5-1988

# The Modeling and Measurement of Respiratory Carbon Use and Net Carbon Gain of Two Agropyron

Halldor Thorgeirsson
*Utah State University*

THE MODELING AND MEASUREMENT OF RESPIRATORY CARBON

USE AND NET CARBON GAIN OF TWO *AGROPYRON*

BUNCHGRASSES

by

Halldor Thorgeirsson

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1988

# ACKNOWLEDGEMENTS

I would like to thank my major professor, Dr. James H. Richards for his support and encouragement during all stages of my work on this dissertation. His thoughtful guidance contributed greatly to this research. I am also grateful to Dr. Keith J. McCree of Texas A&M University for his help. He reviewed my proposal, and subsequent discussions with him have sharpened my understanding of respiratory carbon use and plant carbon balance in general. Dr. M.M. Caldwell provided valuable input and encouragement for which I am grateful.

Gary W. Harris worked closely with me on the development and construction of the laboratory gas-exchange system. Without his talent and dedication the system could not have been brought to the level of sophistication it is at now. I would like to thank him for his efforts. Help by Charles W. Ashurst on the construction of the system is greatly appreciated.

Dr. Jerry Chatterton conducted detailed analysis of plant carbohydrate content and aided in the interpretation of the results. His help is greatly appreciated. I would like to thank Drs. M.M. Caldwell, N.J. Chatterton, K. Mott, F. Senft, and D. Roberts for serving on my advisory committee.

I would like to thank my wife, Heida, and my children, Berglind and Hakon Atli, for their support. Discussion with fellow graduate students

and other coworkers helped me on several occasions in the course of my research. I am grateful for their input.

## TABLE OF CONTENTS

# LIST OF TABLES

## LIST OF FIGURES

LIST OF SYMBOLS

| | |
|---|---|
| $t$ | Time (d) |
| $T$ | Temperature (°C) |
| $T_r$ | Reference temperature (°C) |
| $CER_l$ | Plant net carbon exchange rate during the light period (mmol C plant$^{-1}$ 12h$^{-1}$) |
| $CER_d$ | Plant net carbon exchange rate during the dark period (mmol C plant$^{-1}$ 12h$^{-1}$) |
| $^sCER_d$ | Shoot net carbon exchange rate during the dark period (mmol C plant$^{-1}$ 12h$^{-1}$) |
| $^rCER_d$ | Root net carbon exchange rate during the dark period (mmol C plant$^{-1}$ 12h$^{-1}$) |
| $^rCER_l$ | Root net carbon exchange rate during the light period (mmol C plant$^{-1}$ 12h$^{-1}$) |
| $P_g$ | Daily gross rate of substrate input from photosynthetic carbon fixation (mmol C plant$^{-1}$ d$^{-1}$, Chapter III, or mmol C mol C$^{-1}$ d$^{-1}$, Chapter IV) |
| $P_n$ | Daily net rate of substrate input from photosynthetic carbon fixation (mmol C mol C$^{-1}$ d$^{-1}$) |
| $R$ | Daily rate of whole-plant respiratory carbon use (mmol C plant$^{-1}$ d$^{-1}$) |
| $^sR$ | Daily rate of shoot respiratory carbon use (mmol C plant$^{-1}$ d$^{-1}$) |
| $^rR$ | Daily rate of root respiratory carbon use (mmol C plant$^{-1}$ d$^{-1}$) |
| $^sr$ | Daily mass specific rate of root respiratory carbon use (mmol C mol C$^{-1}$ d$^{-1}$) |
| $^rr$ | Daily mass specific rate of shoot respiratory carbon use (mmol C mol C$^{-1}$ d$^{-1}$) |
| $^sn$ | Integrated or instantaneous mass specific rate of shoot respiratory carbon use during the light period (mmol C mol C$^{-1}$ d$^{-1}$, or µmol C mol C$^{-1}$ s$^{-1}$) |

$^s r_d$      Integrated or instantaneous mass specific rate of shoot respiratory carbon use during the dark period (mmol C mol $C^{-1}$ $d^{-1}$, or μmol C mol $C^{-1}$ $s^{-1}$)

$\Delta S_m/\Delta t$      Daily maintenance requirement (mmol C $plant^{-1}$ $d^{-1}$)

$\Delta S_g/\Delta t$      Daily rate of substrate input for growth (mmol C $plant^{-1}$ $d^{-1}$)

$Y_g$      Efficiency of the conversion of substrate into structural material (conversion efficiency).

$Y$      Growth efficiency

$^s Y$      Shoot growth efficiency

$m$      Maintenance coefficient (mmol C mol $C^{-1}$ $d^{-1}$).

$W$      Plant carbon content (mmol C $plant^{-1}$).

$\Delta W/\Delta t$      Daily net carbon balance (mmol C $plant^{-1}$ $d^{-1}$).

μ      Specific growth rate ($d^{-1}$).

$^s W$      Shoot carbon content (mmol C $plant^{-1}$).

$^r W$      Root carbon content (mmol C $plant^{-1}$).

$^s W_l$      Labile carbon compounds in shoots (mmol C $plant^{-1}$).

$^r W_l$      Labile carbon compounds in roots (mmol C $plant^{-1}$).

$^s W_d$      Degradable structural carbon compounds in shoots (mmol C $plant^{-1}$).

$^r W_d$      Degradable structural carbon compounds in roots (mmol C $plant^{-1}$).

$^s W_n$      Nondegradable structural carbon compounds in shoots (mmol C $plant^{-1}$).

$^r W_n$      Nondegradable structural carbon compounds in roots (mmol C $plant^{-1}$).

$^s W_g$      Shoot structural dry weight (kg structure $plant^{-1}$).

$^r W_g$      Root structural dry weight (kg structure $plant^{-1}$).

$W_g$      Plant structural dry weight (kg structure $plant^{-1}$).

$W_c$      Plant labile carbon content (kg C plant$^{-1}$).

$C_l$      Plant labile carbon concentration [kg C (kg structure)$^{-1}$].

$W_N$      Plant labile nitrogen content (kg N plant$^{-1}$).

$N_l$      Plant labile nitrogen concentration [kg N (kg structure)$^{-1}$].

$f_N$      Fractional nitrogen content of structural dry weight [kg N (kg structure)$^{-1}$].

$^sf_d$      Fraction of shoot carbon content that is degradable structural material.

$^rf_d$      Fraction of root carbon content that is degradable structural material.

$^sf_n$      Fraction of shoot carbon content that is nondegradable structural material.

$^rf_n$      Fraction of root carbon content that is nondegradable structural material.

$^sf_l$      Fraction of shoot carbon content that is labile carbon compounds.

$^rf_l$      Fraction of root carbon content that is labile carbon compounds.

$k_d$      Daily rate of degradation of degradable structural material (d$^{-1}$).

$k_g$      Daily rate of mobilization of labile carbon compounds for growth of structural material (d$^{-1}$).

$Y_d$      Fraction of new structural material that is degradable structural material.

$^sL$      Proportion of daily carbon input from photosynthetic carbon fixation that is partitioned to shoots.

$^rL$      Proportion of daily carbon input from photosynthetic carbon fixation that is partitioned to roots.

$\sigma_n$      Shoot specific activity for nitrogen uptake [kg N (kg structure)$^{-1}$ d$^{-1}$].

$^{max}\sigma_n$     Maximum shoot specific activity for nitrogen uptake [kg N (kg structure)$^{-1}$ d$^{-1}$].

$k_c, k_n$     Constants in equation (14).

$p$     Partition function.

$\alpha$     Partitioning parameter.

$Q_{10}$     The temperature coefficient

# ABSTRACT

The Modeling and Measurement of Respiratory Carbon

Use and Net Carbon Gain of Two *Agropyron*

Bunchgrasses

by

Halldor Thorgeirsson, Doctor of Philosophy

Utah State University, 1988

Major Professor: Dr. James H. Richards
Department: Range Science

The rate of photosynthetic carbon fixation and of root and shoot respiratory carbon use was measured in the laboratory and in the field (shoots only) for *Agropyron desertorum* (Fisch. ex Link) Schult. and *Agropyron spicatum* (Pursh) Scribn. and Smith. The rate of respiratory carbon use of the root system declined within hours of the shading or defoliation of the shoot system, resulting in as much as 60% reduction in specific rate of root respiration. The mean whole-plant growth efficiency (the ratio of whole-plant net carbon gain to gross photosynthetic carbon fixation) in full irradiance in the laboratory was 0.53 and was reduced both by shading and defoliation. The mean conversion efficiency was 0.70 and 0.73, and the mean maintenance coefficient at 20°C was 10.8 and 9.9 mmol C mol $C^{-1}$ $d^{-1}$ for *A. desertorum* and *A. spicatum*, respectively. These maintenance coefficients are lower than previously reported for fast growing crop plants.

The rate of respiratory carbon use and the dynamics of labile carbon compounds were simulated both for intact plants and for plants regrowing following defoliation. The partitioning of assimilates between root and shoot was explicitly modeled to make the separate simulation of root and shoot respiration possible. The simulated daily net mobilization of labile carbon compounds exceeded carbon input from photosynthesis for only the first one-to-two days of regrowth, depending on the severity of the defoliation.

The instantaneous rate of respiratory carbon use of the shoot system in the field during short-term light exclusion during the day was higher than the rate at the same temperature during the subsequent night. The $Q_{10}$ of shoot respiration was estimated to be 2.1-2.2. The mean growth efficiency in the field for the shoots only was 0.65 for sunny days. This efficiency was higher than the whole-plant growth efficiency in the laboratory because root respiration was not measured in the field.

(125 pages)

# CHAPTER I

## OVERVIEW

This dissertation focuses on the daily rates of whole-plant, root, and shoot respiratory carbon use, and the relationship of these rates to the daily rate of whole-plant carbon input from photosynthetic carbon fixation. The effect of net mobilization and net accumulation of labile carbon compounds (nonstructural carbohydrates) on the above relationship was also considered. Together, the rate of carbon fixation and the rate of respiratory carbon use determine net carbon gain. The question of how the two processes interact takes on particular importance during regrowth following defoliation, when the balance between carbon fixation and carbon utilization is disrupted. This study was therefore conducted on both intact plants and on plants regrowing following defoliation, using the cool-season perennial bunchgrasses: *Agropyron desertorum* (Fisch. ex Link) Schult. and *Agropyron spicatum* (Pursh) Scribn. and Smith[1].

This study combines two approaches: the continuous monitoring of root and shoot carbon dioxide exchange, and the mathematical simulation of respiratory carbon use and of pools of labile carbon compounds. Shoot respiratory carbon use was monitored both in the field and in the laboratory. Root respiratory carbon use was monitored in the laboratory only. Continuous monitoring of the rate of respiratory carbon use of entire root systems in the field is still not feasible. The root system must be included a rigorous analysis of whole-plant carbon

---

[1] Recent taxonomic revisions make *A. spicatum* synonymous with *Pseudoroegneria spicata* (Push)Löve (Barkworth & Dewey, 1985).

utilization, however. To achieve my objectives I constructed a laboratory gas-exchange system, capable of separately monitoring root and shoot carbon dioxide exchange of two plants simultaneously. This system was automated to make extended monitoring possible. Shoot respiratory carbon use was monitored in the field using temperature-controlled gas-exchange chambers.

The second approach used in this study was the mathematical simulation of respiratory carbon use. This involved the use of two published models. The first was the classical substrate-balance model (McCree, 1970; Thornley, 1970,1976), which partitions respiration into growth respiration and maintenance respiration. It is termed substrate-balance model because it is designed for conditions were substrate (carbon) use is in balance with substrate supply. I experimentally estimated the parameters of this model, the conversion efficiency and the maintenance coefficient, in the laboratory using intact plants. The second model was a recycling model of respiratory carbon use proposed more recently by Thornley (1977), as a replacement for the classical substrate-balance model. It has a more mechanistic representation of maintenance respiration and includes a pool of labile carbon compounds, making the simulation of transient (nonsubstrate-balance) conditions possible. It is termed recycling model because it includes the internal recycling of degradable structural material. Even though the recycling model has received considerable interest among modelers (Barnes & Hole, 1978; Thornley, 1982; Loehle, 1982; Johnson, 1985), experimental evaluation of the model has been more limited (McCree, 1982; McCree & Amthor, 1982).

Chapters II and III report on the results from the laboratory gas-exchange system. Chapter II reports on the estimation of the conversion efficiency and the maintenance coefficient. It also reports on the measurements of the growth efficiency (the ratio of net daily carbon gain and the gross daily photosynthetic carbon fixation). Whereas the conversion efficiency is the efficiency of the conversion of photosynthates to structural material, the growth efficiency is the overall efficiency of plant growth and includes carbon use for maintenance.

Chapter III focuses on the defoliated plants and the recycling model. The daily rates of carbon input from photosynthetic carbon fixation and of root and shoot respiratory carbon use were monitored during the first 5-19 days of regrowth. Growth efficiency was also measured. The recycling model was modified to enable the separate simulation of the rates of root and shoot respiratory carbon use. This required the explicit simulation of the partitioning of assimilates between root and shoot. I adopted a root-shoot partitioning model proposed by Johnson (1985) for this purpose. The simulated changes in the combined size of the root and shoot pools of labile carbon compounds were used to compare the quantitative contribution of labile carbon compounds and current photosynthate to plant carbon balance during regrowth.

In Chapter IV, I report on the measurements of shoot carbon dioxide exchange of the two plant species in the field. Four plants of each species were monitored for three days each at the end of March and the beginning of April, 1986. The rate of respiratory carbon use during the day was estimated at two times during the day by covering the

plants with opaque plastic bags for fifteen minutes. The rate of respiratory carbon use during the day and the following night was related to temperature and the daily rate of photosynthetic carbon fixation.

Chapter V is a summary and integration chapter. In the Appendix, the FORTRAN implementation of the recycling model and the assimilate partitioning model is printed along with sample input files and samples of model output.

## CHAPTER II

## GROWTH EFFICIENCY, CONVERSION EFFICIENCY

## AND MAINTENANCE COEFFICIENT OF TWO

## *AGROPYRON* BUNCHGRASSES

### Introduction

Growth efficiency is the ratio of net daily carbon gain and daily integrated gross photosynthetic carbon fixation. In the absence of respiratory carbon use, the growth efficiency would be unity; at the whole-plant light compensation point integrated over 24-h it is zero. To determine growth efficiency, and calculate plant growth from measurements of photosynthetic carbon fixation, the rate of respiratory carbon use needs to be measured or estimated. When a balance exists between carbon supply and carbon utilization, the rate of whole-plant respiratory carbon use can be successfully simulated using a simple, two-parameter, linear model (McCree, 1970; Thornley, 1970). This model has one state variable: total plant dry weight, and the two parameters are: the efficiency of conversion of assimilates to structural material (conversion efficiency) and the maintenance coefficient. For a given growth rate, growth efficiency is determined by the maintenance coefficient and the conversion efficiency (see below). The simplicity of this model stems from the fact that when balance exists between the fixation and the use of carbon, the dynamics of labile carbon compounds and of assimilate partitioning can be safely ignored for certain purposes. This limits its scope to conditions of steady-state rate of substrate input, however.

The parameters of this substrate-balance model have been estimated experimentally using various methods (for reviews see: Hesketh, Alberte, and Jones, 1980; Lambers, Szaniawski, and de Visser, 1983; Amthor, 1984). All the experimental methods involve the monitoring of plant carbon balance for two or more different rates of substrate input from photosynthetic carbon fixation where balance has been reached between carbon fixation and carbon utilization. The problem inherent in this approach is that changes in conditions, such as irradiance, can trigger adaptive changes in the physiology of the plant, which in turn can change the values of the maintenance coefficient. The greater the change in conditions, the more likely such changes are.

Previous attempts at parameter estimation have focused on crop and pasture plants (see tables in: Amthor, 1984; Hesketh *et al.* 1980), and only a few wildland plants have been studied (Miller & Stoner, 1979; Lambers, 1979; Schwarz & Gale, 1981; Szaniawski, 1981; Merino, Field, & Mooney, 1982; Reekie & Redmann, 1987). In this Chapter, I report on the measurement of the growth efficiency and the experimental estimation of the two parameters that determine it for two cool-season bunchgrasses, *Agropyron desertorum* (Fisch. ex Link) Schult. and *Agropyron spicatum* (Pursh) Scribn. and Smith. To make these measurements and estimates I used changes in irradiance large enough to alter the balance of substrate use, but not large enough to result in adaptive changes to the physiology of the plants.

**Theory**

Thornley's formulation of the substrate-balance model (Thornley, 1970,1976), which I used, is based on the assumption that all substrate fixed by photosynthesis during a simulation period ($\Delta S/\Delta t$, here set equal to $P_g$, mmol C plant$^{-1}$ d$^{-1}$; the simulation period is 1 d in this case) is completely utilized during that same period. $P_g$ is equivalent to the daily integral of whole-plant gross photosynthesis. A portion of $P_g$ is used to meet the daily maintenance requirement ($\Delta S_m/\Delta t$, mmol C plant$^{-1}$ d$^{-1}$). The remainder ($\Delta S_g/\Delta t$, mmol C plant$^{-1}$ d$^{-1}$) is converted to new plant material with a conversion efficiency of $Y_g$ (unitless ratio):

$$Y_g = (\Delta W/\Delta t)/(\Delta S_g/\Delta t) \tag{1}$$

where $\Delta W/\Delta t$ is the daily net carbon gain (mmol C plant$^{-1}$ d$^{-1}$). $Y_g$ is independent of temperature (Penning de Vries, Brunsting, & Van Laar, 1974).

The daily rate of respiratory carbon use ($R$, mmol C plant$^{-1}$ d$^{-1}$) is:

$$R = (1-Y_g)P_g + Y_g(\Delta S_m/\Delta t) \tag{2}$$

The maintenance coefficient ($m$, mmol C mol C$^{-1}$ d$^{-1}$) is the daily maintenance requirement per unit of carbon in the plant ($W$, mol C plant$^{-1}$):

$$m = (\Delta S_m/\Delta t)/W \tag{3}$$

The growth efficiency ($Y$, unitless ratio) is the proportion of $P_g$ that is retained by the plant through the 24-h period:

$$Y = (\Delta W/\Delta t)/(P_g) \tag{4}$$

For plant productivity studies $Y$ is the parameter of interest because it

links net carbon gain directly to the rate of carbon input, as can be seen by solving equation (4) for net carbon gain:

$$\Delta W/\Delta t = YP_g \tag{5}$$

The growth efficiency is a function of $Y_g$, $m$, and the specific growth rate (Johnson, 1987):

$$Y = (Y_g\mu)/(\mu+mY_g) \tag{6}$$

where $\mu$ is specific growth rate calculated as:

$$\mu = (\Delta W/\Delta t)/W \tag{7}$$

## Materials and methods

*Plant material*

Plants of *A. desertorum* and *A. spicatum* were grown from seeds collected from experimental plots in northern Utah (Caldwell *et al.* 1981). The plants were grown in fritted clay (Absorb-N-Dry, Balcones Minerals, Flatonia, TX, USA) in 28-cm deep, 2200-cm³, PVC pots in an environmentally controlled growth chamber (M-13, Environmental Growth Chambers, Chagrin Falls, OH, USA), at a constant 20±2°C air temperature with 12-h of 900 $\mu$mol m$^{-2}$ s$^{-1}$ photosynthetic photon flux density (PPFD). An 100-W incandescent light bulb was used to provide supplemental far-red radiation during the 12-h light period and for 1-h at the beginning and the end of the 'dark' period.

The plants were watered to excess every third day with a nutrient solution of the following composition: macronutrients (mol m$^{-3}$): $NH_4NO_3$ 1.5; $KNO_3$ 5.0; $Ca(NO_3)_2$ 5.0; $MgSO_4$ 2.0; $KH_2PO_4$ 1.0; micronutrients (mmol m$^{-3}$): $HBO_3$ 20.0; $MnCl_2$ 10.0; $ZnSO_4$ 0.4; $CuSO_4$ 0.1; $Na_2MoO_4$ 0.4; $FeCl_3$ 50.0; HEDTA 50.0.

*Measurement of carbon dioxide exchange*

Two identical sets of chambers allowed the roots and shoots of two plants to be monitored simultaneously. Each root chamber was a double-walled stainless steel chamber with the same internal dimensions as the PVC pots. Water circulated between the two walls by a temperature-controlled water bath (Lauda RMS-20, Brinkmann Instruments, Westbury, NY, USA) maintained a constant $20\pm1°C$ root temperature. A perforated plate was mounted 2-cm from the bottom of the chamber to facilitate drainage. Nutrient solution was added at the top every day and fifteen minutes allowed for drainage. Air was forced through the highly porous fritted clay (van Bavel, Lascano, and Wilson, 1978) from an air inlet below the perforated plate to an air outlet at the top. The root chamber was separated from the top chamber using two stainless steel semi-circular plates. The shoots of the plants extended though a hole in the center of the plates. Glazing putty was used to provide an airtight seal around the stems.

The plexiglass shoot chamber was 30-cm high and had a total volume of 11800-cm³. The chamber walls were covered with transparent Teflon film (S-115, Saunders, Los Angeles, CA, USA), all air lines were made of Teflon or stainless steel, and all internal aluminum surfaces were nickel plated to reduce carbon dioxide and water vapor adsorption (Parkinson, 1985). The shoot chamber was maintained at $20\pm1°C$ using thermoelectric heat exchangers and a fan. Air flow to the shoot chambers was controlled and measured with mass flow controllers (PC-261, Tylan, Torrance, CA, USA). The flow to the root chambers was

controlled manually and measured using pneumotachometers (4600, Hans Rudolph, Kansas City, MO, USA). The mole fraction of water vapor of inlet and outlet airstreams was measured with dew-point mirrors (Dew-10, General Eastern, Watertown, MA, USA), and the mole fraction of carbon dioxide was measured using a differential IRGA (Binos, Inficon Leybold-Heraeus, East Syracuse, NY, USA). The IRGA was fitted with an interference filter to eliminate water vapor interference, but to further reduce the effect of water vapor on the $CO_2$ measurements the air was brought to a constant dew-point of 4°C before entering the IRGA.

Two-to-three-month-old plants were transferred to the carbon dioxide exchange measurement chambers. The fritted clay growing media was carefully washed off the roots before placing them in fresh clay in the root chambers to reduce microbial growth. Monitoring started 2 to 4 d after transplanting. Four plants of each species were measured. Each plant was measured for 12–17 d. The first 3–6 d were in high irradiance (900 $\mu$mol m$^{-2}$ s$^{-1}$, PPFD) then irradiance was reduced to (200–300 $\mu$mol m$^{-2}$ s$^{-1}$) for 3–4 d. Finally measurements were again made for 2–4 d in high irradiance. Following the second high-irradiance period, the plants were defoliated and monitored further for 6–20 d (Chapter III). At the end of this second monitoring period, the plants were harvested and freeze dried.

The two root chambers and two shoot chambers were monitored in a continuous rotation with five minutes spent on each chamber. The data for the first 90 s on a new chamber were not used. The output from the sensors was routed through a multiplexed relay scanner and

digitized every 10 s using a datalogger (AM32 and 21XL, respectively, Campbell Scientific, Logan, UT, USA).

*Calculation of carbon balance parameters*

For the parameterization of the substrate-balance model, all carbon balance parameters needed to be integrated for a complete light and dark period (McCree, 1986). The carbon exchange rate ($CER$, mmol C plant$^{-1}$ 12h$^{-1}$, a negative value for respiration) was integrated separately for the root (superscript r) and the shoot system (superscript s), for the light (subscript l) and dark (subscript d) periods. The rate of respiratory carbon use of the shoot system during the light period was assumed to be equal to the rate during the dark period. The daily carbon balance parameters (mmol C plant$^{-1}$ d$^{-1}$) were calculated in the following manner (McCree 1986):

$$\Delta W/\Delta t = CER_l + CER_d \tag{8}$$

$$P_g = CER_l - CER_d \tag{9}$$

$$^rR = -(^rCER_l + ^rCER_d) \tag{10}$$

$$^sR = -2(^sCER_d) \tag{11}$$

$$R = {}^sR + {}^rR \tag{12}$$

where $^sR$, $^rR$, and $R$, (mmol C plant$^{-1}$ d$^{-1}$) are the daily rates of respiratory carbon use of the shoot, the root system, and the whole plant, respectively.

$\Delta W/\Delta t$ and the final carbon content were used to back-calculate plant carbon content ($W$, mmol C plant$^{-1}$) at the beginning of each day.

*Estimation of respiratory*
*parameters*

Least squares regression was used to fit equation (2) to the data from days where substrate use was in balance. Determining if the plant was at substrate balance is a subjective decision and can best be done by comparing data from a series of days. As an aid in this determination, I used $Y$ and $^rR$, expressed as a fraction of $R$. In some cases new substrate balance was reached immediately; in others it took as long as 3 d. The mean reduction in $P_g$ on the first day of the shading period was 54% and ranged from 35-62%. The reduction in net carbon balance was slightly greater due to the delay in the response of respiration. The reduction in $\Delta W/\Delta t$ exceeded 87% for only one plant. That plant (*A. spicatum*, plant 4) had negative $\Delta W/\Delta t$ for the first two d of shading.

For the calculation of $m$, [equation (3)], total plant dry matter was converted to $W$ using a carbon percentage of 39.0% of dry matter (J. H. Richards, unpublished data).

## Results

Figure II.1 shows the time course of $P_g$, $^sR$ and $^rR$ for a representative plant of *A. desertorum* (plant 1). $P_g$ increased gradually with time due to the growth of the plants. The time course of $P_g$ after the return to high irradiance was a direct continuation of the preshading time course allowing for growth during the shading period. This suggests minimal effect of the shading on the photosynthetic characteristics. $^sR$ declined immediately when $P_g$ was reduced and recovered quickly when $P_g$ was increased again (Fig. II.1b). The
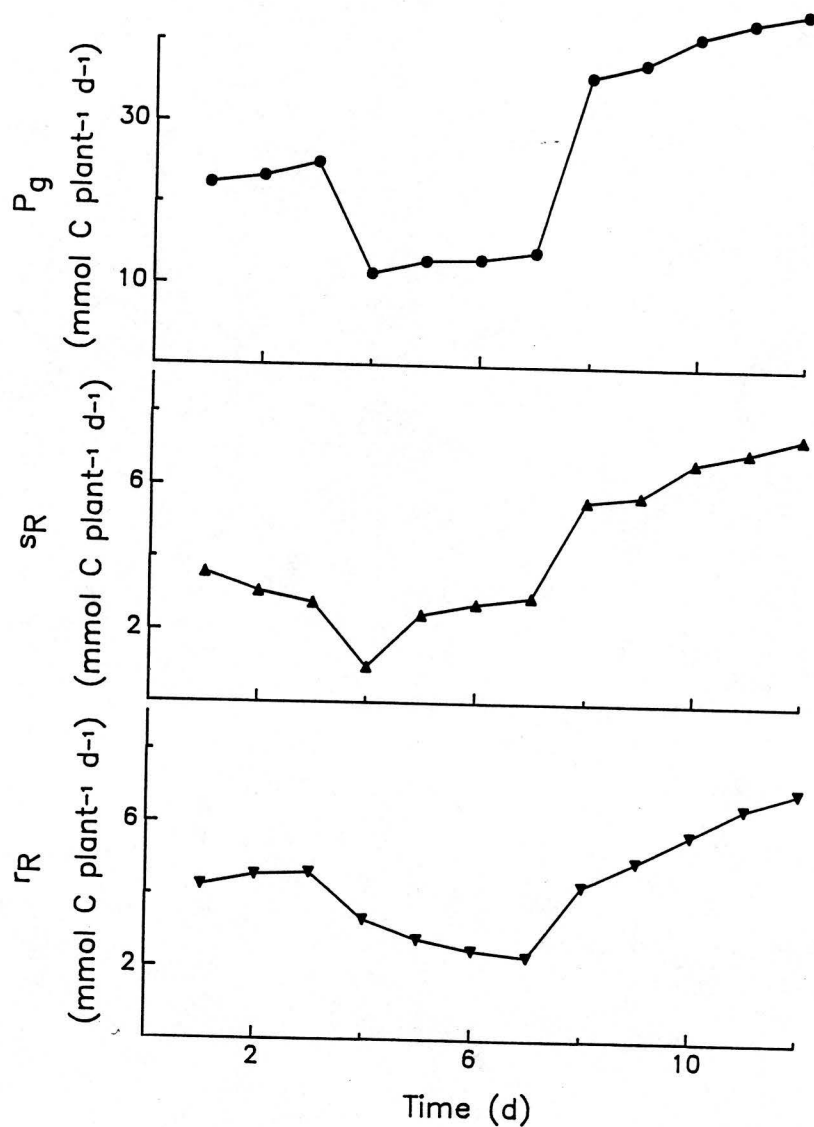
**Figure II.1.** The daily rate of substrate input from photosynthetic carbon fixation ($P_g$), the daily rate of shoot respiratory carbon use ($^sR$), and the daily rate of root respiratory carbon use ($^rR$) for *A. desertorum* no. 1 as a function of time. On d 4 the irradiance was lowered from 900 µmol m$^{-2}$ s$^{-1}$ to 300 µmol m$^{-2}$ s$^{-1}$ for 4 d.

response in $^rR$ was more gradual (Fig. II.1c). A new substrate balance

was reached immediately after the shading (a 55% reduction in $P_g$).

When the irradiance was increased again, however, the absolute change

in $P_g$ was greater (21.6 compared to 13.6 mmol C plant$^{-1}$ d$^{-1}$) and substrate balance was not reached until two days later.

Figure II.2 shows the measured $R$ as a function of $P_g$ for both steady-state and transient conditions and the fitted $R$ using equation (2) for the plant shown in Fig. II.1. The fitted $Y_g$ was 0.71 and $\Delta S_m/\Delta t$ was 1.6 mmol C plant$^{-1}$. The calculated $W$ for d 1 was 173.9 mmol C plant$^{-1}$, resulting in $m$ of 9.2 mmol C mol C$^{-1}$ d$^{-1}$. Table II.1 shows $W$ on d 1, mean $\mu$, $Y_g$, and $m$ for each of the plants measured. The number of days of substrate balance included in the estimation of $Y_g$ and $m$ ranged from 5-11. The coefficient of determination ranged from 0.91-0.98.

