Photosynthetic Energy Conversion Efficiency: Setting a Baseline for Gauging Future Improvements in Important Food and Biofuel Crops[1]

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The conversion efficiency (ε_c) of absorbed radiation into biomass (MJ of dry matter per MJ of absorbed photosynthetically active radiation) is a component of yield potential that has been estimated at less than half the theoretical maximum. Various strategies have been proposed to improve ε_c, but a statistical analysis to establish baseline ε_c levels across different crop functional types is lacking. Data from 164 published ε_c studies conducted in relatively unstressed growth conditions were used to determine the means, greatest contributors to variation, and genetic trends in ε_c across important food and biofuel crop species. ε_c was greatest in biofuel crops (0.049–0.066), followed by C_4 food crops (0.046–0.049), C_3 nonlegumes (0.036–0.041), and finally C_3 legumes (0.028–0.035). Despite confining our analysis to relatively unstressed growth conditions, total incident solar radiation and average growing season temperature most often accounted for the largest portion of ε_c variability. Genetic improvements in ε_c, when present, were less than 0.7% per year, revealing the unrealized potential of improving ε_c as a promising contributing strategy to meet projected future agricultural demand.

Substantial increases in yield are needed to feed and fuel the world's growing human population. With an estimated population of nine billion people by the middle of this century (Lutz and Samir, 2010) and rising affluence resulting in greater consumption of grain-fed animal products (Cirera and Masset, 2010), different studies predict that, by midcentury, global crop production will need to increase 60% to 120% over 2005 levels without the expansion of agricultural land area (Tilman et al., 2011; Alexandratos and Bruinsma, 2012).

Doubling yields in major food and fuel crops requires considerable effort, especially as yields are beginning to plateau in many major food crops. Yield increases necessary for doubling productivity by midcentury are estimated at 1.16% to 1.31% each year in all cereals (Hall and Richards, 2013), 1.7% per year in wheat (*Triticum aestivum*; Rosegrant and Agcaoili, 2010), and 2.4% (noncompounding average per year) across all major grain crops (Ray et al., 2013). However, global mean increases from the past 20 to 30 years suggest that yield gains in rice (*Oryza sativa*) and wheat are approximately 1% (Lopes et al., 2012; Manès et al, 2012; Ray et al., 2013) and declining in some areas of the world (Cassman et al., 2010; Fischer and Edmeades, 2010; Long and Ort, 2010; Ray et al., 2013). Global yearly increases are estimated at 1.3% in soybean (*Glycine max*) and 1.6% in maize (*Zea mays*), with similar concerns that yield trends may also be decreasing in some major growing regions (Lobell and Gourdji, 2012; Ray et al., 2013).

Efforts to increase yields in the next few decades must also account for environmental and sustainability goals (Sayer et al., 2013) as well as heightened environmental stresses predicted to occur due to climate change, which are already responsible for some of the stagnation in yield increases. Anthropogenic sources of greenhouse gases have caused an approximately 1°C increase in land surface temperatures since 1900, and global mean surface temperatures are likely to increase by up to 2.4°C to 4.8°C by the end of the century (IPCC, 2013). Drought is also expected to become more frequent and intense in many regions of the world (Dai, 2011; IPCC, 2013). Of the variability present in major food crop yield gains, 30% can be explained by climate change alone (Lobell and Field, 2007), with drastic decreases in barley (*Hordeum vulgare*), maize, rice, sorghum (*Sorghum bicolor*), soybean, and wheat yields as average growing season temperatures surpass the temperature optimum for each crop (Lobell and Gourdji, 2012). Current levels of atmospheric CO_2 concentration [CO_2] are the highest they have been in at least 800,000 years (IPCC, 2013). Elevated [CO_2] increases water use efficiency (Ainsworth and Long, 2005, Bernacchi et al., 2007, Leakey et al., 2009), but probably not to an extent that would mitigate the resulting reductions in yield caused by higher temperature and higher vapor pressure deficit (Ort and Long, 2014). Additionally, any fertilization effects on C_3 yields due to elevated [CO_2] would be at least in part negated by drought and temperature stress, leaving yield increases

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far from optimal (Long et al., 2006a; Lobell and Gourdji, 2012).

