Limits to Yield Revisited

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Abstract
An early effort aimed at exploring limits to radiation-use efficiency of crops (Crop Sci 3:67-72, 1963) is reexamined in light of current knowledge of photosynthesis and respiration. Light-limited gross photosynthesis estimated with a quantum requirement (qr) of 10 to 16 photons per CO₂ reduced to CH₂O can be translated to wheat biomass with a growth yield near 0.7 g biomass g⁻¹ glucose (to account for respiration associated with growth). Using that approach, it seems that RUE might be considerably more than values observed for real wheat crops (near 3 g DM MJ⁻¹ solar radiation intercepted). With further allowances for maintenance respiration (Rm), down-regulation of photosynthesis when light is not limiting, and other matters, however, qr rises towards 24 and the ‘gap’ between observed and potential productivity largely disappears. Values between 3 and 3.8 g DM MJ⁻¹ seem to represent a practical limit for wheat RUE. Maximum RUE is found to vary strongly with size of crop, temperature, radiation level, and ambient [CO₂]. In contrast to variations in those factors, variations in specific Rm have relatively little influence on RUE. Increase in ambient [CO₂] towards 600 vppm dramatically lowers qr, however, and RUE rises towards 5 g DM MJ⁻¹ at 600 vppm CO₂.

Introduction
Agronomists worry about crop yields reaching a limit that their continued efforts cannot raise. Over three decades ago, Loomis and Williams (1963) argued that maximum crop yields could be significantly greater than those yet achieved. Now, after a generation of research by plant physiologists and breeders, and technological innovation by farmers, it is time to look again at limits to yield.

Yield Levels of Agriculture
As yield depends in part on management and local environment, three measures of regional yield find use. Average yield for a region reflects farmers’ success with the many certainties and uncertainties surrounding production, and their average employment of technology. Some farmers regularly obtain high yields. They stand out above the average as a measure of what is attainable by skilled people employing the best available technology. Record yields and maximum yields, as predicted by models, are important in defining not only progress in breeding and agronomy but also ‘gaps’ between what is achieved and what might be possible.

The reasons why average yields lag behind attainable yields are sometimes readily apparent in poor stands or lack of nutrients. Other times, yield is influenced by a complex of factors including weather, soil fertility, pressures due to disease, pests and weeds,
market prices for inputs and produce, farmer skill, and luck. Given limitations of labor and machinery, for example, it is almost inevitable that some fields in a region will be sown too early and some too late. The optimum sowing date varies with the weather, and thus over years, and is difficult to predict.

Conditions necessary for reaching attainable yields are generally known including freedom from weeds and disease, and soil with appropriate pH and drainage. Identifying the factors contributing to the gap between average and attainable yields within a region, while difficult and, in some cases, impossible, can serve as a basis for improving farm practices. Economic and environmental factors dictate that gaps should always exist between actual and attainable yields, on one hand, and potential yield, on the other. Carrying inputs to the necessary levels of diminishing returns greatly lowers the efficiency in use of expensive inputs and greatly increases the potential for environmental damage.

To produce a record crop, weather, technology, farmer skill and other matters must all be favorable. Record yields serve as one measure of 'genetic potential'. Knowledge of such values for wheat is sparse, however, particularly on a regional basis, although values near 11 t dry grain ha\(^{-1}\) (1100 g m\(^{-2}\)) are not uncommon. That is much greater than the current average yield for any region of the world. Assuming a harvest index of 0.45 for modern wheat, 11 t corresponds to production of 24.5 t of aboveground biomass. Recent reports of 15 t grain ha\(^{-1}\) being obtained in Chile and the UK translate to nearly 30 t biomass ha\(^{-1}\) after correction for moisture content.

Because technology, farmer skill, and weather change with time, genetic advances cannot be calculated directly from changes in real yields. This was revealed nicely in studies by M.A. Bell and colleagues for the Yaqui Valley in northwestern Mexico. Since 1968, that region has been sown almost exclusively with a series of modern semidwarf cultivars of wheat. A linear regression of average yield over years indicated a yearly increase of 57(±13 SE) kg ha\(^{-1}\), from 3860 kg grain ha\(^{-1}\) in 1969 to 1991 (Bell and Fischer, 1994). Much of the variability was due to weather. When average yields were adjusted with a model for weather variations (including a trend towards less favorable weather in recent years), the yearly increase was seen to be 103 (±15 SE) kg ha\(^{-1}\). Through survey research, Bell et al. (1995) were able to define and then isolate several factors contributing to that gain (Table 1). In line with other recent studies, genetic gains were relatively small, particularly in recent years.

