

Global synthesis of drought effects on cereal, legume, tuber and root crops production: A review

Stefani Daryanto, Lixin Wang*, Pierre André Jacinthe

Department of Earth Sciences, Indiana University-Purdue University Indianapolis (IUPUI),
Indianapolis 46202, USA

*Corresponding author

Lixin Wang

Department of Earth Sciences

Indiana University-Purdue University Indianapolis

Indianapolis, IN, 46202, USA

Office phone number: 317-274-7764

Email: lxwang@iupui.edu

This is the author's manuscript of the article published in final edited form as:

Daryanto, S., Wang, L., & Jacinthe, P.-A. (2016). Global synthesis of drought effects on cereal, legume, tuber and root crops production: A review. *Agricultural Water Management*.
<https://doi.org/10.1016/j.agwat.2016.04.022>

Abstract

As a result of climate change, drought is predicted to pose greater pressure on food production system than in the past. At the same time, crop yield co-varies with both environmental (e.g., water, temperature, aridity) and agronomic variables (i.e., crop species, soil texture, phenological phase). To improve our quantitative understanding on the effect of these co-varying factors on agricultural productivity, we synthesized previous meta-analysis studies summarizing the results of numerous independent field experiments on drought and its effect on the production of cereal, legume, root and/or tuber (root/tuber) crops. We also included new crops species that were not covered in previous meta-analyses and the effects of heat stress. Our results indicated that cereals tended to be more drought resistant than legumes and root/tubers. Most crops were more sensitive to drought during their reproductive (i.e., grains filling, tuber initiation) than during their vegetative phase, except for wheat, which was also sensitive during vegetative phase. Recovery from drought impact at reproductive phase was either: (i) unfeasible for crops experiencing damage to their reproductive organs (e.g., maize, rice) or (ii) limited for root/tuber crops, provided that water was abundant during the subsequent root/tuber bulking period. Across soil texture, the variability of yield reduction for cereals was also lower in comparison to legume or root/tuber crops, probably due to the extensive and deep rooting system of cereal crops. As crop species, plant phenology, and soil texture were important co-varying factors in determining drought-induced crop yield reduction, no single approach would be sufficient to improve crop performance during drought. Consequently, a combination of approaches, particularly site-specific management practices that consider soil conditions (i.e., intercropping, mulching, and crop rotation) and selection of crop varieties adjusted to the local climate should be adopted in order to improve the sustainability of agricultural production in a changing climate.

Keywords: drought, cereal, legume, tuber, meta-analysis, climate change

1. Introduction

The majority of human food source has been largely supplied by three different types of crop groups: cereals, legumes, roots and/or tubers (root/tuber). Globally, three major cereal grains (i.e., maize, wheat and rice) and other minor grains (e.g., barley, sorghum, oat, rye, millet) provided 56% of the food energy and 50% of the protein consumed on earth (Cordain, 1999). Legumes ranked second after cereal in terms of food production, which accounted for 27% of the world's primary crop production and contributed 33% of protein needs (Graham and Vance, 2003). They also contributed more than 35% of the world's vegetable oil production, particularly from the processing of soybean and groundnut (Graham and Vance, 2003). The other major crop group, root and tuber, is an important calorie source in certain regions. For example, in the sub-Saharan Africa, root and tuber provided up to 30% of total calorie consumption, and could even reach 50% in some countries such as Congo and Rwanda (Alexandratos and Bruinsma, 2012). Humanity's dependence on these three groups of crop is expected to continue although their demand may increase at different rate due to, for example, shifts towards livestock products and vegetable oils, resulting in a projected decline in the share of cereals in total calorie to 47% in 2050 (Alexandratos and Bruinsma, 2012).

During the last few decades, major drought events have been recorded and were projected to intensify in many parts of Asia and beyond (Miyan, 2014), which could make farming exceedingly challenging in some countries (e.g., Pakistan), particularly those located in the dryland regions (Wang et al., 2012) such as Sahelian zone (Fussell et al., 1991) and Mediterranean

(Hoerling et al., 2012). Early termination of rainy season in the lowland rain-fed areas of the Mekong region of Cambodia and Laos negatively affected the productivity of rice genotypes that flowered late and required a longer growing period (Tsubo et al., 2009). In the Mediterranean climate of North Africa, erratic and inadequate rainfall significantly depressed the important durum wheat production (El Hafid et al., 1998). The yield of food legumes grown in arid to semi-arid environments or drylands such as the Mediterranean (e.g., faba beans, chickpea and lentil), was usually variable or low due to terminal droughts that characterize these areas (Karou and Oweis, 2012; Mafakheri et al., 2010). Even in non-dryland countries like Brazil where precipitation was generally sufficient for legume (i.e., soybean) cultivation, water deficiency might still occur over a period of a few weeks, causing significant yield loss (Oya et al., 2004). Similar findings were also observed for various tuber/root crops, including those generally regarded as “drought-resistant” such as cassava (Burns et al., 2010) and sweet potato (Onwoume and Charles, 1994).

More than in the past, the sustainability of food production systems for a growing world population has therefore become a much greater concern, particularly with the changing climate. Global maize and wheat productions, for example, were projected to decline by 3.8% and 5.5% respectively with increasing temperature but decreasing precipitation, despite improved agricultural technologies and the “carbon dioxide fertilization” effect (Lobell et al., 2011). Similarly, world’s cereal production was only projected to grow by 0.9% annually from 2007 to 2050, down from previously 1.9% per year in the past four decades, largely as a consequence of reductions in irrigated food production system (Alexandratos and Bruinsma, 2012). Further expansion of irrigation is questionable due to, among other factors, competition for water from

urban and industrial sectors, lowering of water table, and potential salinization (Alexandratos and Bruinsma, 2012). Indeed, the conversion of irrigated cropland to rainfed system in heavily-populated China and South Asia as well as western United States (US) due to projected freshwater limitations by the end of the century could translate in the loss of 600 to 2,900 Petacalories (Pcal) of food production (equivalent to 8-43% of present day total production) (Elliott et al., 2014).

Crop yield is affected by agronomic factors and various environmental variables with water availability and temperature being the most critical environmental factors (Awika, 2011). As yield variability in many rainfed areas tends to be large, it will affect food security in these marginal environments (e.g., semi-arid regions) due to water limitation and year to year fluctuations of meteorological conditions. Frequent multi-year droughts over large areas have been observed in both tropical and subtropical regions, and this trend is expected to continue with changes in atmospheric composition and rising global temperature (Dore, 2005). In the US, major drought events were recorded during the 1930s, early 1950s, and more recently in 2007, 2012, and 2014 (Mallya et al., 2013). These alterations in the hydrological cycle (e.g., declines in soil moisture and precipitation during critical plant growth periods) could create high level of uncertainty, particularly for rainfed agricultural system. Groundnut yield in India, for example, varied between 550 and 1100 kg ha⁻¹ mainly due to fluctuation in annual rainfall (Reddy and Reddy, 1993). The impact of those factors across different crop groups and site conditions, however, have not been fully elucidated, but this understanding is necessary to develop agricultural practices aimed at minimizing the impact of drought. One approach to documenting such effects is by examining past results using meta-analysis of large datasets to identify general trends among numerous independent drought-related experiments (Hedges et al., 1999). The effects of drought on global

legume (Daryanto et al., 2015), wheat, maize (Daryanto et al., in review-a) and root/tuber (Daryanto et al., in review-b) production were assessed separately using meta-analysis techniques. However, we still lack: (i) the quantitative comparisons among the three major crop groups with regard to their performance under drought, and (ii) the information on the response to drought of other major cereal crops such as rice, sorghum, barley, and millet. In this review, we synthesized published studies that investigated the effect of drought on various crop species within the three major crop groups listed above and examined the data with due consideration of phenological phases, agro-ecological regions, and soil texture. In addition to legume, wheat, maize and root/tuber group, we included cereal crops such as rice, sorghum, barley, and millet that were not examined in the earlier assessments. We also discussed the importance of heat as another co-varying factor affecting crop yield during drought events, as well as agronomic and plant breeding approaches that could be adopted to mitigate the impact of drought on the production of these major crop groups.