USING PAST LITERATURE TO BETTER UNDERSTAND THE ROLE THAT IMPROVEMENTS IN CONVERSION EFFICIENCY HAVE PLAYED IN INCREASED YIELDS

To double yields in less than 50 years with the additional challenges of climate change, research needs to target yield-related processes that have potential for considerable improvement. The theoretical maximum conversion efficiency (ε_c) of photosynthetically active radiation (PAR) into plant biomass has been calculated in C_3 (0.094) and C_4 (0.123) plants in optimal conditions. The calculations are based on the minimal amounts of energy that could be lost due to various steps in transforming intercepted PAR into plant biomass. The steps where energy is lost include light reflection and transmission, photochemical inefficiency resulting from excess energy in absorbed blue light, thermodynamic limitations, carbohydrate synthesis, photorespiration (C_3 only), and respiration (Zhu et al., 2008, 2010). Estimated at less than half of the theoretical maximum in C_3 and C_4 plants in optimal conditions, ε_c appears to be an ideal candidate for increasing yield potential (Beadle and Long, 1985; Zhu et al., 2010). Moreover, considerable variation is present in ε_c, as it is sensitive to greenhouse gases and weather-related variables predicted to intensify due to climate change (Sinclair and Muchow, 1999; Slattery et al., 2013). Because ε_c is seemingly well below its theoretical maximum and is a highly variable parameter across growing environments and crop species, potential methods to improve ε_c have been identified and reviewed. The most general strategy for improving ε_c at the leaf level involves improving the efficiency of carboxylation by Rubisco while limiting oxygenation in C_3 plants (Zhu et al., 2010; Parry et al., 2011; Raines, 2011; Ainsworth et al., 2012; Evans, 2013). At the canopy level, targets include using altered canopy architecture and antenna size to improve light distribution in dense-canopy crops (Zhu et al., 2010; Ort et al., 2011; Parry et al., 2011; Ainsworth et al., 2012; Reynolds et al., 2012), maximizing nitrogen partitioning, and enhancing spike photosynthesis (Reynolds et al., 2012).

While there is seemingly substantial potential for increasing ε_c in major food and biofuel crops, judging the effectiveness of each strategy is difficult without baseline estimates of ε_c and rates of gain to date in individual crops. Sensitivity to environmental conditions implies that using single studies may not be the best method for gauging the status of ε_c within individual crop species. Therefore, a meta study of the large body of literature that exists on ε_c should provide insight into the current status of ε_c in individual crops, the extent that ε_c varies among food and biofuel crop species, which crops demonstrate greater potential for ε_c improvements, and inherent characteristics that may be benefitting crops with greater realized ε_c. Since the literature spans several decades, the extent to which genetic improvements versus climate change have contributed to changes in ε_c can also be assessed in individual crop species.

These analyses used primary literature to compare the mean ε_c among and within several food and biofuel crop species (Table I). Additionally, the relationships between ε_c and environmental and genetic variables were examined over several decades within major food crops. Briefly, studies containing ε_c (also referred to as radiation use efficiency) measurements under relatively unstressed growing conditions were collected. ε_c values were extracted from the resulting 164 studies (Supplemental Table S1). ε_c is generally calculated as the slope of crop accumulated biomass (in terms of mass or energy) versus intercepted or absorbed solar energy or PAR by the canopy. For the purpose of these analyses, all values were standardized to units of MJ of dry matter per MJ of absorbed PAR before statistically testing differences at $\alpha = 0.1$. An additional aim was to estimate rates of gain in ε_c due to breeding and to determine whether ε_c variation in major food crops over time was more significantly associated with breeding or climate variables. When available, crop information and growing conditions from each study were used as independent variables in multiple regression analyses. These variables included year of release (YOR), mean annual [CO_2] for the years that the experiments were conducted, mean growing season temperature (T), available incident solar radiation during the growing season (S_t), the amount of precipitation (rain and irrigation) available during the growing season, and plant density (maize only). Varieties included in the analyses were indicated for each crop and subgroup (Supplemental Table S2). In food crops with significant positive correlations between ε_c and YOR, the regression coefficient was used to determine the time to double or reach the maximum ε_c, assuming no major changes in trends due to genetic or environmental factors. (For a fully detailed explanation of the methods used in this study, see Supplemental Materials and Methods S1.)

STATUS OF ε_C IN MAJOR FOOD CROP SPECIES

Previous estimates putting ε_c means in food crops at approximately one-third to one-half of the maximum (Beadle and Long, 1985; Zhu et al., 2010) were consistent with the results from this study, with the exception of many legumes demonstrating values below one-third the C_3 maximum. Maize, a highly developed and intensively grown crop, had the greatest mean ε_c among food crops included in the analysis (0.0488; Fig. 1; Table II) but was still less than one-half the predicted maximum of 0.123 (Zhu et al., 2010). Grain sorghum was slightly lower than maize (0.0455; $P = 0.10$; Fig. 1) and was only 37% of the maximum. C_3 nonlegume crop means were significantly lower than C_4 means and ranged from 40% to 45% of the predicted maximum, with the greatest C_3 mean in potato (*Solanum tuberosum*; 0.0414; Fig. 1; Table II). Except for peanut (*Arachis hypogaea*), which had a mean ε_c of 0.0346 (Fig. 1; Table II)

Table I. *Important food and C_4 biofuel crop species used in ε_c analyses*

Species further divided into genetic components are indicated. Biomass energy content for vegetative (V) and combined vegetative and reproductive (V+R) stages used for converting ε_c values to energy units are indicated for each crop.