The principal question before us now is whether photosynthetic systems are capable of much higher yields than observed records, or whether only further small improvements are possible.

Table 1. Summary of sources of gain in average yield of wheat in the Yaqui Valley of Mexico, 1969-1991 (adapted from Bell et al., 1995).

<table>
<thead>
<tr>
<th>Source of gain</th>
<th>kg ha(^{-1})</th>
<th>kg ha(^{-1}) y(^{-1})</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>2370</td>
<td>103</td>
<td>100</td>
</tr>
<tr>
<td>Genetic</td>
<td>660</td>
<td>29</td>
<td>28</td>
</tr>
<tr>
<td>N fertilizer</td>
<td>1140</td>
<td>50</td>
<td>48</td>
</tr>
<tr>
<td>Other</td>
<td>570</td>
<td>25</td>
<td>24</td>
</tr>
</tbody>
</table>
The Basis of Yield

Crop growth and yield are derived from photosynthesis and therefore dependent on receipt and capture of solar radiation. Correlations between leaf photosynthetic rates measured at points in time and yield are, unfortunately, weak (Evans 1993). Leaf photosynthetic rates vary widely, depending on a developmental history in the past environment leading to differences in leaf thickness, stomatal frequency, chlorophyll and enzyme contents, and other parameters. Also, leaf photosynthetic rates change quickly as \([\text{CO}_2]\), temperature, water status and irradiance change. The individual leaves perform according to their age and place in complex canopies that progress from sparse to complete cover and then senescence during the season. Additional complexity arises from the metabolism involved in the biosynthesis, partitioning, and maintenance of biomass. Therefore, about the only way to relate leaf rates with yield is through dynamic models that embrace the key elements of that complexity (Amthor and Loomis 1995).

Much can be learned, however, through consideration of net biomass production per unit solar radiation absorbed by the entire canopy, the so-called radiation-use efficiency (RUE). RUE can be presented in various units; g DM MJ\(^{-1}\) radiation are used here. DM production (crop growth rate) is obtained through periodic sampling of the crop and radiation absorption is measured with sensors placed above and below the canopy. In simple terms, final yield is the product of cumulative seasonal radiation absorption, RUE, and the portion of total biomass that appears as grain.

Potential Radiation-Use Efficiency

Potential RUE can be calculated from physiological principles relating to photosynthesis and respiration, as was done by Loomis and Williams (1963). Steps in the analysis (Table 2) involve: 1) receipt and capture of photosynthetic photon (quantum) flux, 2) gross assimilation of \(\text{CO}_2\) per photon of such light, and 3) correction for carbon losses associated with respiratory metabolism and conversion of photosynthate to biomass.

The photon flux in solar radiation

The absorption spectrum of chloroplast pigments and the level of energy required for a single photochemical event—electron transport, the first step towards production of energy carriers, ATP and NADPH, that do the work of \(\text{CO}_2\) reduction—result in photosynthesis being limited to only some of the wavelengths found in solar radiation. For rough purposes, 400 to 700 nm define photosynthetically active radiation (PAR). This band is essentially the same as that for human vision. On an energy basis, PAR amounts to about 0.5 J J\(^{-1}\) solar radiation.

Because light is captured as individual quanta, an estimate is needed of the number of photosynthetically active quanta per MJ of solar radiation. That number varies with atmospheric conditions and the path length through the atmosphere of direct rays (and thus with time of day and year, and latitude). Loomis and Williams (1963) calculated 2.06 mol quanta MJ\(^{-1}\) total radiation based on P. Moon’s spectrum for direct sunshine through air mass 2. That has been criticized
as not giving sufficient weight to the greater fraction of useful quanta present in diffuse radiation. Monteith and Unsworth (1990, p. 49), for example, give a value for 2.3 mol PAR MJ\(^{-1}\) from England and a range of 2.1 to 2.9 mol PAR MJ\(^{-1}\) from other locations.

In addition to natural variation in the photon content of solar radiation, it is important to remember that the instruments in common use for measuring solar radiation in energy or quantum terms are usually accurate to only about ±5%. The calculations in Table 2 are based on 2.2 mol quanta MJ\(^{-1}\), which seems appropriate to intermediate and lower latitudes during spring.

### Table 2. Estimates of potential radiation-use efficiency (RUE) of a C3 crop with various values of gr. Assumptions are for a wheat crop at midseason with a closed canopy (LAI=3 to 4) completely intercepting incident solar radiation.

