THEORETICAL MAXIMUM ALGAL OIL PRODUCTION

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ABSTRACT

Interest in algae as a feedstock for biofuel production has risen in recent years, due to projections that algae can produce lipids (oil) at a rate significantly higher than agriculture-based feedstocks. Current research and development of photobioreactors for commercial-scale algal oil production is directed towards pushing the upper limit of productivity beyond that of open ponds. So far most of this development is in a prototype stage, so working production metrics for a commercial-scale photobioreactor system are still unknown, and projections are largely based on small-scale experimental data. Given this research climate, a methodical analysis of a maximum algal oil production rate from a theoretical perspective will be useful to the emerging industry for understanding the upper limits that will bound the production capabilities of new photobioreactor designs. This paper presents a theoretical approach to calculating an absolute upper limit to algal production based on physical laws and assumptions of perfect efficiencies. In addition, it presents a practical case that represents a feasible target for production based on realistic efficiencies and is calculated for six global sites. The theoretical limit was found to be 38,000 $\text{gal}\cdot\text{ac}^{-1}\cdot\text{yr}^{-1}$ (354,000 $\text{L}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of unrefined oil, while limits for the practical cases examined in this report range from 4,900 to 6,500 $\text{gal}\cdot\text{ac}^{-1}\cdot\text{yr}^{-1}$ (46,300-60,500 $\text{L}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of unrefined oil.

KEYWORDS: Algae; Biofuels; Theoretical yield; Oil production; Second-generation feedstock

ABBREVIATIONS:

DCW	Dry Cell Weight
NREL	National Renewable Energy Laboratory
PAR	Photosynthetically Active Radiation
PE	Photosynthetic Efficiency

INTRODUCTION

Algae as a feedstock is emerging at the forefront of biofuel research due to increasing awareness of global energy issues in conjunction with the production limitations of agriculture-based oilseed crops [7, 27]. Many species of algae exhibit promise in this capacity because of their characteristics of high lipid content and rapid growth, which result in areal productivity significantly higher than oilseed crops. Additionally, because algae are grown in water rather than soil, algal production can be sited on land not suitable for agricultural use.

The potential of algae as a biofuels feedstock was investigated extensively by the Aquatic Species Program of the National Renewable Energy Laboratory (NREL), focusing specifically on open-pond production designs [28]. That program concluded that large-scale algal production could be an economically-competitive source of renewable energy. Recent years have seen the emergence of new enclosed photobioreactor designs, which are expected to improve yields over the open-pond design by protecting productive strains from contamination and using higher surface-area-to-volume ratios to optimize light utilization. In light of the recent research, a calculation of the theoretical limits of algal production will provide a useful benchmark for understanding the yields that can be realistically expected from this new biofuel technology.

While numerous studies have addressed maximum theoretical efficiency of photosynthesis [5, 8, 22, 24], they have not been applied specifically to algal biofuel production or extrapolated to calculate maximum instantaneous efficiency and maximum annual production yield. Calculations by Raven [24] and Goldman [12] are the closest in methodology to this work, but they focus primarily on daily rather than annual yields and include assumptions of unknown efficiencies akin to the practical case in this work, but do not address a purely theoretical case. Likewise, many projections have been made of expected production yields, but are frequently based on small-scale experiments or include estimations of future advances [7, 27, 28].

The limits presented in this paper apply to any large-scale algal production system that relies only on solar energy input to drive growth and oil production. Systems that use artificial lighting or other additional energy inputs, such as sugars for heterotrophic growth, are not considered. The calculation for theoretical maximum yield is based on physical laws, an established value for quantum yield, solar irradiance assuming perfectly clear weather and atmospheric conditions, and assumes 100% for unknown efficiencies. Thus, the theoretical maximum yield is a true upper limit: a value that cannot be surpassed without breaking fundamental physical laws. Due to the numerous assumptions of perfect efficiency employed in the theoretical calculation, it is an unattainable goal. A practical case is also calculated, in order to provide designers with a realistic goal, which employs solar irradiance data for several sites and reasonable but conservatively high values for some efficiencies that were assumed to be 100% in the theoretical case. The practical case therefore represents what may be possible with system optimization. Uncertainties in several terms were used to provide error bars on both yield results. These values provide a benchmark against which to gauge predicted and achieved yields both to the designers of algae production systems and those seeking to implement the technology.

Calculations are expressed in SI units, but the final areal productivity is also presented in $gal \cdot ac^{-1} \cdot yr^{-1}$ *to provide a meaningful number to English-unit readers.*

METHODS

The primary physical law that limits the production capabilities of algae is the first law of thermodynamics, which states conservation of energy for any system: $\dot{E}_{in} \geq \dot{E}_{stored}$. For a system of photosynthesizing algae, $\dot{E}_{in}$ is the rate of incident solar irradiance on the production area and $\dot{E}_{stored}$ is the rate of chemical energy storage by the algae as oil and other biomass. Thus, the amount of stored chemical energy is directly limited by the amount of solar irradiance available.

