META-ANALYSIS

Quantifying the potential of 'on-farm' seed priming to increase crop performance in developing countries. A meta-analysis

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Abstract

Low-input agriculture in marginal areas of developing countries faces considerable challenges during crop development. A key stage in crop growth is seed germination, which is often constrained by abiotic factors such as low water potential, high temperatures and soil crusting, which can result in poor establishment. This is exacerbated by low soil fertility, salinity, drought, pests and diseases, which ultimately leads to reduced yields. Over the last 20 years, the potential of 'on-farm' seed priming, a traditional, low-cost technique, consisting of soaking seeds in water prior to sowing, has been applied to different crops and conditions with varying degrees of success. To understand the significance of this potentially transformative agronomic strategy, we have conducted a global meta-analysis of on-farm seed priming by quantifying (i) the rate of emergence, (ii) final emergence and (iii) total yield from 44 published papers on 17 crops across 10 countries. Our results show that on-farm seed priming has a significantly positive effect on crop performance: seeds emerge 22% faster, with an increased final emergence of 11%, with total yields 21% higher than conventionally sown seeds. Furthermore, sub-group analyses demonstrated that on-farm seed priming is more advantageous under stressful abiotic conditions with case studies categorized as being either 'nutrient deficient', 'salinity-stressed' or 'dry climates' gaining the highest yield improvements (22–28%). On-farm seed priming can be particularly beneficial to resource-poor farmers working in low-input agricultural systems where yield potential is limited by intrinsically stressed agronomic environments. Here, we demonstrate for the first time that on-farm seed priming is perfectly adapted to local situations in developing countries. Our results provide the evidence that on-farm seed priming could be effectively adopted by resource-poor farmers as a strategy to increase food security in some of the most marginal agricultural areas.

Keywords Crop yield . Germination . Low-input agriculture . Seed technology

Abbreviations

1 Introduction

Low-input agriculture in marginal and semi-arid areas of developing countries encounters many challenges that limit yield potential and thus restricts food security (Tittonell and Giller [2013](#page-11-0); Aune et al. [2017](#page-10-0)). This is further intensified by predicted climate change scenarios such as increasingly unpredictable rainfalls and extreme temperatures (Knox et al. [2012\)](#page-11-0). For example, in semi-arid agricultural systems, important physical constraints in the seedbed, such as low water potential and soil crusting, have frequently been identified as the most significant issues for successful crop establishment (Townend et al. [1996;](#page-11-0) Tisdall [1996](#page-11-0); Nabi et al. [2001;](#page-11-0) Passioura and Angus [2010](#page-11-0)). Tillage, fertilizers and amendments of the seedbed, together with timely irrigation, may ameliorate some of these constraints, although are often

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unaffordable or not accessible to smallholder farmers (Chianu et al. [2012](#page-10-0); Tittonell and Giller [2013](#page-11-0); Tonitto and Ricker-Gilbert [2016\)](#page-11-0). Therefore, inexpensive and sustainable strategies with the potential to alleviate unfavourable conditions and reduce input (e.g., cover crops, water harvesting or organic fertilizer) are becoming more relevant for ensuring food security in semi-arid agro-ecosystems (Branca et al. [2013\)](#page-10-0).

Over the past three decades, there has been a renewed interest in a traditional agronomic technique known as 'on-farm' seed priming, in part because of its simplicity and low-cost (Murungu et al. [2004a](#page-11-0); Rashid et al., [2006](#page-11-0)). On-farm seed priming is a form of hydro-priming, which consists of soaking seeds in water for a number of hours, usually overnight, surface drying them (to allow limited storage) and sowing soon after (Fig. 1) (Harris, [1996\)](#page-10-0). Prior soaking of seeds in water decreases the time needed for seed imbibition in the soil after sowing; thus, on-farm seed priming shortens the exposure of the seed to adverse soil conditions such as limited soil moisture (Harris et al. [2001a\)](#page-11-0). On-farm seed priming technology has been tested in a wide variety of crops and environmental conditions, and has been extensively developed through participatory trials with local farmers (Harris et al., [1999,](#page-11-0) [2001a;](#page-11-0) Rashid et al., [2006a,](#page-11-0) [b\)](#page-13-0). Reports from participatory workshops and research-managed trials have largely agreed that crops grown from on-farm primed seeds emerge faster, obtain higher plant density and vigour, reach flowering and harvest more rapidly, and ultimately, result in higher yields compared with nonprimed crops (Harris, [1996a](#page-10-0), [b](#page-12-0); Harris et al., [1999a](#page-11-0), [b](#page-12-0), [2001a,](#page-11-0) [b;](#page-12-0) Murungu et al. [2003,](#page-11-0) [2004b;](#page-13-0) Farooq et al., [2008](#page-10-0)). However, the extent of these benefits varies widely even under similar contexts; for example, yield improvement of chickpea ranged from 25 to 67% and 4 to 35% in two different villages in India (Harris et al., [1999a,](#page-11-0) [b\)](#page-12-0). There have also been cases where