2. Materials and Methods

In this review, besides the data synthesized in three previous meta-analysis studies on maize, wheat, legume, and root/tuber crops, we included the following cereal species that were not covered in those earlier meta-analyses: durum wheat (*Triticum durum*), aerobic and anaerobic rice (*Oryza sativa*), barley (*Hordeum vulgare*), sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*), proso millet (*Panicum miliaceum*), and oat (*Avena sativa*). The database for this study was collected from peer-reviewed journal articles published in English from 1980 to 2015 based on Google Scholar search using the following two sets of keywords: (i) species common name, water, stress, yield, and field, or (ii) species common name, irrigation, deficit,

yield, and field. Only articles that meet the following criteria were included in the database: (i) plants that experienced drought under field conditions (excluding pot studies), (ii) the effect of water deficit was considered in comparison with well-watered condition and not in combination with other treatments (e.g., addition of fertilizers or growth hormones, modification of temperature or CO₂), (iii) the reported plants were monoculture species cultivation, and (iv) the articles reported crop response as yield per unit area. For cereal crops, the total number of data points before averaging (including genotypes and cultivars) was 5485 from 228 studies. After averaging to the species level, the total number of data points used for cereal meta-analysis was 1674. Although we were only interested in evaluating the effect of drought on crop performance at the species level, we separated the response of aerobic and anaerobic rice due to their disparity in water requirement during cultivation. The other two groups have the same number of data points as Daryanto et al. (2015) and Daryanto et al. (in review-b).

The magnitude of yield responses was examined based on the following categorical variables: (i) species, (ii) agro-ecosystem types (dryland and non-dryland), (iii) drought timing (i.e., vegetative phase or early season, reproductive phase or late season, and during both the vegetative and reproductive phases or throughout season), and (iv) soil texture (fine-, medium-, or coarse-textured soil). To compare the differences in observed yield reduction between each categorical variable, meta-analysis was used to construct the confidence intervals. We performed an unweighted analysis using the log response ratio (lnR) to calculate bootstrapped confidence limits in order to include those studies that did not adequately report sample size or standard deviation using the statistical software MetaWin 2.0 (Rosenberg et al., 2000). The response ratio is the ratio between the outcome of experimental group (i.e., drought) to that of the control group

(i.e., well-watered condition) and the difference is considered significant if the bootstrap confidence interval does not overlap with each other using a statistical significance level of $P < 0.05$.

Since not all articles reported the amount of water used in their experiment, we took the subset of the data that reported it to calculate drought sensitivity, defined as the relationship between yield response ratio (i.e., the ratio between yield during drought and during well-watered condition) and water availability ratio (i.e., the ratio between water during drought and during well-watered condition or control) (Daryanto et al., in review-a). We used water availability ratio instead of the widely-accepted drought intensity indices such as Palmer index because most of the studies were controlled experiments (i.e., comparing irrigated conditions and irrigation reduction instead of observing natural rainfall deficit) (Wells et al., 2004). Water availability ratio might or might not include rainfall (i.e., depending on the study), but the inclusion or exclusion was consistent for each ratio. The highest water level in a study (i.e., well-watered condition, $\leq 100\%$ ET) was then used as control for all data in the corresponding study. Apart from using them for calculating drought sensitivity, we also used the data of water during drought and during well-watered condition (i.e., control) to calculate the difference among observed water reductions within a categorical variable using one-way ANOVA. Some exceptions, however, were applied to species with limited number of data (i.e., oat, Bambara bean, lablab bean, black gram, taro, and yautia). With these species, we used either single amount of water reduction or other quantitative indication (e.g., soil moisture) from the corresponding article as proxy to report the observed water reduction. Further details of the methodology used can be found in Daryanto et al. (2015), Daryanto et al. (in

review-a), and Daryanto et al. (in review-b). The geographical distribution of the study sites is listed in Table 1.

3. Results

3.1. Crop species variations

Our results have shown that the extent of yield reduction due to drought was largely determined by crop species. Within the cereal group, wheat demonstrated the lowest (i.e., <25%) yield reduction under similar water stress (i.e., ~40% water deficit) compared to other species such as durum wheat, pearl millet, and maize (Figs. 1A, 1B). Anaerobic rice, on the other hand, showed a greater yield reduction (>50%) under a similar level of water deficit (Figs. 1A, 1B). When compared to other crop groups, we found that variation in yield reduction range among legume species varied greatly, with some species (e.g., soybean, field pea, groundnut) had smaller variation in yield reduction compared to other species (e.g., lentil, pigeon pea, Bambara bean, common bean) (Fig. 1C). Contrasting to our expectation that high variability in the response of root/tuber crops to drought might occur due to differences in plant families (e.g., Solanaceae, Euphorbiaceae, Convolvulaceae), our results indicated that most root/tuber species showed similar yield reduction (Fig. 1E) under comparable water deficit (Fig. 1F). Sweet potato even showed greater drought sensitivity when compared to potato (Fig. 2). Across the three crop groups, we observed that there was a greater range (i.e., variability) of yield loss in legume (20-85%) and root/tuber groups (25-70%) compared to cereal (25-40%, except for anaerobic rice; Figs. 1A, 1C, 1E). As a group, cereal category also tended to exhibit lower yield reduction compared to legume or root/tuber crops (Figs. 1A, 1C, 1E).

3.2. Phenological phase

Our results suggested that drought occurring during vegetative phase (i.e., early season) generated smaller yield reduction compared to that during reproductive phase (i.e., late season) in all crop groups (Fig. 3). While the range and amount of yield and water reduction were more consistent across cereal, legume or root/tuber crops (Fig. 3), the sensitivity of different crop species during certain growth phase might vary. Maize, in particular, showed greater sensitive to drought during reproductive phase compared to other cereal species such as wheat (Fig. 4).

3.3. Soil texture

The effects of soil texture were more variable across legume crop group compared with cereal (Figs. 5A, 5C), with higher yield reduction generally found in medium-textured soils for legume crop (Fig. 5C). Within the legume group, despite having similarities in drought sensitivity (Fig. 6) likely due to the associated root characteristics, soybean had lower yield reduction to drought compared to common bean (Fig. 1B). Surprisingly, we did not find any difference between root/tuber yield: (i) grown in contrasting soil texture (coarse vs fine; Fig. 5E) despite some species might have shallower root than the others or (ii) when it was compared with relatively deep-rooted cereals (Fig. 5A).

3.4. Agro-ecological region

Despite the difference in relative humidity, temperature and consequently potential evapotranspiration demand, we found no difference in yield reduction between crops grown in dryland versus non-dryland conditions consistently across the three crop groups (Fig. 7).

4. Discussion

4.1. Crop species variation

Variability of yield responses of various cereal species could be related to variations in plant physiological traits as different cereal species adopted different adaptation mechanisms to drought (Daryanto et al., in review-a). Even within the same genera, differences between cereal species have been observed with regard to their adaptation to drought. Lower performance of durum wheat compared to bread wheat (Fig. 1A) under similar osmotic adjustment (OA) (Morgan et al., 1986) could be due to the unrecovered low CO₂ exchange rate and water loss rate in previously droughted plants, resulting from persistent abscisic acid production in durum wheat (El Hafid et al., 1998). A long history of domestication and hybridization in wheat might further explain variation within the same genera since genome-wide diversity between wild and domesticated species has indicated that wheat and durum wheat have lost 69% and 84%, respectively of their nucleotide diversity (Haudry et al., 2007). The severity of water deficit variably affected yield-related traits in durum wheat. While moderate droughts (40% water reduction) only affected grain weight, severe water deficits (>50% water reduction) caused reductions in both the number of fertile ears per unit area and the number of grains per ear (Giunta et al., 1993).

