Rice yield improvements through plant breeding are offset by inherent yield declines over time

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ABSTRACT
Meeting the challenge of feeding a growing population with limited resources will require increasing the yield potential of staple crops, such as rice. Yet many high-yielding, intensive production systems have experienced slow rates of yield improvement in recent years despite a demonstrated increase in the yield potential of new crop cultivars. We analyzed experimental data from one such cropping system, i.e., California (CA) rice, in order to quantify improvements made in the genetic yield potential obtained through plant breeding. California rice systems are among the highest in the world and close to maximum yield potential. Specifically, the hypothesis was tested that if rice cultivar yields decline over time then apparent yield increases in side-by-side yield comparison tests will not reflect increases in yield potential. This hypothesis was tested using 33 years of experimental yield data from the California Cooperative Rice Research Foundation Rice Experiment Station. Based on side-by-side comparisons of old and new rice cultivars which do not consider yield decline over time, there was an apparent increase in yield. However, the yields of older cultivars were found to decline at an estimated rate of 29.3 kg ha⁻¹ year⁻¹ (90% credible interval – 4.4 to –53.3) after initial selection. Once this effect was considered, the yield advantage of newer cultivars over old was uncertain (–3.3 kg ha⁻¹ year⁻¹, 90% credible interval –36.1 to 31.5). These results highlight (1) the importance of continuous crop improvement and deployment of new cultivars simply to maintain existing yields, and (2) to increase the genetic yield potential, higher yield targets are needed. Importantly, when breeding near the yield potential, despite the limited yield gains, significant advances in improving quality and reducing crop duration have been made.

1. Introduction

Constraints on arable land are increasing simultaneous with the need to increase total food production to meet a growing demand (Foley et al., 2011; Godfray et al., 2010; Mueller et al., 2012), which has necessitated harvesting more grain per unit land area (Lobell et al., 2009; Tittonell, 2014). Historically, agricultural research has been successful in staving off the "Malthusian catastrophe" of demand surpassing supply via continued yield improvement of staple crops. However, many production systems are experiencing plateaus in grain yield (Grassini et al., 2013). If this trend continues, improvements per unit land area are no longer possible, and an increase in the area under cultivation will be needed to meet food demand, which carries undesirable ecological implications (Foley et al., 2011; Tilman et al., 2011). Therefore, it is of critical importance to better understand why the rate of increase in grain yields has declined or leveled off in intensified production systems.

California (CA) rice represents one such production system. Rice is grown primarily in the Sacramento Valley, which is characterized by having a Mediterranean climate with long days, a dry growing season relatively free of pests and diseases. These conditions lead to some of the highest yields in the world FAOSTAT, 2016. Production in CA is predominately focused on premium quality medium grain japonica cultivars (e.g., CalRose rice), and rice from CA is recognized globally for its quality (http://agfax.com/2015/11/03/rice-calrose-wins-best-rice-world-competition/). Most cultivars in use in CA are developed by the California Cooperative Rice Research Foundation (CCRRF; a collaboration between the University of California, the USDA-Agricultural Research Service, California Rice Experiment Station, and the California Rice Board). California rice is grown primarily in the Sacramento Valley, which is characterized by a Mediterranean climate with long days, a dry growing season relatively free of pests and diseases. These conditions lead to some of the highest yields in the world FAOSTAT, 2016. Production in CA is predominately focused on premium quality medium grain japonica cultivars (e.g., CalRose rice), and rice from CA is recognized globally for its quality (http://agfax.com/2015/11/03/rice-calrose-wins-best-rice-world-competition/). Most cultivars in use in CA are developed by the California Cooperative Rice Research Foundation (CCRRF; a collaboration between the University of California, the USDA-Agricultural Research Service, California Rice Experiment Station, and the California Rice Board).
Research Service, and farmer-funded research). In part due to improvements in rice genetics, rice yields in CA increased rapidly during the period from 1920 to 1990; however, since the 1990s, the rate of yield increase has slowed (Fig. S2) despite continuous crop improvement. Based on a yield-gap analysis, on-farm yields in the major rice growing region of CA is 73–76% of maximum yield potential (Espe et al., 2016). In highly intensive systems such as this, Grassini et al. (2011) have shown that farmers are capable of attaining 85% of the maximum yield potential. Thus, given that farmers are near the attainable yield potential, increases in yield are likely to be relatively slow and Espe et al. (2016) reported that indeed this was the case with yields on average increasing by about 50–62 kg ha\(^{-1}\) year\(^{-1}\) between 1999 and 2014.