Fig. 1 'On-farm' seed priming steps carried out with maize seeds in Kenya. a Pouring seeds into buckets. b Soaking seeds. c Surface drying after priming. d Effect on emergence of wheat in Pakistan: non-primed (left) vs. primed (right). (Photos courtesy of H. Wainwright and A. Rashid)

soaking seeds has turned out to be counterproductive, e.g., for cotton (Murungu et al. [2004b\)](#page-13-0), barley (Rashid et al., [2006a](#page-11-0), [b\)](#page-13-0), pearl millet (Aune and Ousman, [2011\)](#page-10-0) and sesame (Ousman and Aune, [2011](#page-11-0)). Consequently, it is unclear to what extent onfarm seed priming can improve crop performance and what factors influence the outcome, and a greater understanding is needed to identify the environments where it may be detrimental and where it can best be applied.

The most important aspect of on-farm seed priming is the duration of the soaking, which must be calculated for each crop species, and even for each variety or cultivar of crop (Harris [2006](#page-11-0)). Exceeding a 'safe limit' of soaking will trigger premature germination, which could lead to damage of the radicle during sowing, or if seeds are left in the priming water for too long, or not surface dried properly, they will begin to rot (Harris [2006](#page-11-0)). Although farmers have some knowledge of the advantages of soaking seeds prior to sowing (Harris et al., [1999a,](#page-11-0) [b,](#page-12-0) [2001a](#page-11-0)), it is often only carried out on seeds for re-sowing in order to 'catch up' with the rest of crop and is rarely used as a routine practice. In general, farmers who have used on-farm seed priming are unaware of safe limits and therefore have had varying degrees of success or failure with this method (Harris et al., [1999a,](#page-11-0) [b,](#page-12-0) [2001a\)](#page-11-0).

To date, only narrative reviews about on-farm seed priming have been published (Ashraf and Foolad [2005;](#page-10-0) Harris [2006](#page-11-0)); therefore, a more systematic approach, such as meta-analysis, is needed to quantitatively review this simple technology in terms of increased crop establishment and production. Metaanalysis is a powerful synthesis tool that is being increasingly adopted in agro-ecological disciplines (e.g. Tonitto and Ricker-Gilbert [2016](#page-11-0)), and using this approach will allow a large number of independent on-farm seed priming case studies to be objectively analysed across different crop types and

environments. A better understanding of the potential of onfarm seed priming, and in which environments it could be most usefully promoted, could provide governmental institutions and policymakers in developing countries with the evidence to promote its adoption as recommended practice. Therefore, the overarching aim of this paper was to quantify the effect of on-farm seed priming compared to conventional sowing and identify the context where it can best be applied. Specifically, our objectives were to quantify the effect of onfarm seed priming on crop performance (speed of germination, final emergence and yield) and evaluate the impact of climate, crop type and common yield-limiting factors on the final outcome of crops grown from on-farm primed seed.

2 Material and methods

2.1 Sources of data

A literature search was carried out in 'Web of Science Core Collection' on 15 November 2017 using the key-words: 'on farm seed priming', 'on station seed priming', 'pre-sowing seed soak*' or 'hydro*priming', which resulted in a total of 293 articles. Titles and abstracts were screened and unrelated papers, or studies focussed on tree seeds were discarded. The full text of the remaining papers was examined and had to meet the following criteria: (1) The study had to contain a dry seed sample (control) and primed seed samples (treatment) consisting of seeds submerged in water with no additional oxygenation, and (2) seeds had to be surface dried or partially dried after priming (maximum air-drying duration of less than 24 h). Artificial drying methods such as ovens or air-conditioned cabinets and seeds re-dried to their original moisture, regardless of the methods used, were not included. Other priming strategies, e.g. seeds placed between filter paper and saturated jute mat, were also excluded due to the confounding effects of matric potential. We excluded 141 articles that did not match these requirements. In addition, studies performing other types of seed treatments (19), not containing or missing data (15), lacking or giving ambiguous description of priming (8) and reviews (5) were excluded, and a further 23 papers without full-text, and five more because the same data had been used in several publications, were also excluded. Six additional papers were identified in the reference list of one of the selected papers, which gave a total of 44 valid papers available for meta-analysis (Table [1\)](#page-3-0).