The intention of the theoretical maximum yield calculation is to provide a value that relies only on physical laws and well-known values so that it cannot be disputed as the upper limit to production. For this reason, several efficiencies that reasonably cannot be 100% have been conservatively included in the calculation as 100% because a value has not yet been well-established. Thus, the calculated theoretical maximum yield is not dependent on estimates that could easily change depending on new experimental results or species. Because the intention of the practical case is to provide a value that gives a realistic production goal, estimates of known phenomena are included in the calculation for the practical case.

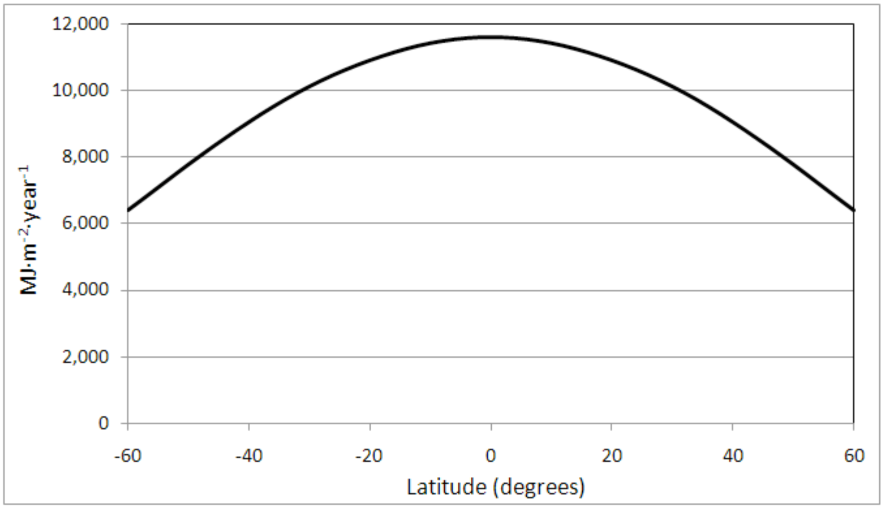
The equation to calculate total yield for both the theoretical and practical cases is identical. The calculations differ only due to different values used for the two cases. The equation includes eleven terms and gives annual production yield, in volume·area^{-1}·year^{-1} of unrefined oil. Several subsets of the terms produce other metrics of note. The first three terms combined result in total photons of average energy in the photosynthetically active portion of the spectrum. Terms 3, 6 and 7 combined result in maximum photosynthetic efficiency, which is a measure of energy stored as biomass per incident solar energy. The first nine terms combined result in growth rate, given as mass·area^{-1}·day^{-1} of biomass.

Term 1: Full-spectrum Solar Energy

The term *Full-spectrum Solar Energy,* ($E_{full-spectrum}$), represents the total solar irradiance incident on the algal production system. The solar spectrum is a function of atmospheric conditions (including clouds, aerosols, ozone and other gases), which affect both the magnitude and spectral distribution of solar irradiance that reaches the earth's surface.

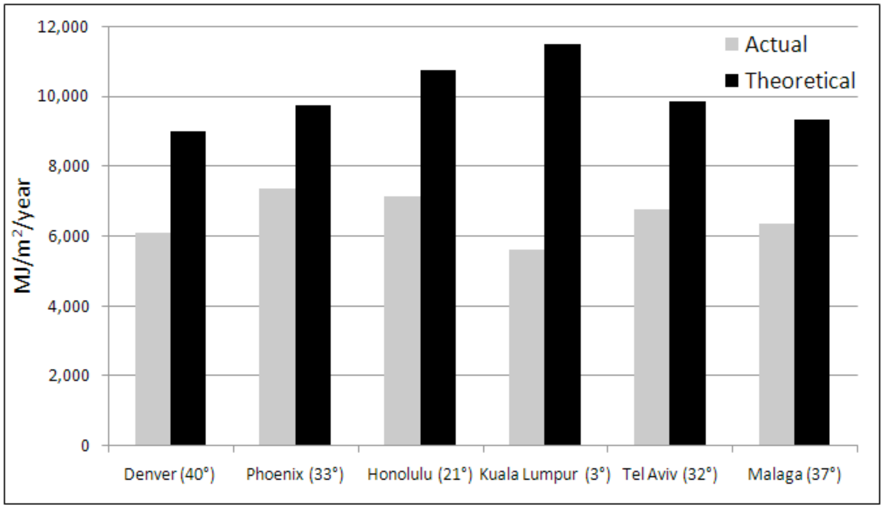
For the theoretical case, total solar irradiance was calculated assuming year-round clear skies and minimal atmospheric absorption. With these assumptions, theoretically maximum total solar irradiance is a function of latitude alone, shown in Figure 1. Calculations for this graph used the Bird Clear Sky Model [3].