<table>
<thead>
<tr>
<th>Solar radiation intercepted</th>
<th>1 MJ</th>
</tr>
</thead>
<tbody>
<tr>
<td>PAR quanta intercepted by canopy</td>
<td>2.2 mol</td>
</tr>
<tr>
<td>Canopy reflection</td>
<td>-0.13</td>
</tr>
<tr>
<td>PAR quanta absorbed by canopy</td>
<td>2.07 mol</td>
</tr>
</tbody>
</table>

**RUE calculation:**

<table>
<thead>
<tr>
<th>gr, quantum requirement</th>
<th>CH(_2)O produced(^b)</th>
<th>CH(_2)O use in R(_m) (^c)</th>
<th>CH(_2)O available for growth</th>
<th>Biomass produced at Y(_g) = 0.72(^d)</th>
<th>Total respiration/gross photosynthesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>(mol/mol CO(_2))</td>
<td>(mmol)</td>
<td>(mmol)</td>
<td>(mmol)</td>
<td>(g)</td>
<td>(g MJ(^{-1}))</td>
</tr>
<tr>
<td>10</td>
<td>207</td>
<td>18</td>
<td>189</td>
<td>5.67</td>
<td>4.1</td>
</tr>
<tr>
<td>15</td>
<td>138</td>
<td>18</td>
<td>120</td>
<td>3.60</td>
<td>2.6</td>
</tr>
<tr>
<td>20</td>
<td>104</td>
<td>18</td>
<td>86</td>
<td>2.58</td>
<td>1.9</td>
</tr>
<tr>
<td>25</td>
<td>83</td>
<td>18</td>
<td>65</td>
<td>1.95</td>
<td>1.4</td>
</tr>
<tr>
<td>30</td>
<td>69</td>
<td>18</td>
<td>51</td>
<td>1.53</td>
<td>1.1</td>
</tr>
</tbody>
</table>

\(^a\) Perhaps 10% of this is 'inactive' absorption (see text). Here, that loss is embodied in elevated grs, comparable to measured values.

\(^b\) Gross photosynthesis; CH\(_2\)O represents a mol of C as carbohydrate with mol weight of 30 g.

\(^c\) Maintenance respiration at 0.015 mmol CH\(_2\)O g\(^{-1}\) biomass d\(^{-1}\) (15°C; cool season). Standing crop of 1000 g m\(^{-2}\), radiation at 20 MJ m\(^{-2}\) d\(^{-1}\), and PAR as 0.5 of solar irradiance.

\(^d\) By definition, values in these columns are estimates of RUE.

**Absorption of PAR**

Only a portion of the light intercepted by leaves is absorbed usefully in chloroplasts by chlorophylls a and b and accessory pigments such as carotenoids. Some light is lost to reflection or transmission and through absorption by structures other than green tissues and by cell components other than those contributing to photosynthesis. For closed canopies (generally LAI=4 or more), about 6% of the light is reflected to the sky (Goudriaan and van Laar 1994). By contrast, most transmitted light (principally in the green region) can be captured deeper within the canopy; that loss is therefore small and may be ignored for our purposes. Absorption by other structures and pigments is not so easily assessed. Allowances can be made for absorption by nongreen tissues, and by green tissues such as stems with less photosynthetic capability than leaves. Comparison of albino and green leaves (Seybold 1933), for example, indicate that inactive absorption may amount to 10% of intercepted quanta.

In Table 2, 6% of the intercepted visible quanta are indicated as lost to reflection while losses due to inactive absorption and
less-effective absorption by stems are ignored. This bases the calculations on all light absorbed by the canopy, in line with experimental measurements, rather than on light actually absorbed by chlorophyll.

**Quantum yield/requirement in photosynthesis**

*C3 and C4 photosynthetic systems*—Given extreme variations in light flux, a dry aerial environment containing a small concentration of CO₂ (near 350 vppm) and a large concentration of O₂ (near 21%), higher plants encounter difficulty in maintaining efficient photosynthesis over time. A major problem is that rubisco, the carboxylating enzyme for CO₂ fixation into the Benson-Calvin cycle, also acts as an oxygenase, releasing CO₂ from previously fixed carbon. Ribulose bisphosphate (rubP) is the substrate in both reactions. The relative rates of carboxylation and oxygenation of rubP depends on the concentrations of CO₂ and O₂ at the enzyme’s active site.