With results from cereals suggested that small yield variation could be related to genetic development and agronomic practice of the associated species (Monneveux et al., 2013), having a large range of yield reduction (Fig. 1C) suggested that some legumes (e.g., lentil and pigeon pea) could be developed into more drought-resistant species by shifting the yield reduction range towards the smaller one. The opportunity appeared as traditionally, pigeon pea and lentil have been regarded as drought-tolerant crops in areas where they have been cultivated (e.g., India, East

Africa) (Materne and Reddy, 2007; Saxena, 2008). Agronomic practices that promoted water conservation and soil fertility (e.g., mulching) had been shown to produce higher lentil yield under rainfed condition (Singh et al., 2009). Similar practice might also improve the yield of common bean as nitrogen (N₂) fixation of the species was particularly sensitive to high soil temperature (Piha and Munns, 1987) and water stress (Ramos et al., 2003). Breeding for drought-tolerant lentil, common bean, and pigeon pea, however, might require combination with their wild species, considering that the cultivated species exhibited narrow level of genetic diversity due to geographical isolation during domestication events (Ferguson et al., 1998; Kwak and Gepts, 2009; Yang et al., 2006).

Unlike cereals or legumes where all species in each crop group belong to the same family (i.e., Gramineae for cereals and Fabaceae for legumes), root/tuber crops consist of different families of plants (e.g., Solanaceae, Euphorbiaceae, Convolvulaceae), and therefore one may expect greater variability in the response of root/tuber crops to drought compared to that of legumes or cereals. We found, however, that there was no significant difference in yield reduction, for example, between the commonly known “drought-sensitive” potato and “drought-resistant” sweet potato (Onwoume and Charles, 1994; Woolfe, 1992) under similar amount of water reduction (i.e., 35%; Figs. 1E & 1F). While sweet potato might be resistant to drought in terms of its survival rather than its capacity to maintain high yield (Daryanto et al., in review-b), we also suggested that dry matter produced by a crop was proportional to the amount of solar radiation intercepted by the canopy across different root/tuber species (Gomes et al., 2005). Lower carbon (C) partitioning to the storage organ in potato during drought was an indirect response of reduced radiation energy interception resulting from lower leaf area index (LAI) of droughted plants

(Jefferies, 1995). Similarly in cassava and sweet potato, shoot and root developed simultaneously throughout the growth season, leading to the existence of optimum leaf area index (LAI) value that allowed a balanced distribution of assimilate to the two competing organs (El-Sharkawy, 2003; Haimeirong and Kubota, 2003). This reduction in LAI was supported by previous research that showed the increase of root:shoot ratio of potato during drought (Jefferies, 1995), resulting from a decrease in shoot biomass in comparison to root biomass (Prasad et al., 2008). At the same time, the ratio between root length and root weight also increased with drought since the developed roots tended to be thinner (Jefferies, 1995), presumably to improve water uptake. Such conditions, however, were reversed under well-watered condition where growth of the storage roots was favored (Gomes et al., 2005).

While the inherited properties of different species affected the extent of yield reduction, greater yield loss was likely to be found in species that were less common in the developed world within each food group (e.g., black gram, lablab bean, yautia, or taro) (Figs. 1C & 1E). These “less common species” also showed a greater yield range within the species (e.g., bambara bean, lentil, pigeon pea, cassava, taro, yautia) compared to the species that are more common in the developed countries (e.g., maize, wheat, soybean, potato), which showed relatively less variability in yield (Figs. 1A, 1C, 1E). We suggested that the robustness of yield of the “more common cereal species” to drought was likely linked to the higher level of agronomic and genetic development that these species underwent. In accord with that contention, it has been suggested that yield improvement in temperate cereals could be attributed to greater stress tolerance that has been obtained through continuous genetic improvement and field trials (Tollenaar and Wu, 1999). The number of studies dedicated to a crop species can be taken as a proxy of genetic improvement. There have been more

than twice as many of drought-related studies for cereals (i.e., 228) compared to legumes (i.e., 111) or root/tuber (i.e., 85) (Daryanto et al., 2015, in review-b). Similarly, there have been six times as many published studies on potato (i.e., 62) than cassava (i.e., 10) (Daryanto et al., in review-b), further underscoring the knowledge gap that likely exists between the “more common” and “less common” crop species with respect to their response to drought. In addition, better agricultural practices are generally adopted where the “more common” species is grown; therefore, when comparing crop species sensitivity to drought, one needs to be aware of the bias that such a disparity can introduce.

Studies on crop breeding efforts, although appeared later in the literature compared to crop and soil management, seemed to contribute significantly to improve crop adaptation, particularly cereal, to drought. A classic example probably would be the selection for short anthesis-silking interval in maize which successfully reduced yield loss during drought (Bolaños and Edmeades, 1996). In general, the focus of breeding efforts has been on the mechanisms on how crops respond to drought, which could be divided into three categories – drought escape, drought avoidance and drought tolerance (Barnábas et al., 2008). The development of shorter cycle crops usually became the target for drought escape category in many rainfed-dependent areas as the majority of yield loss here was caused by early rain termination, generating a significant decline in stored soil moisture during critical grain filling period (Fussell et al., 1991; Tsubo et al., 2009). More variable traits were identified for drought avoidance (e.g., leaf area index or LAI, root density and depth, plant surface structure, osmotic adjustment, delayed senescence or stay-green) and drought tolerance (e.g., stem reserve utilization, cellular membrane stability, antioxidant property, stress protein, and abscisic acid or ABA) criteria (Barnábas et al., 2008). In general the selection favored

for the above-mentioned secondary traits (including anthesis-silking interval) rather than the yield itself *per se* due to the low heritability and possible interactions with other agronomic factors (e.g., nutrient stress, pathogen) of the latter (Fussell et al., 1991; Monneveux et al., 2008).

Apart from the number of studies dedicated to a given crop group or species, intrinsic factors such as physiological and biochemical differences among different crop species were also responsible for variable yield responses within a crop group (i.e., legumes; Fig. 1C), which might later be translated into differences across crop groups (i.e., legumes and cereals; Figs. 1A & 1C). While the capability of legume to fix N_2 could be the most notable difference between legumes and the other crop groups, it was also likely that this hallmark trait made legumes less efficient than cereals in its photosynthetic biochemistry. These inherent differences in resource partitioning (i.e., cost of N_2 fixation, oil, and protein production in legumes) could limit legume yield improvement compared to cereals. Legumes (i.e., soybean) were known to require a much higher leaf N investment than cereals (i.e., rice or maize) to achieve comparable photosynthetic rate (Sinclair, 2004). The relative abundance of N in legume tissues as a result of N_2 fixation was considered as the cause of this high leaf N requirement (Sinclair, 2004). Different legume species, however, had different N_2 fixation sensitivities to drought which were linked to the amide or ureide transport system (Sinclair, 2004). Nitrogen fixation rates in the ureide group (e.g., soybean, green gram, black gram, and cowpea) declined more rapidly than any physiological processes as a result of drought (Sinclair, 2004). Increasing ureide concentration in the shoot and nodules under drought created a strong negative feedback on N_2 fixation (Serraj, 2003). Repressed N_2 fixation in legume plants resulted in significant yield loss (Sinclair, 2004), which could be responsible for the higher yield loss during drought observed in the ureide group (with the exception of soybean) compared

to the amide group (e.g., faba bean, lentil, pigeon pea, and groundnut). This interpretation was consistent with our results. Among the legumes, lentil, groundnut, pigeon pea, soybean exhibited the lowest (<30%) while common bean exhibited the highest yield reduction (>60%) under comparable water reduction (i.e., 40%; Figs. 1C & 1D). It could also be suggested that higher level of genetic modification in soybean, and to a lesser extent in groundnut, compared to other legume species (Somers et al., 2003) might contribute to these trends. Additionally, higher yield variability with drought in legumes might also result from different ability of the various crop species to mobilize phosphorus (P) in the soil (Sinclair, 2004). Pigeon pea, chickpea, common bean, and groundnut were able to tolerate lower P availability compared to soybean, including some cereal species such as maize, pearl millet, or sorghum (Beebe et al., 2008; Sinclair, 2004).