The plants were grown from seeds collected from wild plants in the field and therefore varied greatly in size and growth rate ($\mu$). Considerable variation was also found in the respiratory parameters (Table II.1), particularly in $m$. $Y_g$ ranged from 0.67 to 0.78, while $m$ ranged from 5.6 to 19.0. $m$ can be expected to increase with growth rate (see Discussion). This relationship was not clearly displayed by the plants studied here (Fig. II.3) due to large variation in $m$ and small sample size.

Growth efficiency relates net carbon gain directly to $P_g$ [equation (5)]. When substrate balance has been reached, $Y$ can be calculated from equation (6). The maximum value of $Y$ is set by $Y_g$. Maintenance respiration reduces $Y$ from this maximum value. Figure II.4 shows the calculated $Y$ for five different values of $\mu$ (within the range of values observed in this study) as a function of $m$ between 1 and 30 [equation (6)]. The sensitivity of $Y$ to $m$ increases as $\mu$ is reduced. Figure II.4

also shows the mean value of $Y$ for the experimental plants prior to the shading.
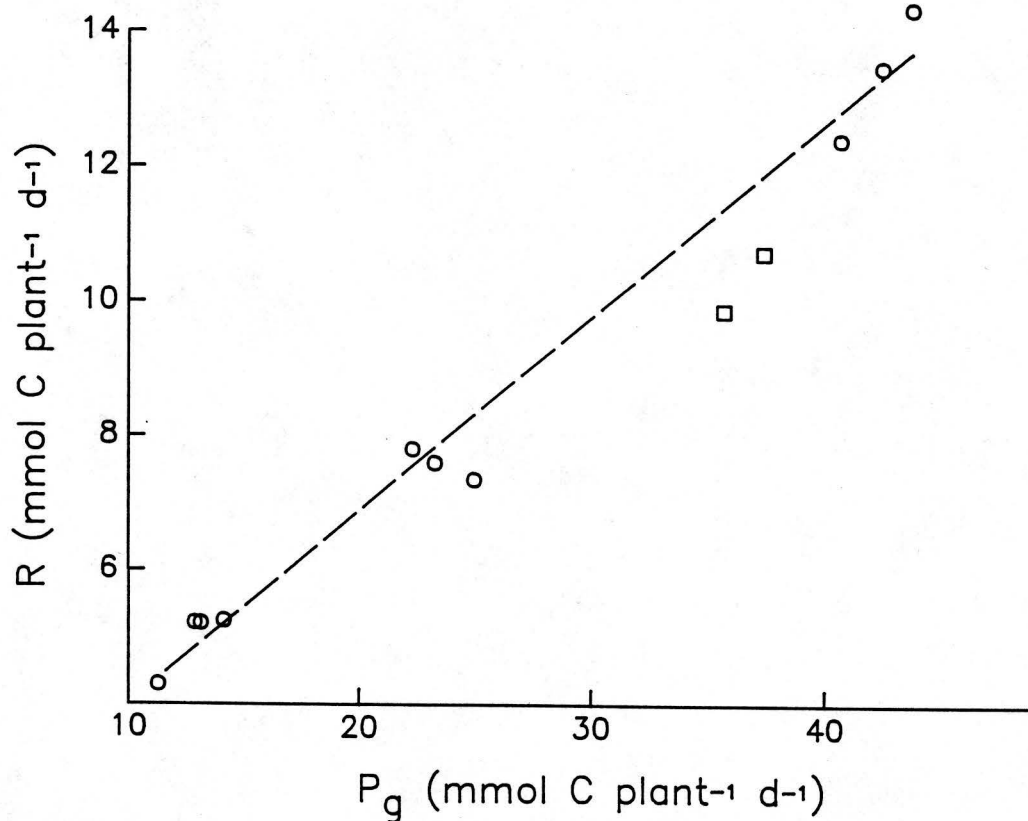


**Figure II.2.** The daily rate of whole-plant respiratory carbon use ($R$) as a function of the daily rate of substrate input from photosynthetic carbon fixation ($P_g$) for *A. desertorum* no. 1, for days when balance in substrate use had been reached (circles), and for days of transients in substrate use (squares). The dashed line is equation (2) fitted to the circles ($R = .29P_g + 1.1$, $r^2 = .98$).

**Table II.1.** Plant carbon content ($W$) at d 1 (mmol C plant$^{-1}$), mean specific growth rate ($\mu$, d$^{-1}$) prior to the experimental shading, conversion efficiency ($Yg$, unitless ratio) and the maintenance coefficient ($m$, mmol C mol C$^{-1}$ d$^{-1}$) for the individual plants.

| Species | No. | $W$ | mean $\mu$ | $Y_g$ | $m$ |
|---|---|---|---|---|---|
| *A. desertorum* | 1 | 173.9 | 0.072 | 0.71 | 9.2 |
| | 2 | 92.9 | 0.076 | 0.68 | 8.3 |
| | 3 | 272.8 | 0.018 | 0.72 | 11.5 |
| | 4 | 312.1 | 0.030 | 0.69 | 14.2 |
| Mean for species: | | 212.9 | 0.049 | 0.70 | 10.8 |
| *A. spicatum* | 1 | 364.4 | 0.040 | 0.71 | 19.0 |
| | 2 | 109.3 | 0.019 | 0.67 | 7.6 |
| | 3 | 359.4 | 0.023 | 0.77 | 5.6 |
| | 4 | 73.3 | 0.003 | 0.78 | 7.5 |
| Mean for species: | | 226.6 | 0.021 | 0.73 | 9.9 |
| Overall mean: | | 219.8 | 0.035 | 0.72 | 10.4 |

Net mobilization or net accumulation of labile carbon compounds causes $Y$ to deviate from the theoretical value calculated from equation (6) (Fig. II.5). Mobilization of labile carbon compounds, such as results from the shading of a previously well illuminated plant, will result in higher $R$ than expected based on $P_g$ alone and a lower $Y$ than predicted from equation (6) (see d 5 and 6, Fig. II.5). This was seen in most of the plants when they were shaded. Conversely, when the supply of carbon temporarily exceeds the demand for carbon, labile carbon compounds accumulate. This accumulation results in a lower $R$ than when all the incoming photosynthate is utilized for growth and maintenance. This increases $Y$ above the theoretical value (see d 8-11, Fig. II.5).
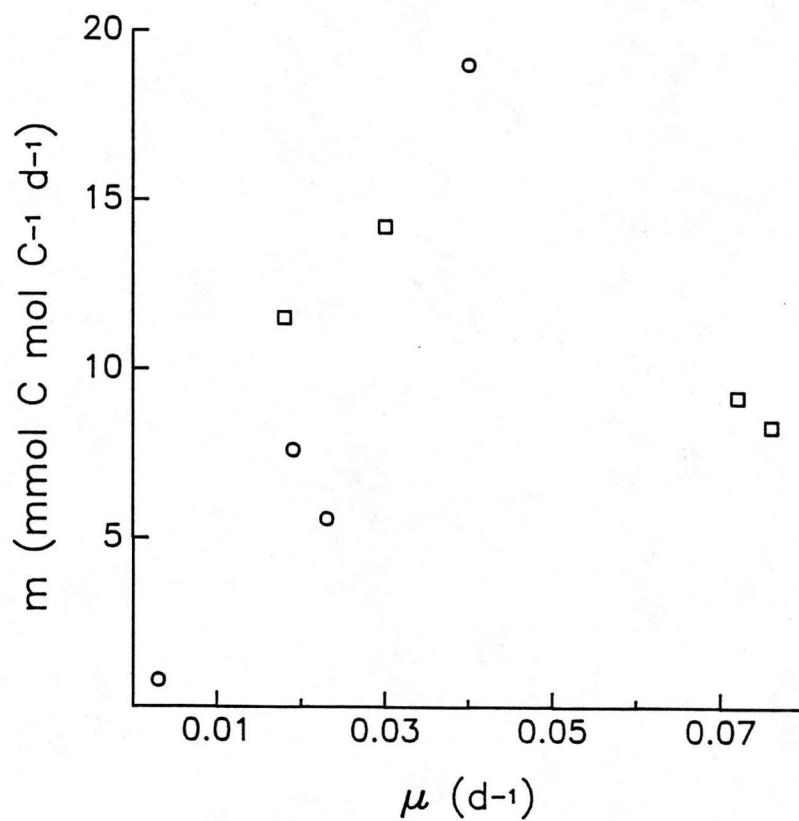
**Figure II.3.** The maintenance coefficient (*m*) as a function of mean specific growth rate (μ) during the preshading period for *A. desertorum* (squares) and *A. spicatum* (circles) plants. Each point represents one plant.
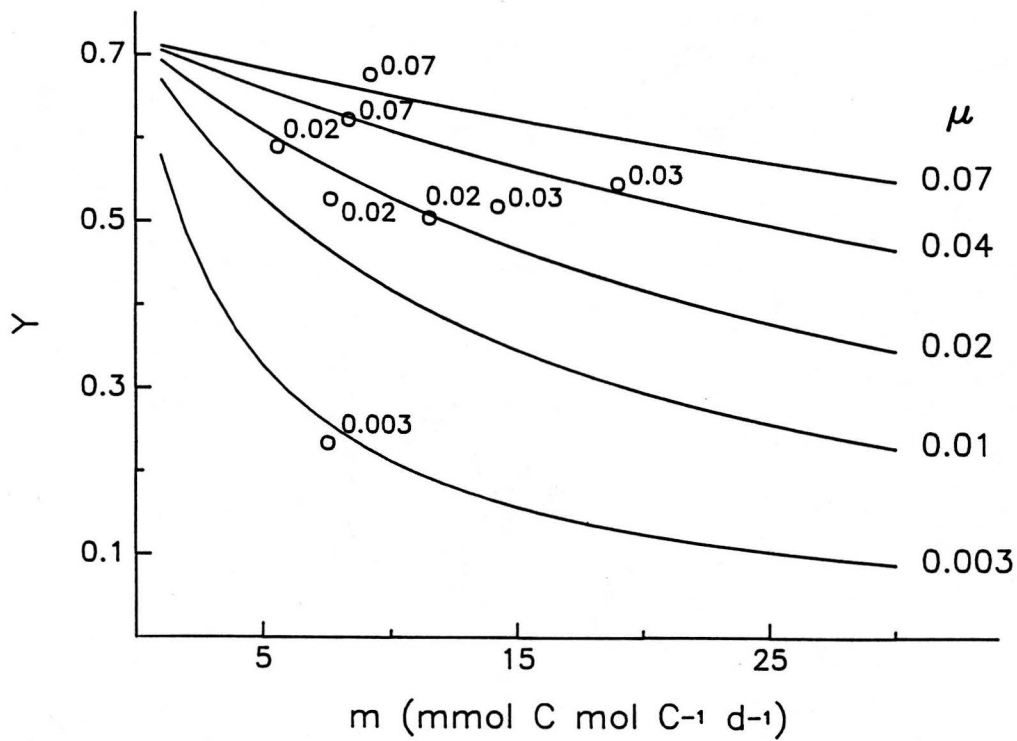
**Figure II.4.** The growth efficiency (*Y*) as a function of the maintenance coefficient (*m*) [equation (6)] for five different mean specific growth rates (μ) (solid lines), and the measured mean *Y* for the preshading period (circles). The numbers next to the circles are the mean specific growth rates for the plants during the same period.
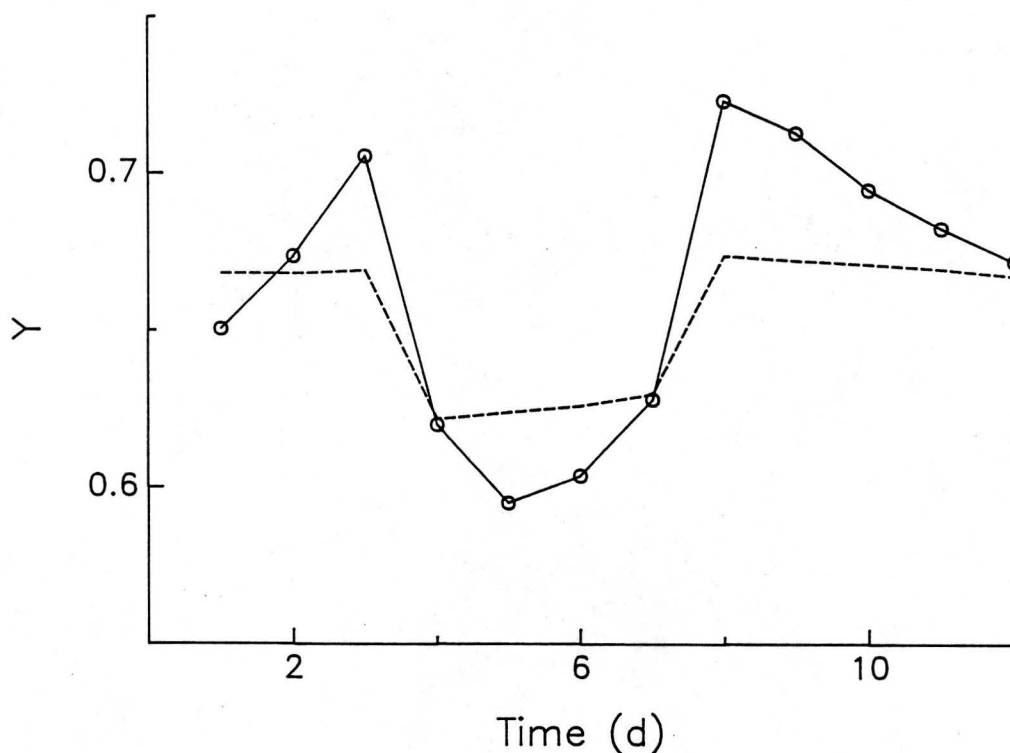
**Figure II.5.** Measured growth efficiency (*Y*) of *A. desertorum* plant 1 (solid line, circles), and the calculated *Y* [equation (6)] (dotted line). The plant was at high irradiance on d 1-3 and d 8-12; during d 4-7 the plant was shaded.

## Discussion

The estimated values of $Y_g$ are consistent with $Y_g$ values estimated for other plants. Hesketh *et al.* (1980) reported 18 $Y_g$ values from the literature, ranging from 0.62 to 0.84, with a mean of 0.74. Similarly, Penning de Vries *et al.* (1974) calculated a $Y_g$ of 0.7 from the stoichiometry of the biosynthesis of vegetative plant tissue from photosynthate. These calculations were based on the assumptions that biosynthesis is operating at maximum theoretical efficiency. This

efficiency can be reduced by nonphosphorylating electron transport, however.

The activity of the cyanide-resistant nonphosphorylating electron transport pathway (Lambers, 1985; Lance, Chauveau, & Dizengremel, 1985) was not quantified in this study. Activity of this cyanide-resistant pathway reduces the mitochondrial respiratory efficiency (i.e. the ADP:O ratio). A reduction in ADP:O ratio of respiration from 3 to 2 will only reduce $Y_g$ by 5%, however (Penning de Vries *et al.*, 1974). For such reduction in ADP:O ratio, 35% of total respiration would have to be due to the cyanide-resistant pathway (Lambers, Szaniawski, & de Visser, 1983). Possible engagement of the cyanide-resistant pathway would, therefore, not have affected my results significantly.

*m* is a composite parameter reflecting the level of metabolic activity in the plant (Amthor, 1984). The term maintenance coefficient is in fact misleading; a metabolic activity coefficient would more accurately reflect its true meaning. *m* actually reaches its lowest value when the plant is just maintaining the *status quo* (McCree, 1982). The level of metabolic activity in a plant changes with factors such as: growth rate, size, age, nutrient supply, and temperature. All of these factors will change the value of *m*. It is, therefore, a simplification to consider *m* a constant. McCree (submitted to Crop Science) demonstrated that season-long growth of sorghum could not be successfully simulated using a constant value for *m*. The large variations in *m* among plants in this study could be due to a combination of several of the sources of variation discussed above. No single factor alone could account for the

variation, however. This is most likely due to the large genetic variation among the plants.

There is some evidence for lower $Y_g$ and higher $m$ in roots compared to the shoot (Hansen & Jensen, 1977; Szaniawski, 1981; Lambers, *et al.*, 1983). The lower $Y_g$ has been related to greater activity of the cyanide-resistant pathway in roots (Lambers, 1985; Lambers, *et al.*, 1983). The higher $m$ in roots can be assumed to be largely a result of the metabolic cost of nutrient uptake (Veen, 1981). The respiratory parameters estimated in this study are whole-plant parameters. Any differences between root and shoot in $Y_g$ or $m$ would have affected individual plants differently since there was large variation in the root weight fraction (from 0.24 to 0.66).

The values for the maintenance coefficient estimated in this study were lower than the average values reported in the literature. In his review, Amthor (1984) lists 48 $m$ values for 18 different species, ranging from 4.0 to 93.0 (mmol C mol $C^{-1}$ $d^{-1}$) with a mean of 30.3, for temperatures ranging from 15.6 to 30°C [$m$ can be assumed to have a $Q_{10}$ of 1.8 to 2.2 (McCree, 1974; Ryle, Cobby, & Powell, 1976)]. Most of the values listed in the review were for fast growing crop plants. The few slower growing wildland plants included had the lowest values and tended to be consistent with the values observed in this study. It appears that most of the variation reported in $m$ values in this study, and in other studies, is real, even though differences in methods also contribute to this variation (Lambers *et al.*, 1983; Amthor, 1984; Irving & Silsbury, 1987).

*m* has been estimated for wildland shrubs and tree seedlings. Schwarz
& Gale (1981) estimated a *m* value of 4 for *Atriplex halimus* at 25/18°C
day/night temperatures. Miller & Stoner (1979) estimated *m* of 1.6 to
3.2 for leaves of two evergreen chaparral species, and Merino, Field, &
Mooney (1982) estimated *m* at 20°C to be 13.9 and 35.9 for leaves of an
evergreen and a drought deciduous chaparral shrub, respectively. *m*
estimated from leaves will be lower than whole-plant values, however,
because a major fraction of the carbon fixed by the leaf is exported
and therefore utilized and respired in other parts of the plant.
Szaniawski (1981) estimated *m* at 20-27°C to be 12.5 and 42.0 for shoots
and roots, respectively, for one-year old scots pine seedlings.

*Yg* and *m* have been estimated for roots of a closely related species:
*Agropyron dasystachyum*[2] (Reekie & Redmann, 1987). They estimated $Y_g$
to be only 0.54 and *m* to be 37 at 20°C. They grew the plants
hydroponically, which tends to change root physiology and morphology.
Plants grow fewer, more succulent, roots when grown hydroponically
than in soils. Total root system activity is therefore distributed among
fewer root elements. It is therefore not surprising that Reekie &
Redmann (1987) measured rather high *m* values. Indeed, Lambers (1979)
measured very high *m* values for hydroponically grown roots [64-302,
mmol C mol C$^{-1}$ d$^{-1}$, corrected to 20°C by Reekie and Redman (1987)].

*Y* can be expected to vary greatly as it is simultaneously influenced
by $Y_g$, *m*, and μ (Fig. II.4). In addition, there is variation caused by
nonsteady-state behavior (net mobilization or net accumulation of labile

---

[2] Recent taxonomic revisions make this species synonymous with
*Elymus lanceolatus* (Scribn. & Smith)Gould, (Barkworth & Dewey, 1985).

carbon compounds) (Fig. II.5). Under field conditions, net mobilization and net accumulation can be expected to balance each other when several days are considered together, making the mean $Y$ approach the theoretical value. $Y$ is a useful parameter for whole-plant studies because it summarizes the effects of both growth and maintenance respiration and therefore allows net carbon gain to be calculated directly from measurements of whole-plant gross photosynthetic carbon fixation. In an extensive study, Yamaguchi (1978) measured $Y$ of crop plants at different stages of development and under different environmental conditions. His values ranged from 0 to 0.75 but most fell between 0.55 and 0.65. Robson (1973) measured $Y$ of 0.55 for seedling swords of perennial ryegrass (*Lolium perenne* L.). $Y$ in this study ranged from 0.24 to 0.69 for *Agropyron* plants with widely varying $\mu$ and $m$ (Fig. II.4).

Better quantitative understanding of the sources of variation in the maintenance coefficient is needed, in particular in the relationship between respiratory carbon use and nutrient uptake. Another promising area is the parameterization of Thornley's (1977) recycling model. This model can shed some light on the sources of variation in the maintenance coefficient because it explicitly models one of the underlying processes: the turnover of degradable structural material.

CHAPTER III

THE DYNAMICS OF RESPIRATORY CARBON USE AND OF LABILE

CARBON DURING REGROWTH FOLLOWING DEFOLIATION:

MEASUREMENTS AND SIMULATIONS USING

THORNLEY'S RECYCLING MODEL

## Introduction

Immediately following severe defoliation, when the rate of carbon fixation falls short of the demand for carbon, the concentration of labile carbon compounds (nonstructural carbohydrates) has been shown to fall (Alberda, 1960; Davidson & Milthorpe, 1966). The quantitative contribution of this carbon mobilization to whole-plant carbon balance has rarely been estimated, however. In a landmark study, Davidson & Milthorpe (1966) showed that the mobilization of labile carbon in roots following severe defoliation of *Dactylis glomerata* did not account for the measured respiration of the root system. For the shoot system the mobilization of labile carbon exceeded input from photosynthesis for only the first two days of regrowth. Richards & Caldwell (1985) showed that the maximum potential mobilization of labile carbon, as estimated from etiolated regrowth of two *Agropyron* bunchgrasses in the field, exceeded the rate of photosynthetic carbon fixation of comparable plants for only three days.

Simultaneous measurements of the rate of photosynthetic carbon fixation, the rate of respiratory carbon use, and the rate of change in the total amount of labile carbon are needed to assess the quantitative significance of labile carbon dynamics for whole-plant carbon balance.

Since the measurement of labile carbon content is destructive, paired sets of plants must be compared (Davidson & Milthorpe, 1966; Richards & Caldwell, 1985). Pairing plants for such comparisons can be difficult for the genetically variable wildland plants. An alternative to the sequential destructive chemical analysis of labile carbon pools is the simulation of the dynamics of these pools using the strong relationship between the rate of carbon utilization and the rate of respiratory carbon dioxide efflux (Penning de Vries, Brunsting, & Van Laar, 1974).

Thornley (1977) has proposed a recycling model of respiratory carbon use which includes the dynamics of labile carbon. In this model, the plant is partitioned into three state variables: a pool of labile carbon compounds, a pool of degradable structural carbon compounds, and a pool of nondegradable structural carbon compounds, hereafter referred to as a labile carbon pool, degradable structural carbon, and nondegradable structural carbon, respectively. Carbon compounds derived from the degradation of structural carbon are recycled through the labile carbon pool, hence the term recycling model. The model has been tested on white clover (McCree, 1982; McCree & Amthor, 1982) but has never been used to simulate a regrowing plant.

In this Chapter I use Thornley's model to simulate the dynamics of respiratory carbon use and of labile carbon for the first 5-19 d of regrowth of *Agropyron desertorum* (Fisch. ex Link) Schult. and *Agropyron spicatum* (Pursh) Scribn. and Smith in the laboratory. Continuous measurements of root and shoot carbon dioxide exchange were used to calibrate the model. I also compare the simulated amount

of labile carbon mobilization to measurements of whole-plant carbon input from photosynthetic carbon fixation.

## The model

I extended Thornley's (1977) recycling model to include two submodels, one for the root system and another for the shoot system (Fig. III.1). The incoming photosynthate was partitioned between the two submodels using an assimilate partitioning model proposed by Johnson (1985).
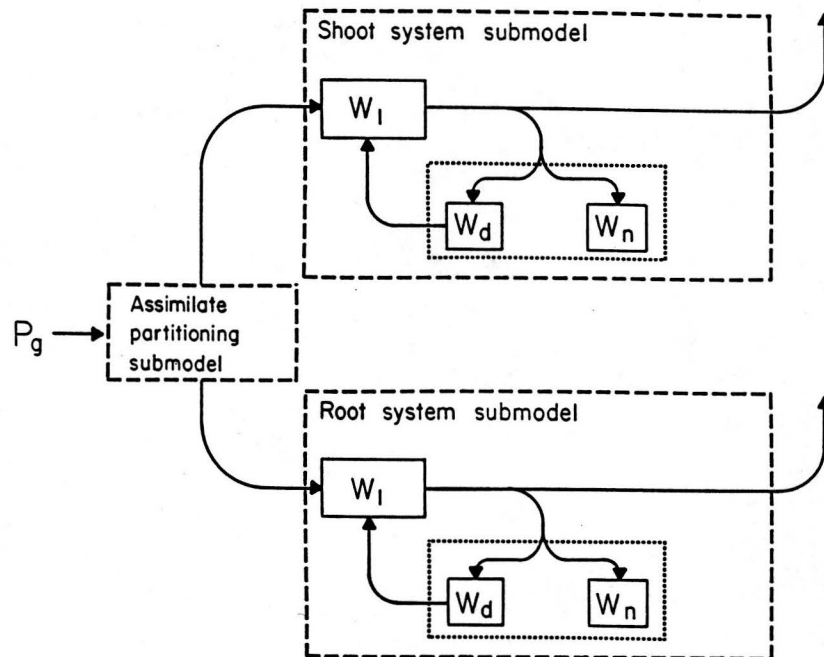


**Figure III.1.** A diagram of the relationship among the three submodels. The rate of carbon input from photosynthetic carbon fixation, $P_g$, is a driving variable. The assimilate partitioning submodel partitions $P_g$ between the two respiratory carbon use submodels. The state variables of the respiratory carbon use submodel are also shown. The dotted boxes represent structural material.

*The respiratory carbon use submodels*

The respiratory carbon use submodels only consider the carbon in the plant. All state variables are expressed in the units of mmol C plant$^{-1}$. In the following, the superscripts s and r refer to the shoot and root submodels, respectively. Following Thornley (1977), each of the respiratory carbon use submodels have three state variables: a labile carbon pool ($^sW_l$, $^rW_l$, mmol C plant$^{-1}$), nondegradable structural material ($^sW_n$, $^rW_n$, mmol C plant$^{-1}$), and degradable structural material ($^sW_d$, $^rW_d$, mmol C plant$^{-1}$). Total shoot, root, and plant carbon contents (mmol C plant$^{-1}$) are:

$$^sW = {}^sW_l + {}^sW_n + {}^sW_d \tag{1}$$

$$^rW = {}^rW_l + {}^rW_n + {}^rW_d \tag{2}$$

$$W = {}^sW + {}^rW \tag{3}$$

The fractions of root and shoot carbon content in each of the compartments are:

$$^sf_l = {}^sW_l/{}^sW; \quad {}^sf_n = {}^sW_n/{}^sW; \quad {}^sf_d = {}^sW_d/{}^sW;$$

$$^rf_l = {}^rW_l/{}^rW; \quad {}^rf_n = {}^rW_n/{}^rW; \quad {}^rf_d = {}^rW_d/{}^rW \tag{4}$$

The rate of gross substrate input from photosynthetic carbon fixation ($P_g$, mmol C plant$^{-1}$ d$^{-1}$) is a driving variable in the model. The assimilate partitioning submodel partitions $P_g$ between $^sW_l$ and $^rW_l$. The daily rate of substrate input to the root and shoot submodels is $P_g{}^rL$ and $P_g{}^sL$, respectively, where $^rL$ and $^sL$ is the proportional partitioning to the roots and the shoots, respectively. The calculation of these partitioning parameters will be discussed below.

The following is a description of the processes taking place within the respiratory carbon use submodels. It follows Thornley (1977), with

the exception that $P_g$ is partitioned between root and shoot. Only the shoot submodel is discussed; the root submodel is identical.

The labile carbon in $^sW_l$ is mobilized and converted to structural material at a rate of $k_g$ (d$^{-1}$), with a conversion efficiency of $Y_g$ (unitless ratio) such that, for each unit of labile carbon mobilized for growth, $Y_g$ units of structural material and $(1-Y_g)$ units of respiration result. $Y_g$ is assumed to be the same as the $Y_g$ of the substrate balance model (Chapter II). Theoretically the $Y_g$ of the recycling model is slightly lower (Thornley, 1982). This difference increases with $^sf_i$ and $^rf_i$, but was found to be small for the plants studied here. Of the new units of structural material, $Y_d$ (unitless ratio) are degradable structure and $(1-Y_d)$ are nondegradable structure. $^sW_d$ is degraded at a rate of $k_d$ (d$^{-1}$). The labile carbon which results from this degradation returns to $^sW_l$. The dynamics of the three state variables can, therefore, be described using the following first-order differential equations:

$$d^sW_l/dt = P_g{}^sL - k_g{}^sW_l + k_d{}^sW_d \qquad (5)$$

$$d^sW_d/dt = Y_d Y_g k_g{}^sW_l - k_d{}^sW_d \qquad (6)$$

$$d^sW_n/dt = (1-Y_d) Y_g k_g{}^sW_l \qquad (7)$$

The rate of shoot respiratory carbon use ($^sR$, mmol C plant$^{-1}$ d$^{-1}$) is calculated using:

$$^sR = k_g{}^sW_l(1-Y_g) \qquad (8)$$

*The assimilate partitioning
submodel*

The assimilate partitioning submodel follows Johnson's (1985) model except were noted. Since this submodel considers nitrogen in addition to carbon, all the state variables are expressed in weight units rather

than molar units. Following Johnson (1985), concentrations of labile carbon and nitrogen are expressed per unit of structural (nonstorage) dry weight, rather than total dry weight. This provides a consistent denominator and confines the effect of substrate levels to the numerator. The submodel has four state variables: shoot structural dry weight ($^sW_g$, kg structure plant$^{-1}$); root structural dry weight ($^rW_g$, kg structure plant$^{-1}$); plant labile carbon content ($W_c$, kg C plant$^{-1}$); and plant labile nitrogen content ($W_N$, kg N plant$^{-1}$). The first three state variables are calculated directly from the respiratory carbon use submodels in the following manner [multiplying by 0.012 converts mmol C to g C, dividing by 0.39 converts g C to g structure (see below), dividing by 1000 converts g structure to kg structure]:

$$^sW_g = [(^sW_d + ^sW_n)0.012]/(0.39 * 1000) \tag{9}$$

$$^rW_g = [(^rW_d + ^rW_n)0.012]/(0.39 * 1000) \tag{10}$$

$$W_c = (^sW_l + ^rW_l)0.012/1000 \tag{11}$$

Since photosynthate directly enters $^sW_l$ and $^rW_l$ at the rate of $P_g$, equation (11) in fact makes $P_g$ a driving variable of the assimilate partitioning model. This approach differs from Johnson's (1985) model, where the rate of carbon uptake is calculated from shoot size and the shoot specific activity for carbon uptake. The rate of change in $^sW_g$ and $^rW_g$ in Johnson's (1985) model is determined by a growth rate constant and the carbon and nitrogen substrate levels.