Species	Common Name	Type	Food or Energy Crop	Groups by Cultivar, Species, or Hybrid	Energy Content		Energy Content Data Source
					V	V+R	
					MJ kg^{-1}		
Z. mays	Maize	C_4	Both[a]		17.0	17.0	Penning de Vries et al. (1989)
S. bicolor	Sorghum	C_4	Both[a]	Energy/biomass/forage grain	17.6	17.3	Amthor et al. (1994)
S. tuberosum	Potato	C_3	Food		17.0	15.8	Penning de Vries et al. (1989)
O. sativa	Rice	C_3	Food	New hybrids *indica* *japonica* Basmati	15.1	15.9	Penning de Vries et al. (1989)
T. aestivum	Wheat	C_3	Food	Spring Winter	17.0	16.6	Penning de Vries et al. (1989)
H. vulgare	Barley	C_3	Food		16.1	15.6	McKendry (2002; V); Sinha et al. (1982; V+R)
A. hypogaea	Peanut	C_3	Food		17.9	23.3	Penning de Vries et al. (1989)
G. max	Soybean	C_3	Food		18.1	19.8	Amthor et al. (1994)
Cicer arietinum	Chickpea	C_3	Food		17.9	18.6	Penning de Vries et al. (1989)
Cajanus cajan	Pigeonpea	C_3	Food		17.9	18.4	Penning de Vries et al. (1989)
P. virgatum	Switchgrass	C_4	Energy		17.4	17.4	McKendry (2002)
Saccharum spp.	Sugarcane	C_4	Energy		17.4	17.4	Botha (2009)
Miscanthus spp.	Miscanthus	C_4	Energy	*M. giganteus* *M. sinensis*	18.5	18.5	McKendry (2002)

[a] Maize studies completely overlapped from food to energy analyses. Sorghum food and energy cultivars were separated and analyzed in the respective analyses.

and was approximately 38% of the maximum, all legume means were approximately 0.028 and 31% of the possible maximum for C_3 crops (Fig. 1; Table II).

One caveat is that this study omitted values from the literature that included belowground biomass, with the exception of peanut and potato, because (1) studies basing ε_c measurements on total aboveground and belowground biomass were minimal and (2) belowground harvesting methods differed greatly and, therefore, may have skewed the results. ε_c is estimated to increase by 10% to 20% when accounting for belowground biomass in annual plants (Sinclair and Muchow, 1999), which would result in an approximate increase of 0.01 in ε_c in food crops from this analysis, but this still would not account for the large disparity between measured and theoretical values. The greatest C_3 ε_c was in potato, which included belowground biomass but was still only 44% of the theoretical maximum. However, the omission of belowground biomass in the calculation of ε_c could have contributed to the disproportionately lower ε_c in legume crops if belowground biomass energy is greater in legumes compared with other crops. Indeed, belowground biomass (roots and nodules) of soybean contains more energy (18.3 MJ kg^{-1}) than sorghum belowground tissue (16.7 MJ kg^{-1}; Amthor et al., 1994). Based on energy contents reported on a per area basis by Amthor et al. (1994), accounting for soybean belowground biomass would increase whole-plant energy content by almost 6%. However, this would only increase soybean ε_c to approximately 0.03, which is still well below the ε_c of C_3 nonlegume crops (Fig. 1; Table II).

Additionally, legume ε_c may have been affected by nitrogen fixation, the costs of which have been determined and vary by study. One study reports a 5% greater photon energy requirement for nitrogen fixation compared with the combined cost of NH_4^+ and NO_3^- assimilation that occurs in most nonlegume crops (Andrews et al., 2009). In terms of carbon usage, the proportion of

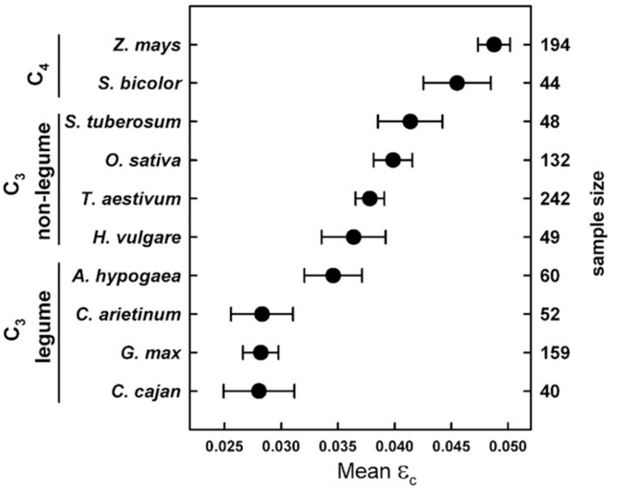

Figure 1. Calculated ε_c means in 10 major food crops. Crops are organized by C_4, C_3 nonlegume, and C_3 legume categories. Sample size is shown on the right axis. Error bars represent 90% confidence intervals.