Fig. 1: Theoretical maximum annual solar irradiance as a function of latitude ($\mathbf{E_{full-spectrum}}$)



For the practical case, total solar irradiance was calculated using weather data for six global climates, because the actual amount of irradiance is greatly reduced from the theoretical by clouds and other absorptive atmospheric conditions. Weather data that represents typical conditions were used from the Department of Energy's EnergyPlus® weather data set. The six sites and their latitudes are Denver, Colorado (40°N); Phoenix, Arizona (33°N); Honolulu, Hawaii (21°N); Kuala Lumpur, Malaysia (3°N); Tel Aviv, Israel (32°N); and Màlaga, Spain (37°N). Figure 2 shows a comparison of theoretical and actual values on an annual basis. As this figure shows, solar irradiance is strongly dependent on the climate, not only latitude. For example, Phoenix has the highest total annual solar irradiance despite its relatively high latitude. Kuala Lumpur, close to the equator and with the highest theoretical solar irradiance, has the lowest.

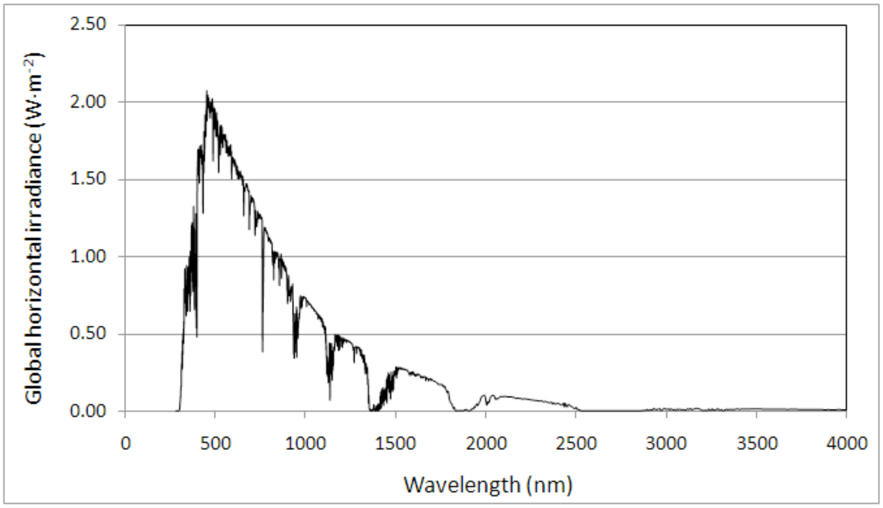
Fig. 2: Annual theoretical and actual solar irradiance by site



Term 2: Photosynthetic Portion of Spectrum

The term *Photosynthetic Portion of Spectrum (%PAR)* accounts for the fact that only a portion of the solar spectrum is utilizable for photosynthesis. That portion is known as PAR (photosynthetically active radiation) and is commonly defined as 400-700 nm. The curve of intensity as a function of wavelength ($E_{solar}(\lambda)$) was calculated with clear-sky assumptions using the SMARTS model [15, 16] (Fig. 3).

Fig. 3: Spectral distribution of solar irradiance ($E_{solar}(\lambda)$)



$E_{solar}(\lambda)$ was used to calculate term 2, *%PAR*, the ratio of PAR to full-spectrum solar energy by Equation A, where 99% of the solar spectrum falls in λ≤4000 nm:

$$\%PAR = \frac{PAR\ energy}{FS\ energy} \times 100 = \frac{\int_{\lambda=400\ nm}^{700\ nm} E_{solar}(\lambda)\, d\lambda}{\int_{\lambda=0\ nm}^{4000\ nm} E_{solar}(\lambda)\, d\lambda} \times 100 \qquad \text{(A)}$$

%PAR was calculated to be 45.8%, which is in agreement with published literature [12, 13, 20]. *%PAR* was assumed to be constant, though it does vary a small amount depending on the ratio of direct to diffusion solar irradiance.

It should be noted that although the entire 400-700 nm portion of the spectrum is considered to be "photosynthetically active", the absorption spectrum of chlorophyll for any oxygenic photosynthesizing organism absorbs best at the edges of this range (blue and red light), and not as well in the middle (green). Therefore *%PAR* may conservatively overestimate the actual solar energy available for photosynthesis.

Term 3: Photon Energy

The term *Photon Energy,* ($\overline{E_{photon}}$) converts PAR as energy to number of photons. $E_{solar}(\lambda)$, calculated in term 2, was used to calculate term 3, the wavelength-weighted average photon energy, $\overline{E_{photon}}$. Within the PAR range, photon energy ranges from most energetic (299 kJ·mol^{-1}) at 400 nm (blue) to least energetic (171 kJ·mol^{-1}) at 700 nm (red). These are calculated using Planck's law ($E_{photon} = h \cdot c/\lambda$, where *h* is Planck's constant (6.63E-34 J·s), *c* is the speed of light (2.998E8 m·s^{-1}), and λ is wavelength). $\overline{E_{photon}}$ was calculated to be 225.3 kJ·mol^{-1}, or 0.2253 MJ·mol^{-1}, also in good agreement with published values [13, 20]. This corresponds to a wavelength of 531 nm (green).