Following Johnson (1985) the rate change in $W_N$ is determined from the balance between the simulated rates of nitrogen uptake and nitrogen mobilization for new structural material:

$$dW_N/dt = \sigma_n{}^rW_g - f_N(dW_g/dt) \tag{12}$$

were $\sigma_n$ is root specific activity for nitrogen uptake [kg N (kg structure)$^{-1}$ d$^{-1}$], $f_N$ is the fractional nitrogen content of structural dry weight, and:

$$W_g = {}^r W_g + {}^s W_g \qquad (13)$$

$\sigma_n$ is allowed to vary in Johnson's (1985) model. The following standard relationship from enzyme kinetics for enzyme-substrate reactions with a fully competitive inhibitor is used. Carbon is the substrate and nitrogen (internal to the plant) is the inhibitor. The rate of nitrogen uptake is therefore driven by the plant demand for nitrogen rather than the availability of nitrogen in the environment. From a constant maximum root specific activity for nitrogen uptake of $^{max}\sigma_n$, the $\sigma_n$ is reduced when the concentration of labile carbon, $C_l$ [kg C (kg structure)$^{-1}$] falls, or when the concentration of labile nitrogen, $N_l$ [kg N (kg structure)$^{-1}$] increases:

$$\sigma_n = {}^{max}\sigma_n / [1 + (k_c / C_l)(1 + N_l / k_n)] \qquad (14)$$

were $k_c$ and $k_n$ are constants. $C_l$ and $N_l$ are calculated as:

$$C_l = W_C / W_g \qquad (15)$$

$$N_l = W_N / W_g \qquad (16)$$

Labile carbon and nitrogen compounds are assumed to be uniformly distributed throughout the plant (Johnson, 1985), and that they can be translocated to any point within the plant.

To calculate the partitioning of $P_g$ between $^s W_l$ and $^r W_l$, the first step is the calculation the partitioning function $p$ (Johnson, 1985; see also: Johnson and Thornley, 1987). This function responds both to the $^r W_g / {}^s W_g$ ratio and to the ratio of the concentrations of labile nitrogen and carbon $N_l / C_l$:

$$p \quad = \alpha \; (N_l/C_l) \; (^rW_g/^sW_g) \tag{17}$$

where $\alpha$ is a partitioning parameter. A reduction in $^sW_g$ as a result of defoliation, or the reduction in $C_l$ from shading will increase $p$. The proportion of $P_g$ that is partitioned to each of the submodels, $^rL$ and $^sL$, for the root and shoot submodel, respectively, is calculated from $p$ in the following manner:

$$^rL \quad = 1/(1+p) \tag{18}$$

$$^sL \quad = p/(1+p) \tag{19}$$

The sum of $^sL$ and $^rL$ is 1, and when $p = 1$, $^rL$ equals $^sL$.

## Materials and methods

### Carbon balance monitoring

The carbon balance of the plants was monitored continuously for 12-17 d before the defoliations, during which time the conversion efficiency and the maintenance coefficient of the classical substrate-balance model (McCree, 1970; Thornley, 1970,1976) was estimated (see Chapter II). This involved shading of the plants for 3-5 d. The plants were monitored for 5-19 d following the defoliations. Four plants of A. desertorum were monitored. Only one out of the four A. spicatum plants tested regrew following the defoliation. The other three had been induced to flower. Defoliation after floral induction removes all active meristematic tissue and no basal meristems were activated (Richards & Caldwell, 1985).

The carbon dioxide exchange of the roots was monitored separately from the shoot system. The temperature of both the root and the shoots was 20±1°C with 12-h of 900 µmol m$^{-2}$ s$^{-1}$ photosynthetic photon flux density (PPFD). Three of the plants were induced to flower

by exposing them to 14-16-h photoperiod using an 100-W incandescent lamp. The roots were in fritted clay, watered to excess daily with a full-strength nutrient solution. Details of the growing conditions and the gas-exchange system can be found in Chapter II.

The carbon exchange rate ($CER$, µmol C plant$^{-1}$ s$^{-1}$, a negative value for respiration) of each chamber was monitored for 5 minutes, every 20 minutes. The $CER$ was integrated for the 12-h light period ($^sCER_l$, $^rCER_l$, $CER_l$, mmol C plant$^{-1}$ 12h$^{-1}$, for the shoot, the roots, and the whole plant, respectively), and for the 12-h dark period ($^sCER_d$, $^rCER_d$, $CER_d$). The rate of shoot respiratory carbon use during the light period was assumed to be equal to the rate during the dark period. The daily rate of substrate input from carbon fixation ($P_g$, mmol C plant$^{-1}$ d$^{-1}$), the net daily gain in biomass carbon ($\Delta W/\Delta t$, mmol C plant$^{-1}$ d$^{-1}$), and the daily rate of respiratory carbon use of whole plants, shoots, and roots ($R$, $^sR$, and $^rR$, mmol C plant$^{-1}$ d$^{-1}$) were calculated as:

$$P_g \qquad = CER_l - CER_d \qquad\qquad (20)$$

$$\Delta W/\Delta t \ = CER_l + CER_d \qquad\qquad (21)$$

$$^sR \qquad = -2(^sCER_d) \qquad\qquad (22)$$

$$^rR \qquad = -(^rCER_l + ^rCER_d) \qquad\qquad (23)$$

$$R \qquad = {}^sR + {}^rR \qquad\qquad (24)$$

At the end of the carbon balance monitoring, the plants were harvested and freeze dried. The dry mass of the plants at harvest was converted to $W$ using a carbon percentage of 39.0% of dry mass, derived from combustion in oxygen (Richards, unpublished information). $W$ at the beginning of each day was calculated from $W$ at harvest, $\Delta W/\Delta t$, and the carbon content of the tissue removed by the defoliations. The

shoot and root carbon contents at the beginning of each day ($^sW$, $^rW$, mmol C plant$^{-1}$) were estimated, based on the assumption that the defoliation resulted in the cessation of root growth (Crider, 1955; Davidson & Milthorpe, 1966), and that $^rW$ did not change during the regrowth period.

The root weight fraction ($^rf$, unitless ratio) was calculated for each day:

$$^rf \quad = \; ^rW/W \tag{25}$$

Mass specific rate of shoot and root respiratory carbon use was calculated as:

$$^sr = \; ^sR/^sW; \qquad ^rr = \; ^rR/^rW \tag{26}$$

The growth efficiency, $Y$, is the ratio of net daily carbon gain to daily photosynthetic carbon fixation:

$$Y \; = \; (\Delta W/\Delta t)/P_g \tag{27}$$

The growth efficiency is different from the conversion efficiency (the efficiency of the conversion of photosynthate to structural material) in that it includes maintenance costs. $Y$ will therefore always be lower than $Y_g$.

*Defoliations*

Two modes of defoliations were used: the removal of all exposed leaf blades leaving sheaths intact, or the removal of all tissue down to a stubble height of 1-cm. For *A. desertorum* plants 1 and 2, and *A. spicatum* plant 1, all exposed leaf blades were removed. *Agropyron desertorum* plants 3 and 4 were cut to a stubble height of 1-cm. *Agropyron desertorum* plants 1 and 2 were defoliated twice, all other plants were defoliated once. The intensity of the defoliations was

measured directly by the reduction in $P_g$. The former mode reduced the rate of substrate input on the day of the defoliations by 78-97%; the latter reduced it to zero.

*Carbohydrate analysis*

Leaf blades, sheath and stem tissue, infloresences, crowns, and roots were analyzed separately for carbohydrates in the laboratory of Dr. J. Chatterton, USDA-ARS, Logan, UT, USA. The tissue was placed in a freezer as soon as possible following cutting. Freeze-dried samples were analyzed for total nonstructural carbohydrates (TNC): fructans, sucrose, glucose, fructose, water soluble starch, and water insoluble starch, using methods developed by Chatterton, Harrison, & Bennett (1986). TNC were determined colorimetrically by the potassium ferricyanide method for reducing sugars following digestion with amylase. Fructan content was determined from the difference between reducing sugar determinations made on samples with and without acid hydrolysis treatment. Mono- and disaccharide concentrations were determined from additional samples extracted twice in boiling water followed by acid hydrolysis, hydrolysis with invertase, or no hydrolysis.

The measured TNC concentrations are reported in the units of mg glucose (g structural d.w.)$^{-1}$, where structural dry weight is: total dry weight $-$ TNC (Moser, Volenec, & Nelson, 1982). In the model, the root and shoot concentrations of labile carbon (nonstructural carbohydrates), $^r\!fi$ and $^s\!fi$, respectively, are expressed as mol C mol C$^{-1}$, using total plant-part carbon contents as the denominator [equation (4)], rather than structural carbon content. While this is different from the expression of the measured values, it has the advantage that the

individual fractions ($f_i$, $f_d$, and $f_n$) add up to one. Shoot system concentrations are weighted averages using the weight fractions of each plant part.

### Initial conditions and parameter values

The model was parameterized using the measurements of respiratory carbon use and the chemical analysis of plant tissue removed by the defoliations and by the final harvest. Table III.1 lists the initial conditions used in the simulations. The initial values for $^sf_i$ and $^rf_i$ were set such that $^rf_i$ and $^sf_i$ at the defoliation would match the measured TNC concentrations (after unit conversions) of the tissue removed by the defoliations. The initial values for $^sf_d$ and $^rf_d$ were 0.2. This is an estimate of the combined concentration of nucleic acids and of soluble protein (in mol C mol $C^{-1}$), assuming that the carbon content of proteins was 45%, that the nitrogen concentration of plant tissue

**Table III.1.** The initial conditions of state variables used in the simulations for *A. desertorum* plants 1-4, and *A. spicatum* plant 1. For the respiratory carbon use submodels, the initial conditions are expressed as the fraction of total shoot or root carbon content in each state variable.

| Plant No.: | | A. desertorum: | | | | A. spicatum: |
|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 1 |
| Variable: | | | | | | |
| | $^sW$ | 60.3 | 36.8 | 182.4 | 150.2 | 175.6 |
| | $^sf_l$ | 0.09 | 0.07 | 0.17 | 0.07 | 0.10 |
| | $^sf_d$ | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 |
| | $^sf_n$ | 0.71 | 0.73 | 0.63 | 0.63 | 0.70 |
| | $^rW$ | 113.6 | 56.12 | 90.4 | 161.9 | 188.8 |
| | $^rf_l$ | 0.06 | 0.05 | 0.05 | 0.04 | 0.08 |
| | $^rf_d$ | 0.20 | 0.20 | 0.20 | 0.20 | 0.20 |
| | $^rf_n$ | 0.74 | 0.75 | 0.75 | 0.76 | 0.72 |
| | $W_N$ | 0.11 | 0.08 | 0.17 | 0.19 | 0.22 |

was 5.0% (Caldwell *et al.*, 1981), and that 60% of total protein was soluble protein (Johnson, 1985). The initial conditions for $^{s}f_{n}$ and $^{r}f_{n}$ were obtained by subtraction. The initial conditions for $W_{N}$ were calculated based on the assumption that 40% of total nitrogen is substrate nitrogen (Johnson, 1985).

Table III.2 lists the parameter values used in the simulations. The same parameter values were used for both respiratory carbon use submodels with the exception of $k_{g}$, see below. As discussed above, the $Y_{g}$ values were assumed to equal the $Y_{g}$ values estimated experimentally on the same plants (see Chapter II). $k_{d}$ was calculated from the experimentally estimated maintenance coefficient using the following relationship (Thornley, 1982):

$$k_{d} = (1-f_{i})Y_{g}m/(1-Y_{g})f_{d} \tag{28}$$

**Table III.2.** Parameter values used in the simulations for *A. desertorum* plants 1-4 and *A. spicatum* plant 1.

| Plant No.: | *A. desertorum*: | | | | *A. spicatum*: |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 1 |
| **Parameter:** | | | | | |
| Predefoliation: | | | | | |
| Shoot $k_{g}$ | 2.0 | 2.4 | 0.3 | 1.2 | 1.2 |
| Root $k_{g}$ | 2.0 | 2.4 | 1.2 | 2.0 | 1.2 |
| $Y_{g}$ | 0.71 | 0.68 | 0.73 | 0.69 | 0.71 |
| $Y_{d}$ | 0.39 | 0.39 | 0.70 | 0.60 | 0.55 |
| $k_{d}$ | 0.10 | 0.08 | 0.12 | 0.14 | 0.21 |
| $\alpha$ | 0.74 | 0.67 | 6.51 | 1.40 | 2.41 |
| $^{max}\sigma_{n}$ | 0.10 | 0.20 | 0.01 | 0.02 | 0.05 |
| Defoliation 1: | | | | | |
| Shoot $k_{g}$ | 2.3 | 2.5 | 1.0 | 2.3 | 1.2 |
| Root $k_{g}$ | 2.0 | 2.4 | 1.2 | 2.0 | 1.2 |
| $Y_{g}$ | 0.72 | 0.72 | 0.73 | 0.72 | 0.72 |
| Defoliation 2: | | | | | |
| Shoot $k_{g}$ | 2.5 | 2.5 | – | – | – |
| Root $k_{g}$ | 2.0 | 2.4 | – | – | – |
| $Y_{g}$ | 0.72 | 0.72 | – | – | – |

$Y_d$ was selected such that $^sf_d$ and $^rf_d$ did not change significantly during the predefoliation period. $k_g$ was used to fit predicted $^sR$ and $^rR$ to the measured rates while matching the measured labile carbon levels as closely as possible. To achieve this, the $k_g$ values had to be changed at defoliation and set differently for the roots in some cases (see Discussion).

The parameter values for the assimilate partitioning submodel were set such that the root–shoot balance in the model before the defoliation would tend to be reestablished after the defoliation. First, the value for $^sL$ which best fit the predefoliation conditions was determined and used to solve equation (19) for $p$. This value for $p$ was then used to solve equation (17) for $\alpha$, using the predefoliation conditions. This value of $\alpha$ was kept constant for the entire simulation period. $\sigma_n$ was fitted individually for each plant such that $M$ was constant during the period before shading. The fitted values were quite variable among plants (Table III.2). This is primarily due to differences in $^rW$ and in nitrogen demands for growth.

*Simulations and comparisons
to data*

The model was integrated numerically with a time step of 1 d using fourth-order Runge–Kutta integration with adaptive step-size control, as implemented by Press *et al.* (1986). The model can be solved analytically by making $P_g$ a function of $W_d$ (Thornley, 1977; Barnes & Hole, 1978). This eliminates $P_g$ as a driving variable making the analytical solution unsuitable for the simulation of transient conditions that result from changes in $P_g$.

The predicted $R$, $^sR$, and $^rR$ were compared to the measured rates using a paired t-test and the coefficient of determination, $r^2$, of a first-order line, fitted to the predicted rates as a function of the observed rates. The t-test compares the mean of the predicted rates to the mean of the observed rates while $r^2$ indicates the proportion of the variation among the predicted rates accounted for by the observed rates.

## Results

### Dynamics of substrate input and plant carbon content following defoliation

The rate of substrate input from photosynthetic carbon fixation, $P_g$, is the only driving variable of the model. This rate was manipulated experimentally by defoliating the plants. An attempt was made to produce a variety of dynamics rather than replicate individual patterns. Below I will use two *A. desertorum* plants as examples to illustrate the differences among the dynamics produced (Fig. III.2 and III.3). The results shown in these figures are from plants 2 and 4, respectively.

Figure III.2 shows $P_g$, $W$, and $Y$, for plant 2. This plant was shaded on day 4 for four days during the estimation of $Y_g$ and the maintenance coefficient (Chapter II). After the shading and an additional 5 d in full irradiance, all exposed leaf blades were removed. The remaining sheath and stem tissue was photosynthetic, accounting for the nonzero $P_g$ on the day of the defoliation (Fig. III.2a). The defoliation occurred at the end of the dark period, just before the lights were turned on. The rapid rate of refoliation was primarily due

to the extension of leaf blades from within the subtending sheaths. Figure III.2b shows the calculated carbon content, $W$, for each day. $\Delta W/\Delta t$ was only negative for one day, on d 13, the first d after the first defoliation. After 13 d of regrowth, exposed leaf blades were again removed and the plant allowed to regrow again. By this time, however, most of the shoots had been induced to flower and leaf production had therefore ceased. Nevertheless, rapid culm extension and photosynthetic activity of the stem and sheaths caused $\Delta W/\Delta t$ to remain positive even on the day of the defoliation. The average daily rate of increase in $P_g$ (Fig. III.2a) was 3.5 mmol C plant$^{-1}$ d$^{-1}$ during the first regrowth period and 1.8 mmol C plant$^{-1}$ d$^{-1}$ during the second regrowth period. A replicate plant (plant 1, not shown), which had similar dynamics to plant 2 during the first regrowth period, but was not induced to flower, regrew even faster during the second regrowth period. The average rate of increase in $P_g$ for that plant was 3.2 mmol C plant$^{-1}$ d$^{-1}$ during the first and 4.6 mmol C plant$^{-1}$ d$^{-1}$ during the second regrowth period.

The growth efficiency, $Y$, was only temporarily reduced by the defoliations (Fig. III.2c). $Y$ was reduced because $P_g$ had been reduced to a greater degree than $R$. This resulted in a greater proportion of $P_g$ being respired than prior to the defoliations. When $R$ had reached a new minimum, and $P_g$ had recovered a bit, $Y$ returned to the predefoliation value. $Y$ is negative (set to zero on Fig. III.2c) when $\Delta W/\Delta t$ is negative. This occurred on the first day of the first regrowth period, but not during the second regrowth period.
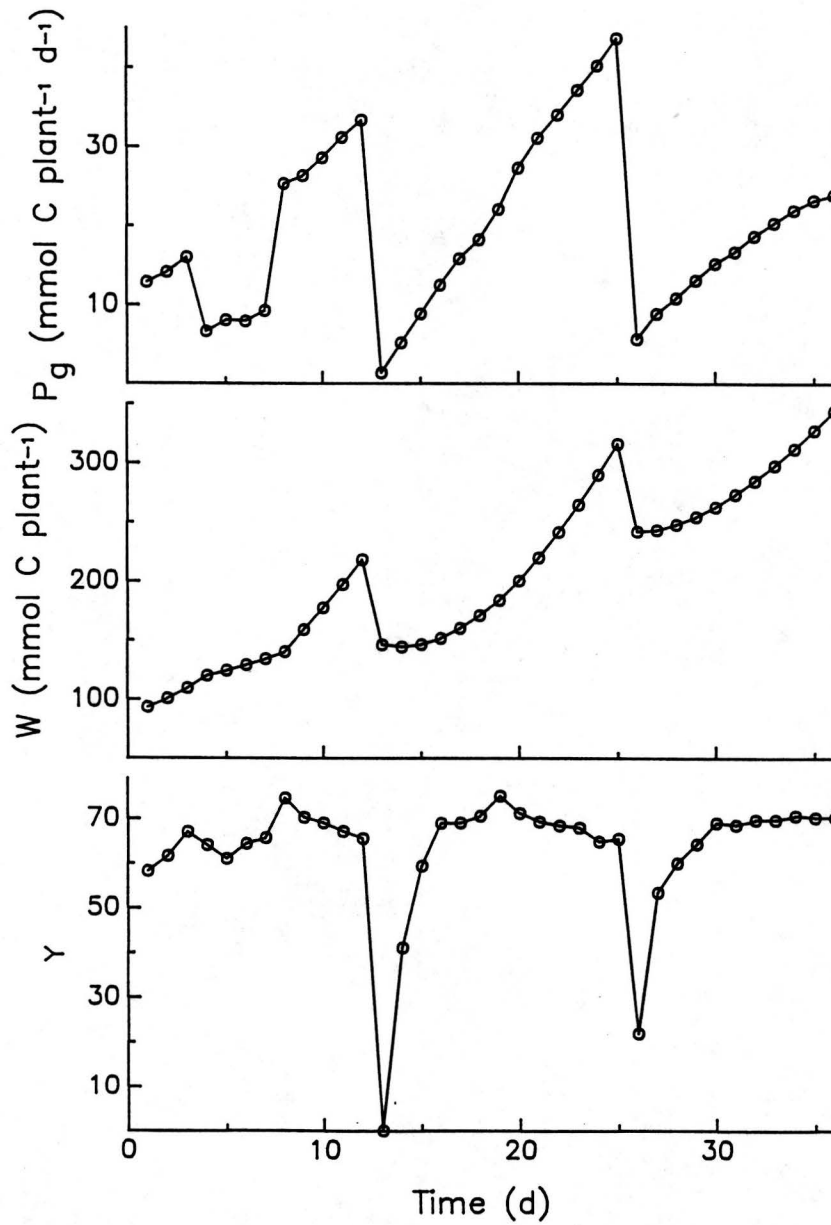
**Figure III.2.** The measured daily rate of substrate input, $P_g$ (mmol C plant$^{-1}$ d$^{-1}$), calculated total carbon content, $W$ (mmol C plant$^{-1}$), and growth efficiency, $Y$, for *Agropyron desertorum* plant 2.
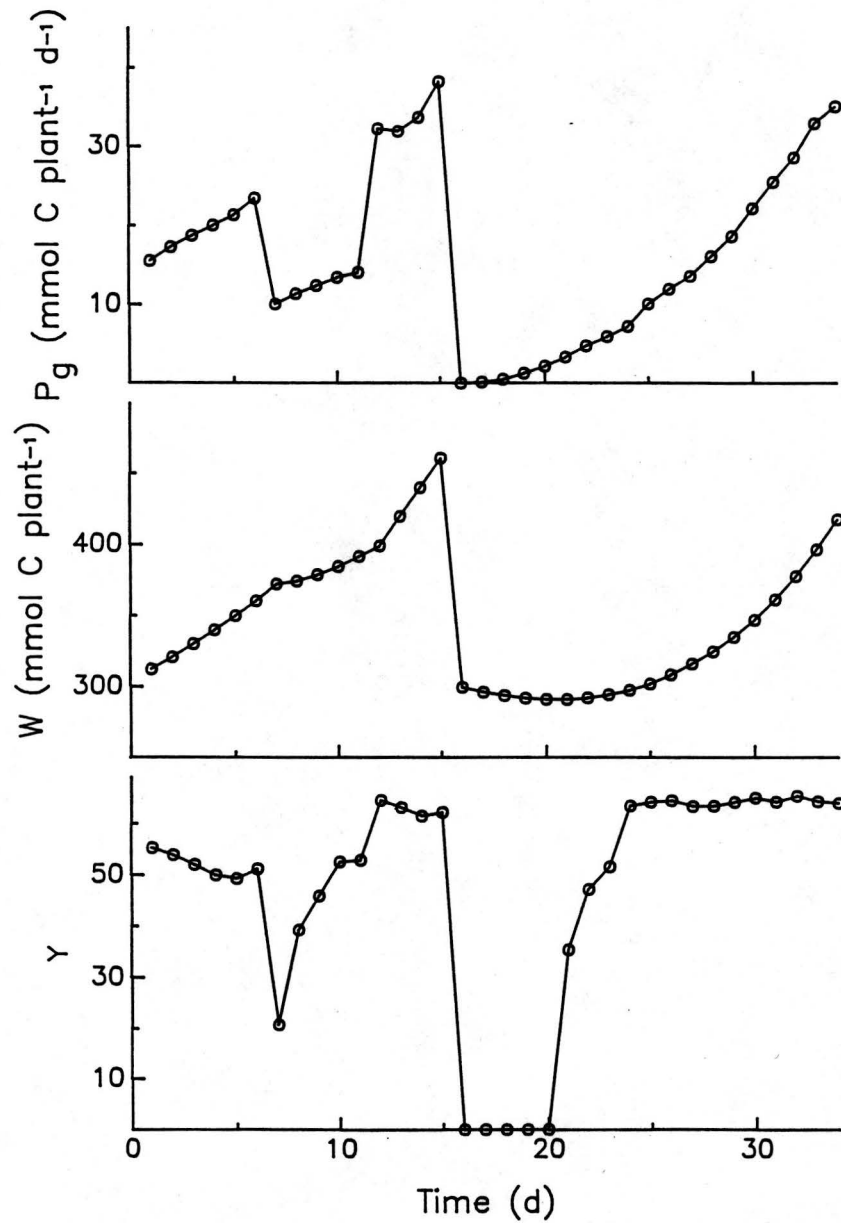
**Figure III.3.** The measured daily rate of substrate input, $P_g$ (mmol C plant$^{-1}$ d$^{-1}$), calculated total carbon content, $W$ (mmol C plant$^{-1}$), and growth efficiency, $Y$, for *Agropyron desertorum* plant 4.

Plant 4 (Fig. III.3) was defoliated more severely than plant 2. In addition to removing all exposed leaf blades, the sheath, and the leaf tissue enclosed by the sheath, were cut to a stubble height of 1-cm. This resulted in a reduction of $P_g$ to zero for two d (Fig. III.3a) and a negative carbon balance, $\Delta W/\Delta t$, for five days (Fig. III.3b). The average daily rate of increase in $P_g$ was 1.9 mmol C plant$^{-1}$ d$^{-1}$. $Y$ was negative while the plant continued to loose carbon (Fig. III.3c), and did not reach the predefoliation value until eight d into the regrowth period.

Each of the other plants monitored had slightly different dynamics. These differences were quantitative rather than qualitative and resulted from differences in the absolute reduction in $P_g$ that resulted from the defoliations. *Agropyron spicatum* plant 1, which was defoliated in the same manner as *A. desertorum* plants 1 and 2, regrew slower that the two *A. desertorum* plants, however. The average rate of increase in $P_g$ for that plant was 1.3 mmol C plant$^{-1}$ d$^{-1}$.

*Rate of respiratory carbon*
*use and root-shoot*
*partitioning*

Figures III.4 and III.5 show the observed $^sR$ and $^rR$ for plants 2 and 4, respectively. The rates of both root and shoot respiratory carbon use were reduced by the defoliations. For the shoot systems (Figs. III.4a and 5a), this reduction was a result of the removal of tissue. Changes in $^sr$ (not shown) were less important. For the root systems (Figs. III.4b and III.5b), however, the changes in $^rR$ were due to changes in $^rr$. For the first defoliation of plant 2, $^rr$ was reduced from 44.0 to 9.3 mmol C mol C$^{-1}$ d$^{-1}$ in two d, and for the second defoliation from 36.4

to 9.4 mmol C mol C$^{-1}$ d$^{-1}$ in two d. For plant 4 the reduction in $^r r$

was from 26.3 to 7.72 mmol C mol C$^{-1}$ d$^{-1}$ in two d, with further

reduction the next 4 d to reach a minimum of 4.7.

Figures III.4 and III.5 also show the predicted rates of root and shoot

respiration. The r$^2$ values for predicted $^s R$ and $^r R$ as a function of

observed $^s R$ and $^r R$ for plant 2 were 0.78 and 0.92, respectively (Fig.
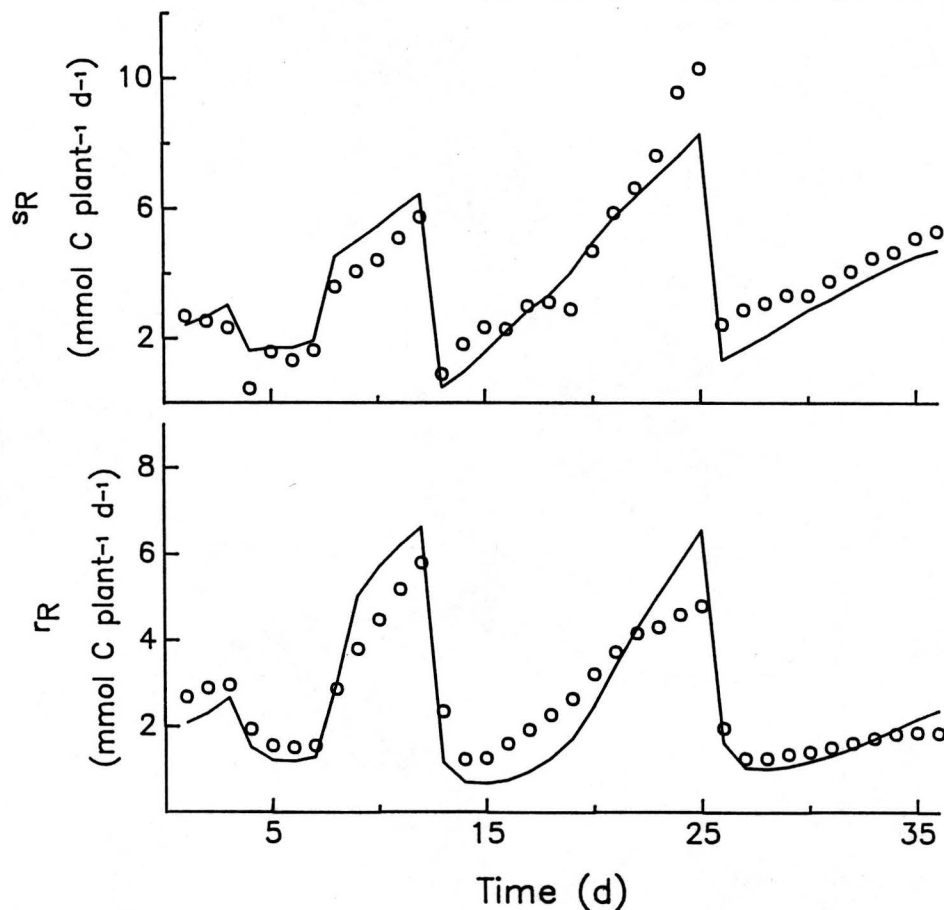


**Figure III.4.** Observed (circles) and predicted (lines) rates of shoot, $^s R$, and root ,$^r R$, respiratory carbon use (mmol C plant$^{-1}$ d$^{-1}$) for *Agropyron desertorum* plant 2. The plant was shaded for four d on d 4 and defoliated on d 13 and d 26.

