

Perspective

Why high yield QTLs failed in preventing yield stagnation in rice?



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ABSTRACT

Rice plays a vital role in global food security, and its yield needs to be increased to meet escalating demand. Although many high yield quantitative trait loci (QTLs) have been identified in the last decades, rice grain yield in the main rice-producing countries is stagnating. By summarizing the yield performance of high-yielding QTL lines, we highlighted that almost all the high-yielding QTL introduced lines had no practical usage in current high yield breeding programs, mainly due to their low absolute grain yield. Further analysis showed that scientists primarily focused on spikelet number per panicle alone rather than other yield traits, and, in most of the studies, the yield increase was referenced to very old cultivars. By analyzing the yield traits correlations across cultivars in both field and pot conditions and different eco-sites using the same cultivars, we emphasized that the rice high yield will be rarely achieved by using single trait approaches due to the counteracting effects of yield components. Finally, several recommendations are provided to the next generation of biotechnological breeding in rice.

1. Introduction

Enhancing crop production is a global challenge since the rate of population growth currently exceeds the increase of food production (Godfray et al., 2010). It has been forecasted that about 70% more primary foodstuffs would be needed by 2050 (Long et al., 2015). Rice (*Oryza sativa* L.) is one of the most important food crops for more than half of the world's population. Because of rapid urbanization, available land for rice cultivation is seriously decreasing, and, therefore, increasing grain yield per unit land area is the only way to meet increasing global food demand (Long et al., 2015). Rice grain yield is determined by four components, including number of panicles per unit area, spikelet number per panicle, seed setting rate, and grain weight. Theoretically, improving rice grain yield can potentially be achieved by increasing a single yield component or any combination of the four (Miura et al., 2011).

The well sequenced, structural and functional rice genomics facilitated molecular marker development and quantitative trait loci (QTLs) identification (Chen et al., 2014; Xu et al., 2011). Over the last decades, many high-yielding rice QTLs have been identified (Miura et al., 2011; Wing et al., 2018; Xing and Zhang, 2010), such as *GN1a* (Ashikari et al., 2005), *Ghd7* (Xue et al., 2008), *SPIKE* (Fujita et al., 2013) and *TGW6* (Ishimaru et al., 2013). For instance, it has been reported that grain yield increased over 70% under experimental conditions by integrating a single QTL of *Ghd8* to the modern rice cultivar 93–11 (Yan et al., 2011). Authors frequently highlighted in papers that their QTLs could be used in high-yielding improvement breeding projects.

In principle, rice yield QTLs can be easily applied in high-yield breeding projects using the molecular marker technique. Indeed, many studies highlighted that improved commercial varieties by transferring a specific QTL from another genotype can be finished in a few years

(reviewed by Nadeem et al., 2018). In other words, these identified high-yield QTLs should have increased rice grain yield significantly if they have a similar efficiency in breeding practice as the finders reported in their original papers. However, the average annual rice grain yield of China and Japan—where most of the high yield QTLs were identified—have been stagnant for decades (Fig. 1). The reasons that high-yield QTLs failed in preventing rice yield stagnation are rarely discussed. Here, we summarized the yield improvement efficiency of identified QTLs for various yield components in past decades, and then discussed the potential reasons why high-yield QTLs failed in preventing rice yield stagnation via highlighting the counteracting effects among yield components.

2. High yield QTLs and their contribution to improving grain yield

To evaluate the contributions of high yield QTLs to rice grain yield under non-stress conditions, a systematic search for peer-reviewed articles was done in the Web of Science database (Clarivate Analytics, Boston, MA) using the search string: TS= ('rice' OR 'Oryza sativa' OR 'O. sativa') AND ('high yield' OR 'high grain yield') AND ('QTL' OR 'gene' OR 'Quantitative trait locus'). To date, hundreds of QTLs for rice yield have been reported in literature, however, only a few of these QTLs have been functionally analyzed. To ensure the conclusions reliable, only the clearly characterized QTLs (genes) were included. The studies without grain yield of the wild-type and/or its QTL introduced mutants were excluded from our analysis. Hence, some reputed high yield QTLs, such as *GN1a* (Ashikari et al., 2005), *Ghd7* (Xue et al., 2008), *GS5* (Li et al., 2011) and *DTH8* (Wei et al., 2010), had to be excluded due to the lack of grain yield values. Moreover, the high yield QTLs analyzed under stress treatments were also excluded. Grain yield of both wild-type and its QTL introduced mutants