Table II. *Numerical data from mean ε_c analyses in major food crops*

Species, common name, photosynthetic type, and any groups or specifications within species are indicated. ε_c means and SE are reported along with sample size (*n*) for each species and group within species.

Species	Common Name	Type	Groups by Cultivar, Species, or Hybrid	Mean ε_c	SE	*n*
Z. mays	Maize	C_4		0.0488	0.001	194
S. bicolor	Sorghum	C_4	Grain type only	0.0455	0.002	44
S. tuberosum	Potato	C_3		0.0414	0.002	48
O. sativa	Rice	C_3		0.0399	0.001	132
			New hybrids	0.0472	0.002	29
			indica	0.0442	0.002	25
			japonica	0.0388	0.002	57
			Basmati	0.0273	0.003	21
T. aestivum	Wheat	C_3		0.0378	0.001	242
			Spring	0.0352	0.001	105
			Winter	0.0399	0.001	137
H. vulgare	Barley	C_3		0.0364	0.002	49
A. hypogaea	Peanut	C_3		0.0346	0.002	60
G. max	Soybean	C_3		0.0282	0.001	159
C. arietinum	Chickpea	C_3		0.0283	0.002	52
C. cajan	Pigeonpea	C_3		0.0280	0.002	40

assimilated carbon that is diverted to the nodules for nitrogen fixation is reported as 7% to 19% (Gordon et al., 1987; Vessey et al., 1988; Hansen et al., 1992, 1993; Fujikake et al., 2003; Ito et al., 2006). Correcting for these costs on ε_c would result in a range of 0.03 to 0.034 for the legumes in this study (excluding peanut). These values are still lower than nonlegume ε_c values (Fig. 1; Table II), but other factors related to nitrogen fixation may also limit legumes, such as the delay in forming mature nodules early in the growing season (Andrews et al., 2009). Therefore, increasing the efficiency of nitrogen fixation may represent an additional means to improve ε_c in legumes that has previously received little attention with regard to increasing photosynthetic efficiency.

Peanut was the anomaly within the legume group, with ε_c more similar to nonlegume C_3 crops than to legumes. Although a portion of belowground biomass was included in the analyses of all peanut studies included, this only comprised the fruiting bodies growing underground and did not include the rest of the root biomass. A more likely explanation for the disparity between peanut and other legumes in this study was the difference in reported energy contents. Peanut whole-plant energy content was 1.2 times greater than that in the rest of the legumes (Table I), which corresponded to an approximately 1.2 times greater efficiency (Fig. 1; Table II).

ε_C VARIES AMONG GROUPS WITHIN RICE AND WHEAT, BUT THIS MAY BE THE RESULT OF VARYING GROWTH CONDITIONS

Significant differences in ε_c were evident within the subgroups of rice and wheat (Fig. 2) but may have been confounded by differences in growth environments (Supplemental Table S3). At approximately one-half of the C_3 theoretical maximum, the ε_c of new hybrid (0.0472) and *indica* (0.0442) rice varieties was significantly greater than that of *japonica* (0.0388) and basmati rice (0.0273; Fig. 2). New hybrid rice ε_c was not significantly different from maize ε_c ($P = 0.51$), and neither new hybrid nor *indica* ε_c was significantly different from grain sorghum ε_c ($P = 0.49$ and $P = 0.72$, respectively). However, a negative relationship between available S_t and subgroup ε_c suggested that the significantly greater ε_c in new hybrid and *indica* varieties may be associated with growth conditions rather than genetic enhancements (Supplemental Table S3). Significant differences were also evident between the ε_c means of spring wheat (0.0352) and winter wheat (0.0399; $P < 0.01$; Fig. 2; Table II). However, mean S_t and T were once again lower in

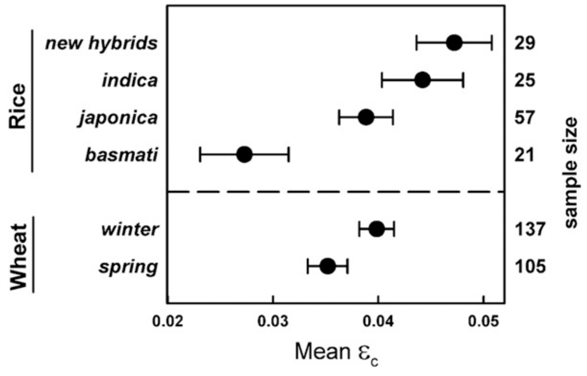

Figure 2. Calculated ε_c means for categories within rice (top) and wheat (bottom). Sample size is shown on the right axis. Error bars represent 90% confidence intervals.

winter wheat compared with spring wheat (Supplemental Table S3), the effects of which are discussed below.

