Respiration II – Functional Components of Respiration

What is the purpose of crop respiration? Could yield be increased by reducing respiration?

Learning Objectives

1. Understand how total crop respiration can be divided conceptually into “growth” and “maintenance” functional components.

2. Understand how the composition of new biomass affects the respiratory costs of biosynthesis.

3. Be able to calculate whole crop carbon fluxes to growth and different respiration components.

Introduction

Our consideration of plant respiration has so far focused on biochemical processes occurring at the cell and organelle levels. In this lecture we consider the phenomenon of respiration in the context of whole plant canopies, to uncover the relationships between photosynthesis, dry matter accumulation, respiration, and crop growth.
Early Models of Crop Respiration

The biomass in a plant canopy, as living tissue, must expend a certain amount of energy simply to maintain itself; this energy is supplied through the process of respiration. Before approximately 1965, crop scientists assumed that the respiration rates of crop canopies must be in some way proportional to the total biomass present, or perhaps to the total leaf area. This assumption had important implications with respect to the relationship between leaf area and crop productivity. For instance, it led to the prediction that as LAI increased, canopy respiration should increase in a linear fashion.

When the increase in gross photosynthesis associated with the increased LAI was greater than the increase in respiration, then there was a net benefit associated with the additional LAI. However, when LAI was increased further, the resulting small increase in canopy gross photosynthesis would not be enough to compensate for the additional respiration of the added leaves, and net canopy photosynthesis would decline. Thus, the shaded leaves at the bottom of the canopy could be considered "parasitic", since they released more CO$_2$ in maintenance respiratory processes than they fixed through photosynthesis.

Two models of how whole-canopy gross CO$_2$ assimilation ($A_G$), respiration (R) and net CO$_2$ assimilation ($A_N$) are affected by leaf area index. On the left, respiration increases linearly with LAI, and net photosynthesis declines at high LAI due to CO$_2$ losses from "parasitic" leaves near the bottom of the canopy. On the right, shaded leaves lower in the canopy are assumed to have lower respiration rates than sunlit leaves, and therefore detract little from canopy net photosynthesis.
The fallacy of this model became apparent when crop modellers found that canopy photosynthesis was underestimated when leaf respiration rates were assumed to be uniform throughout the canopy. Instead, canopy photosynthesis could only be accurately modeled if shaded leaves lower in the canopy were assumed to have lower respiration rates than upper, sunlit leaves. Apparently, leaf respiration was a function not only of biomass, but also of photosynthetic activity.

An elegant experiment that demonstrated this relationship between canopy light environment and canopy respiration was reported by Ludwig et al. in 1965. They grew cotton plants under controlled environment conditions at very wide plant spacings (i.e., low LAI), and then rearranged the plants into more dense communities, with various LAIs between 1 and 12. Immediately upon rearranging the plants, the high-LAI canopies showed very low net photosynthetic rates, as would be expected if canopy respiration was simply proportional to leaf area. However, over time the net photosynthetic rates of the high-LAI canopies rose to nearly the same level as those of the low-LAI canopies, indicating a decline in the respiration rates of some of the leaves.

Net canopy photosynthetic rates for cotton plants growing under controlled environment conditions. Plants were transferred from wide spacing to spacings that produced LAIs of between 1 and 12, and canopy photosynthesis was determined 0, 2, 24 and 72 hours after transfer (Data of Ludwig et al., 1965; Figure from Loomis et al., 1967).
The Two-Component Model of Respiration

Such observations of respiration in whole crop canopies led to the development of the two-component model of respiration by McCree in 1970.

This model states that there are two functionally distinct components to crop respiration - a maintenance component, which is proportional to crop biomass, and a growth component, which is proportional to current photosynthesis. The model can be expressed in the form:

\[ R_T = a \times A_G + b \times W, \]

where

- \( R_T \) is total daily respiration (mol CO\(_2\) m\(^{-2}\) ground d\(^{-1}\))
- \( a \) is the growth coefficient (dimensionless)
- \( A_G \) is the daily gross CO\(_2\) assimilation (mol CO\(_2\) m\(^{-2}\) ground d\(^{-1}\))
- \( b \) is the maintenance coefficient (mol CO\(_2\) g\(^{-1}\) dry matter d\(^{-1}\))
- \( W \) is the current crop dry weight (g dry matter m\(^{-2}\))

The maintenance coefficient (\( b \)) implies that, in the absence of any photosynthesis, a certain proportion of the total crop carbon would be lost each day to meet the maintenance energy requirements of the existing biomass. A typical value might be \( 5.0 \times 10^{-4} \) mol g\(^{-1}\) d\(^{-1}\), indicating that 0.0005 mol of CO\(_2\) would be released each day for every g of crop dry weight, due to respiration supporting maintenance processes. For a crop with 40-% carbon content, this would be equivalent to 1.5% of the crop dry weight.