III.4). The mean of predicted $^s R$ was 0.26 mmol C plant$^{-1}$ d$^{-1}$ higher

than the mean of the observed rates (t=−1.5, P=0.15), while the mean of

the predicted $^r R$ was 0.06 mmol C plant$^{-1}$ d$^{-1}$ lower than the mean of

the observed rates (t=0.5, P=0.61). For plant 4, the r$^2$ values for

predicted $^sR$ and $^rR$ as a function of observed $^sR$ and $^rR$ were 0.88 and

0.78, respectively (Fig. III.5). The mean of the predicted $^sR$ was 0.31

mmol C plant$^{-1}$ d$^{-1}$ higher than the mean of the observed (t=−2.3,

$P$=0.03), while the mean of the predicted $^rR$ was 0.03 mmol C plant$^{-1}$ d$^{-1}$

$^1$ lower than the mean of the observed rates (t=−1.6, $P$=0.87).
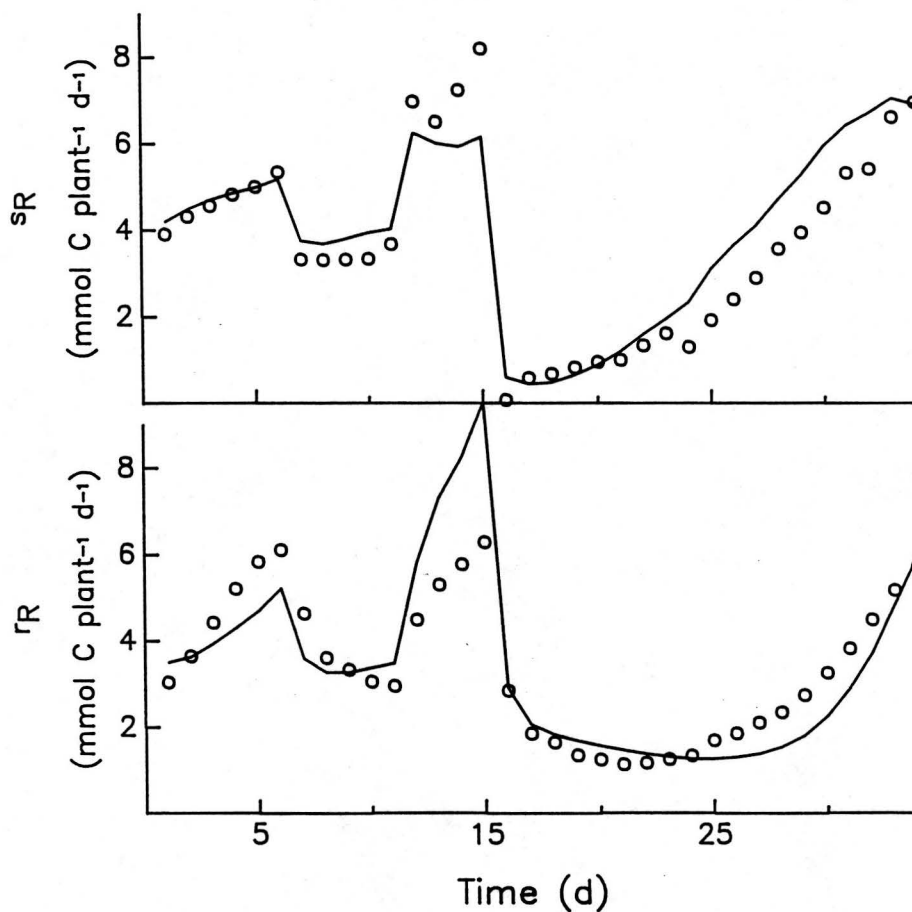


**Figure III.5.** Observed (circles) and predicted (lines) rates of shoot, $^sR$, and root, $^rR$, respiratory carbon use (mmol C plant$^{-1}$ d$^{-1}$) for *Agropyron desertorum* plant 4. The plant was shaded for five d on d 7 and defoliated on d 16.

These simulations were based on root−shoot partitioning predicted by

the assimilate partitioning submodel (Fig. III.6). The model predicted a

slight reduction in $^rL$ when the plants were shaded. This was a result

of a reduction in $C_l$. $^sL$ was again reduced at defoliation as a result of the reduction in $^sW_g$ and $C_l$ [equations (17 & 18)]. $^rL$ for plant 2 (Fig. III.6a) returned fairly rapidly to the predefoliation value during the first regrowth period. This was due to the increase in $^sW_g$ and the simulated depletion of $W_N$ by the rapid regrowth. This depletion
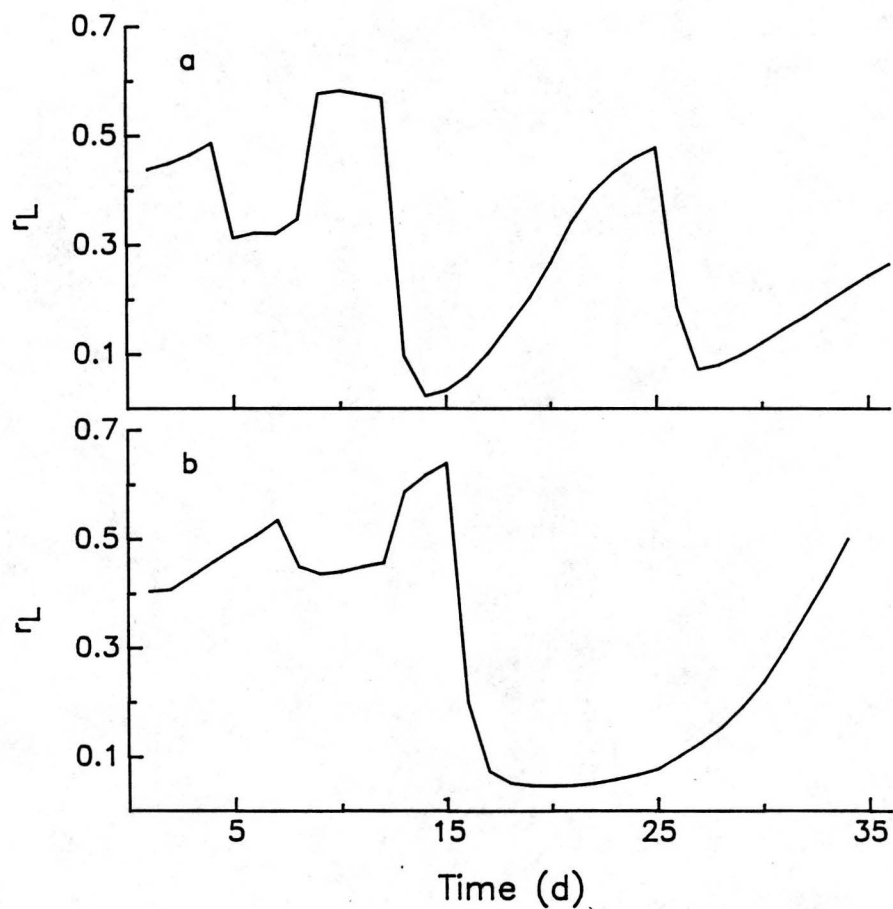


**Figure III.6.** Predicted partitioning of incoming photosynthate to roots, $^rL$, for a) *Agropyron desertorum* plant 2, and b) plant 4. $^rL$ ranges from 0.0 (no partitioning to roots) to 1.0 (all incoming photosynthate partitioned to roots).

increased the $C_i/M$ ratio, which in turn lowered $p$ [equation (17)]. $^rL$ did not return as rapidly to the predefoliation value during the second regrowth of plant 2 (Fig. III.6a) due to the lower simulated demand for nitrogen for regrowth. As would be expected, the lower rate of regrowth of plant 4 resulted in slower return of $^rL$ to the predefoliation value (Fig. III.6b).

The whole-plant rate of respiratory carbon use could be predicted with considerably greater accuracy than the root or shoot rates of respiratory carbon use because assimilate partitioning between root and shoot did not need to be included. The $r^2$ values for predicted $R$ as a function of observed $R$ for plant 2 and 4 were 0.94 and 0.97, respectively. For plant 2, the mean of the predicted $R$ was 0.19 mmol C plant$^{-1}$ d$^{-1}$ higher than the mean of the observed rates (t=−1.4, $P$=0.17). For plant 4, the mean of the predicted $R$ was 0.33 mmol C plant$^{-1}$ d$^{-1}$ lower than the mean of the observed rates (t=−3.2, $P$=0.003). This indicates that while the dynamics could be simulated quite well (as indicated by the high $r^2$ values) there was a small but significant underestimation of $R$ for plant 4. The $r^2$ value is insensitive to the direction of the errors, however.

There was nearly a 1:1 relationship between the predicted and the observed values (slope=0.97), and the $r^2$ was 0.96, when all five plants were combined (Fig. III.7). The slope for individual plants ranged from 0.77 to 0.99, the intercept from 0.43 to 1.13 mmol C plant$^{-1}$ d$^{-1}$, and the $r^2$ values ranged from 0.94 to 0.98.

*Labile carbon pools*

The means and standard errors of the means of the measured TNC concentrations are shown in Table III.3. Also shown are the mean total starch and fructan concentrations. Information on carbohydrate concentrations in leaf blades at the first defoliation is available for all five plants, while the concentrations in the sheath tissue are only available for the plants which had their sheaths removed at the
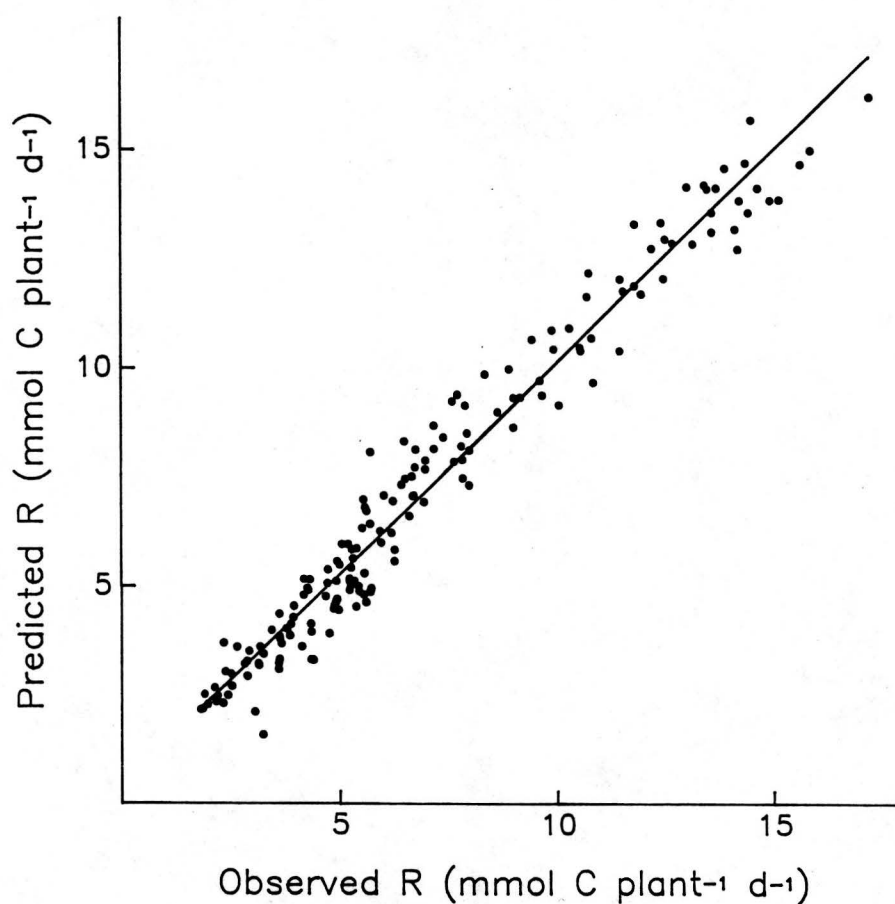


**Figure III.7**. Predicted rates of whole-plant respiratory carbon use (mmol C plant$^{-1}$ d$^{-1}$) as a function of observed rates for each day for all five plants. The slope of the regression line is 0.97 and the intercept is 0.41 mmol C plant$^{-1}$ d$^{-1}$ ($r^2$ = 0.96, n=146).

defoliation, i.e. *A. desertorum* plants 3 and 4. *Agropyron desertorum* plants 1 and 2 were the only two plants defoliated twice. Information on carbohydrate concentrations in crowns and roots is only available for the final harvest.

The TNC concentrations in sheath and stem tissue were significantly higher than the concentrations in other parts ($F=14.1$, $P=0.001$, using *post hoc* contrasts, defoliation 1 and final harvest combined). The highest starch concentrations were found in sheaths and the lowest in roots. The starch concentrations of crowns and leaf blades were intermediate. Fructan concentrations were lower than total starch concentrations in all but two samples. The fructan concentrations were highest in sheaths and roots. *Agropyron desertorum* plant 3 was particularly high in fructan [as high as 170 mg glucose equivalent (g structural d.w.)$^{-1}$ in sheath tissue and 28.4 in leaf blades]. This plant showed symptoms of water stress during measurement (see Discussion).

Table III.3. The mean and standard error of the mean for the measured total nonstructural carbohydrate (TNC) concentrations [mg glucose (g structural d.w.)$^{-1}$], and the mean total starch, fructan, and free sugar concentrations, for *A. desertorum* plants 1-4 and *A. spicatum* plant 1.

| | TNC | n | S.E | Starch | Fructan | Free sugars |
|---|---|---|---|---|---|---|
| **Defoliation 1:** | | | | | | |
| Leaf blades | 82.7 | 5 | 12.0 | 46.7 | 8.0 | 28.6 |
| Sheaths, stems | 282.9 | 2 | 123.9 | 84.4 | 88.1 | 113.9 |
| **Defoliation 2:** | | | | | | |
| Leaf blades | 54.0 | 2 | 0.1 | 40.7 | 0.0 | 14.5 |
| **Final harvest:** | | | | | | |
| Leaf blades | 55.0 | 5 | 4.4 | 40.0 | 1.4 | 12.4 |
| Sheaths, stems | 105.6 | 5 | 24.0 | 58.7 | 7.7 | 40.3 |
| Crowns | 42.4 | 5 | 5.5 | 22.6 | 5.1 | 15.0 |
| Roots | 28.5 | 5 | 7.6 | 11.3 | 10.5 | 6.6 |

Glucose was 3.9 to 25.0% of TNC for individual samples and fructose 6.3 to 39.4%, with no consistent differences between plant parts. Sucrose concentrations were negligible.

The defoliations reduced the TNC concentrations in four out of five plants, judging from a comparison of the leaf and sheath concentrations of tissue removed at defoliation 1, and after the regrowth period (Table III.3). The fructan concentrations were reduced to a greater extent than the starch concentrations. The reduction in free sugars, mostly glucose and fructose, was intermediate.

The TNC concentration values for the root and shoot system (weighted average for component parts) were used to guide the parameterization of the model. Figure III.8 shows the simulated $^{s}fi$ and $^{r}fi$ values for plant 2 and 4. Also shown are the measured $fi$ values. Both the shading and defoliations reduce $^{s}fi$ and $^{r}fi$. For plant 2, the reduction in $^{s}fi$ at defoliation was only temporary. In fact, the predicted $^{s}fi$ was higher during the first part of the first regrowth period than during the predefoliation period. This prediction was corroborated by high $^{s}r$ during the first part of the first regrowth period (data not shown).

The combined size of the root and shoot labile carbon pools was slightly less than one day's $P_g$ for all but *A. desertorum* plant 3 during the predefoliation period. This suggests a high rate of turnover of carbon compounds in the labile carbon pool. When a balance existed between the rate of carbon utilization and the rate of carbon supply, the size of the labile carbon pool remained constant and no significant net accumulation or net mobilization of labile carbon occurred (Fig.

III.9). When $P_g$ was reduced, however, the demand for carbon was
temporarily met by net mobilization of labile carbon. This mobilization
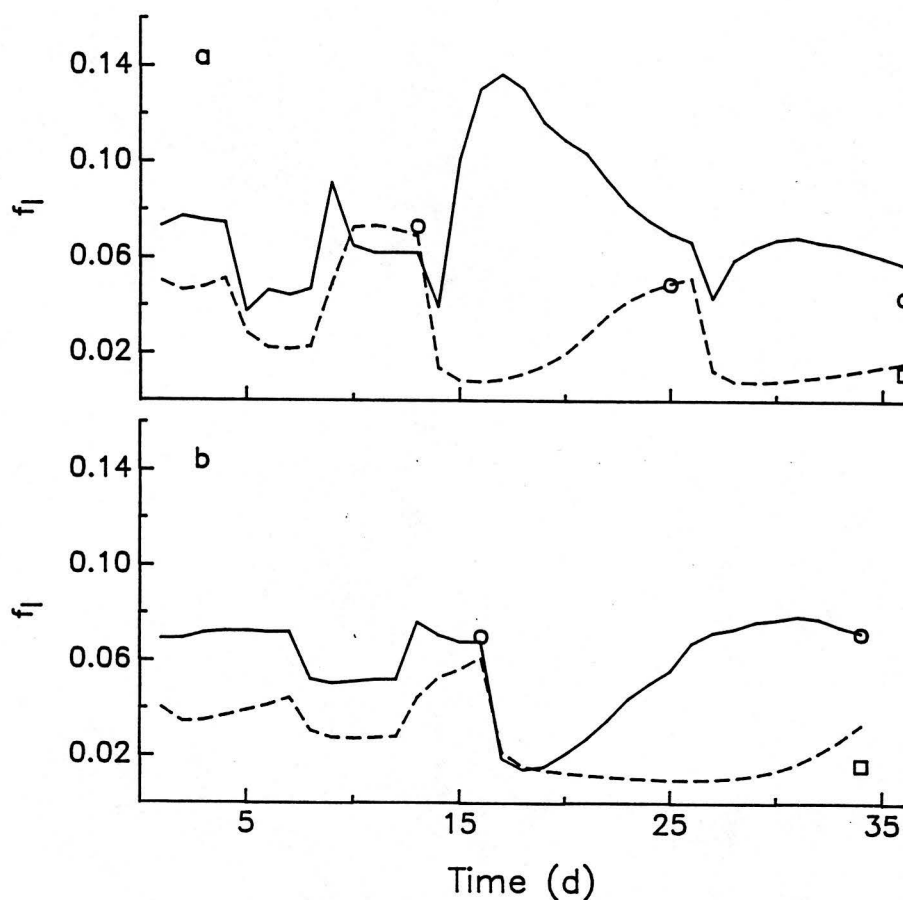


**Figure III.8.** Predicted fraction of total carbon that is labile carbon for
shoots ($^s f_l$, solid line) and roots ($^r f_l$, dashed line) for *A. desertorum*
plants 2 (a) and 4 (b). Also shown are the measured TNC concentrations
for shoots (circles) and roots (squares) (mol C mol C$^{-1}$).

of labile carbon exceeded $P_g$ for the day of the defoliation for plant 2
and for the first two d of regrowth for plant 4. After that, net
accumulation of labile carbon started again, indicated by net
mobilization of less than zero (Fig. III.9).
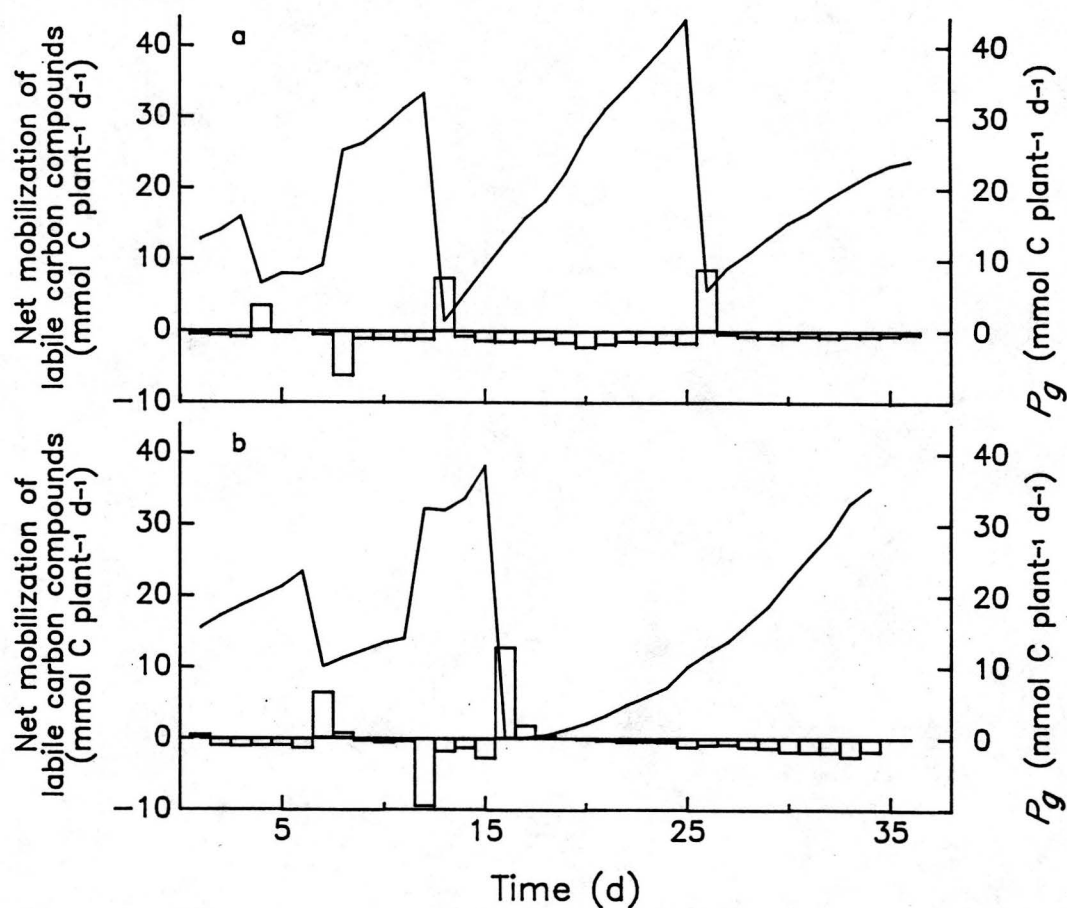
**Figure III.9.** Calculated net whole-plant mobilization (open bars) of labile carbon compounds for *A. desertorum* plants 2 (a) and 4 (b), based on the simulated labile carbon pool sizes. When net mobilization is negative, net accumulation takes place. Also shown are the daily rates of carbon input from photosynthetic carbon fixation, $P_g$, from figures III.2 and III.3.

## Discussion

One of the distinguishing features of the dynamics of plant carbon balance reported in this Chapter was the rapid reduction in the rate of root respiratory carbon use following defoliation (Fig. III.3 and III.4). Both *A. desertorum* and *A. spicatum* have fine fibrous roots with no specialized storage tissue. The crowns do not contain any specialized

storage tissue either, judging from their low carbohydrate content (Table III.3) (Caldwell *et al.*, 1981; Richards & Caldwell, 1985). The root system was dependent on a continuous supply of carbon from the shoot system. When this supply was reduced, the rate of respiratory carbon use was immediately reduced. The labile carbon content in the roots was generally slightly greater than the amount of carbon consumed by root respiratory carbon use in one day (data not shown) (Massimino *et al.* 1981). This suggests that the root system in these plants was a net sink for carbon even immediately following the severe defoliations. It is therefore unlikely that labile carbon was mobilized from roots to meet carbon demands of the shoot system. Davidson & Milthorpe (1966) reached a similar conclusion from their measurements of *Dactylis glomerata*.

The fact that the shading of the shoot system alone reduced the specific rate of root respiration by as much as 60%, suggests that information on the rate of photosynthetic carbon fixation, at the time of the measurement of the rate of root respiratory carbon use, is needed to interpret the results. The rate of respiratory carbon use of the root system cannot, therefore, be considered to be a fixed plant characteristic, independent of the rate of carbon fixation by the shoot system.

When only leaf blades were removed and the remaining sheath tissue was photosynthetic, the rate of carbon fixation recovered quickly (Fig. III.2a) and after 8-9 d of regrowth of *A. desertorum* plant 2, the carbon removed by the defoliation had been completely replaced (Fig. III.2b). For *A. spicatum* plant 1, 80% of the carbon removed by the

defoliation had been replaced after 18 d of regrowth. When all shoot tissue was removed to a stubble height of 1-cm, the recovery of carbon fixation rate took longer (Fig. III.3a), and after 19 d of regrowth of *A. desertorum* plant 4, 76% of the carbon removed had been replaced (Fig. III.3b).

The growth efficiency of these grasses was reduced by defoliation (Figs III.2c and III.3c). This does not suggest any loss in conversion efficiency, however. It simply reflects the fact that $\Delta W/\Delta t$ was reduced to a greater extent than $P_g$, due to the mobilization and respiratory use of labile carbon compounds (Fig. III.9). The rate at which the growth efficiency returns to its previous value will be determined by how rapidly a new balance between carbon supply and carbon demand is reached. The recovery was considerably more rapid when only leaf blades were removed (compare Fig. III.2c to Fig. III.3c). For *A. spicatum* plant 1, the growth efficiency reached the predefoliation value 2-3 d later than *A. desertorum* plants 1 and 2 (7 d compared to 4 and 5 d, respectively).

Richards & Caldwell (1985) measured the regrowth produced from labile carbon only in the field by the same two plant species. They prevented photosynthetic carbon fixation by covering the plants. By monitoring the carbon dioxide efflux of the shoot system, they were able to calculate the shoot regrowth efficiency (regrowth C / (C efflux + regrowth C)) for one week at a time. Root respiration could not be measured in these field studies. Shoot regrowth efficiency is comparable to a growth efficiency for the shoots only, calculated over a longer time span [see equation (27)], if regrowth produced is considered a

measure of "net carbon gain" and $P_g$ is replaced by the amount of carbon mobilized from labile carbon pools (C efflux + regrowth C). Richards & Caldwell (1985) did not report absolute values for the shoot regrowth efficiency, but showed a reduction in the relative shoot regrowth efficiency when the apical and the intercalary meristems were removed. This was primarily due to a greater reduction in the amount of regrowth produced than in the rate of respiratory carbon use.

*Agropyron spicatum* was shown to have lower relative regrowth efficiency than *A. desertorum* (Richards & Caldwell, 1985). This was due to its lower amount of regrowth produced for comparable rates of respiratory carbon use. There is no indication from the present study of differences between the two species in the growth efficiency. However, the *A. spicatum* plant produced lower amounts of regrowth than the two comparable *A. desertorum*.

Thornley's (1977) recycling model was found to be quite suitable for the simulation of whole-plant respiratory carbon use (Fig. III.7). Regression analysis, such as used in Figure III.7, assumes that the independent variable is measured without error. All the residual variation is therefore assumed to be due to variation in the dependent variable. This is not the case here. Errors in the measurements of the observed $R$ contributed to the residual variation and thus lowered the $r^2$ value. Simulation of root and shoot respiratory carbon use proved to be more difficult than the simulation of whole-plant respiratory carbon use (Figs. III.4 and III.5). The main difficulty involved the partitioning of substrate input between root and shoot. The assimilate partitioning submodel tended to allocate too much to roots when irradiance was

increased after the shading period (Fig. III.6, see also d 12-15 on Fig. III.5). This high partitioning to roots resulted from an abrupt increase in the $C_i/M_i$ ratio when the $P_g$ increased as the irradiance was increased following the shading period.

The inclusion of the assimilate partitioning model improved the simulation compared to fixed partitioning, however. Fixed partitioning (not shown) consistently resulted in overestimation of $^rR$ and a corresponding underestimation in $^sR$.

The predicted dynamics of shoot labile carbon pools (Fig. III.8) were very reasonable. The increase in $^s\!f\!i$ during the first part of the regrowth of *A. desertorum* plant 2 cannot be directly verified from the tissue sampling in this study. Such a temporary increase in labile carbon pools could result, however, if the rate of regrowth lagged behind the rate of substrate input. The dynamics of root labile carbon compounds cannot be directly corroborated since the roots were only sampled after the regrowth. The simulated dynamics are reasonable, however, with the exception of the period immediately before the first defoliation, when assimilate partitioning to roots was too high. Errors in the simulation of root and shoot labile carbon pools that result from errors in assimilate partitioning do not affect the calculation of net whole-plant mobilization of labile carbon compounds (Fig. III.9).

These calculations suggest that net mobilization of labile carbon compounds is confined to the first one or two d of regrowth (Fig. III.9). This study was not designed to evaluate the importance of this mobilization in terms of possible feedback effects on the rate of refoliation and photosynthetic carbon fixation, however.

Chatterton *et al.* (1986) found fructan concentrations in *A. desertorum* to be significantly higher when the plants were grown at 10/5°C day/night temperatures, compared to 20/15°C day/night temperatures. The fructan concentrations reported in Table III.3 fall between the mean values reported by Chatterton *et al.* (1986) for the two temperatures.

An important parameter of the respiratory carbon use submodel, which is not directly estimated from the parameters of the substrate-balance model, is $k_g$. This parameter determines the rate of mobilization of carbon compounds from the labile carbon pools. During conditions of steady rate of substrate input, a value of one for $k_g$ causes $W_l$ to assume the value of $P_g$ [equation (5)]. The measured combined size of the root and shoot labile carbon pools was slightly less than $P_g$ during the predefoliation period, indicating that $k_g$ is higher than one. The fitted values for $k_g$ during the predefoliation period ranged from 0.2 to 2.4 (Table III.2). The lowest values were for *A. desertorum*, plant 3. This plant showed symptoms of water stress during the measurements and had the highest TNC concentrations [406.8 and 127.6 mg glucose (g structural d.w.)$^{-1}$, for leaves and sheath, respectively, at the first defoliation]. This suggests direct effects of the water stress on growth and that carbon-supply was nonlimiting. $k_g$ can therefore be considered to be related to the ratio of sink demand to source supply. It is interesting to note that for the second regrowth period for plant 2 (Fig. III.2, Table III.2), $k_g$ was not reduced. This suggest that meristematic limitations during this regrowth period reduced sink demand and source supply to a similar degree.