4.2. Phenological phase

Our results showed that plants usually exhibited lower degree of sensitivity to drought during their vegetative phase (Fig. 3), consistent with previous studies across the three crop groups (e.g., Bolaños and Edmeades, 1996; Farooq et al., 2009; Monneveux et al., 2013). Although some exceptions were found (e.g., wheat, which would be discussed later), smaller yield loss was observed because photosynthesis and development could be adjusted by the production of osmolytes, heat shock protein, or other growth regulators during vegetative phase (Prasad et al., 2008). Further, most of the carbohydrate in cereal grains was derived from post-anthesis photosynthesis (Evans et al., 1975), minimizing potential yield loss due to drought during vegetative phase. In cereal crops, drought during vegetative phase was considered reparable because stomatal closure and partial inhibition of photosynthesis only limited carbohydrate synthesis for cell division and expansion (Barnábas et al., 2008). In legumes, drought that

happened during vegetative periods was relatively more tolerable to plants even though they might experience retarded cell elongation, division and differentiation (Farooq et al., 2009). Plants were still able to maintain their growth functions under stress because early drought might lead to immediate survival or acclimation where the plants modified their metabolic and structural capabilities mediated by altered gene expression (Chaves et al., 2002). Similarly, water stress for up to two months during the vegetative growth only delayed normal growth in cassava, and the plant could resume growth once water became available (Lebot, 2009). Other root/tuber crops (i.e., yam) even had better adaptation to early-phase drought where the young plants were devoid of leaves (and therefore had very low transpiration) and could tap most of its early moisture needs from the 'mother' tuber (Lebot, 2009).

Conversely, greater yield reduction during the later phase of grain crop development was observed not only because such proteins and osmolytes were not produced by the reproductive organs, but also because some cereal (e.g., maize, rice) and legume (e.g., soybean) crops experienced flower sterility and abscission, whose effects could not be reversed even with further water addition. Rice and maize were among the most sensitive cereal species, with significant yield reduction occurring when drought struck during flowering (Daryanto et al., in review-a). Maize was particularly sensitive during the reproductive phase compared to other cereal species such as wheat (Fig. 4). Wheat is a monoclinal monoecious plant where the anthers and ovaries develop in the same flower while maize is a diclinous monoecious plant in which competition for water between female and male flowers occurred (Sangoi and Salvador, 1998). As drought favored the development of male rather than female inflorescence (Sangoi and Salvador, 1998), it created significant fertilization failures. The negative effects of water stress on rice was caused by pollen

sterility, due to impairment of sugar metabolism and starch synthesis of the mother cell during meiosis (Sheoran and Saini, 1996). Normal starch accumulation during pollen development failed to occur in stress-affected anthers (Sheoran and Saini, 1996). Rice was very sensitive to drought during the reproductive phase to the extent that even direct selection for drought-tolerant plants using yield *per se* (rather than secondary traits) during reproductive-stage drought was effective (Venuprasad et al., 2007). Within the legume group (i.e., soybean), drought-induced decrease in water potential and increase in ABA content (originated from root and/or leaf) in flowers were recorded to cause flower and pod abortion (Liu et al., 2003). Here the impairment of carbohydrate and sugar metabolisms due to drought during reproductive phase became the primary cellular-level cause of yield reduction (Liu et al., 2004). Drought during the reproductive phase in legumes (i.e., common bean) tended to reduce the total number of flowers per plant (by up to 50%) as well as the percentage of total pods located on the branches rather than on the main stem (Nuñez Barrios et al., 2005).

Although the root/tuber group had a different pattern of resource partitioning compared to grain crops (distinct vegetative and reproductive phases), drought that occurred during storage root initiation was equally devastating to root/tuber crops because this was the phase that largely determined the final number of tubers (Monneveux et al., 2013; Okogbenin et al., 2013; Onwoume and Charles, 1994). As the number of tuber decreased, prolonged stress might cause assimilate to be partitioned to other organs rather than storage roots (Jefferies, 1995). Both cassava and sweet potato were particularly sensitive to drought during storage root initiation, a period that typically occurred after the first three months of growth for cassava (Okogbenin et al., 2013), and between 4-7 weeks after planting for sweet potato (Onwoume and Charles, 1994). Subsequent water stress

during tuber bulking led to malformation of tubers in potatoes, in addition to reduction in the number and size of the tubers (Monneveux et al., 2013).

Some nutrients were known to mitigate the impact of drought stress during the critical reproductive stage. Potassium, for example, was shown to alleviate the impact of drought on potato yield, as it was involved in lowering crop water potential, allowing more water to be absorbed into the plant (Khosravifar et al., 2008). Phosphorus fertilizer application had impact on soybean by increasing energy storage and water concentration in plant tissue, as well as improving root-water-uptake ability and N assimilation (Jin et al., 2006). As higher P requirement in soybean was observed under drought than under well-watered condition, extra P fertilizer during drought (i.e., 15 mg kg⁻¹ soil) might improve soybean yield (Jin et al., 2006). A more recent review in also suggested that foliar P application to cereals, particularly when applied before anthesis could increase the number of fertile tillers and grain yield in wheat (Noack et al., 2010).

Not all crop species, however, are more sensitive to drought during their later phase of growth and development. Most seed plants, including cereals, start to lose their resistance to drought once they are germinated (Blum, 1996). In fact, seeding establishment, including crown root and initial green leaf area development is critical, and drying seedbed is a common cause of crop failure in drought-prone areas (Blum, 1996). This circumstance, however, was not reflected in our analysis since most drought experiments required good germination and initial plant development to observe drought effects during subsequent phases of crop's life. In other cases, similar sensitivity between vegetative and reproductive period was observed in wheat as reduction in the number of ears in wheat was reported when drought occurred during the entire growing season or between

anthesis and early milk development, but not during grain maturity (Sieling et al., 1994). Another review had suggested that wheat yield loss could be substantially greater if drought occurred during tillering (47%) than during booting (21%) (Nezhadahmadi et al., 2013). This was particularly true when grain yield only considered that produced by the normal tiller rather than the combination of late and normal tiller (Mogensen et al., 1985). Wheat could produce late tillers when temporary water stress occurred during early phenological phase (Mogensen et al., 1985). While grains from late tillers might develop and contribute to yield, they ripened later compared to those which produced from the normal tiller (Mogensen et al., 1985), making it difficult to harvest in a satisfactorily dry condition. Wheat was apparently sensitive to water stress during the vegetative phase since during early-season droughts, it allocated more of its assimilates to the roots, resulting in reduced leaf area, number of leaves per plant, leaf size and leaf longevity (Nezhadahmadi et al., 2013). Indeed, research by Hassan et al. (1987) suggested that drought during crown root initiation might reduce yield by 13% and even up to 65% when drought also occurred during jointing. Early drought that happened four weeks before anthesis was also found to reduce yield significantly by lowering the number of grains per ear (Innes and Blackwell, 1981). If drought prolonged to mid-season (i.e., between jointing and anthesis), however, its impact on wheat head size (i.e., the number of spikelet per spike) and root growth could be irreversible since late-emerging tillers would not contribute to yield (Asseng et al., 1998; Wise et al., 2011). The combination of reduction in photosynthetic sink, and nutrient uptake capacity could severely decrease yield. Therefore, traits that allowed soil moisture saving during early growth (e.g., vigorous crop establishment to shade the soil and suppress water competition from weeds, as well as thinner but wider leaves to increase ground cover and radiation-use efficiency) could be particularly important for wheat in dry areas (e.g., Mediterranean) where water loss from soil

evaporation was significant (Monneveux et al., 2011). Understanding the effects of restricted water availability on different phenological phases could minimize yield loss by applying water saving strategies or regulated irrigation during plant's critical growth periods. In the dry regions of China, for example, the use of mulch, was shown to reduce evaporative water loss by up to 46% and 35% for plastic and crop residue mulch, respectively (Li et al., 2013). Similarly, research in several counties in the Gansu Province of China showed that for supplemental irrigation of wheat, rainwater harvesting stored using subsurface tanks, could significantly improve yield in these water-scarce areas (mean annual rainfall = 289 mm). Even a small amount of supplemental irrigation (350-750 m³ ha⁻¹ or 35-75 mm of water depth equivalent) during the growth period generated about 28-88% increase in yield of wheat and maize, respectively. Thus, the yield increase was more than proportional to the increase in water (12-25%) as supplemental irrigation (Li et al., 2000).