The growth coefficient (\( a \)) typically has a value of between 0.25 to 0.5. This indicates that 25 to 50% of all carbon fixed through photosynthesis must be re-released in the process of synthesizing new biomass; i.e., only a portion of the primary products of photosynthesis are actually retained - the rest must be respired to provide energy for anabolic reactions. To understand why this is so, it is necessary to consider biomass production values.

Growth Respiration and Biomass Production Values

The weight of final plant biomass that is produced as the result of a unit of photosynthesis depends on the chemical composition of the new biomass. For instance, if glucose is considered the primary product of photosynthesis, then production values for different chemical components of plant biomass can be expressed in glucose units.

One unit of glucose can be converted to 0.86 units of a complex carbohydrate such as cellulose or starch, but only 0.36 units of an "energy-dense" compound such as lipid. The remaining weight is lost mainly as CO\(_2\) due to respiration. This respiration provides the energy (e.g., ATP)
and reducing electrons required for the synthesis of the various chemical compounds in the new biomass.

"Production values" for the conversion of 1.0 g of glucose into various chemical compounds, using the most efficient biochemical pathway (After Penning deVries, 1972)

<table>
<thead>
<tr>
<th>Compound</th>
<th>Production Value (g g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sucrose</td>
<td>0.92</td>
</tr>
<tr>
<td>Cellulose and starch</td>
<td>0.86</td>
</tr>
<tr>
<td>Nucleic acids*</td>
<td>0.57</td>
</tr>
<tr>
<td>Amino acids*</td>
<td>0.54</td>
</tr>
<tr>
<td>Proteins*</td>
<td>0.45</td>
</tr>
<tr>
<td>Lipids</td>
<td>0.36</td>
</tr>
</tbody>
</table>

*N and S supplied as NO₃⁻ and SO₄²⁻

The "production value" concept can be extended beyond individual chemical substances to calculate the production values for whole plant tissues. The glucose production values for seeds with different carbohydrate, protein and lipid contents are shown below.

<table>
<thead>
<tr>
<th>Seed</th>
<th>Carbohydrate</th>
<th>Protein</th>
<th>Lipid</th>
<th>Ash</th>
<th>Production Value (g g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley</td>
<td>80</td>
<td>9</td>
<td>1</td>
<td>4</td>
<td>0.75</td>
</tr>
<tr>
<td>Rice</td>
<td>88</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>0.75</td>
</tr>
<tr>
<td>Wheat</td>
<td>82</td>
<td>14</td>
<td>2</td>
<td>2</td>
<td>0.71</td>
</tr>
<tr>
<td>Oats</td>
<td>77</td>
<td>13</td>
<td>5</td>
<td>5</td>
<td>0.70</td>
</tr>
<tr>
<td>Pea</td>
<td>68</td>
<td>27</td>
<td>2</td>
<td>3</td>
<td>0.65</td>
</tr>
<tr>
<td>Soybean</td>
<td>38</td>
<td>38</td>
<td>20</td>
<td>4</td>
<td>0.50</td>
</tr>
<tr>
<td>Canola</td>
<td>25</td>
<td>23</td>
<td>48</td>
<td>4</td>
<td>0.43</td>
</tr>
</tbody>
</table>
For most crops, the production value for the bulk vegetative matter can be estimated accurately from the C and N contents of the biomass (Vertregt and Penning de Vries, 1987) using the following formula:

\[
P V = \frac{1}{5.4(C) + 6.0(N) - 1.1}
\]

where PV is the production value in g DM g\(^{-1}\) glucose, and C and N are the proportions of total DM made up by the weight of C and N, respectively.

Remember, the growth coefficient implies that for each unit of substrate available for growth, a certain proportion will be respired in the growth process per se. This respiration that is the result of converting substrate to final biomass is called growth respiration.

Growth respiration is not affected directly by temperature or other factors; it is a constant proportion of new growth, and is determined only by the chemical composition of the new biomass produced.

**Maintenance Respiration Defined**

As mentioned, all of the existing phytomass will respire in order to meet its maintenance requirements. These requirements include:

- maintenance of ion concentrations across membranes
- turnover of cell components - particularly enzymes, but also membrane lipids and other molecules that must occasionally be replaced during the course of normal metabolic activity.

**Temperature Sensitivity**

Maintenance respiration, unlike growth respiration, is temperature-dependent, occurring at a higher rate at higher temperatures. Maintenance respiration is often reported to have a Q\(_{10}\) of approximately 2.0 within the normal physiological temperature range. In other words, for each 10\(^\circ\) C rise in temperature, maintenance respiration per unit dry weight will double.