This study demonstrated that the components of plant carbon balance change rapidly during regrowth following defoliation and that the quantitative contribution of each component depends on the severity of the defoliation. When the rate of photosynthetic carbon fixation was high immediately following the defoliation, net mobilization of labile carbon took place for only one day. When the rate of photosynthetic carbon fixation recovered more slowly, net mobilization of labile carbon took place for three days. The rate of respiratory carbon use adjusted rapidly to the rate of substrate input. Thornley's (1977) model was found to be suitable for the simulation of respiratory carbon use and of labile carbon pools during regrowth. Using Johnson's (1985) assimilate partitioning model significantly improved the simulation compared to a fixed partitioning of incoming photosynthate to roots.

This study was not designed to enable quantitative inferences to be made about the rates or efficiency of regrowth by other individuals of *A. desertorum* or *A. spicatum*, or any differences between the two species. Such a study would take several years to complete. The study focused rather on the underlying processes and their interaction during regrowth as a step towards a predictive understanding of the factors that determine the rate and efficiency of regrowth.

CHAPTER IV

THE RATE OF RESPIRATORY CARBON USE OF THE SHOOT SYSTEM

OF TWO *AGROPYRON* BUNCHGRASSES IN THE FIELD

## Introduction

The rate of respiratory carbon use of grass leaves is usually less than

10% of the rate of photosynthetic carbon fixation at full irradiance

(Woledge & Parsons, 1986). Gross photosynthetic carbon fixation will

therefore not be very different from net photosynthetic carbon fixation

for leaves. This low value is a result of the fact that for fully

expanded leaves, which are almost exclusively used when photosynthesis

of grasses is measured, a large fraction of the photosynthate is

exported and used in other parts of the plant (Gordon, Ryle, & Powell,

1977; Morgan & Austin, 1983). If shaded leaves and heterotrophic parts

of the shoot system are included, a larger proportion of gross

photosynthesis will therefore be respired. Including the root system will

increase this proportion even further. Robson (1973) found respiratory

carbon use of entire shoots systems and roots of *Lolium perenne* to be

45% of gross photosynthetic carbon fixation. In a laboratory study of

two *Agropyron* bunchgrasses growing under steady state condition and

high irradiance this percentage was found to be 47 (Chapter II).

In this Chapter I report on the measurements of net photosynthetic

carbon fixation and shoot respiratory carbon use during the day and

the night in the field for *Agropyron desertorum* (Fisch. ex Link) Schult.

and *Agropyron spicatum* (Pursh) Scribn. and Smith. To measure shoot

respiratory carbon use during the day, light was excluded from the

plants for 10-15 minutes. The measured rate of shoot respiratory carbon

use was used to estimate the gross rate of photosynthetic carbon fixation. The results from this field study were compared with a laboratory study on the same species.

## Methods

This study was conducted in a common garden field site at the Utah State University Green Canyon Ecological Research Area in Northern Utah (42° N latitude, 1,460 m a.s.l.). Individual grass tussocks were surrounded by four *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle. plants with 50-cm interspacing. This shrub commonly occurs with the grasses in their natural habitat. Further site details can be found in Caldwell *et al.* (1981).

### Carbon dioxide exchange measurements

The rate of carbon dioxide exchange of the above ground parts of culmless tussocks (closely bunched clusters of several tillers with 3-5 leaves each, hereafter referred to as shoot systems) was monitored continuously for 3 d at the end of April and the beginning of May, 1986. Four individual plants were monitored simultaneously, first four plants of *A. desertorum* for 3 d and then four plants of *A. spicatum* for 3 d. The soil was moist and the plants showed no signs of water stress.

During carbon dioxide exchange measurements, the shoot systems were enclosed in 0.15-m³ semi-cylindrical plexiglass chambers. The air temperature in each chamber was individually controlled, using a thermoelectric heat exchanger mounted on the north side of the

chambers. Two of the four chambers were controlled to track the ambient temperature, while the other two were controlled at fixed chamber air temperature of 10°C for *A. desertorum* and 20°C for *A. spicatum*. This difference in chamber air temperature was unavoidable because the chambers could not be cooled more than 5-7°C below ambient temperature, which increased abruptly before the monitoring of *A. spicatum* started.

The chamber walls were covered with transparent Teflon film (S-115, Saunders, Los Angeles, CA, USA), all air lines were made of Teflon or stainless steel, and all internal aluminum surfaces were nickel plated to reduce carbon dioxide and water vapor adsorption (Parkinson, 1985). The soil surface formed the bottom of the chambers, with the chamber walls penetrating the soil surface to a depth of 2 cm. A soil slurry was packed against the outside of the chamber walls to provide sufficient seal for a small (2-5-cm $H_2O$ column) positive pressure to be maintained in the chambers and thereby minimize gas efflux from the soil (Leafe, 1972).

The rate of airflow entering the chambers was measured using pneumotachometers (4600, Hans Rudolph, Kansas City, MO, USA). The mole fraction of carbon dioxide in samples of the inlet and outlet airstreams was measured using an IRGA (ADC-225, P.K. Morgan Instruments, North Andover, MA, USA) in the differential mode. The absolute mole fraction of carbon dioxide in the chambers was measured once in the morning using the absolute mode. The mole fraction of water vapor in the inlet and outlet airstreams, as measured by thin-film capacitance sensors (6061 HM, Vaisala, Woburn, MA, USA) was used to

correct for the dilution of the outlet airstream by water vapor (vonCaemmerer & Farquhar, 1981). The air entering the chambers was brought to a dew point of −25°C using heatless dryers (Puregas HF200, General Cable, Westminster, CO, USA). This resulted in chamber relative humidity similar to the ambient air relative humidity.

Leaf temperature of four different leaves was measured using thin-wire (0.13 mm diameter) thermocouples and electrically averaged by connecting them in parallel. Photosynthetic photon flux density (PPFD) above the plants, but inside the chambers, was measured using quantum sensors (LI−190SB, LiCor, Lincoln, NE, USA).

The four chambers were monitored using the same IRGA, flow meters and humidity sensors. The outlet airstream from a given chamber was routed to the instruments for six minutes using a computer controlled gas switch. This switching took place next to the instruments to minimize the required flushing time between chambers. A flushing and settling time of 60 s was used. The output of the sensors was digitized every 10 s using a data logger (Digistrip II, Kaye Instruments, Bedford, MA, USA). Average values for the six minute periods were used in the subsequent calculations. This averaging time was reduced to 60 s when light was excluded during the day.

For the measurement of the rate of respiratory carbon use during the day, light was excluded from the plants by covering the chambers with an opaque plastic bag. The bag was removed as soon as a stable rate of carbon dioxide exchange was reached. This took 10 to 15 minutes. The flushing time of the return air lines from the chambers is 2 to 4 minutes (S.O. Link, unpublished information). This was done once every

afternoon and also in the morning in most cases. There was no consistent difference between the two covering periods, therefore, the two periods were averaged.

### Calculation of carbon dioxide exchange rates

The measured carbon exchange rates are expressed in the units of μmol C mol C s$^{-1}$. The shoot systems were harvested immediately following the measurements and dried at 65°C for 24 h. Total carbon content was calculated using a carbon content of dry weight of 39% (J.H. Richards, unpublished information). The carbon content of the plants ranged from 0.62 to 1.39 mol C (19.2 to 42.8 g d.w.).

The instantaneous mass specific rate of shoot respiratory carbon use, $^s r$ (μmol C mol C$^{-1}$ s$^{-1}$), is taken to be equal to net shoot carbon exchange rate, $CER$ (μmol C mol C$^{-1}$ s$^{-1}$), when this rate was less than zero. The subscripts l and d will be used for shoot respiratory carbon use measured during the light period (with light exclusion during the day) and during the dark period (night), respectively. The instantaneous rate of net photosynthetic carbon fixation, $P_n$ (μmol C mol C$^{-1}$ s$^{-1}$), is taken to be equal to $CER$ when $CER$ is greater than zero.

The instantaneous rates of respiratory carbon use and of net photosynthetic carbon fixation were integrated for the light and the dark period. The morning and evening whole-shoot light compensation points were used to separate the two periods. Determined this way the light period was 12-h and 30 minutes during the days of this study. The integrated values were used to calculate the daily rate of gross photosynthetic carbon fixation (integrated daily net photosynthetic

carbon fixation + integrated shoot respiratory carbon use during the light) and daily net carbon gain (integrated net photosynthetic carbon fixation − integrated shoot respiratory carbon use during the dark period). The gross rate of photosynthetic carbon fixation calculated in this manner does not include photorespiration since it was removed by measuring net photosynthesis. The ratio of daily net carbon gain and daily gross photosynthetic carbon fixation is the shoot growth efficiency.

*Estimation of the response of*
*shoot respiratory carbon use*
*to temperature*

The relationship between the rate of shoot respiratory carbon use during the night and leaf temperature was quantified using the $Q_{10}$ function (Johnson & Thornley, 1985):

$$^sr(T) = {}^sr(Tr)Q_{10}{}^{[(T-Tr)/10]} \tag{1}$$

where $^sr(T)$ is the measured rate of shoot respiratory carbon use at leaf temperature $T$ (°C) and $^sr(Tr)$ is the carbon exchange rate at the reference temperature $Tr$ (°C). $Q_{10}$ was estimated separately for each species combining the data from the two chambers tracking ambient temperatures ($Q_{10}$ did not differ between the two chambers for the same species). $^sr$ values measured shortly after sunset and just before sunrise were not included.

Nonlinear least squares regression (Quasi-Newton method) was used to fit equation (1) to the data using SYSTAT (Wilkinson, 1987). In fitting the function the reference temperature was set at the mean temperature for each species (4.7 and 11.2 °C for *A. desertorum* and *A. spicatum*, respectively, calculated from the data used to fit the

function). The estimated $Q_{10}$ was independent of the initial values used in the iterative parameter estimation process.

## Results

### *The carbon exchange rate of covered plants*

Figure IV.1 shows the instantaneous *CER* before, during, and after the first covering of *A. desertorum*. The *CER* was positive six minutes into the covering period. Most of this delay was due to the flushing time of the outlet air lines between the chambers and the IRGA. The plant shown in this figure was covered for 25 minutes. Subsequent plants were only covered for 10 to 15 minutes. Fourteen minutes after the removal of the bag, the *CER* had completely recovered (Fig. IV.1).

For the plants at ambient air temperature, the mean instantaneous rate of shoot respiratory carbon use while covered during the light period, $s_n$, was higher than the mean shoot respiratory carbon use of the same plants during the subsequent dark period, $s_{rd}$, (data not shown). This is not surprising since chamber air temperatures were lower during the dark period. For plants maintained at constant chamber temperature $s_n$ was higher than $s_{rd}$ in 9 out of 11 cases (Fig. IV.2). For individual plants, the mean $s_n$ for all days combined (n=15-30) was always higher than the mean $s_{rd}$ (n=42-73). For three plants this difference was statistically significant (t=4.2 to 5.8, $P<0.001$) for one plant it was not (t=1.2, $P=0.247$). The higher chamber air temperature for *A. spicatum* will account for the higher $s_n$ for that species (Fig. IV.2). The two values for *A. spicatum* intermediate between the two species are for the only cloudy day of the study (see below).

65
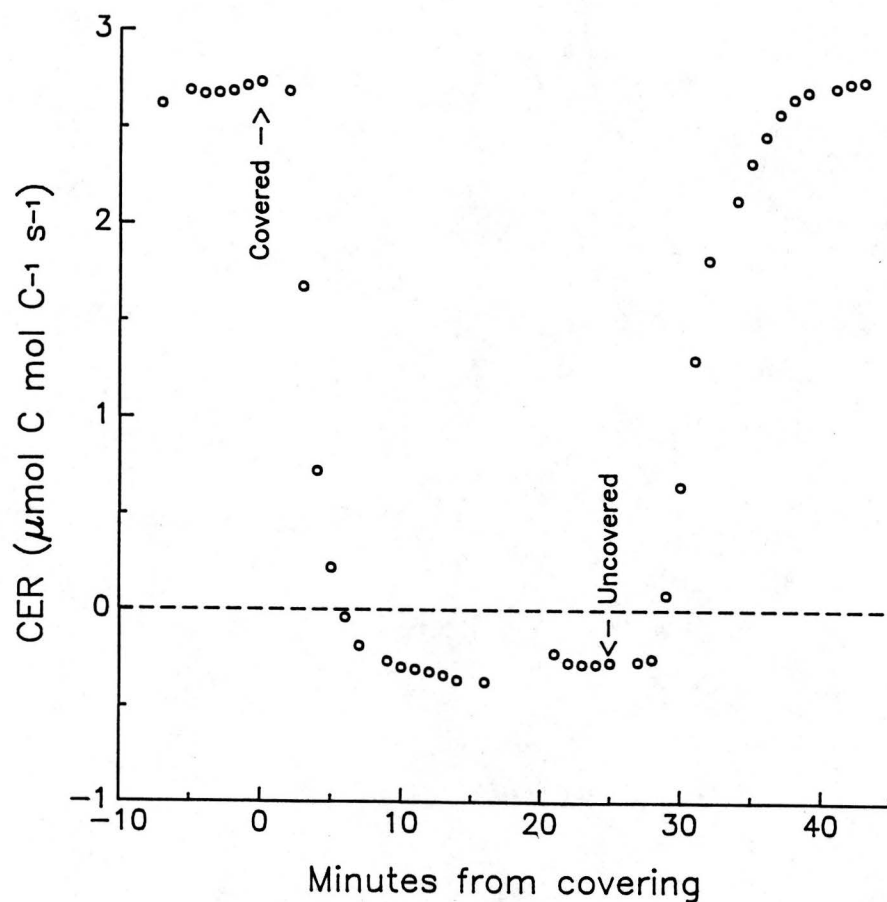


**Figure IV.1.** The instantaneous carbon exchange rate, *CER*, (µmol C mol C$^{-1}$ s$^{-1}$) for a single plant of *A. desertorum*, before, during, and after the covering of the plant with an opaque plastic bag, as a function of the number of minutes from the time the plant was covered.
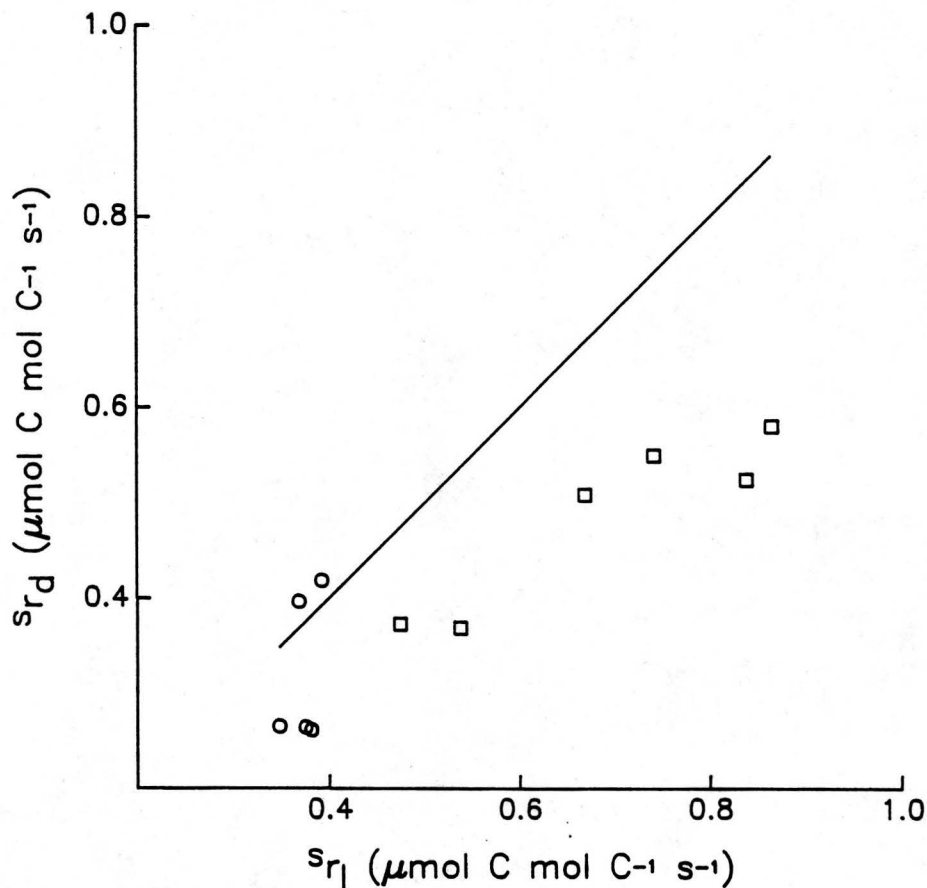
**Figure IV.2.** The mean instantaneous rate of shoot respiratory carbon use during the dark period, $^sr_d$ (μmol C mol C$^{-1}$ s$^{-1}$), as a function of the mean instantaneous rate of shoot respiratory carbon use of the same plants while covered briefly during the preceding light period, $^sr_l$ (μmol C mol C$^{-1}$ s$^{-1}$), for *A. desertorum* (circles) and *A. spicatum* (squares). The solid line is the 1:1 line. The *A. desertorum* plants were controlled at 10°C and the *A. spicatum* plants at 20°C.


*The $Q_{10}$ value of shoot
respiratory carbon use*

Figure IV.3 shows the rate of shoot respiratory carbon use during the

dark period, $^sr_d$, as a function of leaf temperature for the two plants

of *A. desertorum* and *A. spicatum* that were maintained at ambient air

temperature. During the monitoring of *A. desertorum*, the ambient air

temperature at night increased from a sub-zero temperature the first
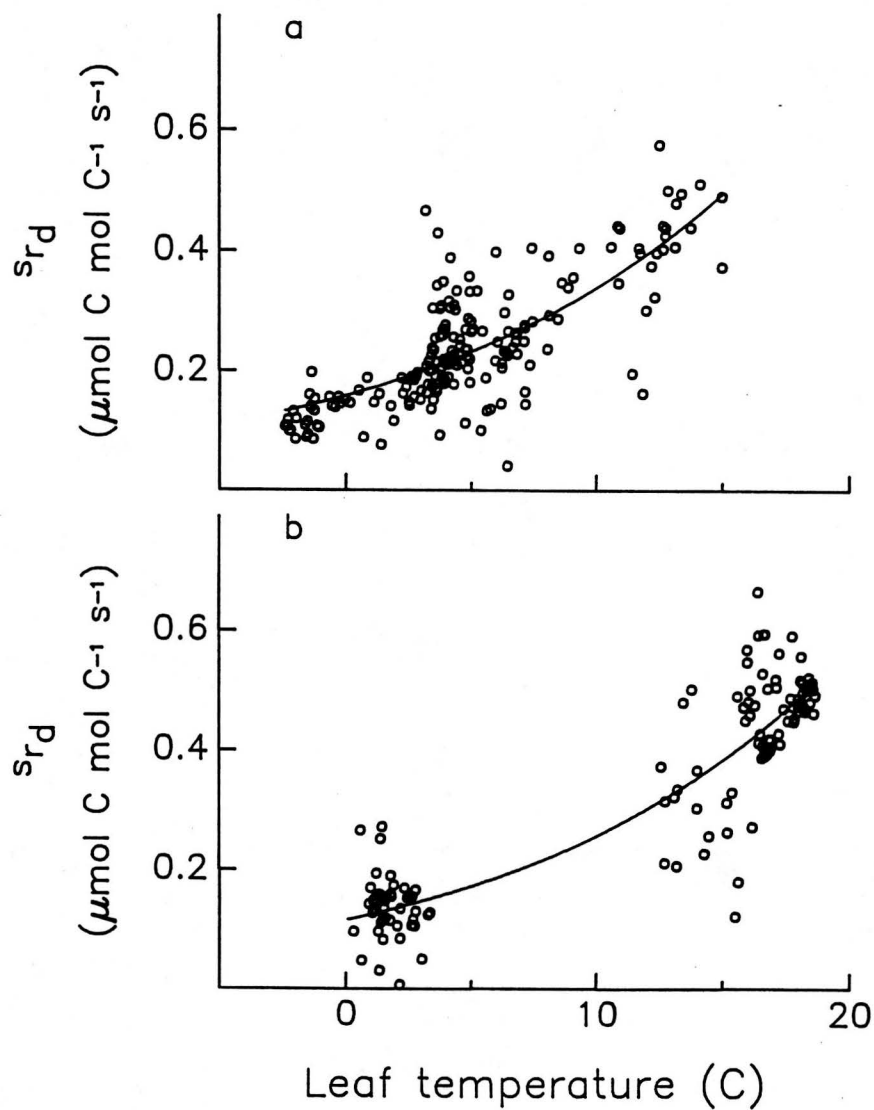
**Figure IV.3.** The instantaneous rates of shoot respiratory carbon use during the dark period, $^sr_d$ (μmol C mol $C^{-1}$ $s^{-1}$), for *A. desertorum* (a) and *A. spicatum* (b), as a function of leaf temperature. Also shown (solid lines) are the calculated rates based on $Q_{10}$ values of 2.1 and 2.2 for *A. desertorum* and *A. spicatum*, respectively. The plants were in gas-exchange chambers with the chamber air temperature equal to the ambient air temperature.

night to 10–15 °C during the last night (Fig. IV.3a). The change in temperature was more abrupt for *A. spicatum*. The first two nights were warm but the last night was cold (Fig. IV.3b).

The natural variation in leaf temperature was used to estimate the $Q_{10}$ value for respiration (the rate of respiratory carbon use at a given temperature divided by the rate at a temperature 10°C lower) using equation (1). The estimated $Q_{10}$ values were 2.1 and 2.2 for *A. desertorum* and *A. spicatum*, respectively (Fig. IV.3).

*Daily integrated carbon
balance parameters*

Cloud cover was minimal during the three days *A. desertorum* was monitored and the first two days *A. spicatum* was monitored with a mean  daily integrated photosynthetic photon flux (PPF) of 46.2 mol. The last day *A. spicatum* was monitored was cloudy, however, and the integrated PPF was only 10.0 mol. That day was also the coldest, with mean air temperature during the light period of 6.1°C. Data from the last day will be reported separately.

The mean daily integrated $P_n$ for the sunny days was 98.9 mmol C mol $C^{-1}$ $d^{-1}$ and ranged from 76.2 to 124.1. The $P_n$ values for the chambers that tracked ambient conditions were slightly higher than the chambers maintained at the slightly lower constant chamber temperatures. The daily integrated $P_n$ was higher for *A. spicatum* than *A. desertorum*. However, this difference can be attributed to the higher chamber air temperatures (see methods).

The mean daily integrated $^s n$ for the sunny days was 30.2 mmol C mol $C^{-1}$ $d^{-1}$ and ranged from 16.3 to 46.8. Adding the $^s n$ values to $P_n$

resulted in mean integrated daily gross photosynthetic carbon fixation, $P_g$, of 129.1 mmol C mol $C^{-1}$ $d^{-1}$, which is 30.5% higher than the mean $P_n$. The mean integrated $^sr_d$ was 14.8 mmol C mol $C^{-1}$ $d^{-1}$, which is significantly lower than the mean daily integrated $^sn$ (paired t=6.1, $P$=0.000). The integrated $^sr_d$ values were lower than the integrated $^sn$ for individual days in all cases.

The shoot growth efficiency, $^sY$, is the ratio of net daily carbon gain and gross photosynthetic carbon fixation. The overall mean $^sY$ for the sunny days was 0.65, and ranged from 0.48 to 0.77 for individual days. The mean shoot growth efficiency was significantly higher for *A. desertorum* than *A. spicatum*, (0.69 and 0.61, respectively, t=2.5, $P$=0.026). Since these two species were measured at different temperatures, however, it is not clear if this is a temperature effect or a species effect.

The cloud cover on the last day *A. spicatum* was monitored reduced both the rate of photosynthetic carbon fixation and the rate of respiratory carbon use. For the plants at ambient air temperature, the rates of photosynthesis and respiration were reduced to a similar degree and the mean integrated $P_n$, $P_g$, $^sn$, and $^sr_d$ were 31.1, 38.9, 7.8, and 4.8 mmol C mol $C^{-1}$ $d^{-1}$, respectively. The mean integrated $P_g$ was 25.1% higher than the mean integrated $P_n$. The $^sY$ (0.67) was not different from the mean for the sunny days. On this day, plants maintained at 20°C had integrated rates of respiratory carbon use that were considerably higher than for the plants at ambient temperature (20.5 and 14.9 for $^sn$ and $^sr_d$, respectively), while the integrated $P_g$ was nearly the same (35.2 mmol C mol $C^{-1}$ $d^{-1}$), making it 39.7% higher

than the integrated $P_n$. This proportionally higher rate of respiratory carbon use reduced the mean net daily carbon gain to $-0.2$ mmol C mol $C^{-1}$ $d^{-1}$. $^sY$ is negative when the net daily carbon gain is less than zero.

## Discussion

As would be expected, the rate of shoot respiratory carbon use at ambient air temperature during the light period was higher than the rate of shoot respiratory carbon use at the lower ambient air temperature during the dark period. This difference was also found when the chamber air temperature was maintained constant, however (Fig. IV.2), suggesting that this is more than a temperature effect.

There is conflicting evidence in the literature on the rate of respiratory carbon use in photosynthetic tissue during the light period. It has most often been shown to decrease, but there is evidence for no change and even an increase in the rate of respiration in the light compared to the dark (Graham, 1980). The reduction in the rate of respiratory carbon use in light can been related to direct interaction with photosynthetic metabolism (Graham, 1980). This effect can therefore be assumed to be confined to photosynthetic tissue. Only a fraction of the respiratory carbon use of a grass shoot system takes place in photosynthetic tissue, however (Morgan & Austin, 1983) and grass leaves rarely grow on their own photosynthate (Penning de Vries, 1983). The rate of respiratory carbon use in heterotrophic tissue in the grass shoot system (stem tissue, crowns, developing leaves enclosed by sheaths etc.) can be expected to only respond to light indirectly through its effect on the rate of carbon substrate supply. The lower

rate of shoot respiratory carbon use during the dark period observed in this study for a constant temperature (Fig. IV.2), suggests that the rate of substrate supply to heterotrophic tissue is lower during the dark period.

The rate of gross photosynthetic carbon fixation was estimated to be 30.5% higher than the net rate of photosynthetic carbon fixation for sunny days. This difference is greater than commonly observed for grass leaves (Woledge & Parsons, 1986). The net daily carbon gain divided by the daily gross rate of photosynthetic carbon fixation is the shoot growth efficiency, $^sY$. For a given value of $P_g$, net carbon gain and therefore $^sY$ will decline as the rate of respiratory carbon use increases. The mean value of $^sY$ was 0.65 (e.i. 35% of daily gross photosynthetic carbon fixation was respired during that same day and the following night). The whole-plant growth efficiency will be lower than $^sY$ due to the respiratory carbon use of the root system, which was not measured in this study. Not including root respiration causes the whole-plant net carbon gain to be overestimated, resulting in overestimation of the growth efficiency. The whole plant growth efficiency is a function of the efficiency of the conversion of photosynthate to structural material, the maintenance coefficient, and the specific growth rate (Chapter II). The conversion efficiency ($Y_g$) determines the maximum growth efficiency. The mean $Y_g$ was estimated to be 0.72 for the two species in the laboratory (Chapter II). The measured $^sY$ exceeded this value in a few cases in this study. This was due to the translocation of photosynthate to the root system and the

fact that respiration associated with this photosynthate was not measured.

A $Q_{10}$ value of 2.0 is commonly assumed for the rate of respiration of intact leaves and fruits (Leafe, 1972; Jones, 1981,1983). Robson (1981) tested this assumption for entire shoot systems of *Lolium perenne* and found a $Q_{10}$ function with a $Q_{10}$ of 2.0 to fit the rate of respiratory carbon use between 5° and 20°C. The $Q_{10}$ values in this study were estimated to be 2.1 and 2.2 for *A. desertorum* and *A. spicatum*, respectively.

This study shows that measuring the rate of shoot respiratory carbon use as a part of shoot carbon dioxide exchange measurements in the field provides additional information that cannot be gathered from the measurement of photosynthetic carbon fixation alone. Information on respiratory carbon use at night makes the calculation of net carbon gain possible, while the measurement of the rate of respiratory carbon use during the day provides information on the gross rate of photosynthetic carbon fixation and the shoot growth efficiency. This study suggests that the rate of respiratory carbon use measured during the night cannot be used to calculate the rate of respiratory carbon use during the day. Such an assumption will lead to the underestimation of gross photosynthesis. Finally this study demonstrated that the $Q_{10}$ response of respiratory carbon use can be estimated using natural variations in temperature.

CHAPTER V

SUMMARY AND INTEGRATION

This study involved the quantification of the dynamics of respiratory carbon use and the mathematical simulation of these dynamics. The rate of respiratory carbon use was studied in the context of two important factors that influence it: the rate of photosynthetic carbon fixation, and the dynamics of labile carbon compounds. This integrated approach made it possible to relate the dynamics of respiratory carbon use to other components of the carbon balance, which would not have been possible if respiratory carbon use had been studied in isolation.

The main objective of this study was to provide a quantitative link between the rate of photosynthetic carbon fixation and the rate of respiratory carbon use, and thereby the rate of net carbon gain. This objective was met by the quantification of the whole-plant growth efficiency in the laboratory and the shoot growth efficiency in the field, and of the factors that determine the growth efficiency: the conversion efficiency, the maintenance coefficient, and specific growth rate. Particular attention was given to the dynamics of respiratory carbon use during regrowth following defoliation.