4.3. Soil texture

While soil texture determined soil water holding capacity, hydraulic conductivity and consequently potential production capacity, plant traits, particularly those related to root structures (e.g., length, density) also played crucial role in determining the ability of plants to extract soil water (Shein and Pachepsky, 1995). Cereal crops, for example, were known to exhibit: (i) greater root mass and root length density (Hamblin and Tennant, 1987; Shein and Pachepsky, 1995), as well as (ii) lower water intake per unit root length compared to legumes (Vadez et al., 2008), likely contributing to the robustness of cereal yield across contrasting soil textures (Fig. 5A). Cereals such as wheat could extend their roots to an average 113 cm and had less than 50% of their total root length in the top 20 cm, while legume (i.e., field pea) to only 65 cm with more than 70% of

the root system in the top 20 cm (Hamblin and Hamblin, 1985). This rapid development of deep rooting system in cereals enabled them to absorb water from deep soil horizon and contributed to the drought avoidance strategy within the crop group (Yue et al., 2006).

The morphology and anatomy of roots largely determined crop adaptability across different types of soil texture and their corresponding water availability (Purushothaman et al., 2013). Xylem vessel size and number were among the most discriminating root traits in relation with their adaptability to different water regimes, at least within legume group with thinner vessel as an indicator of crop adaptability to soils with lower water availability (Purushothaman et al., 2013). Chickpea, for example, was considered to be more adapted for fine-textured soils than common bean, cowpea, or soybean as it had: (i) dense roots (even denser than pearl millet) and root thickening properties where the roots became thicker as soil moisture decreased, and (ii) a large number of thin vessels compared to other legume species which have broader vessels (Purushothaman et al., 2013). As lateral movement of water in fine-textured soil is more restricted than those in coarser soils, these properties allow better absorption of soil water. These traits also allowed chickpea to absorb water without requiring a wide gradient of water potential (Purushothaman et al., 2013). Common bean, on the other hand, had broader vessels, indicating their suitability to soils with high water regimes and should be more productive under regular irrigation (Purushothaman et al. 2013). Despite differences in root morphology and anatomy, chickpea as a species did not performed better than soybean or common bean in term of yield (Fig. 1B). In contrast, soybean had lower yield reduction to drought compared to common bean (Fig. 1B) despite similarities in drought sensitivity (Fig. 6) or root characteristics (Purushothaman et al., 2013), indicating that improving yield performance could not be based on merely a single trait.

Within root/tuber group, potato has been regarded as shallow-rooted species, with most of the roots found in the top 60 cm of soil (Posadas et al., 2008). While this was true particularly for potatoes grown in coarse-textured soils, a more recent finding suggested that potatoes were able to extend their root system down to 1-1.5 m in medium-textured soils where water was more readily available in the deeper soil layers (Ahmadi et al., 2011). Potatoes might therefore have a good root plasticity where: (i) in quick-drained property of coarse-textured soils, they developed higher root production in top soil to accommodate higher water absorption, but (ii) in soils with good water-holding capacity, their roots were capable to extend to the deeper soil layer. As potato roots were able to reach water from depth, yield reduction was also less in medium-textured soil compared to the coarse or fine texture (Fig. 5E). Interestingly, other root/tuber crops such as cassava grown in dried clay soil developed similar behavior to those of potato grown in coarse-textured soils by developing more roots on the top layer of the soils (Iijima et al., 2004). Here cassava was able to horizontally extend their adventitious roots up to 2 m length (Iijima et al., 2004). This lateral roots could compensate for the limited vertical root development which might otherwise limit water uptake in this type of soil, partly explaining the lack of yield difference between root/tuber grown on coarse- and fine-textured soils.

While we suggested that traits related to root structure were likely responsible to the variability of different crop groups on different soil types, they were also considered the most difficult to be assessed within a large set of genotypes (Vadez et al., 2008). Selecting for root-related traits was also time-consuming and complex as the pattern of water uptake was also determined by the pattern of water loss by the shoot (Vadez et al., 2008). Additionally, it required destructive

sampling, allowing only one-time measurement. Currently, recent development using root imaging technique (i.e., minirhizotron tubes) allowed *in-situ* root growth quantification over time, but the technique remained expensive (Prasad et al., 2008). So far, there have been limited breeding achievements which based on root traits in legumes (Vadez et al., 2008) and even cereals (Coudert et al., 2010), except for rice and chickpeas where preliminary breeding efforts have been conducted using root traits (Coudert et al., 2010; Vadez et al., 2008), resulting in more adapted crops with deep root and high root length density. Inexpensive root screening technique using deep-planted herbicide was used to measure the rate and depth of root development in cowpea and peanut (Prasad et al., 2008). Using this method, crops were screened based on how fast and how deep their roots reached the herbicide and wilted. Crop roots that grew faster and deeper would wilt faster than those which did not. Developing crops that have deep rooting characteristic may become important as agriculture is moving towards less water for irrigation (Wasson et al., 2012). A good example for the trend may be the rainfed winter wheat in India, which is typically watered once before sowing to allow the crop to germinate and emerge, then depend solely on soil moisture (Wasson et al., 2012). Similar finding has also been recorded for barley where deep-rooted genotypes were able to survive and produce compared to those with shallow roots (McKenzie et al., 2009). Since biomass production was positively correlated to transpiration, breeding that allowed maximum soil water capture for transpiration (i.e., deep and dense root system) could be important for yield improvement under drought (Blum, 2009). The value of targeting deeper root system, including root length density in medium and deep soil layer but not in the topsoil was two-fold. Apart from being more reliable than rainfall, farmer could pre-condition the amount of soil moisture via management (Wasson et al., 2012). This pre-conditioning soil moisture might aid

crops that relied on drought avoidance strategy by diverting the largest part of the available soil moisture towards stomatal transpiration.

4.4. Agro-ecological region

The lack of significant differences between crop yield grown in the dryland and the non-dryland region was intriguing given the low relative humidity and high temperature of non-dryland regions which increased the potential evapotranspiration demand. We, however, partly attributed the lack of difference to the species differences that were readily adapted to different geographical regions. Faba bean genotypes from North Africa, for example, were generally more drought tolerant than their European counterparts (Stoddard et al. 2006). The dryland origin of wheat was also likely to contribute to its low sensitivity to drought compared to other species (i.e., maize) (Daryanto et al. in review), which came from a much wetter regions (van Heerwaarden et al., 2011). The largely cultivated tuber species (i.e., yam) in West Africa, which was indigenous to the region, also had xerophytic properties (e.g., waxy vines without leaves during emergence), enabling it to absorb water from its ‘mother’ tuber during early-season drought (Asiedu and Sartie, 2010).

The lack of yield difference of crops grown in contrasting eco-regions, however, suggested that there is possibility of: (i) optimizing the use of (irrigation) water using conservation (e.g., mulching, crop rotation) or more advance water saving techniques (e.g., deficit irrigation or DI, partial root-zone drying or PRD) which had been reviewed elsewhere (Blanke et al., 2007; Sepaskhah and Ahmadi, 2010; Turner, 2004), or (ii) minimizing yield loss by applying irrigation during the critical growing period of the plants (e.g., anthesis) in the environments where drought may occur at any time during the growing season. While insights into the mitigating effects of crop

and soil management practices could be obtained by examining previous agricultural practices in the Mediterranean region (Parry et al., 2005) or recent advances on dryland farming reviewed by Davies et al. (2011), the economically viable approaches to support crop production under drought were still limited (Li et al., 2000). Mixed cropping, rainwater harvesting, or no-tillage agriculture were among the more commonly applied strategies to combat drought in dry environment (Davies et al., 2011). Since biomass production was tightly linked to transpiration (Blum, 2009), reduced yield might occur with DI or PRD (Wakrim et al., 2005), although increased water productivity and yield were observed in many other cases (Sadras, 2009; Sepaskhah and Ahmadi, 2010). The ability of soybean to increase their water-use efficiency (WUE) with partial closure of stomata (Liu et al. 2005) could be responsible for their relative production resilience (Fig. 1B). At mild water deficit, photosynthesis decreased less rapidly than stomatal conductance (Liu et al. 2005), enabling soybean to maintain the flow of assimilates to storage organs at lower evapotranspiration rate. Such response indeed has been the basic knowledge for PRD application and it has been successfully applied to reduce water consumption in different crop groups, including root/tuber (e.g., potatoes) (Posadas et al., 2008) and cereal (e.g., wheat) (Condon et al., 2002). Breeding for traits such as small plants, moderate growth, and short growth duration might further improve positive relationship between WUE and yield for crops grown using stored soil moisture in the dryland condition (Blum, 2005). Architectural development of crop roots (i.e., dimorphic root system) and promising association with mycorrhiza have also been proposed to be beneficial during drought particularly in the dryland, allowing re-distribution of soil moisture by roots and access to bound water previously unavailable to crops (Reynolds et al., 2005).