ε_Cs IN BIOENERGY CROPS

Not surprisingly, C_4 crop ε_c was almost always greater than C_3 ε_c due to inherent properties of C_4 photosynthesis. C_4 plants concentrate CO_2 at the site of carboxylation, thereby inhibiting energy losses to photorespiration and increasing the maximum potential ε_c as compared with C_3 plants (Zhu et al., 2008, 2010). However, ε_c was often greater in C_4 energy crops compared with C_4 food crops. At 0.066, nongrain sorghum varieties had the greatest ε_c mean of the energy crops included and reached 54% of the theoretical mean for C_4 crops (Fig. 3; Table III). Switchgrass (*Panicum virgatum*) ε_c was not significantly lower than sorghum ε_c ($P = 0.44$) and was also greater than 50% of theoretical (0.0618; Fig. 3; Table III). Sugarcane (*Saccharum officinarum*) was similar to sorghum ($P = 0.16$) and switchgrass ($P = 0.42$), with a mean of 0.0581 (Fig. 3; Table III), and was not significantly different from the *Miscanthus* × *giganteus* mean of 0.0503 ($P = 0.11$; Fig. 3; Table III). Maize ε_c was the second lowest of the bioenergy crops (0.0488; Fig. 3; Table III), despite having the highest ε_c of the food crops (Fig. 1; Table II). *Miscanthus sinensis* had the lowest mean of the bioenergy crops (0.027) and was only 23% of the maximum theoretical for C_4 crops (Fig. 3; Table III).

The apparent disparity between C_4 food and bioenergy crop ε_c may be the result of plant growth habit. Unlike the annual C_4 food crops, most of the C_4 energy crops were perennial grasses, which are expected to demonstrate greater aboveground biomass than annuals early in the season. Once established, perennials such as *M. giganteus* and switchgrass draw upon belowground reserves from the previous season to facilitate growth after emergence that is independent of absorbed radiation (Dohleman et al., 2012). This would inflate ε_c in perennial C_4 biofuel crops during early crop growth. A comparison by Ceotto et al. (2013) of the C_3 perennial giant reed (*Arundo donax*) and the C_4 annual energy crop sorghum supported this point. ε_c in giant reed, which demonstrates photosynthetic rates typical of C_3 plants (Balota et al., 2008), was greater than the ε_c of the C_4 annual sweet sorghum (Ceotto et al., 2013). However, the intercept of the relationship between aboveground biomass and intercepted radiation in giant reed was greater than zero, suggesting that rhizome energy contributions to aboveground biomass were increasing shoot growth rates independent of radiation absorption (Ceotto et al., 2013).

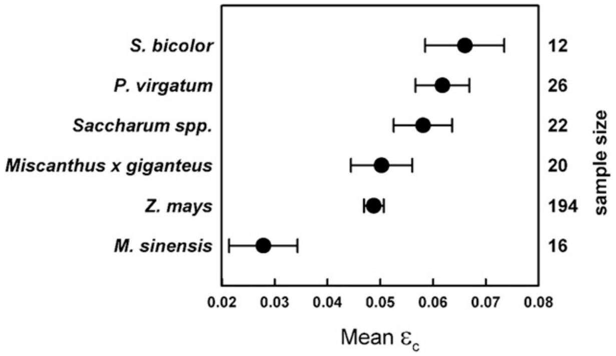

Figure 3. Calculated ε_c means in major C_4 biofuel crops. Sample size is shown on the right axis. Error bars represent 90% confidence intervals.

TRENDS IN MAJOR FOOD CROP ε_C OVER THE PAST FEW DECADES

Prior to conducting multiple regression analyses, the individual relationships between ε_c and independent variables were determined in six major food crops (Fig. 4). In multiple regression analyses, the best model was selected using the lowest corrected Akaike information criterion (AIC_c) score, and inclusion of an independent variable in the model demonstrated that the variable accounted for a large portion of the variability in ε_c for that crop. The variables included in the final model closely matched corresponding partial correlation coefficients, demonstrating that colinearity between independent variables was not a significant factor in the multiple regression results (Supplemental Table S4). The most commonly included variables were T and S_t, which were included in five linear multiple regression models each (Table IV). YOR was only included in four models, and [CO_2] only in one model (Table IV). The AIC_c order of single variables included in the final model indicated relative correlation strengths for each variable. T was the first variable included in three of the models (peanut, soybean, and wheat), S_t in two of the models (rice and sorghum), and YOR in one model (maize; Table IV). Although density was also included in the maize analyses, there was no significant correlation between maize ε_c and density, even though selection for density tolerance is shown to correlate with increasing yield (Duvick, 2005). Additionally, substituting density for YOR did not result in a significant correlation between density and ε_c. Due to reduced sample size, precipitation available during the growing season was only included in the analyses for soybean but was not in the final selected model.