For each publication, three variables were recorded for both control and primed treatments: (i) final emergence, (ii) time to 50% emergence and (iii) yield (i.e. the most common unit of yield for each crop, e.g. grain for cereals, pods for legumes) giving three datasets. The mean and the number of paired observations (n) contributing to that mean value were recorded, e.g. the experimental design of Harris et al.

[\(2005a](#page-11-0), [b\)](#page-12-0) consisted of two cultivars of chickpea with three replications during two seasons, i.e. $n = 12$. When available, standard deviation (SD), standard error (SE) or standard error of the difference in mean (SED) were also collected as a measure of the variance. Mean and variation values from published graphs were extracted taking a snapshot of the figure and scaling the axes with WebPlotDigitizer Version 3.10 (Rohatgi [2010](#page-11-0)) to obtain numerical values. In addition to the statistical data, any characteristics that may have influenced the outcome of the priming treatment and thus could potentially explain heterogeneity in effect size (moderator variables) were also recorded.

If a single publication presented several case studies, the mean effect was calculated (in order to minimize within-study dependence); however, if the moderators differed then, they were considered as independent case studies in the metaanalysis (Koricheva et al. [2013\)](#page-11-0). In cases where several priming outcomes had a common control, the total number of replications of the control group was divided by the number of treatments to avoid overweighting. If papers presented results that had been carried out by distinct groups, e.g. the design of some of the on-station trials, which included both researcher-led and farmer-led experimental and participatory trials, these data were considered as independent. Although these observations cannot be considered fully independent, this approach is commonly used in both plant biology and ecology meta-analyses and allows greater statistical power (Castagneyrol and Jactel [2012;](#page-10-0) Mayerhofer et al. [2013;](#page-11-0) Shrestha et al. [2016](#page-11-0)). The resulting dataset contained 129 case studies derived from 44 papers, which covered 17 crops across ten countries.

2.2 Effect size and meta-analysis

The natural log response ratio (lnR) of the experimental mean divided by the control mean was used as metric of treatment effect (Hedges et al. [1999](#page-11-0)):

$$
lnR = \ln\left(\frac{X_e}{X_c}\right)
$$

where X_e and X_c are the experimental and control mean. Given that more than 50% of the case studies did not provide a measure of variance, case studies were weighted using nonparametric variance (V_{lnR}) (Adams et al. [1997](#page-10-0)):

$$
V_{lnR} = \frac{n_e + n_c}{n_e * n_c}
$$

where n_e and n_c are the experimental and control number of paired observations, respectively.

Bias-corrected bootstrapped 95% confidence intervals based on 10,000 iterations were calculated for overall effect sizes (Adams et al. [1997\)](#page-10-0) and represented as a percentage change relative to controls $(\%)$, transforming them back by

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 Data corresponding to response variable 'yield' b Simulating semi-arid climate conditions in cabinets

^b Simulating semi-arid climate conditions in cabinets

Table 1 (continued)

 $(\exp(LRR) - 1 \times 100)$ for easier interpretation, where LRR is the weighted summary effect size across case studies. Overall effect sizes were considered significant when their confidence intervals did not overlap (Gurevitch and Hedges [1999](#page-10-0)).

A random effects model was chosen because of the high variation expected between studies due to the diversity of crops and environmental factors. In addition, the aim of this study was to obtain mean effects that can be generalized to different scenarios, which is best done with random effects models (Borenstein et al. [2009](#page-10-0)).

To investigate the relationship between emergence and yield, pairs of effect sizes of 'time to 50% emergence' and 'final emergence', and pairs of final emergence and 'yield' from the same case studies were analysed using time to 50% emergence and final emergence as moderators, respectively. The influence of each moderator was assessed with $F_{\rm M}$ (test of moderator) by meta-regression using restricted maximum likelihood with Knapp-Hartung adjustment (Viechtbauer [2010](#page-11-0); Inthout et al. [2014](#page-11-0)), assuming a fixed effect across levels and a random effect within levels (Borenstein et al. [2009](#page-10-0)). Given the importance of soil interactions, papers reporting laboratory-based experiments were omitted from these specific analyses. To further quantify the extent of yield benefits that can be ascribed to emergence, a hypothesized regression line where changes in final emergence are equal to increments in yield was compared against the weighted linear regression obtained from the meta-regression using linear hypothesis testing.

All calculations were conducted with 'metafor' (Viechtbauer [2010](#page-11-0)), 'car' (Fox et al. [2016\)](#page-10-0) and 'boot' packages (Canty and Ripley [2012](#page-10-0)) in R version 3.3.0 (R Development Core Team [2016\)](#page-11-0).