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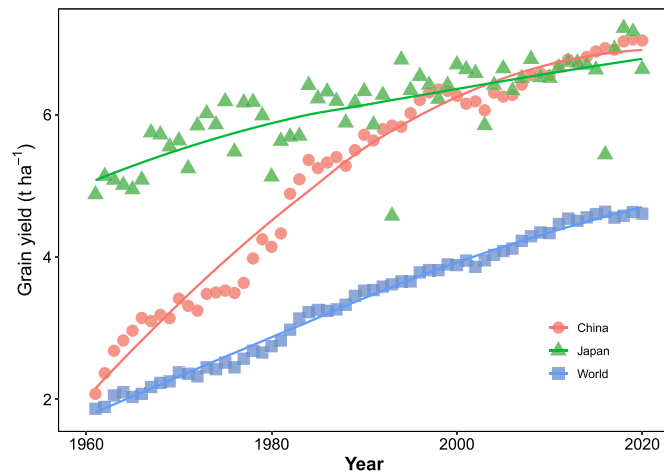


Fig. 1. The average annual grain yield of rice per unit land area. The lines are the loess best fit to the trend of yield against time. Data from FAO (2019).

were extracted as well as yield components when available. As a result, 21 identified rice high yield QTLs were included in our dataset (Table S1).

Overall, high-yielding QTLs contribute differently to the realized grain yield under experimental conditions (Fig. 2A), with a range of from

1.14% (*gw7*) to 70.8% (*Ghd 8*). Comparing with their respective wild types, the plants with a single high-yielding QTL increased grain yield by 22.01% on average. Grain yield of plants with QTLs for panicle number, spikelet number per panicle, seed setting percentage and grain weight increased by -0.58%, 29.51%, 6.17% and 3.78%, respectively (Fig. 2B, Figure S1). The grain yield values of nine QTLs were only expressed on a plant level basis (i.e. g plant⁻¹) rather than on population level base (i.e. t ha⁻¹). To make grain yield comparable, the lines that grain yields were expressed on population level were selected for further comparative analysis (Fig. 3). Note that some QTLs with grain yield expressed on population level (e.g. kg plot⁻¹) were excluded from our analysis, because of lacking plot area values. Surprisingly, the rice grain yields of many high-yielding QTL introduced lines were very low (range from 2.33 to 9.84 t ha⁻¹, with an average of 5.88 t ha⁻¹), and in most of these lines, the grain yield was even lower than the national annual grain yield (2019) in China (7.06 t ha⁻¹) and Japan (6.83 t ha⁻¹), in where these QTLs were identified. In fact, the enhancements of high-yielding QTL lines were based on old rice cultivars that have low yield potential, for instance, Nipponbare (released in 1963) and Zhonghua 11 (released in 1979) in these studies. Disappointingly, only one high-yielding QTL introduced line (*NOG* with background of Teqing) has the grain yield close to the average grain yield of Yangliangyou 6 (YLY6), a widely used reference cultivar in promotion trials of newly developed varieties in China (Fig. 3B), indicating that these high-yielding QTL introduced lines might have no practical usage in high yield breeding, as grain yields of