Two distinct photosynthetic systems have evolved with partial solutions to this problem. The C4 photosynthetic system (e.g., maize) carries out CO₂ fixation in two stages that serve to concentrate the scarce supply of CO₂ into bundle sheath cells, where rubisco and the Benson-Calvin pathway are located in those leaves, sharply raising CO₂/O₂.

Although less efficient in dim light than the C3 photosynthetic system because of the extra stage in fixation, this improves RUE in bright light and with less loss of water than is the case for the C3 system. The C3 system found in wheat, although lacking CO₂-concentrating mechanisms, is able to recover some of the carbon released by rubisco oxygenase activity through a process termed photorespiration, and use it subsequently in rubP regeneration and rubisco carboxylase activity. On average, depending on other activities such as amino acid synthesis, about 3/4 of the carbon in glycolate formed from rubP by rubisco oxygenase activity is saved. Most of the remainder is released as CO₂.

The effect of photorespiration in a C3 leaf is illustrated in Figure 1a, and its absence in a C4 leaf in Figure 1b, by comparing performance in normal air with that in air low in O₂. Photorespiration is also suppressed by supplying CO₂ at a saturating level because, just as O₂ competitively inhibits photosynthesis, CO₂ competitively inhibits oxygenase activity.

*Light-limiting conditions*—Assimilation of CO₂ by leaves of wheat and other C3 plants well nourished for nitrogen increases as light flux increases from 0 towards 800 mmol PAR m⁻² s⁻¹ (about one-half of midday sunlight), beyond which the light-response curve flattens to a plateau. This effect is termed light saturation. C4 species, with their CO₂-concentrating step, saturate at higher light levels. Photosynthesis is therefore most efficient for both C3 and C4 plants, in terms of the most CO₂ being fixed per mol quanta absorbed (quantum yield), in dim light when light supply limits the photosynthesis rate. Canopy photosynthesis flattens less with increasing light and seldom comes to a plateau, even in full sunlight. This occurs because most of the leaves are either displayed obliquely to the sun’s rays (less flux per unit area leaf) or shaded by other leaves. Canopy light-response curves are concave down, however, so canopies also use dim light most efficiently.
Differences in efficiency are grasped more easily from the inverse of the quantum yield, here termed quantum requirement, $q_r$, in mol quanta mol$^{-1}$ CO$_2$ fixed. (Quantum ‘use’ is perhaps a better description.) The theoretical minimum value of $q_r$ is near 9 quanta actually absorbed by photosynthetic pigments (Nobel 1991). Corrected for 10% inactive absorption, minimum $q_r$ would be near 10 mol quanta absorbed by a leaf mol$^{-1}$ CO$_2$ fixed. In their study, Loomis and Williams (1963) used $q_r=10$, based on measurements with green algae in bicarbonate solution (saturating CO$_2$). Values of $q_r=10$ have since been observed for O$_2$ production (a concomitant of CO$_2$ fixation) for C3 higher plants by Björkman and Demmig (1987) when a saturating level of CO$_2$ (5% v/v) was used to suppress photorespiration. Production of O$_2$, while stoichiometrically close to CO$_2$ uptake, may differ from it. At 25°C, the smallest values of $q_r$ for CO$_2$ uptake, obtained with photorespiration suppressed by saturating CO$_2$ or by air with low O$_2$, are near 11. The constancy of this value across all C3 species indicates that very little variation in rubisco has been introduced during millions of years of evolution.

Due to photorespiration, rather different values of $q_r$ are obtained in normal air (325 vppm CO$_2$ and 21% O$_2$; Figure 1a). In C4 leaves (Figure 1b), $q_r$ is unaffected by O$_2$ concentration because photorespiration is inhibited by the high CO$_2$ levels in the bundle sheath cells. Values of C4-leaf $q_r$ exceed those for nonphotorespiratory C3 leaves, however, because extra ATP is required for regeneration of phosphoenolpyruvate in first stage of the C4 cycle.

McCree (1971) found requirements for quanta absorbed by leaves of several C3 crop species in normal air were near $q_r=15$ at

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**Figure 1.** (a) Light-limited photosynthesis rates of C3 *Atriplex patula* in air at 30°C with 325 mbar CO$_2$ and either 1.2% or 21% O$_2$. The quantum requirement ($q_r$) declines from 19.5 to 13.7 when photorespiration is suppressed. (Data from Björkman et al. 1970.)

(b) Similar to (a) except with C4 *A. rosea*. Low O$_2$ has no effect on $q_r$. (Data from Björkman et al. 1970.)