When S_t was included in a model, the simple regression coefficient was always negative (Table IV). Negative correlations of ε_c with S_t within several food crops reinforced the notion that available light in excess of photosynthetic capacity decreases ε_c (Sinclair and Muchow, 1999; Slattery et al., 2013). Lowering S_t to a point near light saturation at the top of the canopy increases ε_c but ultimately depresses yield potential, due to less overall energy available to the crop. Therefore, altering pigment concentrations or canopy architecture in canopies with high leaf area indices can optimize light availability

Table III. *Numerical data from mean ε_c analyses in C_4 bioenergy crops*

Species, common name, photosynthetic type, and any groups or specifications within species are indicated. ε_c means and SE are reported along with sample size (*n*) for each species and group within species.

Species	Common Name	Type	Groups by Cultivar, Species, or Hybrid	Mean ε_c	SE	*n*
Z. mays	Maize	C_4		0.0488	0.001	194
S. bicolor	Sorghum	C_4	Energy, biomass, forage	0.0660	0.005	12
P. virgatum	Switchgrass	C_4		0.0618	0.003	26
Saccharum spp.	Sugarcane	C_4		0.0581	0.003	22
Miscanthus spp.	Miscanthus	C_4	*M. giganteus*	0.0503	0.004	20
			M. sinensis	0.0279	0.004	16

among leaf layers and decrease wasted incident radiation (Long et al., 2006b; Ort et al., 2011; Drewry et al., 2014). This should have been evident in new rice varieties bred for reduced tillering, as fewer tillers was hypothesized to alter canopy structure, allowing greater penetration of light in the canopy and, therefore, greater ε_c (Peng et al., 2008). In fact, ε_c was greatest in the new hybrid varieties (Table II; Fig. 2). However, these new hybrid varieties were also grown in relatively dim conditions as compared with the other subgroups (Supplemental Table S3), preventing any conclusions regarding the effectiveness to this approach in conditions where incident light oversaturates photosynthetic capacity. Nonetheless, frequent negative relationships between ε_c and S_t in food crops present a solid argument for improving light distribution and use in dense food crop canopies.

Multiple regression analyses indicated that, in addition to S_t, T accounted for the greatest proportion of the variation in ε_c in most food crops that were otherwise classified as experiencing optimal growth conditions. T was negatively correlated with rice, wheat, and soybean ε_c (Table IV). Positive correlations were evident between ε_c and T in maize and peanut (Table IV), but as temperatures continue to rise with predicted changes in climate, most likely all food crops will begin to suffer decreases in ε_c. Even in peanut, a crop where increases in T were positively correlated with ε_c in this analysis, recent studies have found that expected increases in T will result in decreases in photosynthesis that will not be alleviated by elevated [CO_2] (Prasad et al., 2003). A similar result was found in soybean grown in the field under elevated [CO_2] and elevated T, where elevated [CO_2] had little effect on photosynthesis when T reached above optimal (Ruiz-Vera et al., 2013). While increasing temperatures can negatively affect crop growth and development in many ways, specific inhibitions to photosynthesis at the leaf level include decreased Rubisco specificity to CO_2, limited ribulose 1,5-bisphosphate regeneration, and destabilization of Rubisco activase, which can have severe implications on C_3 and even C_4 photosynthesis at very high but increasingly frequent temperatures (for review, see Ainsworth and Ort, 2010). Therefore, mitigating these harmful effects on leaf photosynthesis through transgenic approaches should be a priority along with improving leaf photosynthetic efficiency.

Improving ε_c stress tolerance is becoming increasingly important, as current work to increase yields is making crops more sensitive to detrimental climate change effects. Breeding for greater yields in optimal conditions has resulted in greater sensitivity to the environment (i.e. greater yield instability in less favorable conditions) in maize (Lobell et al., 2014) and soybean (Koester et al., 2014; Rincker et al., 2014). This may explain the lack of significant correlations between ε_c and density in maize. Although ε_c was expected to increase with density, a greater sensitivity to temperature and, therefore, vapor pressure deficit could negate those benefits (Lobell et al., 2014). It is also more difficult for newer, high-yielding cultivars of wheat to realize maximum yields in the field as T stress becomes more common (Gourdji et al., 2013). Since ε_c is sensitive to the environment (Table IV; Sinclair and Muchow, 1999; Slattery et al., 2013), improving stress tolerance deserves even greater attention going forward in order to mitigate the negative effects of climate change on yield.

PROJECTED TIME TO DOUBLE CURRENT ε_C VALUES AND REACH THEORETICAL MAXIMUM ε_C IN MAJOR FOOD CROPS

Positive correlation of ε_c with YOR was limited across food crops and only demonstrated rates of increase of less than 0.7% per year. Relationships between ε_c and YOR determined in the absence of environmental variability in wheat (Shearman et al., 2005; Sadras et al., 2012) and soybean (Koester et al., 2014) were reported as less than 0.65% gain per year in ε_c and were consistent with the rates from this study. At best, these rates are half of the rates of yield increase necessary to double crop production by midcentury (Rosegrant and Agcaoili, 2010; Hall and Richards, 2013; Ray et al., 2013). Consequently, projections of when ε_c would double or reach the theoretical maximum suggest that the rate of genetic advancements to the present are not enough to double ε_c by the middle of the century in the crops studied. In maize, the food crop with the greatest mean (Fig. 1) and greatest rate of increase with YOR (Table V), ε_c would not double until the year 2134, and the maximum would be reached approximately 70 years later (Table V). In peanut, the estimated time for ε_c to double was approximately 250 years, while

