



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 $29.3 \text{ kg ha}^{-1} \text{ year}^{-1}$ (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 ($-3.3 \text{ kg ha}^{-1} \text{ year}^{-1}$, 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; Tittone, 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 (CCRFF; a collaboration between the University of California, the USDA-Agricultural

Abbreviations: CA, California; CI, credible interval; RES, Rice Experiment Station; CCRFF, California Cooperative Rice Research Foundation; MC, moisture content

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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 CRRF 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 CRRF Rice Experiment Station (RES) is located near Biggs, CA (39.4648, -121.7342; Fig. S1), and has been the central location for CRRF'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 CRRF 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 m², 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):

$$\begin{aligned} \text{yield}_{ijk} = & \text{Intercept} + (\text{Rate}_{\text{yield decline}} * \text{years since release}_{ik}) \\ & + (\text{Rate}_{\text{yield improvement}} * \text{release year}_{k}) \\ & + \beta_{\text{year}_j} + \beta_{\text{cultivar}_k} + \beta_{\text{cultivar}_k:\text{year}_j} + \epsilon \end{aligned} \quad (1)$$

where yield_i 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, $\text{Rate}_{\text{yield decline}}$ is the rate of yield decline per years since release_{ki} for cultivar k in plot i (mean-centered, i.e., negative for years prior to release, zero at the year of release), $\text{Rate}_{\text{yield improvement}}$ is the rate of yield improvement per year (release year_{ik}), β_{year_j} is the random effect of year j , and $\beta_{\text{cultivar}_k}$ is the random effect of cultivar k , and lastly $\beta_{\text{cultivar}_k:\text{year}_j}$ 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 $\text{Rate}_{\text{yield decline}}$ 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 $\text{Rate}_{\text{yield decline}_k} * \text{years since release}_{ki}$ 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 (Vehtari et al., 2016a), an efficient means of conducting leave-one-out cross validation (Vehtari 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/>.

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