2.3 Moderator variables

Sub-group analysis allowed further exploration of variables in terms of explaining variability and identification of possible trends (Borenstein et al. [2009\)](#page-10-0). We considered levels within moderators to be significantly different from one another when their confidence intervals did not overlap (Gurevitch and Hedges [1999](#page-10-0)).

The effect of climate on total yield was accounted for by categorizing papers as either 'temperate', 'tropical' or 'dry' according to the Köppen-Geiger climate classification (Kottek et al. [2006](#page-11-0)). Dry climates were further subdivided into 'semiarid' or 'arid' to account for potential evapotranspiration as a function of temperature and cycle of precipitation (Kottek et al. [2006\)](#page-11-0). For this purpose, the high-resolution Köppen-Geiger climate world map ([http://koeppen-geiger.vu-wien.ac.at/](http://koeppen-geiger.vu-wien.ac.at/present.htm) [present.htm](http://koeppen-geiger.vu-wien.ac.at/present.htm)) was loaded into Google Earth Pro (Wuthrich [2006](#page-12-0)) and the location of the case studies in each paper used to determine the climate group. When geographical coordinates were not reported, the location of the experimental station or the nearest city at which the study took place was used.

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Based on yield-limiting factors, three agronomic scenarios were commonly identified across the case studies and used for evaluation of on-farm seed priming on yield. The first scenario included case studies where crops were grown without major nutrient and water limitations. The second scenario contained case studies where crops were grown under rain-fed conditions and low soil fertility was identified as a major constraint (by authors stating that there were low levels of the main macronutrients or other known nutrient deficiencies in the area). The third scenario contained case studies where salinity was identified as the main constraint or when trials were designed to test the effect of salinity. These scenarios were named as 'non-stressed', 'nutrient deficient' and 'salinity stressed', respectively. Case studies not mentioning or giving ambiguous descriptions about any of these factors were omitted for categorical analyses.

2.4 Dataset overview

Overall, our analysis comprised work conducted in 10 countries across the Middle East, South Asia and sub-Saharan Africa. The three most globally cultivated cereals, wheat (*Triticum* aestivum), maize (Zea mays) and rice (Oryza sativa), comprised 46% of case studies, whilst 19% of case studies included essential cereals common in semi-arid areas: sorghum (Sorghum bicolor), millet (Pennisetum glaucum and Eleusine coracana) and barley (Hordeum vulgare). Legumes, including chickpea (Cicer arietinum), mungbean (Vigna radiata), cowpea (Vigna unguiculata) and horsegram (Macrotyloma uniflorum), represented 21% of the case studies. Cash crops, such as sesame (Sesamum indicum), cotton (Gossypium hirsutum) and groundnut (Arachis hypogaea), represented 11% of case studies, and minor crops, fennel (Foeniculum vulgare), korarima (Aframomum corrorima) and Dracocephalum kotschyi Boiss (the last two grown for their spice and medicinal properties) accounted for 3% of case studies analysed.

The dataset of time to 50% emergence was mainly characterized by case studies using small-scale trials (three to four replications) testing the response of varieties or cultivars to onfarm seed priming and, to a lesser extent, different soaking durations. The growing conditions included field trials (46%), pots trials (25%) and lab experiments (29%); most case studies were carried out with monocots (83%). The final emergence dataset encompassed small-scale trials and medium size trials repeated over two to three seasons. More than half of the case studies in this dataset were conducted in the field (61%), with fewer laboratory (22%) and pot trials (17%). Monocot (56%) and dicot species (44%) were almost equally represented in this dataset. For the yield dataset (65 case studies), most of the experiments were conducted under field conditions (with only three pot trials), in both irrigated and in rain-fed plots. Over half of the case studies were carried out at research farms, commonly testing priming treatments on different cultivars or varieties over several seasons, averaging 15

experimental replications per study. The remaining 43% of the case studies were mainly participatory trials carried out by local farmers following local practices and constraints. The average experimental replications for these case studies was 38, and the biggest study accounted for 108 trials of wheat across the state of Guajarat in India (Harris et al. [2001b](#page-12-0)).