4.5. Heat

Apart from water, temperature is another critical environmental factor that limits crop survival, distribution and productivity (Prasad et al., 2008). Although drought is not always accompanied by heat and vice versa, it is difficult, however, to separate the contribution of heat and drought stress particularly under field condition since there is a strong relationship between plant water status and temperature (Prasad et al., 2008). At the cellular level, plant responses to either drought or heat stress tend to be similar (e.g., closing their stomata), resulting in higher leaf temperatures (which will be exacerbated if the surrounding temperature is also high) as transpiration rates decrease when stomata is closed (Lopes et al., 2011). Consequently, more latent heat will remain within the leaf's cells and the two major processes determining yield (i.e., photosynthesis and respiration) may become imbalanced under periods of high temperature and/or drought (Lopes et al., 2011). At the whole-plant level, similar responses between drought and heat stress have also been observed with root growth and/or during later phases of crop development (i.e., reproductive phase) where drought and/or heat stress inhibited root growth and caused reproductive failures (Prasad et al., 2008). Contrasting differences, however, have been observed for crops experiencing heat and drought stress during germination and vegetative phases. During germination, crop response to temperature generally follow a bell shape curve where there are minimum, optimum, and maximum temperature for germination rate (Prasad et al., 2008). Crop response to drought, on the other hand, is mostly linear where development process slows then stops completely as drought progresses (Prasad et al. 2008). While heat stress increased leaf elongation rate and leaf number (as long as photosynthetic rate remained constant), drought stress negatively affected them (Prasad et al., 2008).

The mechanisms via which high temperatures resulted in yield reduction were far more complex, involving interactions with other edaphic, biotic, and abiotic factors (Prasad et al., 2008). While the mechanisms of lowering yield differed between drought and heat stress (i.e., drought lowered the amount of assimilates to the sinks (Nuñez Barrios et al., 2005) while heat stress shortened the seed-filling duration), both led to smaller seed size (Prasad et al., 2008). The responses of different crops to heat stress, however, co-varied with species, similar to our findings regarding drought (Daryanto et al., 2015, in review-a, b). Different levels of heat tolerance across different legume species, for example, occurred with groundnut having greater heat tolerance compared to soybean, pigeon pea, and chickpea (Srinivasan et al., 1996). Mechanisms at the cellular level appeared to be important for higher heat tolerance in groundnut than in other legumes as it experienced faster recovery from cell membrane and photosystem II (PSII) damages (Srinivasan et al., 1996). Indeed, a more recent finding suggested that screening for heat-tolerant legumes (i.e., chickpea) and potentially other crop groups was based on membrane stability, photosynthetic efficiency, and pollen germinability at high temperature ($>35^{\circ}\text{C}$) (Basu et al., 2009). PSII has specifically been targeted for heat-tolerance screening because it appeared to be more sensitive to heat than drought as cell fluidity increased with temperature (Prasad et al., 2008). Increasing the efficiency of respiration under heat stress had also been found to reduce yield loss since heat stress was more destructive to mitochondrial than chloroplast activity, generating greater respiratory loss than increased influx of assimilates (Prasad et al., 2008). Similarly, C partitioning was a function of temperature in potato with fewer assimilates translocated to tubers as temperature increased above 24°C (Timlin et al., 2006). The same partitioning, however, was less affected by temperature in sweet potato (Gomes et al., 2005).

Plant sensitivity to heat stress was also affected by phenological phase and soil texture (i.e., soil temperature), although at a lesser extent when compared to drought. Most crops were more sensitive to heat stress during their reproductive phase to an extent that yield reduction was unrecoverable due to flower sterility in rice (Jagadish et al., 2007), wheat (Barnábas et al., 2008), and maize (Cicchino et al., 2010). Significant yield reduction as a result of fewer pollen grains and reduced pollen viability was also observed for groundnut when it was exposed to day temperature of 34°C (Prasad et al., 1999). Temperature as high as 33°C produced plants with fewer pods resulting from fewer reproductive nodes per plant as well as malformed cowpea seeds (Warrag and Hall, 1984). With warming and drying of soils which damaged roots and limit nutrient uptake, prolonged exposure to water and temperature stress ultimately led to plant wilting and death (Smoyer-Tomic et al., 2003). While a greater likelihood of yield loss might exist in fine-textured soils which generally developed lower water potentials and water depletion zones around the roots (Shein and Pachepsky, 1995), high soil temperature during early part of the growing season in medium- to coarse-textured soils remained a constraint to improve soybean yield in the Indo-Gangetic plains of South Asia (Arora et al., 2011). The application of mulch has been shown to improve yield by reducing plant sensitivity to water and temperature stress (but see Chen et al. (2007)), although the extent of the improvement might vary with location (e.g., upland, lowland) (Zhang et al., 2009), type and thickness of mulch (Ramakrishna et al., 2006), as well as soil texture (Gajri et al., 1994).

5. Summary and implications

Our results suggested that drought-induced yield variability in cereal production was lower than observed within the legume and root/tuber crop groups and across different soil textures. We

attributed these results to the more intensive research on cereal group as well as dense and deep rooting systems of cereal crops allowing access to water deep in soil profiles. These results highlighted the importance of genetic development and field trials to improve plant stress tolerance as stated by Tollenaar and Wu (1999). Promising findings from genetic improvement that focus on root traits have been observed for wheat and barley (McKenzie et al., 2009; Wasson et al., 2012), and similar development could be proposed for rice as it has been listed as the cereal with lowest yield to transpiration ratio (i.e., 15-22 kg grain ha⁻¹ mm⁻¹) compared to other cereal grains (Sadras et al., 2011). Currently, rice rooting system could only extract 30% of the available water up to a maximum of 60 cm deep (Fischer et al., 2011), suggesting that rice should be grown in soils that have adequate moisture to support their respiration and transpiration demand.

Most crop groups tended to experience greater yield loss when drought occurred during the later (i.e., reproductive phase for grain crops and root/tuber initiation for root/tuber crops) than earlier (i.e., vegetative) phase of the plant development. While maize and rice were particularly sensitive to drought during flowering, wheat was sensitive during both vegetative and reproductive phases. Since the effects of drought on reproductive organs (including the number storage root and tuber) are usually permanent, the effects of drought on yield during this critical growing period cannot be reversed even with additional water afterwards. Partial improvement, however, might occur for root/tuber if water was available during the subsequent tuber bulking period. Since different crops had different water requirement during different phenological phases, the use of water saving strategies or applying irrigation during different plant's critical growing periods might be important to improve yield particularly in the dryland where greater evapotranspiration demand usually took place.

As various factors (i.e., crop species, plant phenology, and soil texture) determined crop yield during drought, there would be no single approach that might be sufficient to improve plant performance when drought occurred. Consequently, a combination of approaches should be considered to minimize yield reduction. Although plant breeding provided a pathway for the development of drought-resistant crop species and could reduce the vulnerability of agricultural production to the unpredictability of climates, successful applications of these technological innovations required careful consideration of local environmental conditions (e.g., rainfall, temperature and soil nutrients). Site-specific management that considers soil conditions (i.e., intercropping, mulching, and crop rotation) and trait selection that is adjusted to the local climate are more likely to result in sustainable crop yields in a changing climate.