(c) Minimum quantum requirements of C3 *Encelia californica* in normal air and with 2% O$_2$ as a function of temperature. (Data from Ehleringer and Björkman 1977.)
28°C. For oat, at least, \( q_r \) improved to about 13.5 at 11°C. As depicted in Figure 1c, Ehleringer and Björkman (1977) found that \( q_r \) for C3 *Encelia californica* in normal air increased exponentially from near 14.5 at 14°C to almost 24 at 38°C. But, with photorespiration suppressed (air with 2% O\(_2\)), \( q_r \) was 12.5 and unaffected by temperature. This positive response of C3-leaf \( q_r \) to temperature in normal air (Figure 1c) results mainly from the temperature dependence of rubisco’s CO\(_2\)/O\(_2\) specificity, and to some extent from differential effects of temperature on solubilities of O\(_2\) compared to CO\(_2\).

*Light not limiting*—Quantum use per CO\(_2\) increases when the photosynthesis of C3 leaves saturates in bright light. This occurs because the dark reactions of the Benson-Calvin (B-C) cycle fail to keep pace with the photosynthetically limited light reactions. ATP and NADPH go unused and electron transport is ‘closed’. This may occur because the B-C cycle is simply too slow, because inorganic phosphate (Pi), which must cycle between chloroplast and cytosol, becomes tied up in intermediates, or because the CO\(_2\) flux through stomata does not keep pace with fixation, causing the leaf’s internal CO\(_2\) concentration (C\(_i\)) to decline. The decline in C\(_i\) is especially strong when stomata close due to moisture stress.

Continued over-excitation of the light-harvesting system with electron transport shut down causes short- or long-term damage to the system (‘photoinhibition’; Long et al. 1994). The possibility for damage is reduced by ‘down-regulation’ (Weis and Berry 1989) in which excess energy is passed to carotenoids and dissipated through long-wave radiation, convection, and transpiration. Maintenance of the plant’s water status and open stomates is important not only for cooling but also for a high conductance for CO\(_2\), which keeps the dark reactions going and electron transport ‘open’. In C3 leaves, protection from damage is also provided through CO\(_2\)-recycling by photorespiration; ATP and NADPH are used, transport remains open, and \( q_r \) for CO\(_2\) increases.

Down-regulation and photorespiration protect C3 systems from oxidative damage but they sharply increase the apparent quantum requirement. In addition, daily losses due to photoinhibition may easily amount to a 10% increase in \( q_r \) (Long et al. 1994). It is useful to note, however, that Farquhar’s biochemical model of photosynthesis (Farquhar and von Caemmerer 1982), which includes photorespiration but does not consider photoinhibition, generally provides good agreement with leaf rates of well-watered plants (Long 1991; Amthor and Loomis 1995). That model also demonstrates how effects of temperature in increasing photorespiration are offset by a similar stimulation of B-C dark reactions. As a result, light-saturated C3 photosynthesis rates usually have a broad temperature optimum.

An increase in chlorophyll fluorescence is seen when light harvesting exceeds the capacity of the dark reactions. The fluorescence is closely linked with the increase in \( q_r \) and fluorescence measurements are now used widely for
detection and analysis of stress effects on crops (Seaton and Walker 1990; Snel and van Kooten 1990).

It is clear that high RUE in strong light depends on several factors: adequate water to allow high stomatal conductance and transport of CO₂ into leaves; leaf arrangements that avoid excessive display normal to direct beam radiation; adequate leaf nutrition to support a large photosynthetic capacity and rapid processing of assimilated carbon; and canopy ventilation that permits supply of CO₂ and dissipation of heat by convection. It also is clear that qr=10 cannot be achieved by C3 or C4 crops except with limiting light and CO₂ saturation. With so many factors acting to increase qr under field conditions, values from 10 to 30 mol quanta mol⁻¹ CO₂ are employed for calculations presented in Table 2.

Maintenance respiration and growth yield

Dark respiration in plants—Respiration can be partitioned into two functional components, one related to maintenance of existing material (Rₘ), and one related to biosyntheses involved in growth (R₉). Allowance must be made for assimilate use in Rₘ before attempting to estimate net production of biomass.

Rₘ adjustment—Maintenance respiration occurs in all living tissues. It is presumed to relate to repair of existing structures and maintenance of ion balances against leakage and is proportional to the amount of existing biomass and protein content, rather than to radiation intercepted. Rₘ increases exponentially with temperature with a Q₁₀ near 2 over the short term but can acclimate to long-term changes through a smaller Q₁₀. Estimating use of photosynthate in Rₘ is problematic. Observed values of specific Rₘ in crop species are affected by age and plant composition, and may vary over a factor of more than five (Amthor 1989).