**The rate of respiratory
carbon use**

The rate of respiratory carbon use was found to be closely linked to the rate of photosynthetic carbon fixation and to respond immediately to small changes in this rate. There was some delay in this response following large changes in the rate of carbon input. This delay was a result of the buffering action of small pools of labile carbon

compounds. When the rate of substrate utilization was in balance with the rate of substrate supply, carbon was added to the pools of labile carbon compounds at the same rate as it is was removed and no net mobilization or net accumulation of labile carbon compounds took place. When the rate of carbon input from photosynthetic carbon fixation was reduced, however, the demands of carbon utilization were temporarily met by net mobilization of labile carbon compounds. A new balance was rapidly reached as the rate of carbon utilization was reduced in response to the reduced substrate input. The opposite course of events took place if the rate of photosynthetic carbon fixation was abruptly increased again.

The respiratory carbon use of the root system was measured separately from the shoot system in the laboratory. This revealed the rapid response of the root system to the rate of photosynthetic carbon fixation of the shoot system. Within hours of the shading or the defoliation of the shoot system, a reduction was noted in the rate of respiratory carbon use of the root system. When this reduction was complete, the specific rate of respiratory carbon use of the root system had declined by as much as 60%. This rapid response of the root system suggests that the roots did not contain large "reserves" of labile carbon compounds. This was verified by destructive chemical analysis at the end of the experiments.

### Growth efficiency and substrate balance

The growth efficiency is the fraction of the carbon fixed by photosynthesis during a given day that is still a part of plant biomass

at the beginning of the next day (Thornley, 1970,1976; Yamaguchi, 1978). For a given rate of photosynthetic carbon fixation, the growth efficiency will decline as the rate of respiratory carbon use increases. This does not imply, however, that a low rate of respiratory carbon use is always associated with high rate of net carbon gain, because the rate of respiratory carbon use and the rate of photosynthetic carbon fixation are related when the rate of substrate utilization and the rate of substrate supply is in balance.

Most of the growth efficiency values measured in this study fell between 0.5 and 0.7. This is the range of values found for most plants during balanced growth (Yamaguchi, 1978; Robson, 1973). As the specific growth rate is reduced, the carbon requirement for maintenance has greater relative impact. This was exemplified by *A. spicatum*, plant 4, which grew slower than any other plant in this study and had the lowest mean growth efficiency (0.24) in spite of its relatively low maintenance coefficient.

Net mobilization of labile carbon compounds temporarily reduces the growth efficiency. This was seen during the first days of regrowth following defoliation. A reduction in growth efficiency was also observed on the first day of the shading treatment. The assumption that this was due to net mobilization of labile carbon compounds was supported by the simulation of labile carbon dynamics.

The same phenomenon was observed in the field during the only cloudy day of the field study, when the shoot growth efficiency of the plants maintained at 20°C was reduced to the point of becoming slightly negative (net carbon gain less than zero). The fact that the shoot

growth efficiency did not change at the same time for the plants at the cooler ambient air temperature suggests that their rate of carbon utilization did not exceed the reduced rate of carbon input.

## The conversion efficiency and the maintenance coefficient

The mean conversion efficiency was found to be 0.72 and did not vary much. This approximate value was expected based on both published experimental work (Lambers, Szaniawski, & de Visser, 1983) and theoretical analysis (Penning de Vries, Brunsting, & Van Laar, 1974).

Less is known about the maintenance coefficient and how it might differ between plants and growing conditions (Amthor, 1984). The overall mean for the maintenance coefficient was 10.4 mmol C mol $C^{-1}$ $d^{-1}$. This is lower than the values reported for fast growing crop plants (McCree, 1982; Lambers *et al.*, 1983; Amthor, 1984), a fact consistent with the concept that the maintenance coefficient reflects the level of metabolic activity in the plant (Penning de Vries, 1975). The level of metabolic activity can be expected to be higher in fast growing crop plants than the perennial grasses studied here.

## Simulation of respiratory carbon use, labile carbon dynamics and assimilate partitioning

The classical substrate balance model (McCree, 1970; Thornley, 1970,1976) fit the rate of respiratory carbon use of plants at substrate balance quite well ($r^2=0.91-0.98$). In this model the conversion efficiency, the maintenance coefficient, and plant carbon content are used to calculate the rate of respiratory carbon use from the rate of photosynthetic carbon fixation.

The dynamics of labile carbon compounds had to be included to successfully simulate the rate of respiratory carbon use during conditions of transients in substrate use. Thornley's (1977,1982) recycling model of respiratory carbon use was found to be suitable for this purpose, even immediately following a severe defoliation. The simulation of the dynamics of the labile carbon pools also provided valuable insight into the quantitative changes in labile carbon pools during regrowth (see below).

The partitioning of incoming photosynthate between root and shoot had to be explicitly simulated to make a separate simulation of the rate of respiratory carbon use of the root system and the shoot system possible. Johnson's (1985) assimilate partitioning model was used for this purpose. It simulated the changes in partitioning as a result of the defoliation quite well, but was unstable following the short term shading.

## Mobilization of labile carbon compounds during regrowth

The most significant result of this study was the direct quantitative comparison of the magnitude of the daily net mobilization of labile carbon compounds and the rate of carbon input from photosynthetic carbon fixation during each day of regrowth. The mobilization of labile carbon compounds exceeded the rate of carbon input from photosynthetic carbon fixation only for one or two days, depending on the severity of the defoliation.

# REFERENCES

Alberda, T. (1960) The effect of nitrate nutrition on carbohydrate content in *Lolium perenne*. *Proceedings of the 8th International Grassland Congress*, 612-617.

Amthor, J.S. (1984) The role of maintenance respiration in plant growth, *Plant, Cell and Environment*, **7**, 561-569.

Barkworth, M.E. & Dewey, D.R. (1985) Genomically based genera in the perennial Triticeae of North America: identification and membership. *Annals of Botany*, **72**, 767-776.

Barnes, A. & Hole, C.C. (1978) A theoretical basis of growth and maintenance respiration. *Annals of Botany*, **42**, 1217-1221.

Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S. & Dzurec, R.S. (1981) Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia*, **50**, 14-24.

Chatterton, N.J., Harrison, P.A., & Bennett, J.H. (1986) Environmental effects on sucrose and fructan concentrations in leaves of *Agropyron* spp. In *Phloem Transport* (eds Cronshaw, J., Lucas, W.J., & Giaquinta, R.T.), pp. 471-476, Alan R. Liss, Inc., New York.

Crider, F. (1955) Root growth stoppage resulting from defoliation of grass. *USDA Technical Bulletin No. 1102*

Davidson, J.L. & Milthorpe, F.L. (1966) The effect of defoliation on the carbon balance in *Dactylis glomerata*. *Annals of Botany*, **30**, 185-198.

Gordon, A.J., Ryle, G.J.A., & Powell, C.E. (1977) The strategy of carbon utilization in uniculm barley. I. The chemical fate of photosynthetically assimilated $^{14}C$. *Journal of Experimental Botany*, **28**, 1258-1269.

Graham, D. (1980) Effects of light on "dark" respiration. In *The Biochemistry of Plants, Vol. 2, Metabolism and Respiration* (ed. Davies, D.D.), pp. 525-579, Academic Press, New York.

Hansen, G.K. & Jensen, C.R. (1977) Growth and maintenance respiration in whole plants, tops, and roots of *Lolium multiflorum*. *Physiologia Plantarum*, **39**, 275-279.

Hesketh, J.D., Alberte, R.S. & Jones, J.W. (1980) Predicting dark respiration in the soil-plant system. In *Predicting Photosynthesis for Ecosystem Models Vol. II* (eds Hesketh, J.D. & Jones, J.W.), pp 69-84, CRC Press, Boca Raton.

Irving, D.E. & Silsbury, J.H. (1987) A comparison of the rate of maintenance respiration in some crop legumes and tobacco determined by three methods. *Annals of Botany*, **59**, 257-264.

Jones, H.G. (1981) Carbon dioxide exchange of developing apple (*Malus pumila* Mill.) fruits. *Journal of Experimental Botany*, **32**, 1203-1210.

Jones, H.G. (1983) *Plants and microclimate*. Cambridge University Press, Cambridge.

Johnson, I.R. (1985) A model of the partitioning of growth between the shoots and roots of vegetative plants. *Annals of Botany*, **55**, 421-431.

Johnson, I.R. (1987) Models of respiration. In *Plant Growth Modeling for Resource Management Vol. II* (eds K. Wisiol & J.D. Hesketh), pp. 89-108, CRC Press, Boca Raton.

Johnson, I.R. & Thornley, J.H.M. (1985) Temperature dependence of plant and crop production. *Annals of Botany*, **55**, 1–55.

Johnson, I.R. & Thornley, J.H.M. (1987) A model of shoot:root partitioning with optimal growth. *Annals of Botany*, **60**, 133–142.

Lambers, H. (1979) Efficiency of root respiration in relation to growth rate, morphology and soil composition. *Physiologia Plantarum*, **46**, 194–202.

Lambers, H. (1985) Respiration in intact plants and tissues: Its regulation and dependence on environmental factors, metabolism and invaded organisms. In *Higher Plant Cell Respiration, Encyclopedia of Plant Physiology, New Series, Volume 18* (eds Douce, R., & Day, D.A.), pp 418–473, Springer-Verlag, Berlin.

Lambers, H., Szaniawski, R.K. & de Visser, R. (1983) Respiration for growth, maintenance and ion uptake. An evaluation of concepts, methods, values and their significance. *Physiologia Plantarum*, **58**, 556–563.

Lance, C., Chauveau, M., & Dizengremel, P. (1985) The cyanide-resistant pathway of plant mitochondria. In *Higher Plant Cell Respiration, Encyclopedia of Plant Physiology, New Series, Volume 18* (eds Douce, R., & Day, D.A.), pp 202–247, Springer-Verlag, Berlin.

Leafe, E. (1972) Micro-environment, carbon dioxide exchange and growth in grass swards. In *Crop processes in controlled environments* (eds Rees, A, Cockshull, K., Hand, D. & Hurd, R.), pp. 157–174, Academic Press, London.

Loehle, C. (1982) Growth and maintenance respiration: a reconciliation of Thornley's model and the traditional view. *Annals of Botany*, 51, 741–747.

Massimino, D., Andrè, M, Richaud, C, Daguenet, A. Massimino, J. and Vivoli, J. (1981) The effect of a day at low irradiance of maize crop. I. Root respiration and uptake of N, P and K. *Physiologia Plantarum*, 51, 150–155.

McCree, K.J. (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. In *Prediction and Measurement of Photosynthetic Productivity. Proceeding of IBF/PP Technical Meeting, Trebon 1969* (ed. I. Setlik), pp. 221–230, PUDOC, Wageningen.

McCree, K.J. (1974) Equations for the rate of dark respiration of white clover and grain sorghum, as functions of dry weight, photosynthetic rate, and temperature. *Crop Science*, 14, 509–514.

McCree, K.J. (1982) Maintenance requirements of white clover at high and low growth rates. *Crop Science*, 22, 345–351.

McCree, K.J. (1983) Carbon balance as a function of plant size in sorghum plants. *Crop Science*, 23, 1173–1177.

McCree, K.J. (1986) Measuring the whole-plant carbon balance. *Photosynthetica*, 20, 82–93.

McCree, K.J. (1988) Sensitivity of sorghum grain yield to ontogenetic changes in respiration coefficients. *Crop science*, 28, 114–120.

McCree, K.J. & Amthor, M.E. (1982) Effects of diurnal variation in temperature on the carbon balances of white clover plants. *Crop Science*, 22, 822–827.

Merino, J., Field, C., & Mooney, H.A. (1982) Construction and maintenance costs of mediterranean-climate evergreen and deciduous leaves. I. Growth and $CO_2$ exchange analysis. *Oecologia*, **53**, 208-213.

Miller, P.C. & Stoner, W.A. (1979) Canopy structure and environmental interactions. In *Topics in Plant Population Biology* (eds Solbrig, O.T., Johnson, G.B., & Raven, P.H.), pp 428-458, Columbia University Press, New York.

Morgan, C.L. & Austin, R.B. (1983) Respiratory loss of recently assimilated carbon in wheat. *Annals of Botany*, **51**, 85-95.

Moser, L.E., Volenec, J.J., & Nelson, C.J. (1982) Respiration, carbohydrate content, and leaf growth of tall fescue. *Crop Science*, **22**, 781-786.

Parkinson, K.J. (1985) Porometry. In *Instrumentation for Environmental Physiology* (eds Marshall, B. & Woodward, F.I.), pp 171-191, Cambridge University Press, Cambridge.

Penning de Vries, F.W.T. (1975) The cost of maintenance processed in plant cells. *Annals of Botany*, **39**, 77-92.

Penning de Vries, F.W.T. (1983) Modeling of growth and production. In *Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence, Encyclopedia of Plant Physiology, New Series, Volume 12D* (eds Lange, O.L., Nobel, P.S., Osmond, C.B., & Ziegler, H.), pp 117-150, Springer-Verlag, Berlin.

Penning de Vries, F.W.T., Brunsting, A.B., & Van Laar, H.H. (1974) Products, requirements and efficiency of biological synthesis. A quantitative approach. *Journal of Theoretical Biology*, **45**, 339-377.

Press, W.H., Flannery, B.P., Teukolsky, S.A. & Vettering, W.T. (1986) *Numerical Recipes: the Art of Scientific Computing.* Cambridge University Press, Cambridge.

Reekie, E.G. & Redmann, R.E. (1987) Growth and maintenance respiration of perennial root systems in a dry grassland dominated by *Agropyron dasystachyum* (Hook.) Scribn. *New Phytologist*, 105, 595–603.

Richards, J.H. & Caldwell, M.M. (1985) Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *Journal of Applied Ecology*, 22, 907–920.

Robson, M.J. (1973) The growth and development of simulated swards of perennial ryegrass. II. Carbon assimilation and respiration in a seedling sward. *Annals of Botany*, 37, 501–818.

Robson, M.J. (1981) Respiratory efflux in relation to temperature of simulated swards of perennial ryegrass with contrasting soluble carbohydrate contents. *Annals of Botany* 48, 269–273.

Ryle, G.J.A., Cobby, J.M., & Powell, C.E. (1976) Synthetic and maintenance respiratory losses of $^{14}CO_2$ in uniculm barley and maize. *Annals of Botany*, 40, 571–586.

Schwarz, M. & Gale, J. (1981) Maintenance respiration and carbon balance of plants at low levels of sodium chloride salinity. *Journal of Experimental Botany*, 32, 933–941.

Szaniawski, R.K. (1981) Growth and maintenance respiration of shoot and root in Scots pine seedlings. *Zeitschrift für Pflanzenphysiologie*, 101, 391–398.

Thornley, J.H.M. (1970) Respiration, growth and maintenance in plants. *Nature*, **227**, 304–305.

Thornley, J.H.M. (1976) *Mathematical Models in Plant Physiology*, Academic Press, London.

Thornley, J.H.M. (1977) Growth, maintenance and respiration; a reinterpretation. *Annals of Botany*, **41**, 1191–1203.

Thornley, J.H.M. (1982) Interpretation of respiration coefficients. *Annals of Botany*, **49**, 257–259.

van Bavel, C.H.M., Lascano, R., & Wilson, D.R. (1978) Water relations of fritted clay. *Soil Science Society of America Journal*, **42**, 657–659.

Veen, B.W. (1981) Relation between root respiration and root activity. *Plant and Soil*, **63**, 73–76.

vonCaemmerer, S. & Farquhar, G.D. (1981) Some relationship between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, **153**, 376–387.

Wilkinson, L. (1987) *SYSTAT: The System for Statistics*. SYSTAT, Evanston, IL.

Woledge, J. & Parsons, A.J. (1986) *Temperate Grasslands*. In *Photosynthesis in Contrasting Environments* (ed. Baker, N.R. & Long, S.P.), pp. 173–197, Elsevier Science Publishers, New York.

Yamaguchi, J. (1978) Respiration and the growth efficiency in relation to crop productivity. *Journal of the Faculty of Agriculture Hokkaido University*, **59**, 59–129.

APPENDIX

This appendix contains a listing of the FORTRAN implementation of the model used in chapter III. This listing is complete, with the exception of the portions of the code that were adopted from Press *et al.* (1986), (copyright (C) 1985 by Numerical Recipes Software). This appendix also includes sample input files and sample model output using the input files.

DAYMOD.FOR is the main program. COMMON.INC contains variable and common block declarations. INPUT.FOR reads data and parameter files (see below). INIT.FOR initializes variables and arrays used in the simulations. RECMODEL.FOR calculates the derivatives of the state variables of the respiratory carbon use model. It is called directly by the numerical integration routines (not reprinted here). ONECOMP.FOR uses the substrate-balance model (see chapter II) to calculate growth and maintenance respiration. UPDATE.FOR updates the state variables after the call to the numerical integration routines. It also implements the assimilate partitioning submodel. REPORT.FOR writes model output files. STATS.FOR fits predicted rates of respiratory carbon use to observed rates, calculates Chi-squared and $r^2$, and compares the mean observed and predicted rates using a paired t-test.

The input files are for *A. desertorum*, plant 2. DES202.RUN is the first input file. It contains the names of the other input files and the names to be used for the output files. Also included are the number of days the plant was monitored and information on the defoliations. DES202.MOD contains the daily carbon balance information and DES202.WFS the back-calculated weight and weight fraction data. The parameters of the respiratory carbon use submodels are read in from

DES202.MPA and the parameters of the assimilate partitioning model from PART202.INP.

Two of the output files are included. DES202.OUT is a general report on the simulation including the statistical comparison of the predicted and observed values. MOBIL.DAT lists the sizes of the shoot and root labile carbon pools, the substrate input to root and shoot, and net mobilization of whole–plant, shoot, and root labile carbon compounds.

```
DAYMOD.FOR

      program daymod

$NOTRUNCATE

*     Variable declaration *************************************

      real      defolprop,ystart(6),
     &          y(6),h1,hmin,x1,x2,eps,ssqerr,dpar,derr,mse,r2,
     &          meansstor,meanrstor
      integer   nvar,nok,nbad,kmax,kount,dxsav,var
      logical   modpart
      character yn
      external  recmod,rkqc

$INCLUDE:'common.inc'

      common /path/kmax,kount,dxsav,xp(200),yp(10,200)

      call input
      call init(ystart)

      print *,'Use partition model? (y/n)'
      read(*,'(a)')yn
      if (yn .eq. 'y')then
          modpart = .true.
      else
          modpart = .false.
      endif

*     Parameters used by integration routines

      nvar      = 6
      kmax      = 1000
      dxsav     = 0.25
      eps       = 0.001
      h1        = 0.01
      hmin      = 0.00000001

*     Calculate the dynamics of the state variables using 5th order
*     Runge-Kutta numerical integration

      do 20, d = 1,ndays
      x1        = d
      x2        = x1 + 1

      if (d .lt. daydefol1) then
         sm(d)      = im  / 1000.0
         rm(d)      = im  / 1000.0
         shootpart(d) = inisp
         rootpart(d)  = inirp
      else if ((d .ge. daydefol1) .and. (d .lt. daydefol2)) then
         sm(d)      = d1m / 1000.0
         rm(d)      = d1m / 1000.0
         shootpart(d) = df1sp
         rootpart(d)  = df1rp
         skg        = skgd1
         rkg        = rkgd1
         sYg        = sYgd1
```

```
         rYg        = rYgd1
      else if (d .ge. daydefol2) then
         sm(d)      = d2m / 1000.0
         rm(d)      = d2m / 1000.0
         shootpart(d) = df2sp
         rootpart(d)  = df2rp
         skg        = skgd2
         rkg        = rkgd2
         sYg        = sYgd2
         rYg        = rYgd2
      endif

      if (modpart) then
          shootpart(d) = Ls(d)
          rootpart(d)  = Lr(d)
      endif

*     Use the substrate-balance model to calculate RCU for the day

      call onecom

*     Calculate new values for the state variables

*     The odeint subroutine and the subroutines called by it (rkqc and
*     rk4) are not printed in this appendix due to copyright
*     restrictions (Copyright (C) 1985 by Numerical Recipes Software,
*     P.O. Box 243, Cambridge, MA 02238)

      call odeint(ystart,nvar,x1,x2,eps,h1,hmin,nok,nbad,recmod,rkqc)

*     Use the updated ystart array to update the state variables

      call update(ystart)

20    continue

*     Output simulation results to data file: *************************

      call report(outputfile)

99    continue
      stop
      end
```

```
COMMON.INC

      parameter (n = 50)

      real    mtotw(n),mrootw(n),mshootw(n),sfs(n),sfd(n),sfn(n),
     &        rfs(n),rfd(n),rfn(n),subin(n),totcbal(n),shootcbal(n),
     &        mtotrs(n),mshootrs(n),mrootrs(n),measy(n),mshootcer(n),
     &        mrootcer(n),ptotrs(n),pshootrs(n),prootrs(n),ptotw(n),
     &        pshootw(n),prootw(n),etotw(n),dayno(n),defolmass(n),
     &        sstor(n),rstor(n),sdegrad(n),rdegrad(n),snondeg(n),
     &        rnondeg(n),sm(n),rm(n),opshootgrs(n),
     &        opshootmrs(n),oprootgrs(n),oprootmrs(n),optotgrs(n),
     &        optotmrs(n),opshootrs(n),oprootrs(n),optotrs(n),
     &        shootpart(n),rootpart(n),prootwf(n),etotrs(n),
     &        eshootrs(n),erootrs(n),oetotrs(n),oeshootrs(n),
     &        oerootrs(n),mshootrsh(n,0:23),mrootrsh(n,0:23),
     &        subinh(n,0:23),shootcer(n,0:23),inpshootnight(n),
     &        inprootrs(n),ptotmrs(n),ptotgrs(n),pshootmrs(n),
     &        pshootgrs(n),prootmrs(n),prootgrs(n),structg(n),
     &        structrg(n),structsg(n),defno(n),mshootwf(n),mrootwf(n),
     &        mrsratio(n),msgr(n),Wc(n),Wn(n),Wg(n),C(n),
     &        Nc(n),Wsh(n),Wr(n),Lr(n),Ls(n),Ws(n),An(n),Nutil(n),
     &        Nupt(n),dWg(n),part(n),dlt(n),dls(n),dlr(n)
      real    sinifs,sinifd,sinifn,siniw,rinifs,
     &        rinifd,rinifn,riniw,defolmass1,
     &        defolmass2,im,d1m,d2m,shpart,rtpart,mAn,fN,
     &        sumpshootrsh,sumprootrsh,summshootrsh,summrootrsh,
     &        inisp,inirp,df1sp,df1rp,df2sp,df2rp,Mc,Mn,kc,
     &        kn,p,sYg,sYd,skg,skd,rYg,rYd,rkg,rkd,skgd1,skgd2,
     &        rkgd1,rkgd2,sYgd1,sYgd2,rYgd1,rYgd2
      integer d,ndays,ndefol,daydefol1,daydefol2,timestep,hour
      character*80  titleline,textline
      character*20  messagefile,paramfile,outputfile,runfile,input24h,
     &              input1h,massfile,partfile

      common /paramet /sinifs,rinifs,sinifd,rinifd,sinifn,rinifn,
     &        siniw,riniw,shootpart,rootpart,shpart,rtpart,timestep,
     &        hour,sYg,rYg,sYd,rYd,skg,rkg,skd,
     &        rkd,inisp,inirp,df1sp,df1rp,df2sp,df2rp,
     &        mAn,fN,Mc,Mn,kc,kn,p,skgd1,skgd2,
     &        rkgd1,rkgd2,sYgd1,sYgd2,rYgd1,rYgd2

      common /predict /ptotrs,pshootrs,prootrs,sfs,rfs,sfd,rfd,sfn,
     &                 rfn,ptotw,pshootw,prootw,etotw,sstor,rstor,
     &                 sdegrad,rdegrad,snondeg,rnondeg,prootwf,
     &                 maintcoeff,growthresp,maintresp,rcuonecomp,
     &                 etotrs,eshootrs,erootrs,optotrs,opshootrs,
     &                 oprootrs,oetotrs,oeshootrs,oerootrs,opshootgrs,
     &                 opshootmrs,oprootgrs,oprootmrs,optotgrs,
     &                 optotmrs,sumpshootrsh,sumprootrsh,summshootrsh,
     &                 summrootrsh,ptotmrs,ptotgrs,pshootmrs,
     &                 pshootgrs,prootmrs,prootgrs,structrg,structrg,
     &                 structsg,defno,mshootwf,mrootwf,mrsratio,
     &                 msgr,Wc,Wn,Wg,C,Nc,Wsh,Wr,Lr,Ls,Ws,An,Nutil,
     &                 Nupt,dWg,part,dlt,dls,dlr
      common /filename /messagefile,paramfile,outputfile,runfile,
     &              input24h,input1h,massfile,partfile
      common /indata  /mtotw,mrootw,mshootw,subin,totcbal,shootcbal,
     &                 rootcbal,mtotrs,mshootrs,mrootrs,measy,
     &                 mshootcer,mrootcer,dayno,d,ndays,ndefol,
```

```
     &                 daydefol1,defolmass,daydefol2,defolmass1,
     &                 defolmass2,im,d1m,d2m,titleline,mshootrsh,
     &                 mrootrsh,subinh,shootcer,inpshootnight,
     &                 inprootrs,sm,rm
```

INPUT.FOR

```fortran
      subroutine input

$NOTRUNCATE

*     This subroutine reads in initial values, paramater values
*     and data. It also initializes variables used in the simulation

      real    defmass1,defmass2

$INCLUDE:'common.inc'

      print '(a\)',' Name of file containing run instructions ==> '
      read(*,'(a20)')runfile
      open(unit=7,file=runfile,status='old')

      read(7,'(a80)') titleline
      read(7,'(a20)') input24h
      read(7,'(a20)') paramfile
      read(7,'(a20)') outputfile
      read(7,'(a20)') massfile
      read(7,'(a20)') partfile
      read(7,*)       ndays
      read(7,*)       ndefol
      read(7,*)       daydefol1,defmass1
      read(7,*)       daydefol2,defmass2

      close(7)

*     Read in initial conditions and parameter values: *******

      print *
      print *,'Reading in data, initial conditions and parameter values'

      open(unit=1,file=input24h,status='old')

      do 10, i=1,ndays
         read(1,'(4x,f2.0,7f7.3)')defno(i),subin(i),totcbal(i),
     &      mtotrs(i),measy(i),mshootcer(i),mrootcer(i),msgr(i)
         mrootrs(i)    = -mrootcer(i)
         mshootrs(i)   = mtotrs(i) - mrootrs(i)
10    continue
      close(1)

*     Fill the array of defoliation weights

      do 11 i = 1, ndays
         if (i .eq. daydefol1) then
             defolmass(i) = defmass1
         else
             defolmass(i) = 0.0
         endif
         if (ndefol .eq. 2) then
             if (i. eq. daydefol2) then
                   defolmass(i) = defmass2
             endif
         endif
11    continue
```

```fortran
*     Read in parameter values

      open(unit=3,file=paramfile,status='old')
      read(3,101)sinifs,rinifs,sinifd,rinifd,sinifn,rinifn,siniw,
     &    riniw,sYg,sYgd1,sYgd2,rYg,rYgd1,rYgd2,sYd,rYd,skg,skgd1,
     &    skgd2,rkg,rkgd1,rkgd2,skd,rkd,im,d1m,d2m

      read(3,*)inisp,inirp
      read(3,*)df1sp,df1rp
      read(3,*)df2sp,df2rp
      close(3)

      if(((inisp+inirp)-1.0).ge.0.01)stop 'Sum of part. const <> 1.0'
      if(((df1sp+df1rp)-1.0).ge.0.01)stop 'Sum of part. const <> 1.0'
      if(((df2sp+df2rp)-1.0).ge.0.01)stop 'Sum of part. const <> 1.0'
      if(((sinifs+sinifd+sinifn)-100.0) .ge. 0.01) then
          stop 'Sum of shoot fractions <> 100.0'
      endif
      if(((rinifs+rinifd+rinifn)-100.0) .ge. 0.01) then
          stop 'Sum of root fractions <> 100.0'
      endif

*     Read in the mass and mass fraction values

      print *
      print *,'Reading the weight and weightfraction data....'

      open(unit=8,file=massfile)

      do 80 i = 1,ndays
         read(8,'(5x,6f10.3)')mtotw(i),mshootw(i),mrootw(i),
     &       mshootwf(i),mrootwf(i),mrsratio(i)
80    continue
      close(8)

      open(unit=2,file=partfile)

*     Read input for partitioning submodel

      read(2,'(5(t11,f10.5/),t11,f10.5)')fN,p,mAn,kc,kn,Wn(1)

      close(2)

      print *
      print *,'Input complete ....'
      print *

101   format(26(18x,f8.4/),18x,f8.4)

      return
      end
```

INIT.FOR

```
      subroutine init(ystart)

*     This routine loads initial values into arrays for state
*     variables and parameters

$NOTRUNCATE
      real    ystart(6)

$INCLUDE:'common.inc'


      ystart(1)   = (sinifs * siniw)/100.
      ystart(2)   = (sinifd * siniw)/100.
      ystart(3)   = (sinifn * siniw)/100.
      sstor(1)    = ystart(1)
      sdegrad(1)  = ystart(2)
      snondeg(1)  = ystart(3)
      sfs(1)      = sinifs / 100.0
      sfd(1)      = sinifd / 100.0
      sfn(1)      = sinifn / 100.0
      pshootw(1)  = siniw
      ystart(4)   = (rinifs * riniw)/100.
      ystart(5)   = (rinifd * riniw)/100.
      ystart(6)   = (rinifn * riniw)/100.
      rstor(1)    = ystart(4)
      rdegrad(1)  = ystart(5)
      rnondeg(1)  = ystart(6)
      rfs(1)      = rinifs / 100.0
      rfd(1)      = rinifd / 100.0
      rfn(1)      = rinifn / 100.0
      prootw(1)   = riniw
      ptotw(1)    = siniw + riniw
      prootwf(1)  = prootw(1) / ptotw(1)
      dayno(1)    = 1
      sm(1)       = im / 1000.0
      rm(1)       = im / 1000.0
      Mc          = 28.5
      Mn          = 62.0
      Wc(1)       = (sstor(1) + rstor(1)) * 0.012
      Wsh(1)      = ((sdegrad(1)+snondeg(1))*0.012)/0.39
      Wr(1)       = ((rdegrad(1)+rnondeg(1))*0.012)/0.39
      Wg(1)       = Wsh(1) + Wr(1)
      Ws(1)       = ((Mc/12)*Wc(1)) + ((Mn/14)*Wn(1))
      C(1)        = Wc(1) / Wg(1)
      Nc(1)       = Wn(1) / Wg(1)
      An(1)       = mAn / ( 1 + (kc/C(1)) * (1 + Nc(1)/kn))
      part(1)     = (p * Nc(1) * Wr(1)) / (C(1) * Wsh(1))
      Ls(1)       = part(1) / (1 + part(1))
      Lr(1)       = 1 / (1 + part(1))

      return
      end
```