This temperature response can have important implications for productivity and yield, especially when higher temperatures also reduce gross photosynthesis. Consider the figure below, in which
creeping bentgrass, cut to golf green height, is shown to enter negative net carbon assimilation when exposed to excessively high temperatures.

Effect of temperature and time of exposure on the carbon balance of three bentgrass cultivars (Huang and Gao, 2000)

Other Factors Affecting Maintenance Respiration

The magnitude of the maintenance coefficient (b) will also differ for different types of tissue. For instance, active photosynthetic tissue with high enzyme contents will have higher maintenance requirements than storage tissues, such as the endosperm of mature seeds, or structural tissues, such as the stems of woody plants.

Also, under stress conditions maintenance requirements may rise because of the metabolic costs associated with repair of stress-induced cellular damage.

Maintenance vs. Growth Respiration

The distinct separation between maintenance and growth components implied by the two-component model is perhaps somewhat misleading, since "maintenance" requirements will also be partially dependent upon the gross photosynthetic activity. Leaves photosynthesizing at high rates will have greater enzymatic turnover, and will also incur metabolic costs associated with repairing "normal" damage to photosynthetic membrane components under high PPFD ("photodamage").
An analogy would be the increased maintenance costs for a car that is driven fast over long distances, compared to one that is parked most of the time. Even though this additional respiration is proportional in some way to the photosynthetic rate, it still must be considered part of the maintenance component, since it is involved in the maintenance of the existing "photosynthetic factory". Only respiration that results from the conversion of primary substrate into new biomass can be considered true growth respiration.

The Carbon Balance Model of Growth and Maintenance Respiration

Overview of the Model

The two-component model of respiration put forward by McCree is generally very successful in describing the actual respiration rates of crop canopies. However, it has a slight conceptual flaw, in that it describes growth respiration as a function of gross photosynthesis, rather than as a function of new dry matter production per se.

The substrate model of Thornley (1970) accounts for maintenance respiration before calculating growth respiration, which resolves the flaw in the McCree model. The following figure presents an adaptation of the Thornley model that we will use in our discussion.

In this model, daily gross photosynthesis ($A_G$) provides a certain amount of newly fixed carbon ($\Delta C_T$) in the form of, say, glucose.
A proportion of this will be used to support maintenance processes; the carbon lost to maintenance respiration is designated $\Delta C_{Rm}$.

The remaining carbon ($\Delta C_{G}$) is available for growth. Some of this will be retained as carbon in the new crop dry matter ($\Delta C_{DM}$). The rest will be respired to provide energy and reductant for the conversion of glucose into the new biomass - this carbon lost to growth respiration is designated as $\Delta C_{Rg}$ in the diagram. The symbol $Y_g$ is the conversion efficiency; this is the fraction of carbon available for growth that is actually retained in the new biomass. The value of $Y_g$ is a function of the production value (PV), as we will demonstrate below.

**Calculating the Components of the Carbon Balance**

Let's try to use the Thornley model to calculate carbon losses due to maintenance and growth respiration, for the following example:

<table>
<thead>
<tr>
<th></th>
<th>300 g m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Existing crop dry matter</td>
<td></td>
</tr>
<tr>
<td>Crop biomass composition</td>
<td>43% of DM is C by weight 5% of DM is N by weight</td>
</tr>
<tr>
<td>Daily gross photosynthesis</td>
<td>1.2 mol CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>Maintenance coefficient (b)</td>
<td>0.0005 mol CO$_2$ g$^{-1}$ DM d$^{-1}$</td>
</tr>
</tbody>
</table>

**STEP ONE - Calculate $\Delta C_T$ and $\Delta C_{Rm}$**

The amount of glucose made available by photosynthesis (per m$^2$ ground area) can be determined from $A_G$. In our example, 1.2 mol of CO$_2$ are fixed per m$^2$ per day. Since there is 1 mol of carbon in 1 mol of CO$_2$, we can say that 1.2 mol C are fixed per day.

Thus,

$$\Delta C_T = 1.2 \text{ mol C m}^{-2} \text{ d}^{-1}.$$

Of these 1.2 mol C, a certain amount will be lost again, due to maintenance respiration of existing tissues. The amount of this respiration can be calculated as the product of the maintenance coefficient (b) and the existing DM:

$$\Delta C_{Rm} = (0.0005 \text{ mol CO}_2 \text{ g}^{-1} \text{ DM} \text{ d}^{-1}) \times (300 \text{ g DM m}^{-2}) =$$
= 0.15 mol CO₂ m⁻² d⁻¹ =
= 0.15 mol C m⁻² d⁻¹.

