



Calculating maximum theoretical yield in rice



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ABSTRACT

Simple quantitative relationships can be useful in highlighting the characteristics that are key to taking yield towards its theoretical limit. Likewise, calculating maximum yields can be useful in suggesting attainable goals for plant breeders and agronomists. For this purpose we define how the core physiological drivers of yield combine to produce maximum yield. We make simplifications to produce three main equations that trace yield from solar energy through crop photosynthesis and biomass and then using harvest index to maximum grain yield. We focus our investigation on three types of canopy, taking as a starting point the C3 semidwarf elite rice cultivar IR72. We define an ideotype with a canopy of very erect leaves and large leaf area called Vela and consider it both as a C3 and a C4 photosynthetic canopy. We calculate the maximum daily photosynthetic rates and yields of the three canopy types for tropical and subtropical conditions.

Owing to the effects of temperature on quantum yield and maintenance respiration, the conversion of photosynthate to shoot biomass is 40% larger in the subtropics than the tropics. In the tropics, the predicted maximum yields are 12.9 t ha⁻¹ (semidwarf), 14.4 t ha⁻¹ (C3 Vela) and the 17.9 t ha⁻¹ (C4 Vela). In the subtropics those yields are: 20.1 t ha⁻¹, 22.4 t ha⁻¹ and 25.0 t ha⁻¹, respectively. The key factors taking rice yields towards their ultimate limit are canopy architecture, quantum yield, maintenance respiration, and minimizing loss of photosynthetic capacity as lower leaves senesce and nitrogen is recycled to grain after peak photosynthesis has been reached.

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1. Introduction

The current situation for food production in the world can be summarized in a sentence. We must produce more grain, of higher quality, from less land, using less water, less labour, less fertilizer, less pesticide, and with a smaller carbon footprint during an era of climate change (Brown, 2011; Beddington et al., 2012). Sheehy and Mitchell (2011a,b) discussed these global issues from the perspective of the research in rice required to prevent potentially catastrophic consequences of rising populations and climate change. Key to solving the problem is to increase crop yield. However, there are yield barriers which are imposed by physiological and environmental factors.

We can think of crop plants as machines powered by solar energy captured in photosynthesis. At their most efficient, crops intercept essentially all of the incident solar radiation so any

increase in crop biomass must come from more effective use of the radiation or better retention of dry matter in the crop or both (Sheehy, 2000; Thomas and Sadras, 2001). Mineral nutrients are also required of which nitrogen is the most important. Rates of leaf photosynthesis depend linearly on the nitrogen concentration of the leaf, and reach maximum values of 32.5 μmol CO₂ m⁻² s⁻¹ for rice (Peng, 2000) and 56.0 μmol CO₂ m⁻² s⁻¹ for maize (Evans and von Caemmerer, 2000). High-yielding crops need to acquire a substantial amount of nitrogen to maintain high rates of photosynthesis. At later stages of crop growth, some of this nitrogen from shaded leaves which have senesced moves to the grain (Sinclair and Sheehy, 1999); indeed about 30% of the nitrogen in grain has been acquired before panicle initiation (Sheehy et al., 2004a).

Farmers' yields are constrained by many environmental and financial factors so we need to work with yield potential when investigating maximum rice yields and how breeders and agronomists can achieve them. We assume an optimal physical environment in terms of solar radiation, water and mineral nutrients; perfect timing of sowing or transplanting, application of fertilizer and harvest; and that there are no losses to weeds, pests or diseases. The ultimate aim is to answer the questions: what is the maximum yield in rice? what factors limit yield? and is there a

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difference between rice in the tropics and subtropics? We use the three laws of maximum yield (Sheehy and Mitchell, 2013). These state quantitatively (1) how photosynthesis is driven by solar radiation intercepted by the canopy; (2) how shoot biomass is derived from photosynthesis less respiration and allocation to roots; and (3) how grain yield is partitioned from maximum shoot biomass by harvest index. The model follows the transformation of solar energy into the chemical energy of carbohydrates, the transformation of carbohydrates into biomass, and the allocation of some biomass to grain. This approach allows us to identify the important factors contributing to higher yields.

The model of maximum crop yield (Sheehy and Mitchell, 2013) was derived by assuming simple logistic growth and a differential equation for mass continuity describing the rate of change in crop mass as a function of the difference between the rates of resource capture and loss. This approach allowed Sheehy and Mitchell (2013) to provide mathematical equations for the estimation of maximum crop yield which did not require simulation of crop performance throughout crop development. The physiological parameter values used are representative of a crop achieving maximum yield. The advantage of this approach is that considerations of crop development and crop duration are not explicitly required for the calculations.