Certainly one question in looking at this situation is, “do new cultivars have greater yield potential”? Like many breeding programs, one of the goals of the CCRRF is to increase yields through breeding cultivars with increased yield potential. However, when the popular cultivar M-202 was released in 1985, it was reported to yield an average of 11 Mg ha\(^{-1}\) (14% moisture content (MC); Johnson et al. (1985)). In 2015, the reported average yield of the newest released cultivar M-209 was 10.8 Mg ha\(^{-1}\) (14% MC; University of California Cooperative Extension, 2016). However, in annual breeding reports and cultivar release announcements, data based on yield performance in side-by-side cultivar trials show that new cultivars usually out yield the older cultivars, typically by 3–5% (e.g., M-209 release description at http://www.crrf.org/linked/2015annualreport.pdf). In other rice systems, a decrease in a cultivar’s yield performance over time has been observed (Peng et al., 1999, 2010, 2000; De Datta et al., 1995). It has been speculated that this yield decline over time is due to the inability of a cultivar to adapt to changing biotic and abiotic conditions (Peng et al., 1999, 2010, 2000; De Datta et al., 1995). Yield declines over time may explain the apparent contradiction above, in which side-by-side yield comparisons show yield improvements in cultivars while overall there may be little change in yield potential. To address this issue we tested the hypothesis that if rice cultivar yields erode over time then apparent yield increases in side-by-side yield comparison tests will not reflect the true magnitude of yield changes over time.

2. Methods

2.1. Site and data description

The CCRRF Rice Experiment Station (RES) is located near Biggs, CA (39.4648, −121.7342; Fig. S1), and has been the central location for CCRRF’s efforts to develop improved rice cultivars adapted to CA since 1969. The California Statewide Variety Trials evaluate current and promising cultivars at the RES and six to eight on-farm trials around the state each year. To avoid potential complications due to site, climate, and management differences at the farmer-managed trials between years, we focused our investigation on the RES. The RES is researcher-managed and plants the majority of the experimental plots for the statewide program (approximately 3–4 times the number of experimental plots compared to other on-farm locations). The climate at the RES is Mediterranean, characterized by mild winters during which most of the annual precipitation occurs (441–612.5 mm annually) and warm summers largely free of precipitation events. Soils at the RES are classified as Esquon-Neerdobe clays with roughly 2% soil organic matter in the top 15 cm (Soil Survey Staff, 2017).

As part of the annual Statewide Variety Trials, newly developed entries are tested against officially released cultivars (checks) at the RES in several trials spanning multiple planting dates per year. For the purposes of this study, we concentrated on released medium grain cultivars, as these cultivars constitute approximately 90% of the planted rice area in CA. Newly developed entries are typically evaluated in these trials for 3–5 years prior to their official release. For these cultivars planted in breeding trials at the RES from 1984 to 2016 plot level observations (replicated 3–4 times in a completely randomized design) were collected leading to a final data set of 1487 observations representing 14 cultivars and included every publicly released medium grain cultivar developed by the CCRRF from 1981 to 2015. For each cultivar, the official year of public release and the time elapsed (in years) since release was determined.

Experimental plots at the RES are managed similar to University of California Cooperative Extension prescribed best management practice for land preparation, fertility rates, and pest and disease control (University of California Cooperative Extension Staff, 2016). As is typical for water-seeded systems, the plots were planted by pre-germinating rice seed prior to direct-seeding into pre-flooded fields. Plots were rectangular and either 14.0 or 18.5 m\(^2\), and were harvested after physiological maturity using a small-plot combine. All yields were converted to 14% MC prior to reporting.

2.2. Statistical analysis

To test the hypothesis, the influence of breeding and yield decline over time were quantified on yield over time using three nested Bayesian hierarchical models. First, yield was modeled as a response to the number of years since the cultivar was officially released and the year of release using a mixed-effects linear regression. To account for similarities between years and between cultivars, year and cultivar were included in the model as random effects (Model 1):

\[
\text{yield}_{ijk} = \text{Intercept} + (\text{Rate yield decline}_{ik} \times \text{years since release}_{ik}) + (\text{Rate yield improvement}_{jk} \times \text{release year}_{ik}) + \beta_{\text{year}_{ik}} + \beta_{\text{cultivar}_{jk}} + \beta_{\text{cultivar \times year}_{jk}} + \epsilon
\]