For Table 2, 0.015 mmol CH₂O g⁻¹ biomass h⁻¹ is taken to represent a wheat crop in midseason with daily mean temperature of 15°C. This is close to the value calculated with coefficients developed by Mitchell et al. (1991; their Table 3). It is important to remember that crop Rₘ is a function of crop biomass. RUE values are calculated for Table 2 with 1000 g m⁻² near anthesis, which is less than would be the case for truly high yields. Because RUE is expressed per MJ radiation in Table 2, the correction for Rₘ also varies with radiation level. With less than 20 MJ radiation d⁻¹, as used for Table 2, the Rₘ term would be larger.

A slowing of leaf respiration in the light is sometimes observed or inferred (Krömer 1995). The interpretation is that some features of metabolism that use products of 'dark' respiration, such as the step from NO₂⁻ to NH₄⁺ in nitrate reduction, or the active transport of ions across membranes, can be accomplished in the chloroplast or elsewhere with ATP and reductant generated by photosynthetic processes. Given the uncertainties in the occurrence and magnitude of such changes in respiration, it is ignored in Table 2. It might reduce the Rₘ component and/or increase slightly the growth yield, Y₉ (see below).

R₉ evaluated through growth yield, Y₉—

Newly reduced CO₂, represented here as an equivalent amount of simple carbohydrate,
CH$_2$O, can be translated to wheat biomass using a 'growth-yield' factor ($Y_g$, g biomass formed g$^{-1}$ CH$_2$O consumed; Pirt 1965). $Y_g$ (and corresponding respiratory exchanges of CO$_2$ and O$_2$) can now be calculated accurately from either elemental (McDermitt and Loomis 1981; Lafitte and Loomis 1988) or proximal analyses (Penning de Vries et al. 1974).

Assuming that new wheat biomass being formed near anthesis consists of 75% carbohydrate, 12% protein, 5% lignin, 3% lipid and 5% minerals (Subcommittee on Feed Composition 1982), $Y_g$ calculated by the least-cost method of Penning de Vries et al. is 0.72. Thus, 1/0.72=1.38 g CH$_2$O is consumed for carbon skeletons and growth respiration for each g biomass formed. $R_g$ amounts to 0.22 g CH$_2$O g$^{-1}$ biomass formed, and 7.35 mmol CO$_2$ is released. Multiplication of gross photosynthesis, minus maintenance respiration, by 0.72, as is done in Table 2, accounts for the minimum possible amount of respiration ($R_g$) associated with heterotrophic synthesis of biomass with that composition.

During grain filling, protein-N (reduced N) is mobilized from vegetative tissues, lessening the cost of protein synthesis. $Y_g$ can then increase towards 0.8. $Y_g$ also would be greater than 0.72 if some nitrogen is taken up from soil as NH$_4^+$ or if respiration is reduced in the light through, for example, a smaller cost for nitrate reduction.

**Potential RUE of wheat**

The calculations given in Table 2 indicate that potential RUE may range from 4.1 g biomass MJ$^{-1}$ solar radiation with $qr=10$, to 1.1 with $qr=30$. Per MJ PAR, the range is 8.2 to 2.2 g. The dependence of RUE on $qr$ is depicted in Figure 2a. This is total biomass and therefore includes roots. For a rough estimate of RUE based on aboveground material in crops well supplied with nutrients and water, these values can be divided by 1.1.

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**Figure 2.** (a) Calculated potential RUE (per MJ absorbed PAR or total solar radiation; from Table 2) as a function of variations in the quantum requirement, $qr$. (Dashed lines are explained below.) (b) Relation of crop growth rate (CGR), observed by various workers in experiments with wheat (open o) and barley (closed o), to absorbed photosynthetically active radiation (PAR). The slope, 3 g MJ$^{-1}$ PAR, represents radiation-use efficiency (RUE). (After Fischer 1983). The dashed lines in Figure 2a depict interpolation of Fischer’s RUE=3 g MJ$^{-1}$ PAR absorbed to $qr=24$. 
Fischer (1983) compared crop growth rates (CGR) observed in several field experiments with PAR absorbed by the canopies (Figure 2b). (Aboveground biomass was multiplied by 1.1 to account for roots.) The slope of the relation in Figure 2b is very near 3.0 g MJ⁻¹ PAR or 1.5 g MJ⁻¹ total radiation. Because wheat biomass has a heat of combustion near 17 kJ g⁻¹, the corresponding efficiencies are 5.1% of PAR absorbed and 2.6% of total solar absorbed. Interpolating in Figure 2a (with the assumptions given for Table 2), Fischer’s value corresponds to a quantum requirement near 24 mol quanta mol⁻¹ CO₂. Several outliers on the high side of Fischer’s graph are fit by RUE=3.8 g MJ⁻¹; from Figure 2a, this corresponds to qr=20.