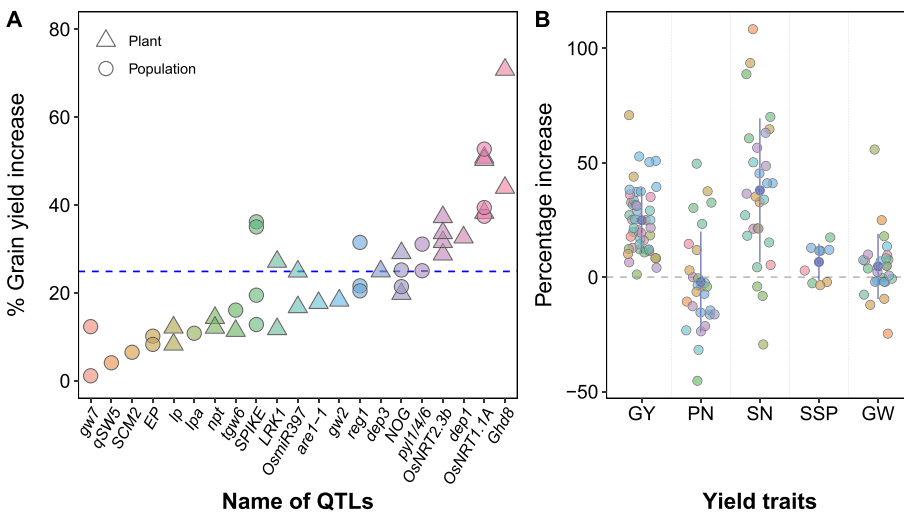


Fig. 2. Contributions of high yield genes on yield increase (A) and average increase of yield and yield components in high-yielding QTL introduced lines (B). The dot line in (A) represents the average grain yield increase (22.01%), and the blue points and bars in (B) represent the means and standard errors. GY, Grain yield; PN, Panicle number; SN, spikelets number; SSP, seed setting percentage; GW, grain weight. The percentage increase was calculated as $100\% \times (X_{QTL} - X_{wild})/X_{wild}$, where the X_{QTL} and X_{wild} represent the parameter values for plants with introduced QTL, and wild type, respectively.

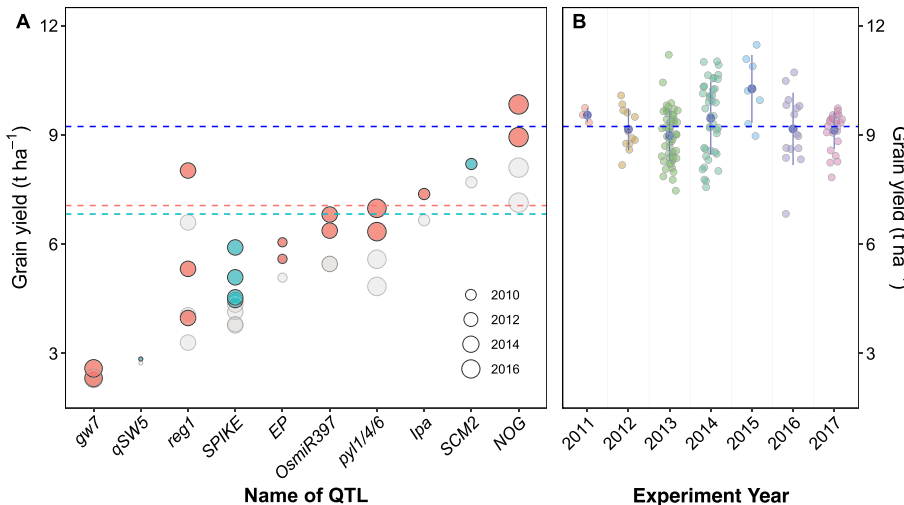


Fig. 3. (A) Effects of high yield QTLs on rice grain yield on population level, and (B) grain yield of Yangliangyou 6 (YLY6) - a widely used reference cultivar in promotion trials of newly developed varieties in China - under field condition at Wuxue, Hubei, China. In panel (A), the red and green points represent the high yield QTL identified in China and Japan, respectively, and the grey points represent the wild types (references). The red and green dot line represent the national average annual grain yield of China and Japan in 2019 (data from FAO), respectively. The blue dot line in both (A) and (B) represents the average grain yield of YLY6 under field condition in over 7 years at Wuxue, Hubei, China.

newly developed rice cultivars are often higher than 10.0 t ha^{-1} in experimental conditions since 2000 in both China and Japan (Njinju et al., 2018). One possibility is that some of these high-yielding QTLs have been unintentionally introduced to the modern rice cultivars by breeders; however, we cannot test this hypothesis in our current analysis. If this is the case, more communication between breeders and QTL biologists is needed to have a more efficient breeding practice in the future.