**STEP TWO - Calculate ΔC₆**

The carbon available from photosynthesis, after maintenance respiration is accounted for, is ΔC₆. In our example, this is:

\[ ΔC₆ = ΔC₇ - ΔC₉m = \]
\[ = 1.2 \text{ mol C m}^{-2} \text{ d}^{-1} - 0.15 \text{ mol C m}^{-2} \text{ d}^{-1} = \]
\[ = 1.05 \text{ mol C m}^{-2} \text{ d}^{-1}. \]

**STEP THREE – Determine the Conversion Efficiency (Y₉) and the Carbon Retained in the New Biomass (ΔC_{DM})**

It should be obvious from our previous discussion that the fraction of ΔC₆ retained in new biomass will depend on the chemical composition of the new biomass. That is, it is a function of the production value.

Recall that the production value can be estimated from the C and N content of the final biomass:

\[ PV = \frac{1}{5.4(C) + 6.0(N) - 1.1} \]

In our example:

\[ PV = \frac{1}{5.4 \times 0.43 + 6.0 \times 0.05 - 1.1} = 0.657 \text{ g DM / g glucose} \]

This is a measure of the **mass of new dry matter** that can be produced from a given mass of **glucose**. As Y₉ is expressed in mol C / mol C, DM and glucose must be converted to mol C:

0.43 g C / g DM × 1 mol C / 12 g C = 0.0358 mol C / g DM and 1 mol glucose / 180 g glucose × 6 mol C / mol glucose = 0.0333 mol C / g glucose

\[ Y₉ = 0.657 \text{ g DM / g glucose} \times 0.0358 \text{ mol C / g DM} \times 0.0333 \text{ mol C} = \]
\[ = 0.706 \text{ mol C mol}^{-1} \text{ C} \]
Therefore, 70.6% of the carbon available as $\Delta C_G$ will be retained as $\Delta C_{DM}$; the remaining 29.4% of $\Delta C_G$ will be respired as growth respiration ($\Delta C_{Rg}$).

(Note that $Y_g = PV$ when carbon content of biomass is 40%)

**STEP FOUR - Calculate $\Delta C_{DM}$, crop growth rate, and growth respiration.**

It is now a simple matter to determine the amount of newly fixed carbon that will be retained as new crop dry matter. This is simply $\Delta C_G \times Y_g$:

$$\Delta C_{DM} = \Delta C_G \times Y_g =$$
$$= 1.05 \text{ mol C m}^{-2} \text{ d}^{-1} \times 0.706 =$$
$$= 0.741 \text{ mol C m}^{-2} \text{ d}^{-1}$$

This is the amount of carbon allocated to new dry matter. So, how much actual dry matter will be produced? That is, what is the crop growth rate? This is also easily calculated, by multiplying $\Delta C_{DM}$ by the molar mass of C (12 g), and then dividing by the fractional carbon content of the new biomass:

$$\text{CGR} = \frac{\Delta C_{DM} \times C_{MW}}{C} =$$
$$= \frac{(0.741 \text{ mol C m}^{-2} \text{ d}^{-1}) \times (12 \text{ g C mol}^{-1} \text{ C})}{(0.43 \text{ g C g}^{-1} \text{ DM})} =$$
$$= 20.7 \text{ g DM m}^{-2} \text{ d}^{-1}$$

And finally, what was the growth respiration rate? Again, this is easily determined if you understand the Thornley model. The $\Delta C_{Rg}$ can be estimated as:

$$\Delta C_{Rg} = \Delta C_G - \Delta C_{DM}$$
$$= 1.05 \text{ mol C m}^{-2} \text{ d}^{-1} - 0.741 \text{ mol C m}^{-2} \text{ d}^{-1}$$
$$= 0.309 \text{ mol C m}^{-2} \text{ d}^{-1}$$

Growth respiration ($\Delta C_{Rg}$) can also be estimated as $(1-Y_g) \times \Delta C_G$. Since there is 1 mol of C in 1 mol of CO$_2$, we could also express the growth respiration rate as 0.309 mol CO$_2$ m$^{-2}$ d$^{-1}$. 

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Summary

In our example, a total of 1.2 mol C were fixed by photosynthesis per m$^2$ of ground area per day. Of this, 62% (0.741 mol) was retained in the new DM produced, 26% (0.309 mol) was lost to growth respiration, and 12% (0.150 mol) was lost to maintenance respiration.

These proportions are fairly typical for a crop during early phases of development (e.g., prior to flowering), but it should be noted that the proportions of new C allocated to growth, maintenance respiration and growth respiration will change over the season. For instance, maintenance respiration becomes a larger percentage of the total carbon balance of the crop as crop DM increases. An example of how respiration rates can change over a growing season is provided in the figure below.

Weekly amounts of gross photosynthesis (AD), maintenance respiration (BC), growth respiration (CD) and net photosynthesis (AB) of a barley crop sown on March 18th and harvested on August 21st. (From Biscoe et al., 1975)