RECMODEL.FOR

```fortran
      subroutine recmod(x,ystart,dydx)

*     This is the statement of Thornley's recycling model.
*     This routine calculates the derivatives of the state
*     variables with respect to time (x). The Runge-Kutta
*     routines call this routine.

$NOTRUNCATE

      real ystart(6),dydx(6),x

$INCLUDE:'common.inc'

      dydx(1) = (shootpart(d) * subin(d)) - skg * ystart(1)
     &          + skd * ystart(2)
      dydx(2) = sYd*sYg*skg*ystart(1)-skd*ystart(2)
      dydx(3) = (1 - sYd) * sYg * skg * ystart(1)
      dydx(4) = (rootpart(d) * subin(d)) - rkg * ystart(4)
     &          + rkd * ystart(5)
      dydx(5) = rYd*rYg*rkg*ystart(4)-rkd*ystart(5)
      dydx(6) = (1 - rYd) * rYg * rkg * ystart(4)

      return
      end
```

```
ONECOMP.FOR

      subroutine onecom

$NOTRUNCATE

*     This routine calculates the rate of respiratory carbon use based
*     on the substrate-balance model. The rate of
*     respiratory carbon use is calculated for both the roots and the
*     shoots using the partitioning constants.
*     This routine is called ones a day.....

$INCLUDE:'common.inc'

*     Respiratory carbon use of shoots:

      opshootgrs(d) = (1 - sYg) * (shootpart(d) * subin(d))
      opshootmrs(d) = sYg * sm(d) * mshootw(d)
      opshootrs(d)  = opshootgrs(d) + opshootmrs(d)

*     Respiratory carbon use of roots:

      oprootgrs(d)  = (1 - rYg) * (rootpart(d) * subin(d))
      oprootmrs(d)  = rYg * rm(d) * mrootw(d)
      oprootrs(d)   = oprootgrs(d) + oprootmrs(d)

*     Total respiratory carbon use:

      optotrs(d)    = opshootrs(d)  + oprootrs(d)
      optotgrs(d)   = opshootgrs(d) + oprootgrs(d)
      optotmrs(d)   = opshootmrs(d) + oprootmrs(d)
      oetotrs(d)    = optotrs(d)    - mtotrs(d)

      return
      end
```

UPDATE.FOR

```fortran
      subroutine update(ystart)

*     This routine updates the state variables after the call to
*     the integration routine

$NOTRUNCATE
      real    ystart(6)

$INCLUDE:'common.inc'

      sstor(d+1)    = ystart(1)
      dls(d)        = -(sstor(d+1) - sstor(d))
      sdegrad(d+1)  = ystart(2)
      snondeg(d+1)  = ystart(3)
      pshootw(d+1)  = ystart(1) + ystart(2) + ystart(3)
      if (pshootw(d+1) .lt. 0.0) then
          print *,'Shootweight less than zero!!'
          print *,'Shootweight: ',pshootw(d+1)
          stop
      endif
      rstor(d+1)    = ystart(4)
      dlr(d)        = -(rstor(d+1) - rstor(d))
      dlt(d)        = dls(d) + dlr(d)
      rdegrad(d+1)  = ystart(5)
      rnondeg(d+1)  = ystart(6)
      prootw(d+1)   = ystart(4) + ystart(5) + ystart(6)
      ptotw(d+1)    = pshootw(d+1) + prootw(d+1)
      prootwf(d+1)  = prootw(d+1) / ptotw(d+1)
      etotw(d+1)    = ptotw(d+1) - mtotw(d+1)
      sfs(d+1)      = (sstor(d+1)/pshootw(d+1))
      sfd(d+1)      = (sdegrad(d+1)/pshootw(d+1))
      sfn(d+1)      = (snondeg(d+1)/pshootw(d+1))
      rfs(d+1)      = (rstor(d+1)/prootw(d+1))
      rfd(d+1)      = (rdegrad(d+1)/prootw(d+1))
      rfn(d+1)      = (rnondeg(d+1)/prootw(d+1))
      dayno(d+1)    = d+1
      structsg(d)   = ((sdegrad(d+1) - sdegrad(d)) +
     &                (snondeg(d+1) - snondeg(d)))
      structrg(d)   = ((rdegrad(d+1) - rdegrad(d)) +
     &                (rnondeg(d+1) - rnondeg(d)))
      structg(d)    = structrg(d) + structsg(d)

*     Calculate the rate of respiration

      pshootrs(d)   = (1-sYg) * skg * sstor(d+1)
      prootrs(d)    = (1-rYg) * rkg * rstor(d+1)
      ptotrs(d)     = pshootrs(d) + prootrs(d)
      etotrs(d)     = ptotrs(d)   - mtotrs(d)
      eshootrs(d)   = pshootrs(d) - mshootrs(d)
      erootrs(d)    = prootrs(d)  - mrootrs(d)
      ssqerr        = ssqerr      + (etotrs(d)**2)

*     Calculate growth and maintenance respiration

      if (structsg(d) .gt. 0.0) then
          pshootgrs(d)  = (1-sYg)/sYg*structsg(d)
      else
          pshootgrs(d)  = 0.0
      endif
      prootgrs(d)   = (1-rYg)/rYg*structrg(d)
      ptotgrs(d)    = pshootgrs(d) + prootgrs(d)

      pshootmrs(d)=(1-sYg)/sYg*skd*sdegrad(d+1)
      prootmrs(d) =(1-rYg)/rYg*rkd*rdegrad(d+1)
      ptotmrs(d)  = pshootmrs(d) + prootmrs(d)

      comptotal     = ptotmrs(d) + ptotgrs(d)

*     'Defoliate' the plant by reducing all the compartments by
*     the defoliation proportion (defolprop)

      if (defolmass(d+1) .gt. 0.0) then
          if (defolmass(d+1) .ge. pshootw(d+1)) then
              print *,'Defoliation mass exceeds shoot mass!!'
              print *,'Defoliation mass:',defolmass(d+1)
              print *,'Shoot mass:       ',pshootw(d+1)
              stop
          endif
          defolprop = defolmass(d+1) / pshootw(d+1)
          print '(f5.2,a,i2)',defolprop,' % defoliation on day: ',d+1
          print *
          do 21 var = 1, 3
              ystart(var) = ystart(var) - ystart(var) * defolprop
21        continue
          sstor(d+1)    = ystart(1)
          sdegrad(d+1)  = ystart(2)
          snondeg(d+1)  = ystart(3)
          pshootw(d+1)  = ystart(1) + ystart(2) + ystart(3)
          ptotw(d+1)    = pshootw(d+1) + prootw(d+1)
          prootwf(d+1)  = prootw(d+1) / ptotw(d+1)
          etotw(d+1)    = ptotw(d+1)   - mtotw(d+1)
      endif

      Wc(d+1)       = (sstor(d+1) + rstor(d+1)) * 0.012
      Wsh(d+1)      = ((sdegrad(d+1)+snondeg(d+1))*0.012)/0.39
      Wr(d+1)       = ((rdegrad(d+1)+rnondeg(d+1))*0.012)/0.39
      Wg(d+1)       = Wsh(d+1) + Wr(d+1)
      dWg(d+1)      = Wg(d+1) - Wg(d)

*     Calculate the size of the nitrogen substrate pool

      Nupt(d+1)     = An(d) * Wr(d+1)
      if (dWg(d+1) .gt. 0.0) then
          Nutil(d+1) = fN * dWg(d+1)
      else
          Nutil(d+1) = 0.0
      endif
      Wn(d+1)     = Wn(d) + Nupt(d+1) - Nutil(d+1)
      if (Wn(d+1) .le. 0.0) then
          print *,'The nitrogen pool is empty!!'
          stop '...can not continue like this'
      endif

      if (defolmass(d+1) .gt. 0.0) then
          Wn(d+1) = Wn(d+1) - (Wn(d+1)*(1-prootwf(d+1))*defolprop)
      endif
```

UPDATE.FOR (continued)

```
Ws(d+1)      = ((Mc/12)*Wc(d+1)) + ((Mn/14)*Wn(d+1))
C(d+1)       = Wc(d+1) / Wg(d+1)
Nc(d+1)      = Wn(d+1) / Wg(d+1)
An(d+1)      = mAn / ( 1 + (kc/C(d+1)) * (1 + Nc(d+1)/kn))
part(d+1)    = (p * Nc(d+1) * Wr(d+1)) / (C(d+1) * Wsh(d+1))
Ls(d+1)      = part(d+1) / (1 + part(d+1))
Lr(d+1)      = 1 / (1 + part(d+1))

return
end
```

```
REPORT.FOR

      Subroutine report

$NOTRUNCATE

$INCLUDE:'common.inc'

      integer*2 year,month,dd,hh,mm,ss,hd
      integer page
      character response*1
      real CN,sin,rin

      call getdat(year,month,dd)
      call gettim(hh,mm,ss,hd)

      open(unit=7,file=outputfile)

*     Print the title and general run information

      page = 1

      write(7,100)page
100   format(' ','Report on carbon balance simulation with root/',
     &'shoot partitioning',t70,'page ',i2/,' ','Timestep of 24 hours')
      write(7,101)titleline
101   format(' ','Data from: ',a80/)
      write(7,102)dd,month,year,hh,mm
102   format(' ','Simulated on ',i2,'-',i2,'-',i4,' at ',i2,':',i2/)
      write(7,103)runfile,paramfile,inputfile
103   format(' ','Run instructions read from:',t30,a20/,
     &         ' ','Parameter values read from:',t30,a20/,
     &         ' ','Input data read from:',t30,a20/)
      write(7,104)
104   format(' ','Following input parameters were used:'/)

      write(7,105)sinifs,sinifd,sinifn,siniw,sYg,sYgd1,sYgd2,sYd,skg,
     &       skgd1,skgd2,skd,rinifs,rinifd,rinifn,riniw,rYg,rYgd1,rYgd2,
     &       rYd,rkg,rkgd1,rkgd2,rkd
105   format(t5,'Shoot parameters:'/,t10,
     &'inifs = ',f10.4/,t10,'inifd = ',f10.4/,t10,'inifn = ',f10.4/,
     &t10,'iniw  = ',f10.4/,t10,
     &'Yg   = ',f10.4/,t10,'Ygd1  = ',f10.4/t10,'Ygd2  = ',f10.4/t10,
     &'Yd   = ',f10.4/,t10,'kg    = ',f10.4/,
     &t10,'kgd1  = ',f10.4/,t10,'kgd2  = ',f10.4/,
     &t10,'kd    = ',f10.4///
     &t5,'Root parameters:'/,t10,
     &'inifs = ',f10.4/,t10,'inifd = ',f10.4/,t10,'inifn = ',f10.4/,
     &t10,'iniw  = ',f10.4/,t10,
     &'Yg   = ',f10.4/,t10,'Ygd1  = ',f10.4/t10,'Ygd2  = ',f10.4/t10,
     &'Yd   = ',f10.4/,t10,'kg    = ',f10.4/,
     &t10,'kgd1  = ',f10.4/,t10,'kgd2  = ',f10.4/,
     &t10,'kd    = ',f10.4///)

      write(7,106)
106   format('Partition model partameters:'/)
      write(7,107)fN,p,mAn,kc,kn,Wn(1)
107   format(t10,
     &'fN   = ',f10.4/,t10,'p    = ',f10.4/,t10,'mAn  = ',f10.4/,
     &t10,'kc   = ',f10.4/,t10,
```

```
     &'kn   = ',f10.4/,t10,'Wn(1) = ',f10.4///)

      page = 2
      write(7,'(a)')char(12)

      write(7,201)dd,month,year,hh,mm,page
201   format(' ',i2,'-',i2,'-',i4,2x,i2,':',i2,t70,'page ',i2/)
      write(7,202)
202   format(' ','Substrate input and assimilate partitioning'/)
      write(7,203)
203   format(' ','  Day:    Subin:      Wr:      Wsh:      part:'
     &      '   Shootpart:  Rootpart: '/)

      do 10 d = 1,ndays
        write(7,'(i5,f10.2,5f10.3)')d,subin(d),Wr(d),Wsh(d),
     &          part(d),shootpart(d),rootpart(d)
10    continue

204   format(i6,10x,f6.2,12x,f5.3,16x,f5.3)

      page = 3
      write(7,'(a)')char(12)

      write(7,201)dd,month,year,hh,mm,page
      write(7,301)
301   format(' ','Total dry weight and root fraction'/)
      write(7,302)
302   format(' ','  Day:    ptotw:    mtotw:    etotw:    pshootw:',
     &'  prootw:   prootwf:'/)

      do 30, d = 1,ndays
        write(7,303)d,ptotw(d),mtotw(d),etotw(d),pshootw(d),
     &   prootw(d),prootwf(d)
30    continue

303   format(i6,6f10.3)

      page = 4
      write(7,'(a)')char(12)

      write(7,201)dd,month,year,hh,mm,page
      write(7,401)
401   format(' ','Dynamics of state variables (expressed as weight',
     &' fractions)'/)
      write(7,402)
402   format(' ',t20,'Shoots',t50,'Roots')
      write(7,403)
403   format('  Day:     fs:      fd:      fn:      fs:',
     &'      fd:      fn:'/)

      do 40 d = 1,ndays
        write(7,404)d,sfs(d),sfd(d),sfn(d),rfs(d),rfd(d),rfn(d)
40    continue

404   format(i6,6f10.3)

      page = 5
      write(7,'(a)')char(12)
```

```fortran
      write(7,201)dd,month,year,hh,mm,page
      write(7,501)
501   format(' ','Rate of respiratory carbon use'/)
      write(7,502)
502   format(' ',t27,'Total',t45,'Shoots',t65,'Roots')
      write(7,503)
503   format(' ',' Day:   pred:   obs:  error:    pred:    obs:',
     &' error:   pred:    obs:  error:'/)

      do 50 d = 1,ndays
         write(7,504)d,ptotrs(d),mtotrs(d),etotrs(d),
     &      pshootrs(d),mshootrs(d),eshootrs(d),prootrs(d),
     &      mrootrs(d),erootrs(d)
50    continue

504   format(i6,9f8.2)

      page = 6
      write(7,'(a)')char(12)

      write(7,201)dd,month,year,hh,mm,page

      write(7,601)
601   format(' ','Components of the rate of respiratory carbon use'/)
      write(7,602)
602   format(' ',t20,'Steady-state model:',t55,'Recycling model:'/)
      write(7,603)
603   format(' ',10x,2('Growth resp:      Maint. resp:      ')/)

      do 60 d = 1,ndays
         write(7,604)d,optotgrs(d),optotmrs(d),ptotgrs(d),ptotmrs(d)
60    continue

604   format(i6,f10.2,3(10x,f10.2))

      page = 7
      write(7,'(a)')char(12)

      write(7,201)dd,month,year,hh,mm,page

      write(7,901)
901   format(' ','The Root/Shoot partitioning parameters'/)
      write(7,902)
902   format(' ','          C:      Nr:      C/N:       An:',
     &'     Wn:       Nupt:    Nutil:')

      do 35 d = 1,ndays
         CN = C(d) / Nc(d)
         write(7,'(i5,7f10.3)')d,C(d),Nc(d),CN,An(d),Wn(d),Nupt(d),
     &         Nutil(d)
35    continue

*     Calculate statistics

      page = 8
      write(7,'(a)')char(12)
```

```fortran
      write(7,201)dd,month,year,hh,mm,page

      print *,'Statistics section.............'
      print *
      print *,'WHOLE PLANT RCU: Predicted vs. observed '
      write(7,*)'WHOLE PLANT RCU: Predicted vs. observed '
      write(7,*)

      call stats(mtotrs,ptotrs,ndays)
      print *
      print *,'Enter RETURN to continue...'
      read(*,*)

      print *
      print *,'SHOOT RCU: Predicted vs. observed '
      write(7,*)
      write(7,*)'SHOOT RCU: Predicted vs. observed '
      write(7,*)

      call stats(mshootrs,pshootrs,ndays)
      print *
      print *,'Enter RETURN to continue...'
      read(*,*)

      print *

      print *,'ROOT RCU: Predicted vs. observed '
      write(7,*)
      write(7,*)'ROOT RCU: Predicted vs. observed '
      write(7,*)

      call stats(mrootrs,prootrs,ndays)

      close(7)

*     Write the plot data file

      open(unit=1,file='daymod.gph')

      do 11 d = 1,ndays
         write(1,6)dayno(d),mtotrs(d),ptotrs(d),mshootrs(d),
     &           pshootrs(d),mrootrs(d),prootrs(d),optotrs(d),
     &           opshootrs(d),oprootrs(d),sfs(d),sfd(d),sfn(d),
     &           rfs(d),rfd(d),rfn(d)
11    continue

      close(1)

*     Write Root/Shoot partitioning data to a plot file

      open(unit=1,file='partplot.gph')

      do 12 d = 1, ndays
         write(1,'(i5,8f10.5)')d,Ls(d),Lr(d),C(d),Nc(d),An(d),
     &         Wn(d),Ws(d),Wg(d)
12    continue
      close(1)
```

REPORT.FOR (continued)

```
*       Write changes in labile carbon pools to a file

        open(unit=1,file='mobil.dat')

        do 13 d = 1, ndays
            sin = subin(d) * shootpart(d)
            rin = subin(d) * rootpart(d)
            write(1,'(i5,7f10.5)')d,sstor(d),rstor(d),sin,rin,
     &      dlt(d),dls(d),dlr(d)
13      continue
        close(1)

801     format(a)
6       format(f3.0,9f9.3,6f8.4)

        return
        end
```

STATS.FOR

```fortran
       subroutine stats(x,y,ndata)

*      Function:
*         Calculate statistics to compare observed and prediced

       parameter (npt=200,npol=2)
       dimension x(npt),y(npt),sig(npt),a(npol),cvm(npol,npol)
       dimension u(npt,npol),v(npol,npol),w(npol)
       real     meanx,meany,sumx,sumy,yhat(200),residual(200)
       real     sse,mse,sumobs,meanobs,ssto,ssr,msr,r2,dmean

       mp      = npt
       np      = npol
       sumx    = 0.0
       sumy    = 0.0

       do 10, i=1,ndata
          sig(i) = 1.0
          sumx    = sumx + x(i)
          sumy    = sumy + y(i)
10     continue

       meanx   = sumx / ndata
       meany   = sumy / ndata

*      Call singular value decomposition linear regression routines
*      from Numerical Recipes. These subroutines are not printed
*      in this appendix due to copyright restrictions.
*      (Copyright (C) 1985 by Numerical Recipes Software,
*      P.O. Box 243, Cambridge, MA 02238)

       call svdfit(x,y,sig,ndata,a,npol,u,v,w,mp,np,chisq)
       call svdvar(v,npol,np,w,cvm,npol)

       sse     = 0.0
       ssto    = 0.0
       ssr     = 0.0

*      Calculate the total sum of squares of the predicted values

       do 20 i = 1,ndata
          ssto    = ssto + (y(i) - meany)**2
20     continue

*      Calculate the residual sum of squares (the error sum of squares).
*      This is the sum of the squared residuals. Yhat is the predicted
*      value.

       do 30 i = 1,ndata
          yhat(i)     = a(1) + (a(2)*x(i))
          residual(i) = (y(i) - yhat(i))
          sse         = sse + residual(i)**2
30     continue

*      The residual sum of squares has n-2 degrees of freedom associated
*      with is. The error mean square or the residual mean square is
*      calculated by dividing sse with the degrees of freedom.

       mse = sse / (ndata - 2)

*      Calculate the regression sum of squares. This sum of squares has
*      only 1 df associated with it ==> msr = ssr.

       do 40 i = 1,ndata
          ssr = ssr + (yhat(i) - meany)**2
40     continue
       msr = ssr
*      Calculate the coefficient of determination (r2)

       r2  = ssr / ssto

       print *
         print *,'===> Fitting first order line to the data'
       print *
       print '(t15,a,i4)',' Number of data points: ',ndata
       write(*,'(t15,a,f10.2,a,f10.2)')' Intercept: ',a(1),' +-',
     &    sqrt(cvm(1,1))
       write(*,'(t15,a,f10.2,a,f10.2)')' Slope:     ',a(2),' +-',
     &    sqrt(cvm(2,2))
         write(*,'(t15,a,f10.2)')' Chi-squared',chisq
       print '(t15,a,f10.2)',' r2           ',r2
       print '(t15,a,f10.2)',' mse          ',mse

       write(7,'(t15,a,i4)')' Number of data points: ',ndata
       write(7,'(t15,a,f10.2,a,f10.2)')' Intercept: ',a(1),' +-',
     &    sqrt(cvm(1,1))
       write(7,'(t15,a,f10.2,a,f10.2)')' Slope:     ',a(2),' +-',
     &    sqrt(cvm(2,2))
         write(7,'(t15,a,f10.2)')' Chi-squared',chisq
       write(7,'(t15,a,f10.2)')' r2           ',r2
       write(7,'(t15,a,f10.2)')' mse          ',mse

       print *

*      Call t-test routines from Numerical Recipes. These routines are
*      not printed in this appendix due to copyright restrictions.
*      (Copyright (C) 1985 by Numerical Recipes Software,
*      P.O. Box 243, Cambridge, MA 02238)

       call tptest(x,y,ndata,t,prob)
       print *,'===> MEAN predicted vs. MEAN observed'
       print *
       print '(t15,a,f10.3)',' Mean observed   ',meanx
       print '(t15,a,f10.3)',' Mean predicted  ',meany
       dmean = meany - meanx
       print '(t15,a,f10.3)',' Difference      ',dmean
       print '(t15,a,f10.3)',' t               ',t
       print '(t15,a,f10.3)',' Probability:    ',prob

       write(7,'(t15,a,f10.3)')' Mean observed   ',meanx
       write(7,'(t15,a,f10.3)')' Mean predicted  ',meany
       write(7,'(t15,a,f10.3)')' Difference      ',dmean
       write(7,'(t15,a,f10.3)')' t               ',t
       write(7,'(t15,a,f10.3)')' Probability:    ',prob
       return
```

```
DES202.RUN

Agropyron desertorum 202
des202.mod
des202.mpa
des202.out
des202.wfs
part202.inp
36
2
13    93.925
26   102.700
```

DES202.MOD

```
 1  1  0 12.800   7.444   5.356 58.170 10.126 -2.678    .080
 2  1  0 14.085   8.670   5.415 61.550 11.559 -2.889    .086
 3  1  0 15.989  10.707   5.281 66.960 13.667 -2.959    .098
 4  0  0  6.589   4.215   2.374 63.980  6.148 -1.933    .035
 5  0  0  8.011   4.881   3.130 60.920  6.430 -1.548    .039
 6  0  0  7.885   5.074   2.811 64.350  6.574 -1.500    .039
 7  1  0  9.222   6.056   3.170 65.640  7.600 -1.544    .045
 8  0  0 25.326  18.874   6.452 74.530 21.737 -2.863    .135
 9  0  0 26.341  18.485   7.856 70.180 22.278 -3.793    .116
10  1  0 28.589  19.711   8.878 68.940 24.178 -4.470    .111
11  1  0 31.185  20.911  10.274 67.050 26.096 -5.185    .106
12  1  0 33.378  21.844  11.530 65.450 27.641 -5.796    .100
13  0  1  1.337  -1.889   3.230   .000   .452 -2.341   -.013
14  0  1  5.159   2.119   3.041 41.060  3.341 -1.226    .015
15  0  1  8.830   5.237   3.593 59.300  6.493 -1.256    .036
16  1  1 12.456   8.581   3.874 68.900 10.174 -1.593    .057
17  1  1 15.837  10.926   4.911 68.990 12.841 -1.915    .068
18  1  1 18.226  12.852   5.374 70.520 15.115 -2.259    .075
19  1  1 22.096  16.570   5.522 75.000 19.204 -2.630    .090
20  1  1 27.322  19.422   7.900 71.090 22.630 -3.207    .097
21  1  1 31.141  21.552   9.589 69.200 25.278 -3.726    .098
22  1  1 34.070  23.281  10.789 68.330 27.437 -4.159    .096
23  1  1 37.170  25.222  11.944 67.860 29.526 -4.304    .095
24  1  1 40.259  26.085  14.174 64.790 30.678 -4.593    .090
25  1  1 43.733  28.619  15.115 65.440 33.415 -4.796    .091
26  0  2  5.611   1.230   4.381 21.920  3.181 -1.952    .005
27  0  2  8.848   4.730   4.119 53.450  5.970 -1.244    .019
28  0  2 10.826   6.500   4.326 60.030  7.748 -1.248    .026
29  0  2 13.089   8.419   4.674 64.300  9.763 -1.344    .033
30  1  2 15.222  10.500   4.719 68.990 11.900 -1.400    .040
31  1  2 16.715  11.448   5.263 68.500 12.952 -1.500    .042
32  1  2 18.700  13.026   5.674 69.660 14.633 -1.607    .046
33  1  2 20.378  14.185   6.193 69.620 15.904 -1.719    .048
34  1  2 21.993  15.522   6.474 70.570 17.341 -1.819    .050
35  1  2 23.259  16.319   6.941 70.160 18.170 -1.852    .050
36  1  2 23.919  16.785   7.137 70.170 18.622 -1.837    .049
```

DES202.WFS

| | | | | | | |
|---|---|---|---|---|---|---|
| 1 | 92.937 | 36.814 | 56.123 | .396 | .604 | 1.524 |
| 2 | 100.381 | 39.763 | 60.618 | .396 | .604 | 1.524 |
| 3 | 109.051 | 43.197 | 65.854 | .396 | .604 | 1.524 |
| 4 | 119.758 | 47.438 | 72.320 | .396 | .604 | 1.524 |
| 5 | 123.973 | 49.108 | 74.865 | .396 | .604 | 1.524 |
| 6 | 128.854 | 51.041 | 77.813 | .396 | .604 | 1.524 |
| 7 | 133.928 | 53.051 | 80.877 | .396 | .604 | 1.524 |
| 8 | 139.984 | 55.450 | 84.534 | .396 | .604 | 1.524 |
| 9 | 158.858 | 62.927 | 95.931 | .396 | .604 | 1.524 |
| 10 | 177.343 | 70.249 | 107.094 | .396 | .604 | 1.524 |
| 11 | 197.054 | 78.057 | 118.997 | .396 | .604 | 1.524 |
| 12 | 217.965 | 86.340 | 131.625 | .396 | .604 | 1.524 |
| 13 | 145.884 | 14.259 | 131.625 | .098 | .902 | 9.231 |
| 14 | 143.995 | 12.370 | 131.625 | .086 | .914 | 10.641 |
| 15 | 146.114 | 14.489 | 131.625 | .099 | .901 | 9.084 |
| 16 | 151.351 | 19.726 | 131.625 | .130 | .870 | 6.673 |
| 17 | 159.932 | 28.307 | 131.625 | .177 | .823 | 4.650 |
| 18 | 170.858 | 39.233 | 131.625 | .230 | .770 | 3.355 |
| 19 | 183.710 | 52.085 | 131.625 | .284 | .716 | 2.527 |
| 20 | 200.280 | 68.655 | 131.625 | .343 | .657 | 1.917 |
| 21 | 219.702 | 88.077 | 131.625 | .401 | .599 | 1.494 |
| 22 | 241.254 | 109.629 | 131.625 | .454 | .546 | 1.201 |
| 23 | 264.535 | 132.910 | 131.625 | .502 | .498 | .990 |
| 24 | 289.757 | 158.132 | 131.625 | .546 | .454 | .832 |
| 25 | 315.842 | 184.217 | 131.625 | .583 | .417 | .715 |
| 26 | 241.761 | 110.136 | 131.625 | .456 | .544 | 1.195 |
| 27 | 242.991 | 111.366 | 131.625 | .458 | .542 | 1.182 |
| 28 | 247.721 | 116.096 | 131.625 | .469 | .531 | 1.134 |
| 29 | 254.221 | 122.596 | 131.625 | .482 | .518 | 1.074 |
| 30 | 262.640 | 131.015 | 131.625 | .499 | .501 | 1.005 |
| 31 | 273.140 | 141.515 | 131.625 | .518 | .482 | .930 |
| 32 | 284.588 | 152.963 | 131.625 | .537 | .463 | .861 |
| 33 | 297.614 | 165.989 | 131.625 | .558 | .442 | .793 |
| 34 | 311.799 | 180.174 | 131.625 | .578 | .422 | .731 |
| 35 | 327.321 | 195.696 | 131.625 | .598 | .402 | .673 |
| 36 | 343.640 | 212.015 | 131.625 | .617 | .383 | .621 |

DES202.MPA

| | |
|---|---|
| Initial fs shoots | 7.3 |
| Initial fs roots | 5.0 |
| Initial fd shoots | 20.0 |
| Initial fd roots | 20.0 |
| Initial fn shoots | 72.7 |
| Initial fn roots | 75.0 |
| Initial shoot wgt | 36.814 |
| Initial root wgt | 56.123 |
| Yg shoots | 0.6845 |
| Yg shoots defol 1 | 0.72 |
| Yg shoots defol 2 | 0.72 |
| Yg roots | 0.6845 |
| Yg roots defol 1 | 0.72 |
| Yg roots defol 2 | 0.72 |
| Yd shoots | 0.39 |
| Yd roots | 0.39 |
| kg shoots | 2.4 |
| kg shoots defol 1 | 2.5 |
| kg shoots defol 2 | 2.5 |
| kg roots | 2.4 |
| kg roots defol 1 | 2.4 |
| kg roots defol 2 | 2.4 |
| kd shoots | 0.083 |
| kd roots | 0.083 |
| Initial maintc. | 8.3224 |
| Maintc. defol1 | 8.3224 |
| Maintc. defol2 | 8.3224 |

| | |
|---|---|
| 0.55 | 0.45 |
| 0.55 | 0.45 |
| 0.55 | 0.45 |

```
PART202.INP

fN      =   0.05
p       =   0.6753
mAn     =   0.2
kc      =   0.004
kn      =   0.0003
Wn(1)   =   0.0798
```