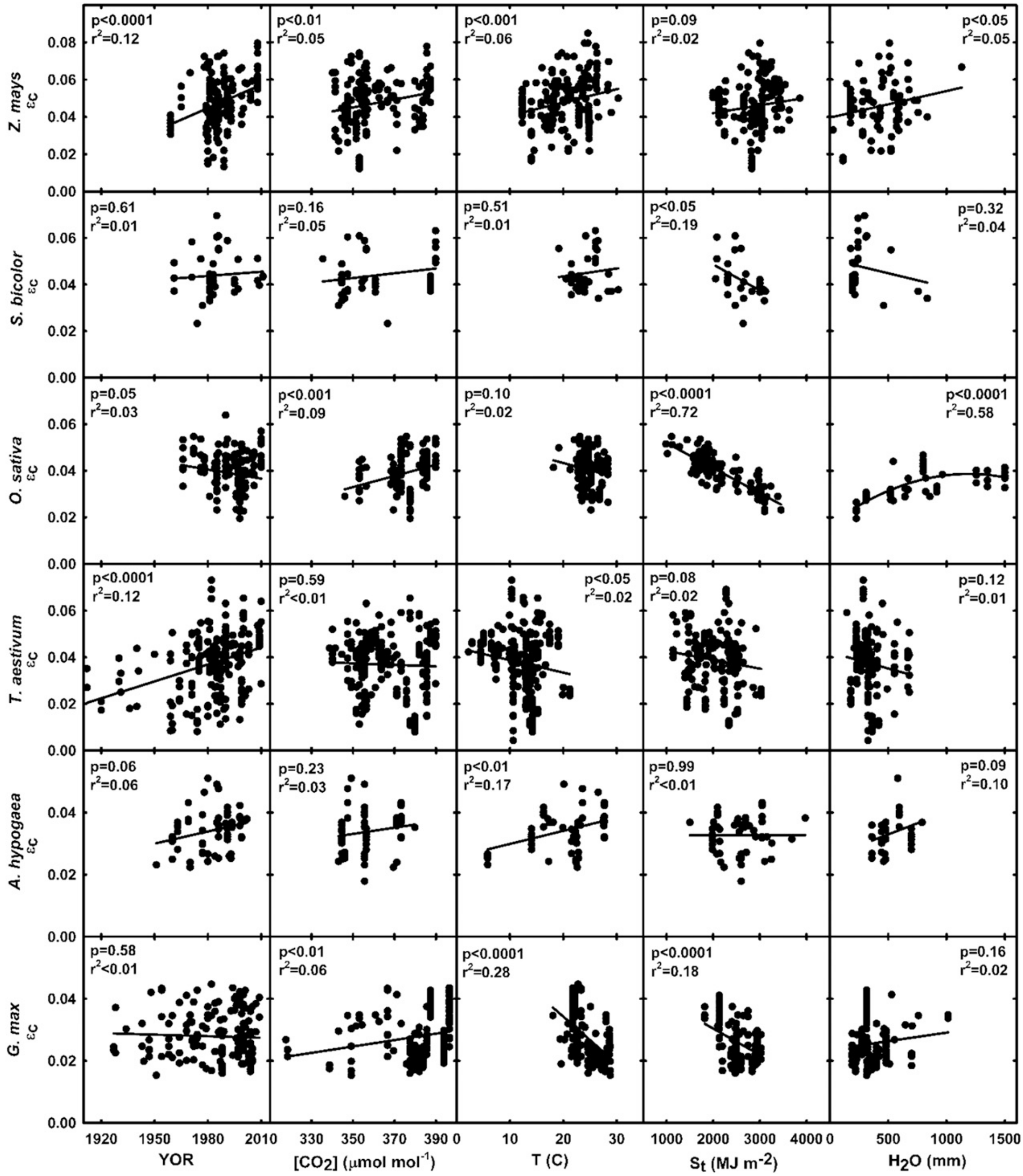

Figure 4. Relationships between ε_c and individual independent variables in six major food crops. Independent variables included YOR, mean annual [CO$_2$] during the measurement period, T, available S$_t$, and water available during the growing season as precipitation and irrigation (H$_2$O). Lines represent least-squares regression, with corresponding significance levels and correlation coefficients in each graph. ε_c versus density in maize is not shown.

reaching the maximum would not occur for at least 400 years (Table V). The year of doubling ε_c in wheat was 2357, whereas reaching the maximum would occur in 2391 (Table V). Due to having the low absolute value of ε_c and the lowest rate of gain in soybean, doubling ε_c would take approximately one millennium (Table V). These projections, based on trends in ε_c spanning several decades, demonstrated that breeding and biotechnology to date have not necessarily selected for increasing ε_c as a high priority. Thus, there is potentially

Table IV. *Multiple regression analyses of ε_c in six major food crops*

The final model and ranking of variables included in the final model were determined using the lowest AIC_c. Variable coefficients and significance were determined using the final model.