2.5 Publication bias and sensitivity analysis

Studies showing negative results are less likely to be published; therefore, effect sizes in meta-analyses could be overestimated (Gurevitch and Hedges [1999\)](#page-10-0). Consequently, indirect methods such as rank correlation tests and funnel plots of effect size vs. variance are commonly used to detect bias (Gurevitch and Hedges [1999;](#page-10-0) Koricheva and Gurevitch 2014). We conducted Kendall's tau test, where significant correlation between effect size and corresponding sample size would indicate asymmetry in the funnel plot and therefore, potential publication bias (Begg and Mazumdar [1994](#page-10-0); Viechtbauer [2010\)](#page-11-0). However, no significant relationship between effect size and increasing number of replicates for any of the three datasets in our analysis was seen. We also performed 'trim and fill' funnel plots to detect potential missing studies. The trim and fill method is a funnel-based test that imputes values that would compensate for the most extreme values in one side of the funnel (Duval et al. [2000](#page-10-0)). In our meta-analysis, trim and fill imputed 12 and 15 potential missing case studies in time to 50% emergence and yield datasets, respectively. In both cases, adjusted summary effects would further deviate from zero suggesting that our results may be conservative (summary tables and funnel plots from these analyses are available at <http://hdl.handle.net/11667/123>).

Sensitivity analyses are also important to determine the robustness of the results (Koricheva and Gurevitch [2014](#page-11-0)). Leaveone-out meta-analysis, i.e. recalculating summary effect size omitting the study with highest effect size for each variable and observing the deviation introduced by this modification, was performed to test robustness of the summary effects. The removal of the study with largest influence in the yield dataset (Harris et al. [2001b\)](#page-12-0) increased the summary effect by 1.42%. The study with the largest influence on final emergence was Finch-Savage et al. ([2004\)](#page-10-0), whose removal changed the summary effect by 1.89%. Lastly, the study with biggest impact on the time to 50% emergence dataset was Harris et al. [\(2001b\)](#page-12-0), and its removal decreased the overall effect size by 6.04%. In conclusion, we did not find evidence of publication bias in our datasets, and although the time to 50% emergence dataset presented some sensitivity, all three datasets were suitable for meta-analysis.

Data availability The datasets generated during and analysed during the current study are available in the Stirling Online Repository for Research Data repository, [http://hdl.handle.](http://hdl.handle.net/11667/123) [net/11667/123](http://hdl.handle.net/11667/123).

3 Results and discussion

3.1 'On-farm' seed priming: an inexpensive technology for increased food security

Our meta-analysis showed that on-farm seed priming has a significantly positive effect on crop performance, from nascence until harvest, relative to conventional ('control') seed sowing (Fig. [2\)](#page-7-0). Although there is substantial variation (ranging from -36 to -7%), on-farm seed priming significantly decreases the time to emergence by 22% compared with nonprimed seeds. On average, the number of plants emerged increased by 11%. Ultimately, yields increased by 21% compared with non-primed seeds, and only six out the 65 case studies reported negative effects on yield (data not shown).

Improved crop performance following on-farm seed priming can have important implications for smallholders' food production. Higher yield is often accompanied by higher straw biomass, which is especially remunerative in mixed croplivestock systems. Enhanced plant density reduces costs and the labour needed for re-sowing, and can also increase the willingness of farmers to invest in fertilizers, as the risk of plant stand failure is lower. Faster emergence typically results in plants reaching flowering and harvest stages earlier (e.g. by several weeks), giving farmers more labour flexibility, for example, by facilitating more optimal sowing for the subsequent crop or including an extra crop in rotation systems, or even by allowing migration for off-season work (Harris et al., [1999a,](#page-11-0) [b](#page-12-0), [2001a;](#page-11-0) Virk et al., [2006](#page-11-0)). Furthermore, the benefits are not restricted to the traits accounted for in our data, as faster development combined with the improved vigour and more uniform emergence in crops from on-farm primed seeds may save labour allocated to weeding. Although it is tempting to suggest that these benefits may increase net incomes, additional costs such as extra fertilizer or extra costs associated with harvesting, processing and storing greater yields, together with access to markets, will determine the final return from adopting on-farm seed priming.

3.2 Relationships between early growth and yield on crops grown from 'on-farm' primed seeds

To further investigate the relationships between rate of emergence, crop establishment and yield, we conducted separate analyses of the effect of time to 50% emergence on final emergence and the effect of final emergence on yield of crops from on-farm primed seeds relative to non-primed. Final emergence versus time to 50% emergence showed that in general, quicker emergence conferred by on-farm seed priming relative to non-primed seeds produced a higher number of successfully emerged seedlings (Fig. [3a](#page-7-0)). Although this relationship was significant ($P < 0.01$), it must be interpreted with caution due to the relatively small number of case studies.