**Assessment**

The earlier study (Loomis and Williams 1963) focused on limitations imposed in real canopies by light saturation, CO₂ supply, pattern of assimilate partitioning, and the amount, duration and manner of leaf display. All of those topics have received attention in wheat and continue to offer avenues for further small improvements in RUE.

**A practical potential RUE**

The estimate of RUE=8.2 g dry matter MJ⁻¹ PAR given in Table 2 with qr=10 is larger than the value of 6.8 g MJ⁻¹ PAR obtained in the earlier study (Loomis and Williams 1963). The difference comes in part from the greater number of quanta per MJ irradiance and inclusion of inactive absorption. In addition, the respiration allowance, now placed on a reasonably mechanistic basis, is smaller at qr=10 (26% of gross photosynthesis; R/P, Table 2) than the 33% used by Loomis and Williams based on measurements for alfalfa crops. In Table 2, R/P increases as qr increases, however, reaching 40% with qr=30. Amthor (1989) summarized observations for ‘growth efficiency’ (1-R/P) observed with wheat. Values of R/P calculated from his Table 6.1 range from 21 to 63% with a central tendency towards 33%, the same as in Table 2 with qr=20. Variations in photosynthesis rather than in respiration seem to be the main cause of the wide variation in R/P.

There is speculation that Rₘ might be reduced in crops through breeding, so the effect of a 20% reduction in Rₘ on RUE outlined in Table 2 was calculated. Reduction in the already small Rₘ used in this exercise did little to increase RUE: with qr=10, 20% smaller Rₘ increased RUE by only 1.9%; with qr=30, 20% reduction in Rₘ increased RUE by 6.8%.

R₉ seems a less likely source of variation in RUE as Y₉ is conservative. In a study with sorghum crops varying in age and nitrogen status, Y₉ calculated from elemental composition was 0.73 to 0.74 with adequate N and 0.77 to 0.78 with limited N (Lafitte and Loomis 1988). Arguably, protein content of wheat growth prior to anthesis may be nearer 18% (3% N) than 12% as used in Table 2, in which case, Y₉ would be near 0.69 (1.46 g CH₂O used per g biomass). Because variation in Y₉ has a direct effect on RUE, changes in Y₉ for Table 2 lead to similar changes in RUE.

If light saturation could be avoided, and with present atmospheres and temperatures near 20°C, wheat might be able to operate at qr=<20 and RUE=<4. Considerable light
saturation is unavoidable, however, and RUE=3.8 g DM MJ⁻¹ (qr=20) seems a practical estimate of maximum RUE of wheat under field conditions with long cool days and moderate radiation (20 MJ m⁻² d⁻¹).

Readers are referred to Austin (1993), Sinclair (1993) and Horton (1994), among others, for consideration of many other factors affecting photosynthesis as well as possibilities for improving production rate through altering system components, including rubisco. A principal conclusion from the present exercise is that RUE is a variable function of size of crop, temperature, radiation level, and ambient [CO₂]. Brief comments on several of these factors are presented in following sections.

[CO₂]
In the field, rapid photosynthesis can lower ambient [CO₂] to well below the current average of 350 vppm. Light saturation occurs at lower PAR, and RUE declines. These effects point up the importance of good ventilation (open canopy and turbulent air) and large canopy conductance (well-watered stand with open stomates).