where \(\text{yield}_{ijk}\) is the grain yield for cultivar \(k\) in plot \(i\) during year \(j\), the Intercept is the average yield for the RES across cultivars and years, \(\text{Rate yield decline}_{ik}\) is the rate of yield decline per years since release\(_{ik}\) for cultivar \(k\) in plot \(i\) (mean-centered, i.e., negative for years prior to release, zero at the year of release), \(\text{Rate yield improvement}_{jk}\) is the rate of yield improvement per year (\(\text{release year}_{ik}\)), \(\beta_{\text{year}_{ik}}\) is the random effect of year \(j\) and \(\beta_{\text{cultivar}_{jk}}\) is the random effect of cultivar \(k\), and lastly \(\beta_{\text{cultivar \times year}_{jk}}\) is the a random effect for the interaction term for cultivar \(k\) in year \(j\). Two variations of this full model were used to further explore yield dynamics over time. For comparison to estimates where yield decline over time is not taken into account, the model was used as described above except omitting the \(\text{Rate yield decline}_{ik}\) term (Model 2). Lastly, a model was fit to estimate if there were differences between cultivars in the rate of yield decline over time by adding allowing the rate of decline to vary by cultivar (i.e., adding a \(\text{Rate yield decline}_{ik} \times \text{years since release}_{ik}\) term to the model for the rate of yield decline for cultivar \(k\) (Model 3).

Data were processed and models fit in R, an environment for statistical computing (R Core Team, 2017). Models were fit using the ‘rstanarm’ package (Stan Development Team, 2016), an interface to Stan, a language for probabilistic programming (Stan Development Team, 2017). All model diagnostics, including \(\hat{R}\), effective size, and posterior predictive checks were examined before reporting results. To test goodness of fit, the full model was compared to models containing only the years since release or the year of release using the ‘loo’ package (Vehari et al., 2016a), an efficient means of conducting leave-one-out cross validation (Vehari et al., 2016b). The 90% credible interval (90% CI), defined as the interval containing 90% of the distribution of estimated credible parameter values given the data, was calculated as a measure of uncertainty in the parameter estimates using the quantile method. The 90% CI is more stable to sample-to-sample variance and hence is preferable to the 95% interval (Stan Development Team, 2016). To verify the estimates, the analysis was also conducted using classical methods, specifically frequentist mixed-effects models fit by maximum likelihood (see supplemental material for details and model results). Complete data and code used for this analysis is available through the Open Science Framework at https://osf.io/6ed5k/.
3. Results

3.1. Cultivar yields at time of release

There was general agreement between the estimates from the Bayesian and classical statistical approaches for all models, with the estimates being similar between similar models. The Bayesian estimates are presented here due to the inherent flexibility of Bayesian inference, though the classical estimates can be found in the supplemental material. Comparing the cultivars' yield during each's initial time (average 3 years) in the experimental trials showed that across cultivars, yields ranged from 9.64 (M-207) to 11.88 Mg ha\(^{-1}\) (M-205) (Fig. 1). The relationship between the year a cultivar was released and yield over the 33-year study period was estimated to be slightly negative (−3.1 kg ha\(^{-1}\) year\(^{-1}\)) and does not provide evidence of genetic yield improvements during this period. Individual exceptions to this were two cultivars (M-204 and M-205) which were observed to have higher yields than the others in the raw data (Fig. 3).

3.2. Yield decline over time

Based on Model 3, there was no evidence of differences between cultivars in the rate of yield decline over time (i.e., all cultivar specific rates of decline overlapped with each other). Differences between cultivars in the decline of yield over time, seen in the raw data (Fig. 2), are therefore likely small and uncertain. Given this, the model excluding varying rates of decline by cultivar (Model 2) is presented here. The yields of each cultivar over time were evaluated relative to when the cultivar was released using the full model which accounts for both yield decline over time and yield improvements over time (Model 2). The average decrease in yield over time following a cultivar's release was estimated at −29.5 kg ha\(^{-1}\) year\(^{-1}\) (90% CI: −4.3 to −56.3) (Fig. 3 and Table 2). The oldest cultivar in the trials (M-401) is estimated to have lost an average of 1.1 Mg ha\(^{-1}\) since its release. Likewise, an estimated 560 kg ha\(^{-1}\) yield advantage of M-206 over M-202 (the current and former predominant cultivars, respectively), can be attributed solely to the decline of M-202's yield over time (Figs. 1 and 4). Further supporting this estimate of yield decline, both M-202 and M-205 yielded similarly at their respective year of release (Fig. 4), despite the fact that M-202 was released 19 years prior to M-206 (Fig. 4 and Table 1).