We focus investigation on three types of canopy, taking as a starting point the semidwarf rice with erect leaves of the current elite cultivar IR72. Unless harvest index can be increased, substantially higher yields will require larger shoot biomass. Stouter stems will be needed to support more grain and resist lodging. Since the grass stem consists of true stem (culm) surrounded by leaf sheaths, achieving more biomass and stouter stems means more leaves. If leaves are to be the same size, there will need to be more of them, from more nodes, so stems may well be taller. Increased leaf area (higher leaf area index) is beneficial only if the leaves are very erect (and if adequate nitrogen concentration can be maintained). The more erect the leaves, the more uniformly is solar radiation distributed down the canopy. Then even the lowermost leaves can make some contribution to crop photosynthesis and, more importantly, each leaf is receiving radiation well below the saturating value for photosynthesis thus raising the efficiency of radiation use. These effects are more marked with high irradiance i.e. sunny days in the tropics with high solar elevation. Higher leaf area index also enlarges the reservoir for nitrogen for later movement to filling grain, essential if improved yields are to maintain the current nitrogen and protein concentrations in the grain. Thus we define an ideotype of very erect leaves and large leaf area called Vela. An ultimate aim is to incorporate C4 photosynthesis into rice (Sheehy et al., 2007a) so a second ideotype is C4 Vela. Applying the model to these canopies allows us to suggest the key features for rice breeders to improve in their quest for advanced high-yielding varieties of irrigated rice.

2. Method of calculating maximum yield

2.1. Outline of the model

The model is derived in full in Sheehy and Mitchell (2013) and is summarized here from the top downwards. Assumptions and simplifications are stated at each stage. Values for the driving variables and parameters are given in Table 1.

Yield of rice (Y , t ha^{-1}), rough rice or paddy rice, as it leaves the field at harvest, is expressed at 14% moisture content (m.c.) on a fresh weight basis, which is obtained from

$$Y = 0.01 W_{g\max}/0.86 \quad (1)$$

where 0.01 converts from g m^{-2} to t ha^{-1} ; $W_{g\max}$ is maximum grain as dry matter (g m^{-2}); and 0.86 is the fraction of dry matter (DM) in yield at 14% m.c.

The maximum amount of grain is computed from

$$W_{g\max} = H W_{s\max} \quad (2)$$

where H is the harvest index (dimensionless), i.e. the fraction of shoot biomass (crop dry matter above ground) which appears as grain; and $W_{s\max}$ is the maximum shoot biomass at the end of growth duration (g DM m^{-2}).

Harvest index is a convenient but entirely empirical method of obtaining yield in crop growth models, and there is scope elsewhere for a more mechanistic formulation. The model applies to 1 m^2 of ground. The carbon content of dry matter is assumed to be 40% (Jimenez and Ladha, 1993) so that carbohydrate (CH_2O) and dry matter can be used interchangeably in the state variables. The driving variables are photosynthetically active radiation (PAR, the waveband 400–700 nm of solar radiation), mean air temperature, and mean leaf temperature during daylight; typical values are discussed below and given in Table 1. The crop is assumed to have a logistic growth pattern in which maximum rate of growth occurs halfway through the growth duration and then decreases to zero as maximum biomass is reached at the end of growth duration (Williams, 1964). The maximum rate of crop photosynthesis is also reached halfway through the duration and decreases thereafter but growth slows faster than photosynthesis because there is more and more biomass needing maintenance respiration. The driving variables are for a day averaged over the second half of growth duration. This is the period when the canopy is complete, interception of PAR is maximal, the rate of canopy photosynthesis is near maximum, and biomass is near maximum so that a high rate of maintenance respiration is occurring. Using single daily values for driving variables is a reasonable assumption in the tropics and subtropics where variations in solar angle and in temperature are relatively small across a period of two or three months. In temperate regions where solar angles and temperature change greatly during the growing season, this assumption—of linear averaging across several months—works less well.

Maximum shoot biomass is given by

$$W_{s\max} = c_T P_{d\max} \quad (3)$$

where c_T is a parameter governing the conversion of photosynthate into shoot biomass ($\text{g DM g}^{-1} \text{CH}_2\text{O d}$); and $P_{d\max}$ is maximum daily canopy gross photosynthesis ($\text{g CH}_2\text{O m}^{-2} \text{ground d}^{-1}$).

The parameter c_T is dependent on mean air temperature through one of its components. It is a collection of other parameters:

$$c_T = \frac{\beta f}{m_T(1 - d_{\max})} \quad (4)$$

where β is a coefficient (dimensionless) taking account of allocation to roots, losses as root exudates, and synthetic respiration; f (dimensionless) reduces $P_{d\max}$ from its peak value as the crop approaches maturity; m_T is the coefficient for maintenance respiration ($\text{g CH}_2\text{O g}^{-1} \text{DM d}^{-1}$); and d_{\max} (dimensionless) is the maximum fraction of shoot biomass which is dead.

Only part of gross photosynthesis can appear in shoot biomass. There are losses to roots and respiration. Roots are assumed to be 0.15 of total crop biomass, a suitable value for rice during the second half of growth duration. Respiration is divided into two components: one associated with synthesis of new biomass, at a cost of 25% of the carbohydrate available; and the other associated with the maintenance of biomass and thus varying with the amount of biomass at any one time and also sensitive to temperature (McCree, 1970; Amthor, 2000). About 5% of daily photosynthesis is lost as root exudates (Marschner, 1995). The parameter β takes account of allocation to roots, exudation from roots, and synthetic respiration

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