Total photon flux over a year can be calculated from a combination of Terms 1, 2 and 3 by Equation B.

$$Photon\ Flux\left(\frac{mol\ photons\ incident}{m^2 \cdot year}\right) = \frac{E_{full-spectrum}\left(\frac{MJ}{m^2 \cdot year}\right) \times \frac{\%PAR}{100}}{\overline{E_{photon}}\left(\frac{MJ}{mol}\right)} \qquad \text{(B)}$$

Term 4: Photon Transmission Efficiency

The term *Photon Transmission Efficiency* accounts for losses in incident solar energy due to the construction or geometry of the growth system, either an open pond or enclosed photobioreactor. Light reflection or absorption by surfaces and materials will be minimized in an optimized design, but any design will have some reduction in the number of incident photons that reach the cells. For the theoretical case, the growing system was assumed to preserve total photon flux, i.e. no reduction to 100% photon transmission efficiency. For the practical case, the reduction in photon flux due to the growth system was modestly assumed to be 10%, resulting in a photon transmission efficiency of 90%.

Term 5: Photon Utilization Efficiency

The term *Photon Utilization Efficiency* accounts for reductions in perfect photon absorption due to suboptimal conditions of the algal culture. A cell under optimal conditions will absorb and use nearly all incident photons. However, under sub-optimal conditions such as high-light levels or non-optimal temperatures under which photoinhibition occurs, some absorbed photons will be re-emitted as heat or cause damage to the cells. For the theoretical case, the culture was assumed to be maintained under perfectly optimal conditions such that all incident photons would be absorbed and used, i.e., there would be no reduction in the 100% photon utilization efficiency. For the practical case, reduction in photon utilization due to high-light levels can be significant for outdoor production. Light utilization efficiency could range from 50-90% under low-light conditions, to 10-30% under high-light conditions [12]. Therefore, for the practical case, a median value of 50% was chosen, which may be conservatively high, given that high-light conditions are likely to be found in outdoor growth systems.

Terms 6 and 7: Quantum Requirement and Carbohydrate Energy Content

The terms *Quantum Requirement* and *Carbohydrate Energy Content* together represent the conversion of light energy to chemical energy via photosynthesis. The basic equation for photosynthesis is commonly expressed by Equation C:

$$CO_2 + H_2O + 8 \text{ photons} \rightarrow CH_2O + O_2 \qquad (C)$$

This equation represents a combination of two reactions: (1) energy transduction in the two photosystems, which produces ATP and NADPH via electron transfer stimulated by photon absorption, and (2) carbon assimilation in the Calvin Cycle, which uses the energy of the ATP and NADPH produced in the photosystems to fix CO_2 and produce chemical energy. In Equation C, CH_2O represents the basic form of chemical energy captured by photosynthesis. Its actual form is triosephosphate ($C_3H_5O_3P$), but the energy content is often calculated from glucose ($C_6H_{12}O_6$). Several reported values for CH_2O include 496, 494, 468.9 and 470 $kJ \cdot mol^{-1}$ [5, 12, 26, 30]. The median of the range of cited values, 482.5 $kJ \cdot mol^{-1}$, was used for term 7, *Carbohydrate Energy Content*.

Term 6, *Quantum Requirement*, represents the energy input on the left side of Equation C of 8 mol photons per mol of CO_2 reduced to CH_2O. At perfect efficiency, the quantum requirement would be 3, because 3 of the least energetic photons (at 700 nm) have an energy of $3 \times 170.9\ kJ \cdot mol^{-1} = 512.7\ kJ \cdot mol^{-1}$. This is slightly higher than the required energy of 482.5 $kJ \cdot mol^{-1}$. However, extensive debates on this topic since the middle of the last century have resulted in a common agreement that the value of 8 mol photons per mol CO_2 reduced to CH_2O corresponds to maximally efficient photosynthesis based on the Z-scheme [5, 9, 14, 22, 23]. While some recent work suggests higher values may be more realistic, because of the methodology of conservatism to produce an absolute maximum, 8 was used because there is not yet consensus on a higher (and thus less efficient) theoretical quantum requirement.

Term 8: Biomass Accumulation Efficiency

The term *Biomass Accumulation Efficiency* accounts for energy that is used for cellular functions rather than stored directly as harvestable biomass. Thus, it is the ratio of the chemical energy stored in the cell (as biomass that can be harvested) to the total energy captured. During normal growth, energy required by the cell may be retrieved by consuming carbohydrates already stored, or by using ATP directly. All cell functions that require energy are included in this term, such as maintenance, repair, and synthesis of complex molecules. The complexities of energy use considered by *Biomass Accumulation Efficiency* are not well-understood, and are highly dependent on factors such as species, temperature, and nitrogen source. Therefore, because the methodology of the theoretical case seeks to avoid disputable assumptions, term 8 was considered to be 100%, perfect efficiency of biomass accumulation, implying that the cell does not require any of its captured energy to maintain itself or synthesize complex molecules.