3.3. Yield gains

When yield decline over time is not accounted for in the analysis (Model 2), there is estimated to be a yield increase of approximately 24.1 kg ha\(^{-1}\) year\(^{-1}\) (90% CI: 1.5 to 48.6) (Fig. 5). In contrast, the full model (Model 1) which accounts for both the year of release and yield decline over time indicates that the estimated change in grain yield per year in the CCRRF's breeding trials at the RES was −3.1 kg ha\(^{-1}\) year\(^{-1}\), with both small positive and negative trends within the credible interval (90% CI: −37.5 to 29.1) (Fig. 1). According to model comparison metrics (PS-LOO, WAIC), Model 1 is estimated to have superior predictive accuracy compared to the model which does not account for yield decline over time.

After correcting for yield decline over time, some cultivars were higher yielding compared to the overall average (as estimated via the random intercept term in the model). The marginal estimate for the performance of a cultivar averaged over the uncertainty in the other parameters in the model (i.e., the random effect) shows three cultivars with higher than average yields: M-201, M-205, M-204 (Fig. S3).

4. Discussion

4.1. Cultivars within the context of the production system

In CA, the cultivars with broad adaptation and adoption over the 33-year period of this study are M-202, M-206, and M-105. Cold tolerance is a major problem for much of the California rice producing region (Espe et al., 2017), although it is a bigger problem in the southern portion of the Sacramento Valley due to the influence of the ocean winds through the San Francisco Bay (Espe et al., 2016) (see Fig. S1 for the geographic orientation of the rice growing area relative to the San Francisco Bay). These three cultivars have a higher degree of cold tolerance, high yield potential, and relatively short duration and are thus broadly grown with over 70% of the area in these cultivars at any given time during the study period (University of California Cooperative Extension Staff, 2016). There are several cultivars that were found to have better than average yields, even after correcting for yield declines over time. However, these cultivars (M-201, M-204, M-205, and possibly M-209; Fig. S3) are not widely adopted. Importantly, not all medium grain cultivars that were released were purported to have higher yields than previous cultivars. Some cultivars had special traits, but upon release had similar yields to more broadly adapted cultivars. Examples of this include M-208, which had resistance to blast disease (Magnaporthe grisea) and M-402 which is a premium quality cultivar. Other cultivars such as M-205 and M-209, while high yielding, do not have the cold tolerance of the other cultivars and are thus only recommended for the northern portion of the Sacramento Valley.

4.2. Yield changes over time

The high yielding variety M-202 was released in 1985 and became the most widely planted cultivar for two decades (McKenzie et al., 2014). At the time of release, M-202 yields were reported at 11.0 Mg ha\(^{-1}\) (Johnson et al., 1985) which is almost identical to what we. This value of 11.0 Mg ha\(^{-1}\) is what we also found in this analysis based on the average experimental yields prior to public release (Fig. 1). Since the release of M-202, the rice yields of newly released varieties cultivars have remained between 10.8 and 11.5 Mg ha\(^{-1}\) (Fig. 1), with the exception of M-204 and M-205 (M-204 is no longer grown and M-205 has limited adaptation range so is only grown in a limited area). The variety cultivar M-206 was released in 2004 and is currently still the most widely grown rice cultivar in California. At the time of its release, M-206 was reported to yield 10.5 Mg ha\(^{-1}\)—similar to what we found based on our analysis (Fig. 1). Based on this premise, it is clear that improvements in yield potential have not been made over the 33-year period of this study. In contrast, both Samonte et al. (2014)
and McKenzie et al. (2014), report yield potential gains in California rice systems based on analyses that showed that newly released cultivars had higher yields than previously released cultivars. Based on their analyses, Samonte et al. (2014) reported yield gains from the rice breeding program of 37–60 kg ha\(^{-1}\) year\(^{-1}\) and McKenzie et al. (2014) a yield increase of 25 kg ha\(^{-1}\) year\(^{-1}\). The simplest model (Model 2) in this study is similar to the procedures used by Samonte et al. (2014) and McKenzie et al. (2014), and results in similar findings; yields were estimated to increase by an average of 24.1 kg ha\(^{-1}\) year\(^{-1}\) (Fig. 5), almost identical to estimates by McKenzie et al. (2014).

