth (78 g C m\(^{-2}\) 127 d\(^{-1}\)) of this grassland (Warembourg & Paul, 1977), together with Eqn (1) and the respiratory parameters determined for laboratory-grown roots (g = 0.85 g g\(^{-1}\), m = 270 mg g\(^{-1}\) d\(^{-1}\)). The m was corrected for temperature differences between laboratory and field using a Q\(_{10}\) of 2.0 and the daily average soil temperature at 20 cm depth. It was assumed that the total root biomass required maintenance; B, calculated as in A, except that the m was expressed on the basis of non-structural carbon in laboratory-grown roots [680 mg (g non-structural C)\(^{-1}\) d\(^{-1}\)]; only the non-structural fraction (0.13) of total root biomass was considered to require maintenance; C, calculated as in B, except that the m was reduced to 0.5 mg (g non-structural C)\(^{-1}\) d\(^{-1}\) for the 63 d during the 127 d period when soil water potential was below -1.5 MPa.

to the higher estimates of 'live' or 'functional' roots obtained in autoradiographic studies (e.g. 60% in Singh & Coleman, 1977). The long root axes of field-grown roots, while structurally intact and functional in the translocation of carbon, water and nutrients, consist primarily of metabolically inactive tissue requiring little maintenance.

Simulation of respiration in field-grown roots

Root respiration for a 127 d growing season was calculated assuming that the total root biomass required maintenance. The result was an unrealistically high value of maintenance respiration (Table 3, simulation A). Assuming that only the non-structural biomass requires maintenance produced a substantially lower maintenance respiration (Table 3, simulation B). In both simulations, maintenance
respiration was much larger than growth respiration (e.g. maintenance respiration in simulation B was 89% of total respiration). Under laboratory conditions, maintenance respiration was only about 50% of total respiration at time of maximum biomass.

Adjustment for water stress reduced maintenance respiration (Table 3, simulation C). The cost of maintaining root systems in arid and semi-arid environments may be substantially reduced by periods of root dormancy induced by environmental factors such as drought, or perhaps by some internal control mechanisms, as proposed by Holthausen & Caldwell (1980). Dormancy mechanisms would allow the development of the large root systems needed during periods of growth, yet substantially reduce the total cost of maintaining these systems over the total growing season.

Root respiration measured independently in this grassland by Warembourg & Paul (1977) totalled 25 g C m\(^{-2}\) (127 d\(^{-1}\)) for the same year used in these simulations. Simulation C gave a total respiration of 327 g C m\(^{-2}\) (127 d\(^{-1}\)). True root respiration probably lies between these two extremes. Warembourg & Paul (1977) reported root growth to be 78 g C m\(^{-2}\) (127 d\(^{-1}\)). Multiplying this value by a conservative estimate of the growth respiration coefficient (0.85 g g\(^{-1}\)) gives a growth respiration of 66 g C m\(^{-2}\) (127 d\(^{-1}\)). Maintenance respiration costs also have to be added on, making the total respiration even higher. True root respiration is probably substantially higher than the estimate by Warembourg & Paul.

Simulation C may have overestimated total respiration if (1) the proportion of roots requiring maintenance was too high, or (2) the \(m\) determined for laboratory-grown roots was too high for field-grown roots. As discussed above, the estimate of the proportion of roots requiring maintenance which was used in these simulations is low compared to previous estimates of the proportion of functional roots in grassland. More measurements of growth and maintenance respiration are required to verify the values of \(g\) and \(m\). In particular, the effect of water stress on maintenance respiration needs to be determined at several stages of root development in order to refine the model presented here.

In summary, maintenance respiration in laboratory-grown roots of \(A.\) dasystachyum is substantially lower than published rates for mesic species. The extensive root system of this species is composed primarily of long axes of vascular tissue which functions in transport between the shoot and root tips, but which has a low maintenance requirement. Differences in the proportions of roots requiring maintenance, together with differences in root growth, temperature and water stress, are able to explain most of the discrepancy between respiration rates of laboratory- and field-grown \(A.\) dasystachyum root systems. Species such as \(A.\) dasystachyum, adapted to semi-arid habitats, have inherently low rates of maintenance respiration and a relatively small degradable fraction. As a result, maintenance costs are smaller than would be predicted using the large root biomasses reported for grassland ecosystems.

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