Fig. 2 Summary analyses of the response of crops to 'on-farm' seed priming. Numbers in parentheses indicate number of case studies. Error bars represent back-transformed 95% bootstrap CIs

Fig. 3 a Relationship between final emergence and time to 50% emergence relative to crops from non-primed seeds $(n = 12)$. **b** Relationship between field and final emergence relative to crops grown from non-primed seeds. Solid line represents the weighted model regression line, and dotted line represents the hypothesized regression line where changes in final emergence cause equal changes in yield $(n=22)$. Bubble size represents the weight of each study in the metaregression

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Meta-regression of yield versus final emergence (relative to crops from non-primed seeds) showed a positive relationship (Fig. 3b), although this relationship was not found significant. We found no difference between the hypothesized line and the meta-regression line ($P > 0.05$), which demonstrates that higher yields are proportional to improvements in emergence. However, in over two-thirds of the case studies, improvements in yield were proportionally higher than the expected gain due solely to improvement in final emergence. This suggests that increments in yield due to on-farm seed priming are not only a consequence of rapid and more prolific emergence, but that additional benefits may persist long after emergence.

Rapid emergence is crucial for the vulnerable seedling to avoid abiotic and biotic stresses and ensure high crop establishment (Gardarin et al. [2016\)](#page-10-0). On-farm seed priming facilitates rapid emergence by accelerating germination through two complementary mechanisms. Firstly, it ensures water availability and the successful completion of phase I (the imbibition phase) prior to sowing, rather than relying on the seed imbibing soil moisture in the field where the water supply can be restricted or discontinuous (Wojtyla et al. [2016](#page-12-0)). Throughout the imbibition phase, both mechanical and biochemical changes, e.g. embryo enlargement, respiration, protein synthesis and DNA repair, are initiated (Gallardo et al. [2001;](#page-10-0) Weitbrecht et al. [2011;](#page-12-0) Steinbrecher and Leubner-Metzger [2017](#page-11-0)). All these processes prepare the seed for cell elongation (phase II, the lag phase); therefore, on-farm primed seeds are developmentally more advanced than dried seeds, resulting in a 'head start of germination' (Chen and Arora [2013\)](#page-10-0). Secondly, on-farm primed seeds are only externally dried so that, once in the field, seeds need to absorb less water from the soil to complete phase III (the post-germination phase) when the radicle emerges from the seed coat. Furthermore, it has been reported that seed soaking enhances the production of the enzyme α-amylase (Ashraf and Foolad [2005;](#page-10-0) Farooq et al., [2017\)](#page-10-0), which plays a crucial role in starch mobilization and provides the embryo with carbohydrates for

respiration during germination and seedling growth (Ashraf and Foolad [2005;](#page-10-0) Farooq et al., [2017a](#page-10-0), [b](#page-12-0)). As a result, seedlings from on-farm primed seeds have more developed roots before the common limiting factors such as declining soil moisture, crust formation and/or high salinity prevent successful emergence.

Our results suggest that the gains in yield due to on-farm seed priming can be mainly attributed to enhanced emergence, i.e. rapid emergence leads to better crop establishment, which is conducive to higher yields. However, advanced establishment may also be coupled with higher vigour of individual plants, which is translated into significantly more tillers, more fruits (cobs/panicles/pods) per plant, greater number of grain and 1000-grain weight, or straw yield (Harris [2006;](#page-11-0) Rashid et al., [2006;](#page-11-0) Harris et al., [2007;](#page-11-0) Farooq et al., [2008](#page-10-0)). In addition to these physiological benefits, other circumstantial benefits are frequently observed, for example, earlier maturation decreases crop exposure to end of season drought, disease and pest attacks (Harris et al. [2001a;](#page-11-0) Rashid et al., [2006a](#page-11-0), [b](#page-13-0)). It is also likely that seed priming exerts important metabolic changes during early plant growth that are able to persist until later stages of development (Ashraf and Foolad [2005;](#page-10-0) Chen and Arora [2013](#page-10-0)); for example, there is evidence for enhanced

Fig. 4 Sub-grouped summary effect sizes and 95% CIs for priming effect on crop yield. Comparisons among a levels of climate, b levels of yieldlimiting factors, and c levels of plant type. Numbers in parentheses indicate number of case studies. Error bars represent back-transformed 95% bootstrap confidence intervals

disease resistance (Musa et al., [2001;](#page-11-0) Rashid et al. [2004;](#page-11-0) Harris et al., [2005\)](#page-11-0) or drought tolerance (Wojtyla et al. [2016\)](#page-12-0).

3.3 What modulates the 'priming' response?

It is important not only to identify the context where on-farm seed priming can best be applied, but also understand the potential situations where it can be counterproductive. Therefore, a subgroup analysis of moderators was conducted to examine potential factors that influence the effect of seed priming.