Crop	Variable Rank	Model[a]	AIC_c	Coefficient (10^{-3})	*P*
Peanut (*n* = 51)		YOR, S_t, T	−540.1		<0.001
	1	T	−536.0	0.426	<0.001
	2	YOR	−531.8	0.123	<0.05
	3	S_t	−526.6	−0.00238	0.12
Soybean (*n* = 117)		YOR, [CO_2], S_t, T	−1,270.2		<0.0001
	1	T	−1,231.8	−1.04	<0.0001
	2	S_t	−1,226.3	−0.00824	<0.0001
	3	[CO_2]	−1,204.3	0.0524	<0.05
	4	YOR	−1,201.3	0.0293	0.21
Rice (*n* = 102)		S_t, T	−1,133.8		<0.0001
	1	S_t	−1,125.0	−0.00960	<0.0001
	2	T	−1,014.3	−0.729	<0.01
Wheat (*n* = 159)		YOR, S_t, T	−1,451.2		<0.0001
	1	T	−1,447.9	−0.746	<0.001
	2	YOR	−1,438.4	0.105	<0.05
	3	S_t	−1,437.8	−0.00284	0.13
Sorghum (*n* = 23)	1	S_t	−228.3	−0.00739	0.11
Maize (*n* = 149)		YOR, T	−1,347.8		<0.0001
	1	YOR	−1,346.0	0.346	<0.0001
	2	T	−1,344.0	0.521	<0.01

[a] Independent variables included YOR, mean annual [CO_2] during the measurement period, T, and available S_t. Water available as precipitation and irrigation was included when sample size changed by less than 10% after including it in the analyses. Density was included in maize analyses but was not in the selected model.

a large amount of room for improvement in this key factor and, therefore, yield potential.

CONCLUSION

As greater increases in yields are needed to feed and fuel the world's population, targets such as ε_c are key to reaching these goals. This assessment aimed to determine the mean ε_c in several important food and biofuel crops, test the key contributors to variation in ε_c, and determine genetic trends in ε_c. As expected, mean ε_c values in food crops were greatest in C_4, followed by nonlegume C_3, and were lowest in legume C_3 plants. All food crop means were lower than one-half the theoretical maximum. Bioenergy crop ε_c means were much greater than those in food crops, and some, including the energy crops sorghum and switchgrass, exceeded 50% of the maximum for C_4 grasses. However, ε_c values for perennial grasses may have been inflated if measured during the growing season interval when stored rhizome reserves are mobilized and contribute to aboveground biomass accumulation. Reported variation in ε_c was found to be generally negatively correlated with S_t and T. Positive correlations with YOR were only present in a few food crops, and rates of increase were relatively low, suggesting that ε_c will not double in most crops before the middle of the century at the current rate of increase.

While these findings show that there has been little progress to date in improving ε_c, the fact that ε_c has room for improvement and is receiving increasing amounts of attention is promising. Targets for improving ε_c in various manners have already been identified and reviewed (Amthor, 2010, Zhu et al., 2010; Parry et al., 2011; Raines, 2011; Ainsworth et al., 2012; Reynolds et al., 2012; Evans, 2013) and have the potential to greatly alter the current trends in ε_c improvement. This study emphasizes the importance of using strategies that improve nitrogen fixation efficiency in legumes, canopy light distribution, and tolerance to higher temperatures to increase genetic gains and limit detrimental environmental effects on ε_c. As these strategies are implemented to improve ε_c and, therefore, yield potential, these ε_c means and trends will serve as a baseline to track the relative success of each approach.

Table V. *Summary of ε_c trends and projections in major food crops*

Positive trends in ε_c from multiple regression analyses were used to project the year in which ε_c will double and reach the theoretical maximum, assuming no changes in the coefficients due to climate change, breeding intensity, etc.

Crop	YOR Slope	Year of Doubling	Year of Maximum
	$year^{-1}$ × 10^{-3}		
Maize	0.346	2134	2176
Wheat	0.105	2357	2391
Peanut	0.123	2273	2317
Soybean	0.029	2966	2986

Supplemental Data

The following supplemental materials are available.

Supplemental Table S1. Data sources used in analyses.

Supplemental Table S2. Varieties included in crop and subgroup analyses.

Supplemental Table S3. Means and ranges of independent variables used in analyses.

Supplemental Table S4. Partial correlation coefficients from regression analyses.

Supplemental Materials and Methods S1. Detailed description of data collection, manipulation, and analysis.

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