For the practical case, the “cost of living" accounted for by this term was estimated from a survey of a variety of sources, some of which consider only respiration, and others which consider cell energy use comprehensively. Sukenik et al. [29] estimated that the costs of living consume 35% of the total energy captured by photosynthesis, meaning a biomass accumulation efficiency of 65%. Falkowski et al. [10] cited values of 47-86% for what the authors call "net growth efficiency" for various species and irradiances. Langdon [21] reported values for a respiration to gross production ratio of 21-89% for various species, which translates to 11-79% for this efficiency term. Goldman [12] used an estimate of 87.5%. For the practical case developed here, a value of 60% was chosen for *Biomass Accumulation Efficiency*.

Term 9: Biomass Energy Content

The term *Biomass Energy Content* describes how much mass will be produced for the amount of captured energy, also called heat of combustion. Values cited in other literature range from 20 to 23.75 kJ/g [2, 11, 12, 19, 28]. A median value of 21.9 kJ/g was chosen.

Terms 1 through 9 combined result in total biomass growth rate, usually expressed as $g \cdot m^{-2} \cdot day^{-1}$.

Term 10: Cell Oil Content

The term *Cell Oil Content* is the portion of the cell that can be refined into a usable biofuel. A theoretical maximum value is not yet known for a cell's oil content, and oil content is highly specific to species and growth conditions. Most values reported in the literature are total lipid content of dry cell weight (DCW), of which only a portion can be refined into a usable biofuel. Chisti et al. [7] present a summary of algal lipid contents ranging from 15 to 77% DCW. Rodolfi et al. [25] present cited values as high as 70 and 85% DCW, but also note that lipid accumulation often corresponds with reduced biomass productivity, so the high-growth requirement of production systems may necessitate species with lower lipid content and higher growth rates. A recent comprehensive survey by Hu et al. [18] shows an average total lipid content for oleaginous green algae of 45.7% DCW under stress conditions. To reiterate, only a portion of the total lipid content can be refined into usable fuel; this portion may reach 80% of total lipid content as an upper limit [18]. An additional overestimation may be introduced because most of the values reported in the literature are based on gravimetric analysis, which may overestimate total lipid content by co-extracting some non-lipid components such as proteins, carbohydrates, and pigments. For this work, 50% oil content was chosen for both the theoretical and practical maximum cases, though it is acknowledged this may be an overestimate of what will be achievable for production systems for the reasons stated above.

Term 11: Oil Density

The term *Oil Density* is the volumetric density of the unrefined oil. This term converts the mass of oil produced to a volume measurement. Because algal oil is a relatively new commodity, not much data exist for its physical properties. Therefore, the density of soybean oil, which is similar to algal oil, was used. The density of soybean oil was taken to be 918 $Kg \cdot m^{-3}$, with a range of 910 - 925 $Kg \cdot m^{-3}$ [4] for both the theoretical and practical cases.

RESULTS

The values used in the calculations and the resulting outputs for the theoretical and practical cases are summarized in Table I. The daily maximum growth for the theoretical case used the daily average, assuming sustained year-round production, because the theoretical case assumed a site on the equator, which has relatively constant solar irradiance. The daily maximum growth for the practical case used the day with peak solar energy, and thus represents a rate that could be achieved over short periods, but not sustained, unless the site sustained a high rate of solar energy, such as those close to the equator.

Table I: Results for Theoretical and Practical Maximum Cases

Term	Theoretical Maximum Case	Practical Maximum Case	Units
[1] Full-spectrum Solar Energy	11,616	5,623-7,349	$\frac{\text{MJ fullspectrum}}{\text{m}^2 \cdot \text{year}}$
[2] Photosynthetic Portion of Spectrum	45.8%	45.8%	$\frac{\text{MJ PAR}}{\text{MJ fullspectrum}}$
[3] Photon Energy	225.3E-3	225.3E-3	$\frac{\text{MJ PAR}}{\text{mol photons incident}}$
[4] Photon Transmission Efficiency	100%	90%	$\frac{\text{mol photons transmitted}}{\text{mol photons incident}}$
[5] Photon Utilization Efficiency	100%	50%	$\frac{\text{mol photons utilized}}{\text{mol photons transmitted}}$
[6] Quantum Requirement	8	8	$\frac{\text{mol photons utilized}}{\text{mol CO}_2\text{ reduced to CH}_2\text{O}}$
[7] Carbohydrate Energy Content	482.5	482.5	$\frac{\text{kJ CH}_2\text{O captured as biomass}}{\text{mol CH}_2\text{O}}$
[8] Biomass Accumulation Efficiency	100%	60%	$\frac{\text{kJ biomass stored}}{\text{kJ CH}_2\text{O captured}}$
[9] Biomass Energy Content	21.9E3	21.9E3	$\frac{\text{kJ biomass stored}}{\text{kg biomass}}$
[10] Cell Oil Content	50%	50%	$\frac{\text{kg oil}}{\text{kg biomass}}$
[11] Oil Density	918	918	$\frac{\text{kg oil}}{\text{m}^3\text{ oil}}$
Maximum daily growth	196	38-47	$\frac{\text{grams biomass}}{\text{m}^2 \cdot \text{day}}$
Annual oil production (English units)	38,000	4,900 (Kuala Lumpur) 5,300 (Denver) 5,600 (Màlaga) 5,900 (Tel Aviv) 6,300 (Honolulu) 6,500 (Phoenix)	$\frac{\text{gallons oil}}{\text{acre} \cdot \text{year}}$
Annual oil production (SI units)	354,000	46,000 (Kuala Lumpur) 50,000 (Denver) 52,000 (Màlaga) 56,000 (Tel Aviv) 59,000 (Honolulu) 60,500 (Phoenix)	$\frac{\text{liters oil}}{\text{hectare} \cdot \text{year}}$