3. Can rice grain yield be enhanced by modifying a single yield component?

Another interesting issue in our analysis is that most of the high-yielding QTLs related to spikelet number per panicle rather than other yield components (Fig. 2). As shown in Fig. 2B, most of the high-yielding QTL introduced lines increased spikelet number per panicle, except the *gw7* and *gw2* which enhanced grain yield mainly through increasing grain weight. Hence, we may ask: can rice grain yield be enhanced by increasing spikelet number per panicle alone? Unfortunately, the data for yield components were rarely provided in these papers and the contribution of each yield component to the grain yield of the high-yielding QTL introduced lines cannot be analyzed. We, therefore, analyzed correlations of the yield components across genotypes with different panicle size and panicle number under both field (55 genotypes) and outdoor pot conditions (88 genotypes) conducted in Wuxue (2013–2015) and Wuhan (2014), Hubei province, respectively. As showed in Figure S2 & S3, no significant correlation between grain yield and any single yield

component was observed, except for a significant correlation between grain yield and spikelets number under field condition and between grain yield and seed setting percentage in pot condition. The extremely low seed setting percentage of some genotypes in pot condition (Figure S3) was intruded by high temperature during the flowering. The analyses indicate that the variation of grain yield is not determined by any single yield component alone.

To validate the statement, a synthesis analysis was performed to compare the rice yield formation of same cultivars in Taoyuan, a well-known rice high-yield eco-site because of its favorable ecological conditions (Katsura et al., 2008; Ying et al., 1998) and in other experimental sites (summarized in Table S3). Over the last decades, many experiments compared the rice grain yield in Taoyuan and other eco-sites in pairs. In these experiments, the same rice cultivars and managements were typically adopted and the yield differences between Taoyuan and other eco-sites were mainly caused by environment factors. As expected, an increase of all the yield components, except grain weight, contributed to the high yield at Taoyuan (Fig. 4, Figure S4). These results, again, suggest that it is necessary to improve multiple yield components synergistically, instead of improving spikelet number per panicle alone, to achieve a higher grain yield.

4. Counteracting effects among yield components

A negative correlation was observed between panicle number and spikelet number per panicle under both field and pot conditions (Fig. 5;