DES202.OUT

Report on carbon balance simulation with root/shoot partitioning     page  1
Timestep of 24 hours
Data from: Agropyron desertorum 202

Simulated on  8- 3-1988 at 22:44

Run instructions read from: des202.run
Parameter values read from: des202.mpa
Input data read from:       des202.mod

Following input parameters were used:

Shoot parameters:
    inifs =    7.3000
    inifd =   20.0000
    inifn =   72.7000
    iniw  =   36.8140
    Yg    =     .7200
    Ygd1  =     .7200
    Ygd2  =     .7200
    Yd    =     .3900
    kg    =    2.5000
    kgd1  =    2.5000
    kgd2  =    2.5000
    kd    =     .0830

Root parameters:
    inifs =    5.0000
    inifd =   20.0000
    inifn =   75.0000
    iniw  =   56.1230
    Yg    =     .7200
    Ygd1  =     .7200
    Ygd2  =     .7200
    Yd    =     .3900
    kg    =    2.4000
    kgd1  =    2.4000
    kgd2  =    2.4000
    kd    =     .0830

Partition model partameters:
    fN    =     .0500
    p     =     .6753
    mAn   =     .2000
    kc    =     .0040
    kn    =     .0003
    Wn(1) =     .0798

Substrate input and assimilate partitioning

| Day: | Subin: | Wr: | Wsh: | part: | Shootpart: | Rootpart: |
|---|---|---|---|---|---|---|
| 1 | 12.80 | 1.641 | 1.050 | 1.277 | .561 | .439 |
| 2 | 14.09 | 1.751 | 1.183 | 1.224 | .550 | .450 |
| 3 | 15.99 | 1.868 | 1.333 | 1.150 | .535 | .465 |
| 4 | 6.59 | 2.003 | 1.496 | 1.055 | .513 | .487 |
| 5 | 8.01 | 2.092 | 1.597 | 2.203 | .688 | .312 |
| 6 | 7.89 | 2.141 | 1.689 | 2.099 | .677 | .323 |
| 7 | 9.22 | 2.184 | 1.791 | 2.117 | .679 | .321 |
| 8 | 25.33 | 2.232 | 1.904 | 1.874 | .652 | .348 |
| 9 | 26.34 | 2.359 | 2.155 | .732 | .423 | .577 |
| 10 | 28.59 | 2.609 | 2.409 | .716 | .417 | .583 |
| 11 | 31.18 | 2.926 | 2.639 | .737 | .424 | .576 |
| 12 | 33.38 | 3.272 | 2.888 | .759 | .432 | .568 |
| 13 | 1.34 | 3.639 | .449 | 9.462 | .904 | .096 |
| 14 | 5.16 | 3.779 | .481 | 42.338 | .977 | .023 |
| 15 | 8.83 | 3.777 | .558 | 28.263 | .966 | .034 |
| 16 | 12.46 | 3.767 | .712 | 15.295 | .939 | .061 |
| 17 | 15.84 | 3.764 | .936 | 8.804 | .898 | .102 |
| 18 | 18.23 | 3.776 | 1.218 | 5.521 | .847 | .153 |
| 19 | 22.10 | 3.813 | 1.537 | 3.905 | .796 | .204 |
| 20 | 27.32 | 3.882 | 1.893 | 2.737 | .732 | .268 |
| 21 | 31.14 | 4.004 | 2.297 | 1.929 | .659 | .341 |
| 22 | 34.07 | 4.192 | 2.725 | 1.521 | .603 | .397 |
| 23 | 37.17 | 4.446 | 3.156 | 1.308 | .567 | .433 |
| 24 | 40.26 | 4.758 | 3.592 | 1.172 | .540 | .460 |
| 25 | 43.73 | 5.123 | 4.038 | 1.087 | .521 | .479 |
| 26 | 5.61 | 5.539 | 1.552 | 4.410 | .815 | .185 |
| 27 | 8.85 | 5.701 | 1.669 | 12.942 | .928 | .072 |
| 28 | 10.83 | 5.710 | 1.811 | 11.274 | .919 | .081 |
| 29 | 13.09 | 5.707 | 2.002 | 9.095 | .901 | .099 |
| 30 | 15.22 | 5.711 | 2.232 | 7.216 | .878 | .122 |
| 31 | 16.72 | 5.727 | 2.497 | 5.826 | .853 | .147 |
| 32 | 18.70 | 5.757 | 2.786 | 4.920 | .831 | .169 |
| 33 | 20.38 | 5.802 | 3.099 | 4.122 | .805 | .195 |
| 34 | 21.99 | 5.864 | 3.432 | 3.538 | .780 | .220 |
| 35 | 23.26 | 5.945 | 3.781 | 3.087 | .755 | .245 |
| 36 | 23.92 | 6.045 | 4.139 | 2.763 | .734 | .266 |

8- 3-1988  22:44                                             page  3

Total dry weight and root fraction

| Day: | ptotw: | mtotw: | etotw: | pshootw: | prootw: | prootwf: |
|---|---|---|---|---|---|---|
| 1 | 92.937 | 92.937 | .000 | 36.814 | 56.123 | .604 |
| 2 | 101.330 | 100.381 | .949 | 41.684 | 59.646 | .589 |
| 3 | 110.582 | 109.051 | 1.531 | 46.838 | 63.745 | .576 |
| 4 | 121.154 | 119.758 | 1.396 | 52.523 | 68.630 | .566 |
| 5 | 123.889 | 123.973 | -.084 | 53.924 | 69.964 | .565 |
| 6 | 128.742 | 128.854 | -.112 | 57.570 | 71.172 | .553 |
| 7 | 133.417 | 133.928 | -.511 | 60.884 | 72.533 | .544 |
| 8 | 139.161 | 139.984 | -.823 | 64.924 | 74.237 | .533 |
| 9 | 157.676 | 158.858 | -1.182 | 77.076 | 80.600 | .511 |
| 10 | 175.153 | 177.343 | -2.190 | 83.720 | 91.433 | .522 |
| 11 | 194.045 | 197.054 | -3.009 | 91.425 | 102.621 | .529 |
| 12 | 214.624 | 217.965 | -3.341 | 100.085 | 114.539 | .534 |
| 13 | 142.592 | 145.884 | -3.292 | 15.564 | 127.028 | .891 |
| 14 | 140.768 | 143.995 | -3.227 | 16.257 | 124.511 | .885 |
| 15 | 143.969 | 146.114 | -2.145 | 20.181 | 123.788 | .860 |
| 16 | 150.009 | 151.351 | -1.342 | 26.601 | 123.408 | .823 |
| 17 | 158.664 | 159.932 | -1.268 | 35.224 | 123.440 | .778 |
| 18 | 169.701 | 170.858 | -1.157 | 45.542 | 124.159 | .732 |
| 19 | 182.306 | 183.710 | -1.404 | 56.519 | 125.787 | .690 |
| 20 | 197.779 | 200.280 | -2.501 | 69.058 | 128.721 | .651 |
| 21 | 217.087 | 219.702 | -2.615 | 83.288 | 133.800 | .616 |
| 22 | 238.909 | 241.254 | -2.345 | 97.585 | 141.324 | .592 |
| 23 | 262.611 | 264.535 | -1.924 | 111.758 | 150.853 | .574 |
| 24 | 288.413 | 289.757 | -1.344 | 126.248 | 162.165 | .562 |
| 25 | 316.286 | 315.842 | .444 | 141.141 | 175.145 | .554 |
| 26 | 243.837 | 241.761 | 2.076 | 54.046 | 189.791 | .778 |
| 27 | 244.318 | 242.991 | 1.327 | 56.664 | 187.654 | .768 |
| 28 | 249.644 | 247.721 | 1.923 | 62.565 | 187.078 | .749 |
| 29 | 256.498 | 254.221 | 2.277 | 69.546 | 186.951 | .729 |
| 30 | 265.022 | 262.640 | 2.382 | 77.822 | 187.200 | .706 |
| 31 | 275.061 | 273.140 | 1.921 | 87.159 | 187.902 | .683 |
| 32 | 286.084 | 284.588 | 1.496 | 97.016 | 189.068 | .661 |
| 33 | 298.548 | 297.614 | .934 | 107.766 | 190.781 | .639 |
| 34 | 312.149 | 311.799 | .350 | 119.032 | 193.117 | .619 |
| 35 | 326.853 | 327.321 | -.468 | 130.757 | 196.096 | .600 |
| 36 | 342.372 | 343.640 | -1.268 | 142.685 | 199.687 | .583 |

8- 3-1988  22:44                                             page  4

Dynamics of state variables (expressed as weight fractions)

| Day: | Shoots fs: | fd: | fn: | Roots fs: | fd: | fn: |
|---|---|---|---|---|---|---|
| 1 | .073 | .200 | .727 | .050 | .200 | .750 |
| 2 | .077 | .207 | .715 | .046 | .202 | .752 |
| 3 | .075 | .215 | .710 | .048 | .202 | .750 |
| 4 | .074 | .221 | .705 | .051 | .203 | .746 |
| 5 | .037 | .227 | .735 | .028 | .205 | .767 |
| 6 | .046 | .222 | .731 | .022 | .200 | .778 |
| 7 | .044 | .220 | .736 | .021 | .194 | .785 |
| 8 | .047 | .218 | .735 | .023 | .188 | .789 |
| 9 | .091 | .215 | .694 | .049 | .184 | .767 |
| 10 | .065 | .226 | .710 | .073 | .188 | .739 |
| 11 | .062 | .228 | .711 | .073 | .198 | .729 |
| 12 | .062 | .228 | .710 | .072 | .206 | .723 |
| 13 | .062 | .229 | .709 | .069 | .212 | .719 |
| 14 | .039 | .232 | .728 | .014 | .219 | .767 |
| 15 | .101 | .226 | .674 | .008 | .210 | .782 |
| 16 | .130 | .234 | .635 | .008 | .199 | .793 |
| 17 | .137 | .247 | .616 | .009 | .189 | .802 |
| 18 | .131 | .258 | .611 | .011 | .180 | .809 |
| 19 | .116 | .267 | .616 | .015 | .172 | .813 |
| 20 | .109 | .272 | .619 | .020 | .166 | .814 |
| 21 | .104 | .274 | .622 | .028 | .163 | .809 |
| 22 | .092 | .277 | .631 | .036 | .164 | .800 |
| 23 | .082 | .277 | .640 | .042 | .167 | .791 |
| 24 | .075 | .276 | .649 | .046 | .171 | .782 |
| 25 | .070 | .274 | .656 | .049 | .176 | .774 |
| 26 | .067 | .271 | .662 | .051 | .182 | .767 |
| 27 | .043 | .271 | .686 | .013 | .185 | .802 |
| 28 | .059 | .262 | .679 | .008 | .177 | .815 |
| 29 | .064 | .258 | .678 | .008 | .169 | .824 |
| 30 | .068 | .255 | .677 | .008 | .160 | .831 |
| 31 | .069 | .254 | .677 | .009 | .153 | .838 |
| 32 | .067 | .254 | .679 | .010 | .146 | .843 |
| 33 | .065 | .253 | .681 | .012 | .141 | .848 |
| 34 | .063 | .253 | .684 | .013 | .136 | .851 |
| 35 | .060 | .252 | .688 | .015 | .133 | .853 |
| 36 | .057 | .250 | .693 | .016 | .130 | .854 |

Rate of respiratory carbon use                                          Components of the rate of respiratory carbon use

|  |  | Total |  |  | Shoots |  |  | Roots |  |
|---|---|---|---|---|---|---|---|---|---|
| Day: | pred: | obs: | error: | pred: | obs: | error: | pred: | obs: | error: |
| 1 | 4.53 | 5.36 | -.82 | 2.44 | 2.68 | -.23 | 2.09 | 2.68 | -.59 |
| 2 | 4.99 | 5.41 | -.43 | 2.68 | 2.53 | .15 | 2.31 | 2.89 | -.58 |
| 3 | 5.64 | 5.28 | .35 | 2.97 | 2.32 | .64 | 2.67 | 2.96 | -.29 |
| 4 | 3.03 | 2.37 | .66 | 1.53 | .44 | 1.09 | 1.50 | 1.93 | -.43 |
| 5 | 3.22 | 3.13 | .09 | 2.02 | 1.58 | .44 | 1.20 | 1.55 | -.35 |
| 6 | 3.21 | 2.81 | .40 | 2.03 | 1.31 | .72 | 1.18 | 1.50 | -.32 |
| 7 | 3.61 | 3.17 | .44 | 2.32 | 1.63 | .69 | 1.29 | 1.54 | -.25 |
| 8 | 8.32 | 6.45 | 1.87 | 5.33 | 3.59 | 1.74 | 2.99 | 2.86 | .13 |
| 9 | 9.15 | 7.86 | 1.29 | 4.12 | 4.06 | .05 | 5.03 | 3.79 | 1.24 |
| 10 | 9.99 | 8.88 | 1.11 | 4.28 | 4.41 | -.13 | 5.70 | 4.47 | 1.23 |
| 11 | 10.93 | 10.27 | .66 | 4.72 | 5.09 | -.37 | 6.21 | 5.18 | 1.03 |
| 12 | 11.78 | 11.53 | .25 | 5.15 | 5.73 | -.59 | 6.63 | 5.80 | .84 |
| 13 | 1.59 | 3.23 | -1.64 | .45 | .89 | -.44 | 1.15 | 2.34 | -1.19 |
| 14 | 2.11 | 3.04 | -.93 | 1.42 | 1.81 | -.39 | .69 | 1.23 | -.53 |
| 15 | 3.10 | 3.59 | -.50 | 2.43 | 2.34 | .09 | .67 | 1.26 | -.59 |
| 16 | 4.13 | 3.87 | .25 | 3.37 | 2.28 | 1.09 | .76 | 1.59 | -.84 |
| 17 | 5.12 | 4.91 | .21 | 4.16 | 3.00 | 1.17 | .96 | 1.91 | -.96 |
| 18 | 5.87 | 5.37 | .49 | 4.61 | 3.12 | 1.49 | 1.26 | 2.26 | -1.00 |
| 19 | 6.99 | 5.52 | 1.47 | 5.28 | 2.89 | 2.38 | 1.71 | 2.63 | -.92 |
| 20 | 8.51 | 7.90 | .61 | 6.04 | 4.69 | 1.34 | 2.48 | 3.21 | -.73 |
| 21 | 9.73 | 9.59 | .14 | 6.32 | 5.86 | .45 | 3.41 | 3.73 | -.31 |
| 22 | 10.70 | 10.79 | -.09 | 6.44 | 6.63 | -.19 | 4.27 | 4.16 | .11 |
| 23 | 11.72 | 11.94 | -.23 | 6.66 | 7.64 | -.98 | 5.06 | 4.30 | .75 |
| 24 | 12.74 | 14.17 | -1.44 | 6.93 | 9.58 | -2.65 | 5.81 | 4.59 | 1.22 |
| 25 | 13.87 | 15.11 | -1.24 | 7.30 | 10.32 | -3.02 | 6.57 | 4.80 | 1.77 |
| 26 | 3.31 | 4.38 | -1.07 | 1.71 | 2.43 | -.72 | 1.60 | 1.95 | -.35 |
| 27 | 3.61 | 4.12 | -.51 | 2.59 | 2.88 | -.28 | 1.02 | 1.24 | -.22 |
| 28 | 4.13 | 4.33 | -.19 | 3.14 | 3.08 | .06 | .99 | 1.25 | -.25 |
| 29 | 4.76 | 4.67 | .09 | 3.70 | 3.33 | .37 | 1.06 | 1.34 | -.28 |
| 30 | 5.38 | 4.72 | .66 | 4.20 | 3.32 | .88 | 1.18 | 1.40 | -.22 |
| 31 | 5.84 | 5.26 | .58 | 4.52 | 3.76 | .76 | 1.32 | 1.50 | -.18 |
| 32 | 6.43 | 5.67 | .75 | 4.93 | 4.07 | .86 | 1.50 | 1.61 | -.11 |
| 33 | 6.95 | 6.19 | .76 | 5.24 | 4.47 | .77 | 1.71 | 1.72 | -.01 |
| 34 | 7.46 | 6.47 | .99 | 5.52 | 4.65 | .87 | 1.94 | 1.82 | .12 |
| 35 | 7.89 | 6.94 | .94 | 5.71 | 5.09 | .62 | 2.17 | 1.85 | .32 |
| 36 | 8.15 | 7.14 | 1.01 | 5.78 | 5.30 | .48 | 2.37 | 1.84 | .53 |

| | Steady-state model: | | Recycling model: | |
|---|---|---|---|---|
| | Growth resp: | Maint. resp: | Growth resp: | Maint. resp: |
| 1 | 4.04 | .53 | 3.65 | .79 |
| 2 | 4.45 | .57 | 4.00 | .88 |
| 3 | 5.05 | .62 | 4.49 | .98 |
| 4 | 2.08 | .68 | 2.85 | 1.02 |
| 5 | 2.53 | .71 | 2.13 | 1.04 |
| 6 | 2.49 | .73 | 2.16 | 1.05 |
| 7 | 2.91 | .76 | 2.41 | 1.08 |
| 8 | 8.00 | .80 | 5.68 | 1.20 |
| 9 | 8.32 | .90 | 7.57 | 1.38 |
| 10 | 9.03 | 1.01 | 8.22 | 1.58 |
| 11 | 9.85 | 1.12 | 8.93 | 1.78 |
| 12 | 10.55 | 1.24 | 9.60 | 1.99 |
| 13 | .37 | .87 | 2.16 | 1.00 |
| 14 | 1.44 | .86 | .97 | .98 |
| 15 | 2.47 | .88 | 1.80 | .99 |
| 16 | 3.49 | .91 | 2.79 | 1.03 |
| 17 | 4.43 | .96 | 3.74 | 1.10 |
| 18 | 5.10 | 1.02 | 4.48 | 1.19 |
| 19 | 6.19 | 1.10 | 5.38 | 1.30 |
| 20 | 7.65 | 1.20 | 6.65 | 1.44 |
| 21 | 8.72 | 1.32 | 7.79 | 1.62 |
| 22 | 9.54 | 1.45 | 8.65 | 1.81 |
| 23 | 10.41 | 1.59 | 9.45 | 2.02 |
| 24 | 11.27 | 1.74 | 10.25 | 2.24 |
| 25 | 12.25 | 1.89 | 11.12 | 2.48 |
| 26 | 1.57 | 1.45 | 3.51 | 1.62 |
| 27 | 2.48 | 1.46 | 1.91 | 1.60 |
| 28 | 3.03 | 1.48 | 2.38 | 1.60 |
| 29 | 3.66 | 1.52 | 2.96 | 1.61 |
| 30 | 4.26 | 1.57 | 3.56 | 1.64 |
| 31 | 4.68 | 1.64 | 4.03 | 1.69 |
| 32 | 5.24 | 1.71 | 4.52 | 1.75 |
| 33 | 5.71 | 1.78 | 4.99 | 1.82 |
| 34 | 6.16 | 1.87 | 5.43 | 1.90 |
| 35 | 6.51 | 1.96 | 5.79 | 1.99 |
| 36 | 6.70 | 2.06 | 6.02 | 2.08 |

The Root/Shoot partitioning parameters

| | C: | Nr: | C/N: | An: | Wn: | Nupt: | Nutil: |
|---|---|---|---|---|---|---|---|
| 1 | .025 | .030 | .826 | .012 | .080 | .000 | .000 |
| 2 | .024 | .030 | .816 | .011 | .088 | .020 | .012 |
| 3 | .025 | .030 | .823 | .012 | .096 | .021 | .013 |
| 4 | .025 | .030 | .857 | .012 | .104 | .023 | .015 |
| 5 | .013 | .032 | .401 | .006 | .120 | .025 | .009 |
| 6 | .013 | .033 | .408 | .006 | .125 | .012 | .007 |
| 7 | .013 | .033 | .389 | .006 | .131 | .013 | .007 |
| 8 | .014 | .033 | .423 | .006 | .135 | .013 | .008 |
| 9 | .029 | .029 | 1.009 | .014 | .130 | .014 | .019 |
| 10 | .029 | .028 | 1.022 | .014 | .142 | .036 | .025 |
| 11 | .028 | .028 | 1.016 | .014 | .156 | .041 | .027 |
| 12 | .028 | .028 | 1.008 | .014 | .172 | .046 | .030 |
| 13 | .028 | .049 | .578 | .008 | .201 | .051 | .000 |
| 14 | .007 | .053 | .125 | .002 | .224 | .031 | .009 |
| 15 | .008 | .052 | .162 | .002 | .227 | .007 | .004 |
| 16 | .012 | .051 | .234 | .003 | .229 | .009 | .007 |
| 17 | .015 | .049 | .309 | .004 | .231 | .013 | .011 |
| 18 | .018 | .047 | .379 | .005 | .233 | .017 | .015 |
| 19 | .019 | .044 | .429 | .006 | .236 | .021 | .018 |
| 20 | .021 | .041 | .506 | .007 | .239 | .024 | .021 |
| 21 | .023 | .038 | .610 | .009 | .242 | .029 | .026 |
| 22 | .024 | .036 | .683 | .010 | .248 | .036 | .031 |
| 23 | .025 | .034 | .728 | .010 | .256 | .043 | .034 |
| 24 | .024 | .032 | .763 | .011 | .268 | .049 | .037 |
| 25 | .024 | .031 | .788 | .011 | .282 | .055 | .041 |
| 26 | .023 | .041 | .546 | .008 | .294 | .061 | .000 |
| 27 | .008 | .044 | .178 | .003 | .324 | .045 | .014 |
| 28 | .008 | .044 | .189 | .003 | .332 | .015 | .008 |
| 29 | .009 | .044 | .212 | .003 | .338 | .016 | .009 |
| 30 | .010 | .043 | .239 | .004 | .344 | .018 | .012 |
| 31 | .011 | .043 | .266 | .004 | .350 | .020 | .014 |
| 32 | .012 | .042 | .284 | .004 | .357 | .022 | .016 |
| 33 | .012 | .041 | .307 | .004 | .363 | .024 | .018 |
| 34 | .013 | .040 | .326 | .005 | .369 | .026 | .020 |
| 35 | .013 | .039 | .344 | .005 | .376 | .028 | .021 |
| 36 | .013 | .038 | .357 | .005 | .383 | .030 | .023 |

WHOLE PLANT RCU: Predicted vs. observed

| Number of data points: | 36 | |
|---|---|---|
| Intercept: | .36 +- | .38 |
| Slope: | .97 +- | .05 |
| Chi-squared | 23.68 | |
| r2 | .94 | |
| mse | .70 | |
| Mean observed | 6.430 | |
| Mean predicted | 6.624 | |
| Difference | .194 | |
| t | -1.410 | |
| Probability: | .167 | |

SHOOT RCU: Predicted vs. observed

| Number of data points: | 36 | |
|---|---|---|
| Intercept: | 1.37 +- | .34 |
| Slope: | .71 +- | .08 |
| Chi-squared | 24.72 | |
| r2 | .78 | |
| mse | .73 | |
| Mean observed | 3.856 | |
| Mean predicted | 4.112 | |
| Difference | .256 | |
| t | -1.461 | |
| Probability: | .153 | |

ROOT RCU: Predicted vs. observed

| Number of data points: | 36 | |
|---|---|---|
| Intercept: | -1.01 +- | .37 |
| Slope: | 1.37 +- | .13 |
| Chi-squared | 10.07 | |
| r2 | .92 | |
| mse | .30 | |
| Mean observed | 2.575 | |
| Mean predicted | 2.513 | |
| Difference | -.062 | |
| t | .517 | |
| Probability: | .608 | |

MOBIL.DAT

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 1 | 2.68742 | 2.80615 | 7.17889 | 5.62111 | -.48352 | -.53497 | .05145 |
| 2 | 3.22239 | 2.75470 | 7.75085 | 6.33415 | -.60022 | -.30877 | -.29145 |
| 3 | 3.53116 | 3.04615 | 8.55243 | 7.43657 | -.85328 | -.37845 | -.47483 |
| 4 | 3.90961 | 3.52098 | 3.38294 | 3.20606 | 3.43017 | 1.89185 | 1.53832 |
| 5 | 2.01776 | 1.98265 | 5.50993 | 2.50107 | -.24301 | -.64923 | .40622 |
| 6 | 2.66699 | 1.57643 | 5.34099 | 2.54401 | .01138 | -.01442 | .02579 |
| 7 | 2.68141 | 1.55064 | 6.26313 | 2.95887 | -.52292 | -.37222 | -.15069 |
| 8 | 3.05363 | 1.70133 | 16.51280 | 8.81320 | -6.21920 | -3.97208 | -2.24712 |
| 9 | 7.02571 | 3.94845 | 11.13401 | 15.20699 | -1.08903 | 1.59670 | -2.68573 |
| 10 | 5.42901 | 6.63418 | 11.92570 | 16.66330 | -1.10432 | -.21692 | -.88740 |
| 11 | 5.64592 | 7.52159 | 13.23089 | 17.95411 | -1.24768 | -.57685 | -.67083 |
| 12 | 6.22277 | 8.19242 | 14.40578 | 18.97222 | -1.11787 | -.56591 | -.55197 |
| 13 | .96502 | 8.74438 | 1.20920 | .12780 | 7.36656 | .32825 | 7.03831 |
| 14 | .63677 | 1.70607 | 5.03996 | .11904 | -.71945 | -1.39577 | .67631 |
| 15 | 2.03254 | 1.02976 | 8.52825 | .30175 | -1.40106 | -1.43798 | .03692 |
| 16 | 3.47052 | .99284 | 11.69159 | .76441 | -1.47824 | -1.34736 | -.13088 |
| 17 | 4.81788 | 1.12372 | 14.22159 | 1.61541 | -1.42814 | -1.12772 | -.30043 |
| 18 | 5.94560 | 1.42414 | 15.43100 | 2.79500 | -1.08698 | -.63680 | -.45018 |
| 19 | 6.58239 | 1.87433 | 17.59128 | 4.50472 | -1.63118 | -.95376 | -.67741 |
| 20 | 7.53616 | 2.55174 | 20.01089 | 7.31111 | -2.21855 | -1.08682 | -1.13172 |
| 21 | 8.62298 | 3.68346 | 20.50797 | 10.63303 | -1.79101 | -.39856 | -1.39246 |
| 22 | 9.02154 | 5.07592 | 20.55404 | 13.51596 | -1.44745 | -.17310 | -1.27435 |
| 23 | 9.19464 | 6.35027 | 21.06310 | 16.10690 | -1.49341 | -.31975 | -1.17365 |
| 24 | 9.51439 | 7.52393 | 21.72208 | 18.53692 | -1.50530 | -.38441 | -1.12089 |
| 25 | 9.89880 | 8.64482 | 22.77497 | 20.95804 | -1.66232 | -.53424 | -1.12808 |
| 26 | 3.59731 | 9.77290 | 4.57391 | 1.03709 | 8.55210 | 1.15972 | 7.39238 |
| 27 | 2.43759 | 2.38052 | 8.21339 | .63461 | -.40184 | -1.26586 | .86401 |
| 28 | 3.70345 | 1.51651 | 9.94396 | .88204 | -.74450 | -.78220 | .03769 |
| 29 | 4.48565 | 1.47881 | 11.79245 | 1.29655 | -.90344 | -.79885 | -.10459 |
| 30 | 5.28450 | 1.58340 | 13.36928 | 1.85272 | -.88929 | -.71161 | -.17768 |
| 31 | 5.99611 | 1.76108 | 14.26618 | 2.44882 | -.66851 | -.46192 | -.20659 |
| 32 | 6.45803 | 1.96767 | 15.54148 | 3.15852 | -.84483 | -.58517 | -.25966 |
| 33 | 7.04320 | 2.22733 | 16.39911 | 3.97889 | -.76064 | -.44634 | -.31430 |
| 34 | 7.48954 | 2.54163 | 17.14662 | 4.84638 | -.74198 | -.39670 | -.34528 |
| 35 | 7.88623 | 2.88691 | 17.56799 | 5.69102 | -.62052 | -.27316 | -.34736 |
| 36 | 8.15940 | 3.23427 | 17.56273 | 6.35627 | -.39021 | -.10378 | -.28643 |

VITA

Halldor Thorgeirsson

Candidate for the Degree of

Doctor of Philosophy

Dissertation: The Modeling and Measurement of Respiratory Carbon Use and Net Carbon Gain of Two *Agropyron* bunchgrasses.

Major Field: Range Ecology

Biographical Information:

Personal Data: Born at Isafjordur, Iceland, July 25, 1956, son of Thorgeir Hjorleifsson and Una Halldorsdottir; married Heida Steinsson, January 4, 1976; children: Berglind and Hakon Atli.

Education: Attended the Isafjordur Grammar School, graduated 1976; received Bachelor of Science degree in biology from the University of Iceland, 1980; completed an one-year non-degree honors program at the University of Iceland, 1982; received Masters of Science degree in range ecology from Utah State University, 1985; completed requirements for the Doctor of Philosophy degree at Utah State University in April 1988, with a major in range ecology and an area of specialization of plant physiological ecology.

Professional Experience: Research Assistant, (plant distribution, plant community structure), Institute of Biology, University of Iceland, 1979-80; Deputy Research Officer, (range ecology, statistics, data processing), Agricultural Research Institute, Iceland, 1981-1982; part-time lecturer in plant physiology, University of Iceland, 1979-1982; Graduate Research Assistant in the Department of Range Science, Utah State University, 1982-1988; Research Officer, (range forage production, plant physiological ecology), Agricultural Research Institute, Iceland, present.