The uncertainties in Terms 1, 7, 9, and 11 should be taken into account and these were used to add error bars to the results. These are the only terms included because the others are assumptions appropriate to the methodology (Terms 4, 5, 8, 10) or are well-established values (Term 6). Any uncertainty in Terms 2 and 3 is assumed to be captured in the uncertainty in Term 1. The effect of the collective uncertainty in Terms 1, 7, 9, and 11 on the final result was calculated by using the sets of values that maximally increase or decrease the final result. For example, if the result were calculated from $C= A/B$, then the highest possible result due to the uncertainties would be calculated from $C_{high}=(A+\Delta A)/(B-\Delta B)$, and the lowest possible result would be calculated from $C_{low}=(A-\Delta A)/(B+\Delta B)$, where ΔA and ΔB are the errors associated with Terms A and B.

The uncertainties in Terms 1, 7, 9, and 11 are illustrated by the error bars in Figures 4 and 5. For Term 1, *Full-spectrum solar energy*, an uncertainty of ±10% was used for the theoretical calculation of total solar based on the two radiation models employed. Term 1 for the practical case has no uncertainty because the dataset is derived from several decades of data and represents typical weather conditions. For Terms 7, 9, and 11, uncertainties of 2.2%, 8.4%, and 1%, respectively, were taken from the ranges of cited values found in the literature. Error bars in Figure 4 increase with latitude because they are calculated as a percent of Term 1, the total solar energy for a particular latitude

Fig. 4: Theoretical maximum yield as a function of latitude

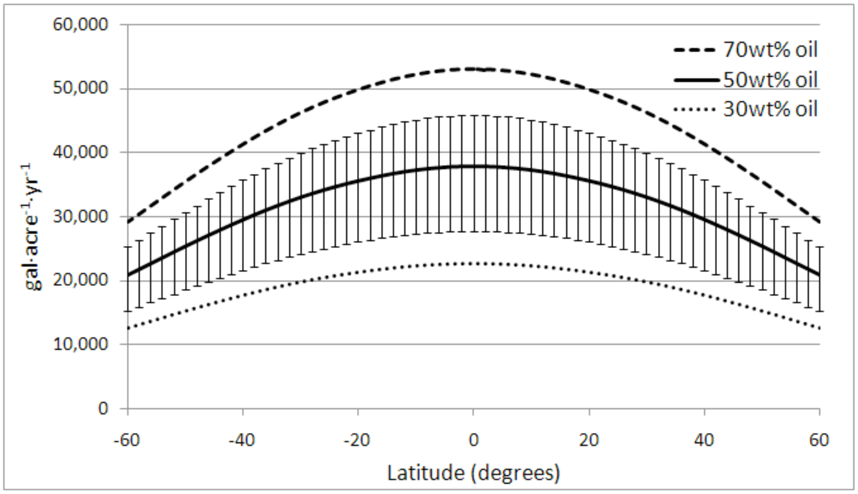
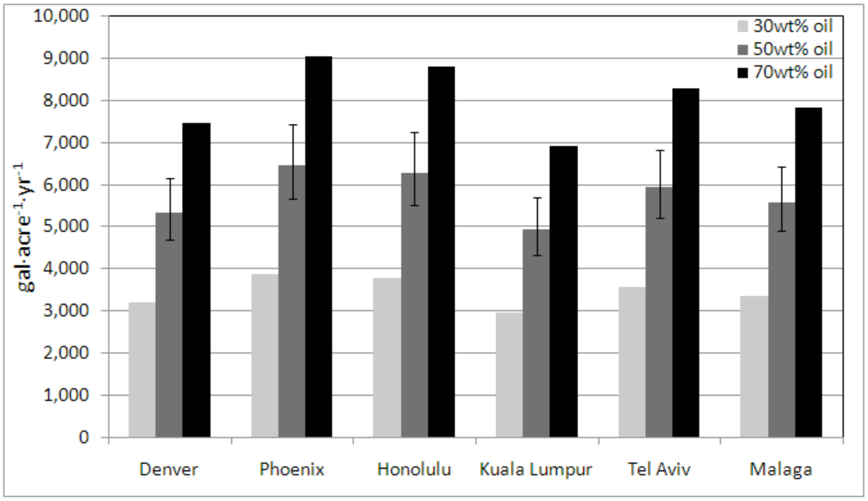
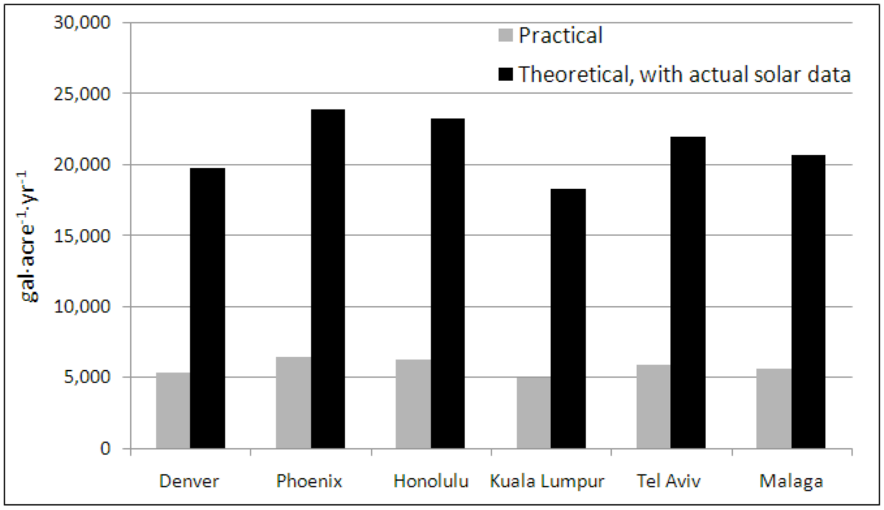