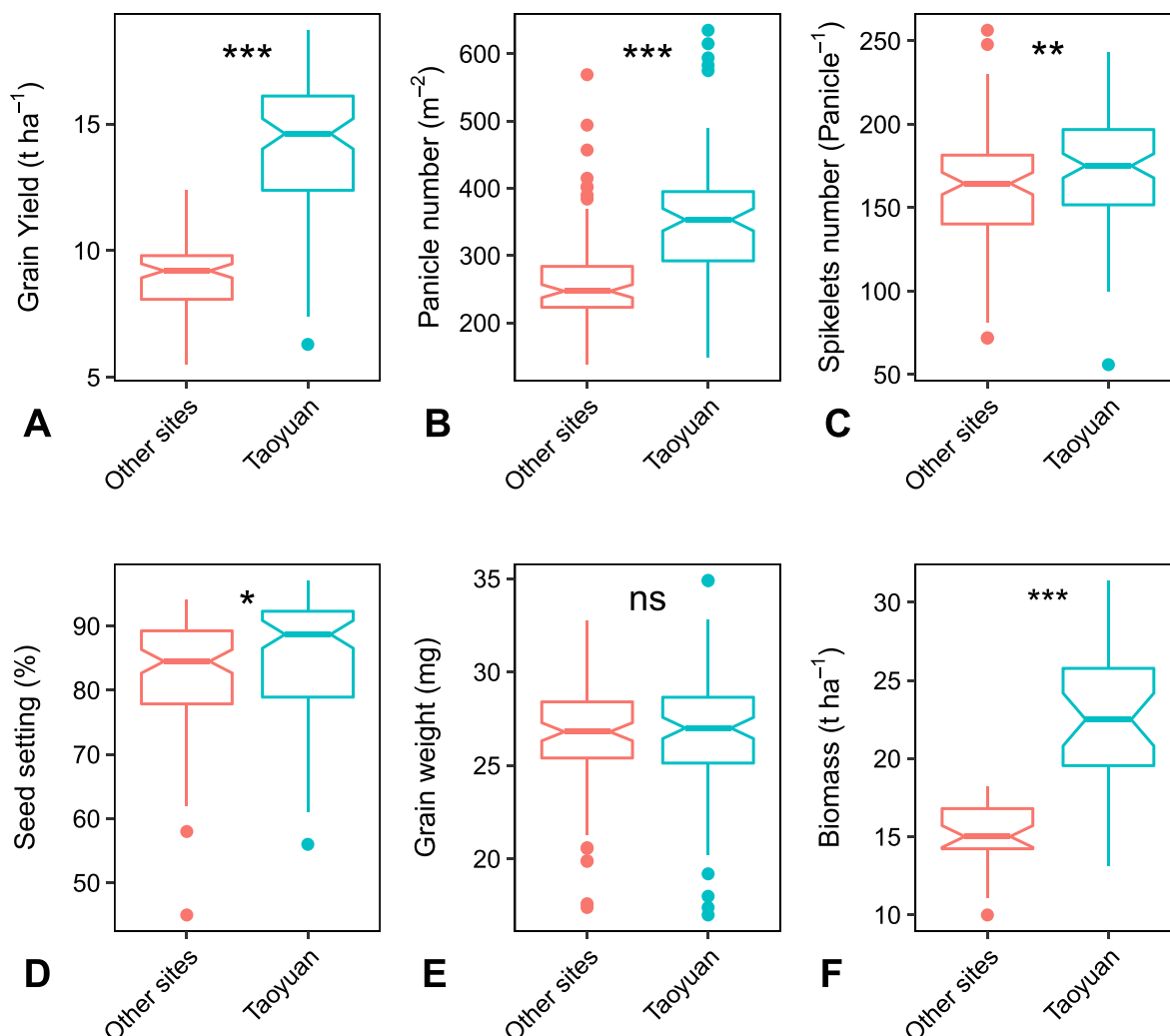


Fig. 4. Rice yield and yield components in a high yield eco-site, Taoyuan, and other eco-sites. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, $p > 0.05$.

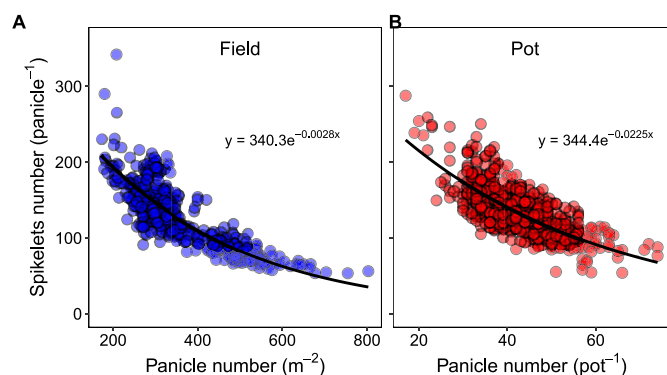


Fig. 5. The correlation between spikelet number per panicle and panicle number across rice genotypes under field (A), and pot (B) conditions.

Figures S2-S3), which indicated the existence of a strong trade-off between these two traits. Considering the grain yields of more than half of the high-yielding QTL lines were reported based on single plant, the effect of increasing spikelet number per panicle on grain yield may be offset by the reduce of panicle number at the population levels. The mechanism for the counteracting effects can be illustrated by the sink – source balance theory: in a unit space, less panicle number may be beneficial for individual panicles to accumulate more carbon during the spike development, which can support more spikelets per panicle. Conversely, more panicle numbers may increase the competition among panicles, and then reduce the investment to spikelets on each panicle. Assuming that seed setting, and grain weight can be maintained, further enhancement of grain yield requires an increase of spikelets number per panicle and

panicle number per land area simultaneously, which likely relays on breaking the trade-off between spikelets number per panicle and panicle number per land area.

Importantly, the negative correlation between panicle number and spikelet number was also observed in Taoyuan and other sites. This confirms the counteracting effects of panicle number and spikelet number. Although the seed setting percentage was slightly higher in Taoyuan (85.2%) than in other sites (82.3%), the higher grain yield at Taoyuan can be largely explained by a shift of the correlation between panicle number and spikelet number per panicle (Fig. 6). Further breeding and agronomic managements for high rice yield should, therefore, target at reducing the counteracting effects of panicle number and spikelet number per panicle.