Acknowledgement

This research was supported by a postdoctoral fellowship from Schlumberger Foundation and USDA grant (2014-51130-22492). The authors thank Xuefei Lu for assistance with the MetaWin software package.

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Figure Captions

Fig. 1. Yield reduction of various cereal (A), legume (C), and root/tuber species (E) and their corresponding water reduction (B, D, F). Letter “a, b, or c” indicates significant difference between observed water reduction, while letter “n” indicates the number of samples. Rectangular point indicates proxy to water reduction obtained from the original research article instead of being calculated using one-way ANOVA.

Fig. 2. Drought sensitivity of potato (A) and sweet potato (B) and their associated confidence intervals (C). Dotted lines indicate 95% prediction band.

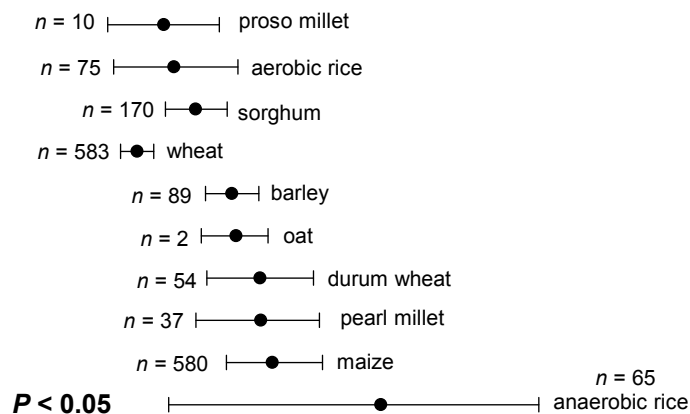
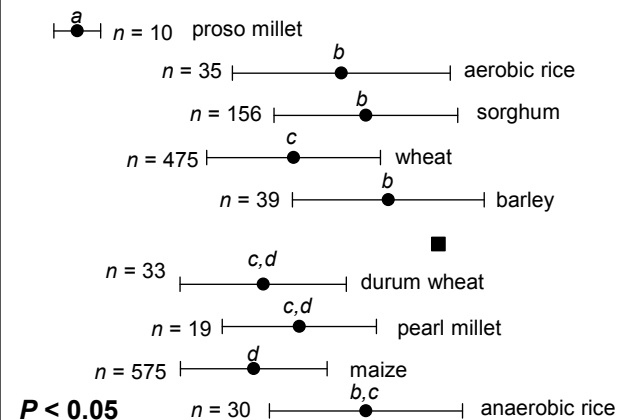
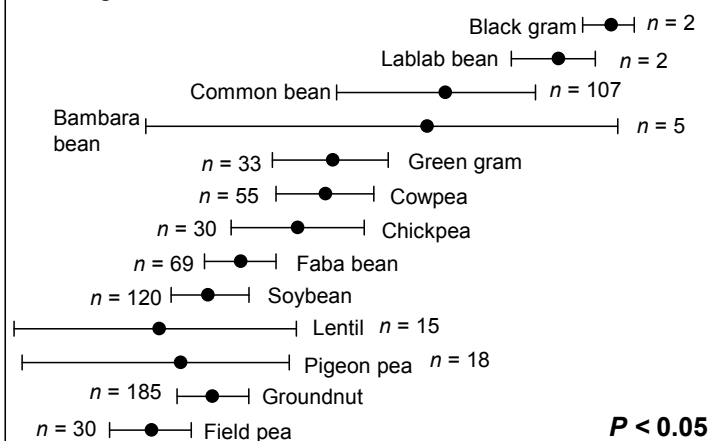
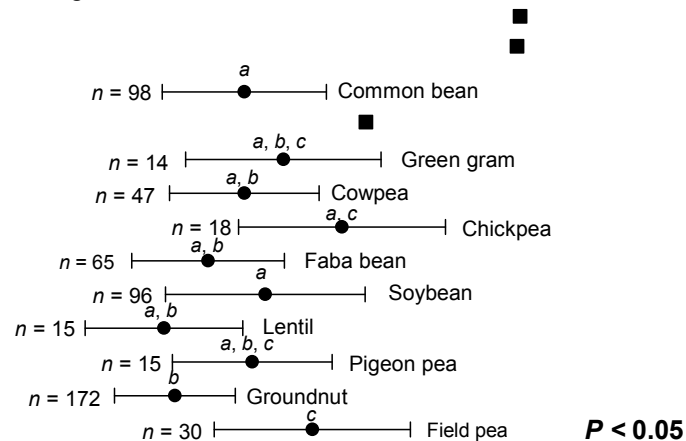
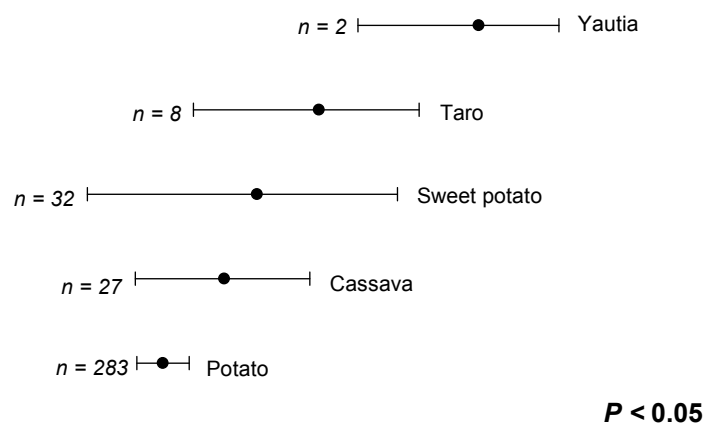
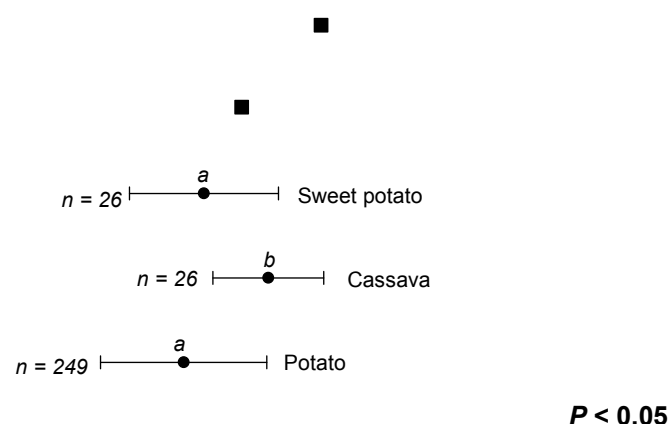
Fig. 3. Yield reduction of cereal (A), legume (C) and root/tuber crops (E) grown during different phenological phases and their corresponding water reduction (B, D, F). Letter “a, b, and c” indicates significant difference between observed water reduction, while letter “n” indicates the number of samples.

Fig. 4. Drought sensitivity of wheat (A) and maize (B) and their associated confidence intervals (C). Dotted lines indicate 95% prediction band.

Fig. 5. Yield reduction of cereal (A), legume (C) and root/tuber crops (E) grown on different soil textures and their corresponding water reduction (B, D, F). Letter “a and b” indicates significant difference between observed water reduction, while letter “n” indicates the number of samples.

Fig. 6. Drought sensitivity of soybean (A) and common bean (B) and their corresponding confidence intervals (C). Dotted lines indicate 95% prediction band.

Fig. 7. Yield reduction of cereal (A), legume (C), and root/tuber crops (E) grown on dryland and non-dryland conditions and their corresponding water reduction (B, D, F). Letter “a and b” indicates significant difference between observed water reduction, while letter “n” indicates the number of samples.