Fig. 5: Practical maximum yield by site



Because the theoretical case uses the assumption of an equatorial site with perfectly clear skies, it represents an unattainable maximum for any location, and it is also much higher than the theoretical limit for any particular site off the equator with realistically cloudy weather. Because the amount of solar energy available is fixed and known from weather data, an additional case can be calculated: a theoretical case using actual solar data for specific sites. This modification only changes Term 1 (*Full-spectrum solar energy*) in the theoretical case. The theoretical maximum yields for the six sites chosen in the paper range from 18,300 to 24,000 gal·ac^{-1}·yr^{-1}, for Kuala Lumpur and Phoenix, respectively (171,000-224,000 $L\cdot ha^{-1}\cdot yr^{-1}$). This case compared to the practical case for the six sites is shown in Figure 6.

Fig 6: Practical and theoretical yields, using actual solar data for both



DISCUSSION

The practical case agrees well with other projections and reported experimental results. The Aquatic Species Program report by NREL included projections based on experiments ranging from 50 to 300 $mt\cdot ha^{-1}\cdot yr^{-1}$, which is equivalent to 2,913-17,478 $gal\cdot ac^{-1}\cdot yr^{-1}$ [28]. Chisti [7] predicted yields of 6,276-14,637 $gal\cdot ac^{-1}\cdot yr^{-1}$ for 30wt%-70wt% oil, respectively, which are somewhat more optimistic than the practical case of this paper, but the climate was unspecified. Other reported projects were often expressed as daily biomass yield, rather than annual oil yield. Daily biomass yields rates reported in the published literature ranged from 10 to 37 $g\cdot m^{-2}\cdot d^{-1}$, average for the production length in a variety of sites; peak rates ranged from 24 to 65 $g\cdot m^{-2}\cdot d^{-1}$ [1]. The recent work by Roldolfi et al. [25] predicts yields of 3,490 $gal\cdot ac^{-1}\cdot yr^{-1}$ for tropical climates, which falls at the lower end of the practical range.

The results cited above also agree well with other reported calculations of theoretical maximum production. Raven [24] calculated a range of theoretical maximum yields for various quantum requirement assumptions; for a quantum requirement of 8, Raven calculated 173 $g\cdot m^{-2}\cdot d^{-1}$. The assumed solar energy in that paper (42.5 MJ·m^{-2}·d^{-1}) is higher than the assumed solar energy in this paper, but is based on an assumption of noontime equator sunlight for a twelve hour day. Goldman's [12] calculation of a production maximum of 58 g·m^{-2}·d^{-1}, from a solar input of 33.5 MJ·m^{-2}·d^{-1}, closely matched the practical case of this paper.