3.3.1 Climate

It is clear that yield benefits are more evident under low and unpredictable rain conditions. The largest response to on-farm seed priming was seen in areas with dry climates (Fig. 4a) with significantly higher yields for both arid (22%) and semi-arid (28%) climates compared to temperate climates (11%). Variation in yield between seasons due to on-farm seed priming has been frequently attributed to rainfall profiles, with greater yield increments commonly reported during rainy seasons with limited precipitation (Rashid et al., [2006a,](#page-11-0) [b](#page-13-0); Virk et al., [2006;](#page-11-0) Ousman and Aune, [2011\)](#page-11-0). Low soil moisture and high evapotranspiration can slow and interrupt imbibition, which is conducive to emergence failure (Harris 1996); however, on-farm seed priming can offset a lack of soil moisture, as seeds have already imbibed water prior to sowing.

Importantly, in crust-prone soils, if rainfall occurs before emergence, shoots from on-farm primed seeds could be mechanically impeded, whilst the later emerging non-primed seedling may find more favourable soil strength (Murungu et al. [2004a](#page-11-0)). Equally, if rainfall is considerably delayed after sowing, seedlings from on-farm primed seeds may be damaged as germination has already been initiated and a lack of water could kill the developing seedling, whereas non-primed seeds will not initiate germinate until the rain comes (Murungu et al. [2003;](#page-11-0) Rashid et al., [2006a](#page-11-0), [b](#page-13-0)). However, the occurrence of these events seems to be very rare (Murungu et al. [2003,](#page-11-0) [2004a](#page-11-0)), and our data at emergence stage is consistent with the yield subgrouping, i.e. showing the higher benefits under dry climates (data not shown).

The interaction between soil temperature and on-farm seed priming, however, is less clear. Primed maize seed is more sensitive to elevated temperature under both dry and wet soil conditions (Finch-Savage et al., [2004a,](#page-10-0) [b;](#page-12-0) Murungu et al. [2004b](#page-13-0)). For the former, internal seed moisture may induce heat stress by acting as a thermal conductor in soils of higher temperatures, while wet soils may exacerbate prolonged hypoxia (Finch-Savage et al., [2004a](#page-10-0), [b\)](#page-12-0). Conversely, late sown wheat and chickpea plants from on-farm primed seeds have shown increased tolerance to chilling temperatures (Farooq et al., [2008a](#page-10-0), [b](#page-12-0), Farooq et al., [2017a](#page-10-0), [b\)](#page-12-0), possibly due to enhanced carbohydrate supply to the germinating embryo, which together

with an accumulation of trehalose, can protect proteins and membranes from oxidative damage under abiotic stress.

3.3.2 Yield-limiting factors

Figure [4](#page-8-0)b shows that crops from on-farm seed grown under 'salinity stress' or in nutrient deficient soils had significantly higher yields compared to crops from on-farm seed grown under non-stressed environments (approximately 16% difference). In saline environments, germination is delayed or inhibited through reduced water availability and/or accumulation of toxic Na+ and Cl[−] . However, primed seeds are already hydrated and therefore less subjected to these constraints (Ibrahim [2016](#page-11-0); Savvides et al. [2016](#page-11-0)). Importantly, case studies growing crops in conditions defined as non-stressed were mostly from research-managed trials using fertilizers and pesticides, whilst case studies grouped as nutrient deficient were mainly from farmer-managed trials with limited access to fertilizers and pesticides, and therefore more accurately reflect resource-poor farming conditions in marginal areas. These data indicate that on-farm seed priming can compensate, to some extent, for low-yielding environments and the lack of inputs that would further limit yields. Under low fertility environments, the quicker development of seedlings from onfarm primed seeds allows greater uptake from fertilizers, before nutrients are leached from the soil surface or become volatized (Harris et al. [2001b;](#page-12-0) Rashid et al., [2006a](#page-11-0), [b](#page-13-0)).

Declining soil fertility together with limited access to affordable mineral fertilizers is a major constraint for achieving optimal yields in marginal areas of developing countries (Chianu et al. [2012](#page-10-0)). However, low-cost strategies that combine on-farm seed priming with low amounts of inorganic fertilizers have been carried out to alleviate nutrient deficiencies with promising results (Aune and Ousman, [2011a](#page-10-0), [b](#page-12-0); Ousman and Aune, [2011a](#page-11-0), [b](#page-13-0)). On-farm seed priming in combination with micro-dosing, i.e. application of small amounts of fertilizer in the planting pocket, demonstrated greater fertilizer use efficiency than micro-dosing alone for all the crops tested (Aune and Ousman, [2011a,](#page-10-0) [b](#page-12-0); Ousman and Aune, [2011a,](#page-11-0) [b\)](#page-13-0). Small amounts of micronutrients added to the water used for on-farm seed priming, e.g. $ZnSO₄$, can also be highly cost-effective (Harris et al., [2007a](#page-11-0), [b,](#page-12-0) Farooq et al., [2008a,](#page-10-0) [b\)](#page-12-0).