The concentration of CO₂ in the atmosphere is expected to increase during the next century from about 350 vppm at present to between 500 to 600 vppm. To test the beneficial effect of increasing [CO₂] in lowering qr, simulations were made using an analytical simulation model based on that of Farquhar and von Caemmerer (1982). The [CO₂] in wheat chloroplasts was assumed to be 50% that in ambient air (von Caemmerer and Evans 1991). At 25°C, predicted light-limited qr declined, and RUE increased, as follows:

<table>
<thead>
<tr>
<th>[CO₂] (vppm)</th>
<th>qr (mol/mol)</th>
<th>RUE (g/MJ PAR)</th>
</tr>
</thead>
<tbody>
<tr>
<td>300</td>
<td>19.2</td>
<td>3.1</td>
</tr>
<tr>
<td>400</td>
<td>16.2</td>
<td>4.0</td>
</tr>
<tr>
<td>500</td>
<td>14.6</td>
<td>4.6</td>
</tr>
<tr>
<td>600</td>
<td>13.6</td>
<td>5.0</td>
</tr>
</tbody>
</table>

**Temperature**

Wheat is a cool-season crop. Both fall- and spring-sown wheat crops generally encounter quite cool temperatures during the vegetative period, whereas grain filling occurs in much warmer weather. The analysis presented here indicates that maximum photosynthetic efficiency (light-limiting conditions) of C₃ plants is favored by cool temperatures (<20°C). On the other hand, the maximum rate of light-saturated photosynthesis occurs at 25 to 30°C because acceleration of the Benson-Calvin cycle partially offsets photorespiration. As Long (1991) showed, the optimum temperature for photosynthesis will increase in the future as photorespiration will be repressed by increased [CO₂].

These effects of temperature on production processes interact with the effect of temperature on wheat’s developmental rate: rates of initiation of leaves (and thus canopy development) and spikelets (influencing potential kernel number) and the duration of grain filling. Temperature-response curves for developmental rate are similar to those for growth rate, perhaps because cell division and enlargement are integral to organ initiation.

The temperature response of development differs from that for photosynthesis leading to rather complex problems in defining ideotypes for crop improvement. Ideotypes that will raise yields beyond present levels may turn out to be more climate-specific (and thus regionally specific) than we have
supposed. Whereas effects of temperature on photosynthesis is well understood, we lack an equivalent understanding of mechanisms controlling development. This is an important area for basic research.

Radiation level

The frequency of light saturation of wheat crops is subject to several factors. The utility of erect leaves in moderating light saturation of crops has been a subject of considerable confusion. The question was analyzed theoretically by Duncan (1971) who made it clear that truly erect leaves offer great advantage only for dense canopies (LAI>5) and only with high solar elevation (e.g., summer and/or low latitude). Achievement of full interception is more important, however, and with less leaf area, that is accomplished best with leaves of moderate inclination. Given that wheat is most exposed to high solar elevation mainly during grain filling, when leaves are senescing and shaded by spikes, extremely erect leaves are not likely to offer the advantage to wheat that they lend to summer crops of maize and rice.

Conclusions

This analysis demonstrates that the upper limit of dry matter production by wheat crops is in the range of 3 to 4 g DM MJ\(^{-1}\) PAR (1.5 to 2 g DM MJ\(^{-1}\) solar radiation). This is considerably less than the 6.8 g MJ\(^{-1}\) PAR predicted by Loomis and Williams (1963) before photorespiration was known. Warm temperature, the small concentration of CO\(_2\) relative to O\(_2\), and light saturation limit attainment of greater RUE. Because present crops reach 3 to 4 g MJ\(^{-1}\) efficiency when conditions are favorable, further efforts at improving wheat yield need to focus on extending the duration of efficient photosynthesis and on improving the conversion to grain.

References


**Questions and answers**

R.A. Fischer:
Since I collected the RUE data of the 1970s and early 1980s to which you referred, I have been collecting whatever else has appeared on wheat RUE. The average number of 3 g Dm/MJ has not changed but there is clear evidence of a positive effect of canopy N concentration on RUE and a negative one of frost. With respect to cultivars there is no evidence that RUE has increased with yield progress over the last 30 years: the only evidence of a cultivar effect is a study showing higher RUE with more erect-leafed cultivars.

R.S. Loomis:
The positive effect with increased N generally relates to increased photosynthetic capacity as chlorophyll and enzyme content increase. Canopy reflectance declines, pointing to the importance of how radiation measurements are made. There are trade-offs, however. Less light may penetrate to shaded leaves, for example, and growth and maintenance respiration are increased.

Because wheat is relatively tolerant of direct freezing damage, the negative association with frost probably arises from increased photoinhibition at low temperatures. With low temperatures, the B-C enzymes fail to keep pace in bright light and photodamage occurs. Long et al. (1994) discuss this problem.

R.A. Fischer:
The N concentration effects were large, on the order of 15%, going from moderate to high concentration, and are unlikely to be compositional ones. Besides, the effects agree with those calculated by Tom Sinclair from individual leaf responses to leaf N concentration.