The only way to reconcile the two apparently contradictory findings above is that the yield of potential of cultivars decline over time such that when newly released cultivars are compared with the older cultivar (as shown by Samonte et al., 2014; McKenzie et al., 2014, and Fig. 5), yields of the new cultivar are greater than those of the older cultivar.
period. In this study, over a 30-year period and a 29.5 kg ha\(^{-1}\) potential declines over time and reported a 15% decline over a 30 year period. Peng et al. (2010) also found that a cultivar’s yield rate of yield increase equal to or greater than 25 kg ha\(^{-1}\) over the study period are unlikely; there is only a 8.2% probability of a rate decreasing the environmental conditions required for higher yield potential. Yield potential can be defined as the yield of optimum cultivar in the absence of biotic and abiotic stresses in a given environment (van Ittersum et al., 2013). However, Espe et al. (2017) found no evidence of sustained trends in growing season temperatures (either high, low, or average temperatures) in the Sacramento Valley during the study period, which does not support this theory that new cultivars have higher yield potential in the face of declining environmental conditions. While our analysis offers inconclusive evidence of differences between cultivars in rate of yield decline (i.e., the CIs for the interactions overlapped with each other and zero), visual examination suggests that cultivars may be different in terms of rates of yield decline (Fig. 2); however, we do not have sufficient data nor the proper controls in the existing data set to fully test this hypothesis. More data is needed to further explore the exact cause of the yield declines observed here, as well to determine if different cultivars have differential declines over time.

4.4. Causes for statewide increases over time

California state average yields have increased slowly during the study period (Fig. S2) (Espe et al., 2016). What are the potential causes? It is not due to the adoption of the broadly adapted cultivars (M-206 and M-105) as there is no evidence of increased yield potential among these (Figs. 1 and Figure 4) compared to M-202 released at the start of this period. Although M-205 is not broadly adapted, it has increased yield potential (Fig. 1) and its adoption (although limited) in the northern and warmer part of CA may contribute to some yield gains reported at the state level. Other factors include improvement in agronomic management, including more efficient nutrient management (Lundy et al., 2012, 2015; Linquist et al., 2009), and weed management (Brim-DeForest et al., 2017; Pittelkow et al., 2012; Caton et al., 2002). However, recent rates of state-wide yield gains are far less than those of the preceding era, consistent with a system near the yield ceiling (Grassini et al., 2013).

It should be noted that while our investigation has been concerned about increasing yield potential, the estimates here might not capture yield stability (how consistent grain yields are from year to year). The occurrence of stress events (e.g., extreme temperatures) are unpredictable across years and are not well captured by the analysis here.
Yield stability is notoriously difficult to quantify (e.g., Lobell et al., 2011), hence further investigation is needed to explore how yield stability has changed over the study period.

Planning to meet future demand necessitates increases in grain yield (Godfray et al., 2010; Foley et al., 2011; Mueller et al., 2012). Meeting the challenge to produce more grain without expansion of land under cultivation will rely on new genetics with increased yield potential. The evidence here suggests that to accomplish true increases over time, the improvement target needs take into account declines in the current “standard” cultivars’ yield over time (Fig. 6). While side-by-side comparisons will continue to be useful, comparisons across years to each cultivar’s benchmark yield at the time of release should provide information on the absolute improvements made in yield potential over time. New technologies may need to be adapted to further increase yield potential, including hybrid rice.

4.5. Other advances from breeding

Our investigation here is narrowly focused on the rough-rice/field grain yield. Other advancements due to plant improvement, including increased quality (McKenzie, 1993) and milling yield (McKenzie et al., 1994), have been made over the study period and are important. Furthermore, as previously mentioned, important disease resistance traits have been developed. Additionally, crop duration has been reduced in CA rice cultivars. For example, while the predominate cultivars M-202 and M-206 had similar yield potentials at the time of release (Fig. 5), M-206 matures about 6 days earlier than M-202 (Table 1). Shorter duration is very important in CA due to an already short growing season and water limitations (shorter duration cultivars would presumably require less irrigation water). For a detailed discussion of cultivars’ agronomic and grain quality characteristics, refer to http://rice.ucanr.edu/Reports-Publications/Rice_Production_Workshop_Manual/.

5. Conclusions

Increasing grain yield is essential to meeting the challenges of feeding a growing population in a changing world. Here we show that side-by-side cultivar comparisons do not necessarily indicate gains in yield potential as they do not account for yield declines over time of the older cultivars being tested. Here we show, as have others, that the yield of a cultivar declines over time. Therefore, quantifying changes in yield potential requires comparing yields of new cultivar yields to yields of the older cultivars when they were first released. Unfortunately, our analysis did not allow us to identify the cause of yield declines in this case. While efforts should be made to identify the cause of yield decline over time, this study highlights both the need for plant breeding to simply maintain current yields, and the challenge of increasing genetic yield potential, especially in systems such as CA where yield is approaching the physiological limit. The goal of increasing yield may require the yield performance of cultivars to be assessed earlier in the selection process to avoid discarding higher yielding entries without full consideration. We suggest here that historical benchmarks be used in to evaluate promising rice cultivars in addition to side-by-side comparisons to maintain perspective of the absolute yield gains being made.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fcr.2018.03.017.

References