3.3.3 Plant type

On-farm seed priming of all the major tropical crops produces similar or greater yields than traditionally sown crops in almost all cases (data not shown). However, decreased performance following on-farm seed priming has also been occasionally reported for barley (Rashid et al., [2006a](#page-11-0), [b](#page-13-0)), pearl millet (Aune and Ousman, [2011a,](#page-10-0) [b](#page-12-0)), rice (Rehman et al. [2011\)](#page-11-0), sesame (Ousman and Aune, [2011a](#page-11-0), [b\)](#page-13-0), maize (Ali et al., [2008\)](#page-10-0), wheat (Islam et al., [2015\)](#page-11-0), and cotton

(Murungu et al. [2004b\)](#page-13-0), although for each of these crops, thee are also studies showing an increased performance (e.g. Harris et al., [2007a](#page-11-0), [b](#page-12-0); Farooq et al., [2008a](#page-10-0), [b](#page-12-0); Rashid et al., [2006a,](#page-11-0) [b](#page-13-0)). Importantly, negative results are rarely attributed to the incompatibility of priming with the crop, but rather to untimely adverse environmental conditions. The largest yield loss due to on-farm seed priming was 8% for pearl millet in a series of on-station trials; however, in this study, the farmermanaged replicates registered a 30% increase in yield (Aune and Ousman, [2011a,](#page-10-0) [b\)](#page-12-0). Therefore, we have found no consistent evidence of negative interactions between specific crops and on-farm seed priming, which suggests that this is therefore a safe practice for all crop species trialled so far.

The effect of categorizing case studies by plant type on total yield is shown in Fig. [4](#page-8-0)c. On average, the yield increase of cereals (monocots) was 13% less than dicots. Dicot plants, broadly represented by legumes with 18 out of 23 case studies, responded better to on-farm seed priming averaging a 28% yield increase. This is in line with our final emergence data where greater effect sizes generally belonged to dicotyledonous crops (data not shown). Cereals were commonly grown with irrigation or during the rainy season, whilst legumes were sown as a component of the rotation after cereals in the post-rainy season or in fallow lands that were unsuitable for the main crop. In these marginal contexts, the benefit of seed being hydrated prior to sowing leads to more rapid emergence and establishment.

We cannot conclude from our data whether specific crops are more responsive to on-farm seed priming than others; however, on-farm seed priming may facilitate the use of legumes into rotational and intercropping systems. Currently, in both rotational and intercropping systems, the adoption of legumes is largely discouraged due to poor establishments of the legume component. In rotation, legumes are commonly grown utilizing residual soil moisture remaining during the dry season, and with no additional fertilization, whilst in intercropping systems, the planting of a legume companion is delayed in order to avoid shading and competition (Masvaya et al. [2017\)](#page-11-0). Therefore, on-farm seed priming may ameliorate these unfavourable planting conditions and boost the benefits of cereal-legume cropping systems, e.g. by improving soil fertility and providing an additional income.

4 Conclusion

In developing regions of the world, tackling yield reductions due to both natural and socio-economic constraints, e.g. increasingly unpredictable rainfalls, declining soil fertility and limited access to inputs and resources, requires inexpensive and sustainable strategies to ensure food production and selfsufficiency. This is the first study quantifying the potential of on-farm seed priming for sustainably increasing food production at a global scale, and our results have shown that it is a

valid approach to closing yield gaps. The literature considered in our meta-analysis encompassed a representative number of agro-environments where on-farm seed priming can be practiced and gives us the basis to draw the following conclusions.

On-farm seed priming attenuates the negative effects of adverse planting conditions, and low inputs, by facilitating rapid and enhanced crop establishment that may also result in improved individual plant performance. These effects are more evident in semi-arid and arid regions and, given that millions of hectares in dry climates are experiencing yield reductions, these findings could have important implications. Our results have also highlighted that crops grown in marginal lands can especially benefit from this intervention. This is particularly important for farmers with limited access to mineral fertilizers where to a large extent an input of N is dependent on N_2 fixed by legumes.

On-farm seed priming can be seen as a starting point towards sustainable intensification in marginal areas of the developing world. This technology requires very few resources and technical knowledge, and its benefits would be compatible with a range of other sustainable strategies such as smartuse of farmyard manure, micro-dosing and water harvesting practices. Therefore, our results provide the evidence needed to encourage governmental institutions and policymakers in developing countries to promote the adoption of on-farm seed priming as recommended practice.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

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