The main differences among approaches to calculating a theoretical maximum involve the assumed solar irradiance, which is the main driving force for photosynthesis, and the quantum requirement. This paper addresses these differences by conservatively choosing values that will maximize the theoretical limit, thus presenting it as a true maximum that cannot be attained in any location.

A calculation of photosynthetic efficiency for algae can be made for the theoretical and practical approaches for comparison to what is observed in terrestrial plants. Maximum theoretical photosynthetic efficiency (PE) applies to any photosynthesizing organism, and is given by Equation D (based on PAR rather than full-spectrum solar irradiance):

$$PE_{PAR} = \frac{482.5\ \left(\frac{kJ}{mol\ CH_2O}\right)}{8\ \left(\frac{mol\ photons}{mol\ CH_2O}\right) \times 225.3\ \left(\frac{kJ}{mol\ photons}\right)} = 26.7\% \qquad \text{(D)}$$

This would be the photosynthetic efficiency for the theoretical case of perfectly efficient algae. For the practical case, the reductions in perfect efficiency from terms 4, 5, and 8 of 90%, 50%, and 60%, respectively, result in a photosynthetic efficiency of 7.2%. In outdoor cultures of *Chlorella* in full sunlight, Burlew [6] achieved 2.6-2.7% photosynthetic efficiency based on PAR; for reduced sunlight (reduced to 22%), he achieved 6.3%. Most terrestrial plants are usually assumed to convert ~0.1% of solar energy into biomass. Zhu et al. [30] reported that the highest efficiencies achieved are 2.4% and 3.7% for C3 and C4 crops, respectively. Even crops considered to be high-productivity, such as the perennial grass Miscanthus, achieve only up to 1-2% efficiency, based on PAR [17].

The calculation methodology of this paper makes evident the areas of focus for maximizing oil production. Just four of the eleven terms used in this calculation reduce the practical case from the theoretical; *Full-spectrum Solar Energy (Term 1),* which accounts for the total solar energy available; *Photon Transmission Efficiency (Term 4)*, which accounts for losses through the growth system geometry; *Photon Utilization Efficiency (Term 5)*, which accounts for losses due to photoinhibitive and other growth inhibiting effects; and *Biomass Accumulation Efficiency (Term 8)*, which accounts for cellular energy requirements. The first is influenced only by site selection and can be easily calculated from weather data. Of the latter three, *Photon Transmission Efficiency* may be increased through careful design of growth system geometry. *Photon Utilization Efficiency* may be maximized by distributing incident light broadly over a wide surface area, or strain improvements that improve a species' tolerance to high-light levels. The costs associated with the last, *Biomass Accumulation Efficiency*, are unavoidable because all cells require some of their captured energy for maintenance and growth, but species selection and other factors such as temperature will influence the magnitude. The success of algal production systems will largely be a function of how well the system is optimized to improve these efficiencies by providing optimal conditions for growth and lipid storage.

While the practical case includes the estimates for efficiencies that may be improved with optimization of the growth system and chosen algal strain, the theoretical case includes no estimates and thus continues to represent an unattainable limit despite system optimization and even genetic improvements to algal strains. Any possible genetic improvements would be aimed at improvements in the efficiencies included in the practical case (terms 4, 5, or 8). These might include decreasing photoreceptor antennae to reduce photoinhibitive effects, increasing temperature tolerance, or improving resistance to predatory species. These effects are already assumed to be nonexistent in the theoretical case.

Despite any discrepancies among approaches, all estimates affirm the productive potential of algae as a biofuel feedstock. The lowest projection in this paper, is 4,900 $gal{\cdot}ac^{-1}{\cdot}yr^{-1}$, for Kuala Lumpur, is drastically higher than reported yields for corn (18 $gal{\cdot}ac^{-1}{\cdot}yr^{-1}$), canola (127 $gal{\cdot}ac^{-1}{\cdot}yr^{-1}$) or even oil palm

(637 gal·ac^{-1}·yr^{-1}) [7]. Thus, the bounds on algal production presented in this paper should not be viewed as unpleasant news about physical realities, but as a realistic check that confirms its potential and will serve the industry in its pursuit of maximum algal biofuel production.

CONCLUSION

A process of employing basic physical laws, known values, and conservative assumptions has resulted in a robust calculation of theoretical maximum and practical algal oil yields. For the theoretical case on the equator with 50% cell oil content, the theoretical maximum annual oil production from algae was calculated to be 38,000 gal·ac^{-1}·yr^{-1} (354,000 L·ha^{-1}·yr^{-1}) with an uncertainty of roughly 10%. The practical maximum was calculated to range from 4,900 to 6,500 gal·ac^{-1}·yr^{-1} (46,000-60,500 L·ha^{-1}·yr^{-1}).

The equations, calculations, and discussions in this paper have shown that, because physical laws dictate the theoretical maximum, it represents a true upper limit to production that cannot be attained regardless of new technology advances. However, if algal biofuel production systems approach even a fraction of the calculated theoretical maximum, they will be extremely productive compared to current production capability of agriculture-based biofuels.

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