5. Conclusion and recommendations

Here we show that almost all the high-yielding QTL introduced lines had no distinct contribution to the current high yield breeding practices, due mainly to their low absolute grain yield in the field. Several possible reasons may be attributed to the limited success in achieving high yield by introducing high-yielding QTLs. Single-trait approaches (specifically on spikelet number per panicle) have been used in most cases, but crop yield is an extremely complex trait that is determined by multiple components as showed in this study and in previous (summarized by Xing and Zhang, 2010). Moreover, the counteracting effects existing between panicle number per land area and spikelet number per panicle further confirm that single trait approaches may be hard to match the high yield breeding goal in rice. These results suggest future research should focus on multiple traits approaches. Fortunately, the multiple traits approach has begun to receive attentions, for instance, a very recent research

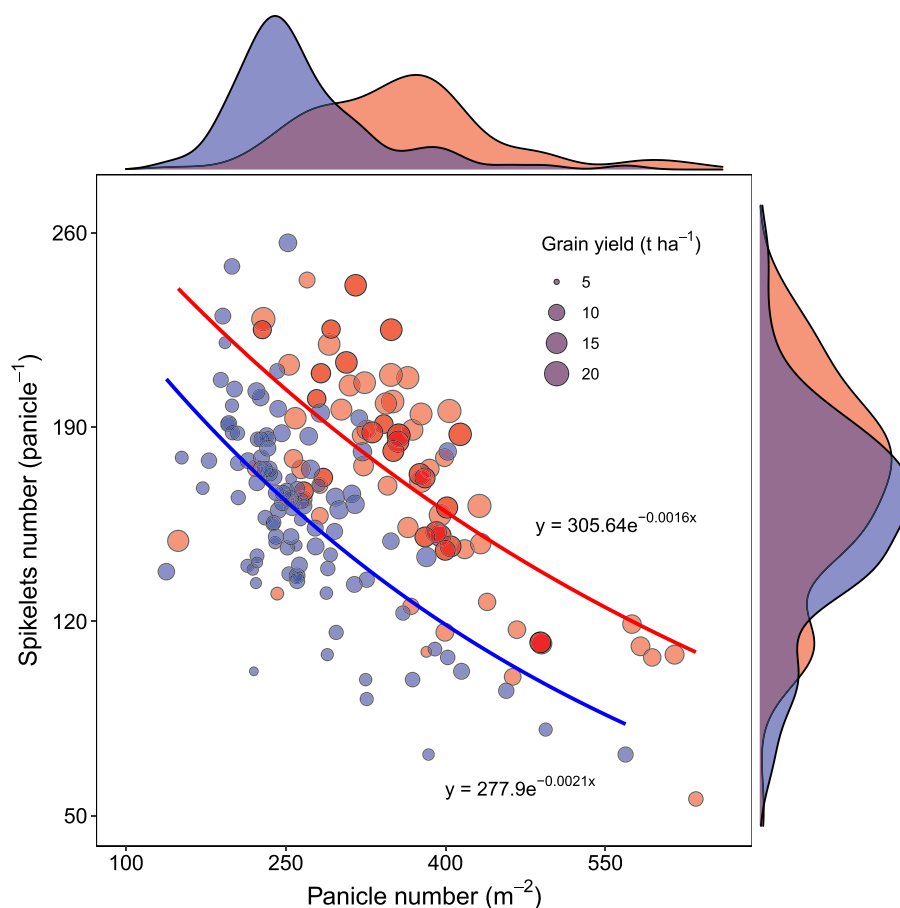


Fig. 6. Correlation between spikelet number per panicle and panicle number per unit land area. The blue and red points represent rice grown at other sites and at Taoyuan, respectively.

showed that rice grain quality of a high yield potential cultivar can be significantly improved without yield loss by introducing multiple grain quality genes (Chen et al., 2021; Zeng et al., 2017).

Another reason may be that the high-yielding QTL lines in most of the studies were created by introducing high-yielding QTLs to very old rice cultivars that usually have low yield potential. Although studies that investigate whether some of these high-yielding QTLs have been introduced to the modern rice cultivars unconsciously by breeders are still needed, we recommend researchers use modern cultivars as recipient or at least add some modern cultivars as high yield references when verifying the functions of the QTLs. Importantly, to take the counteracting effects into account, evaluating the contributions of high-yielding QTLs to grain yield on the population level rather than in individual plant or in panicle level is highly recommended.

Declarations of competing interest

The author declares that he/she has no competing interests. Given his role as Editors-in-Chief, Dongliang Xiong had no involvement in the peer-review of this article and has no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to Shaobing Peng. Jaume Flexas (Editorial Board member) was not involved in the journal's review or decisions related to this manuscript.

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Authors' contributions

DX: conceptualization, data compilation, data analysis and writing; JF: conceptualization, data analysis, and revision; JH, KC, FW, CD and ML: revision, and approval of the final manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.crope.2022.05.002>.

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