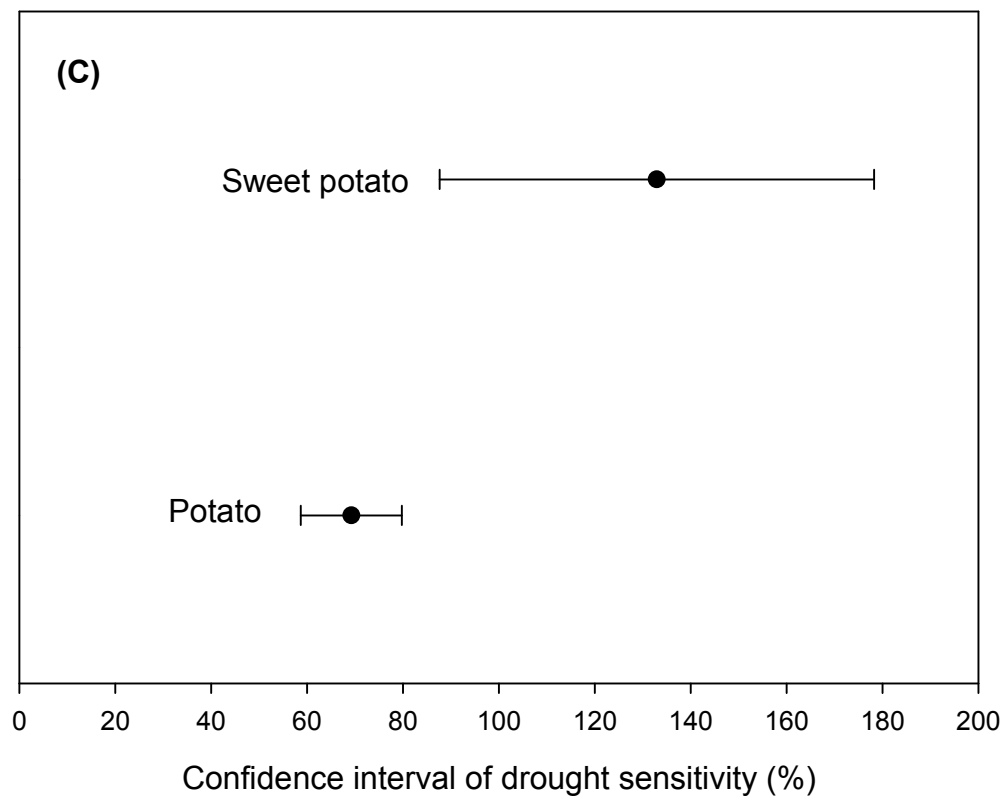
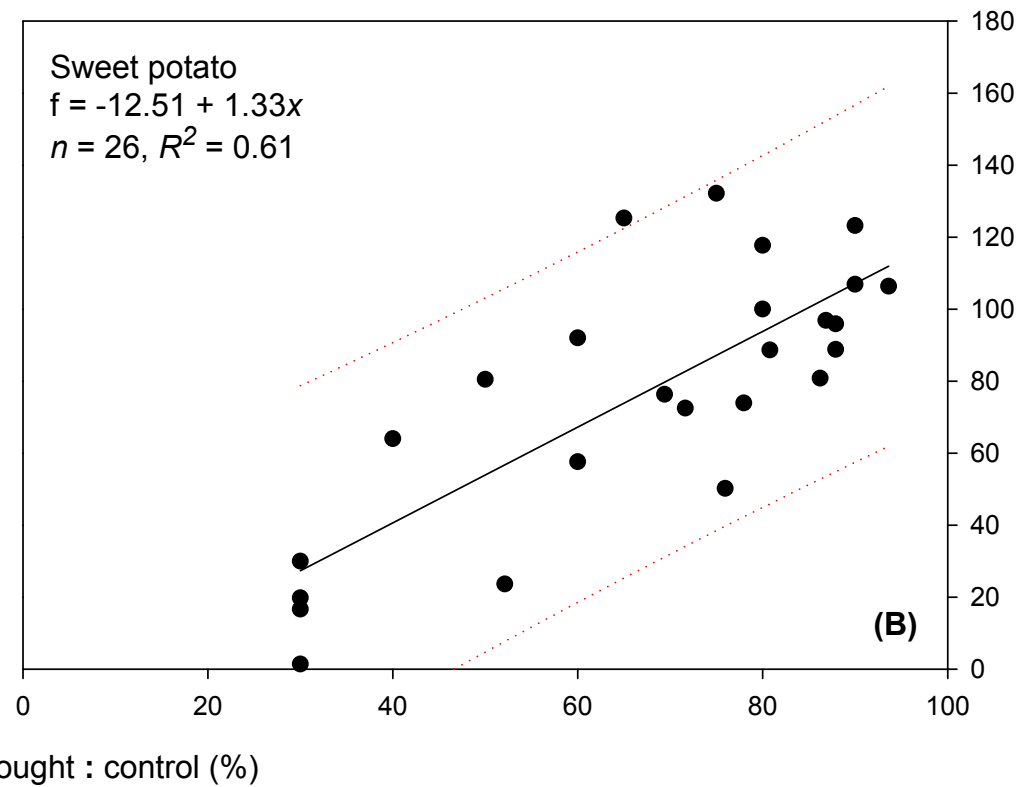
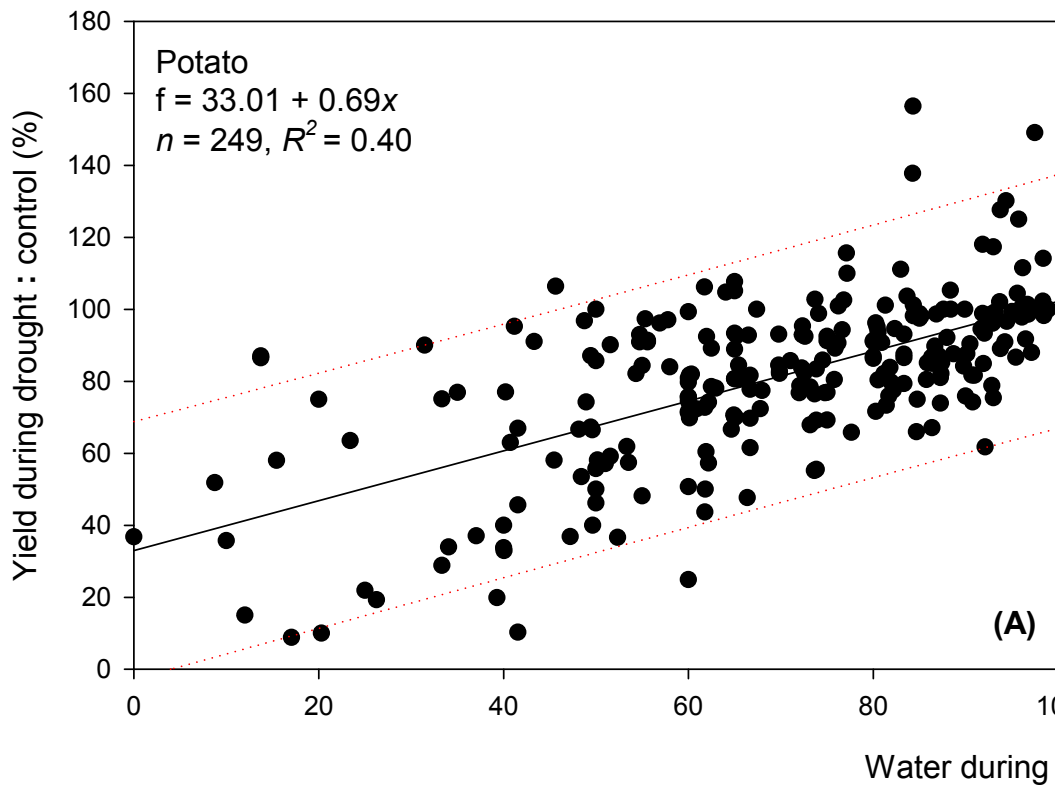
(A) Cereal**(B) Cereal****(C) Legume****(D) Legume****(E) Root/Tuber****(F) Root/Tuber**

0 20 40 60 80 1000

Observed yield reduction (%)

20 40 60 80 100

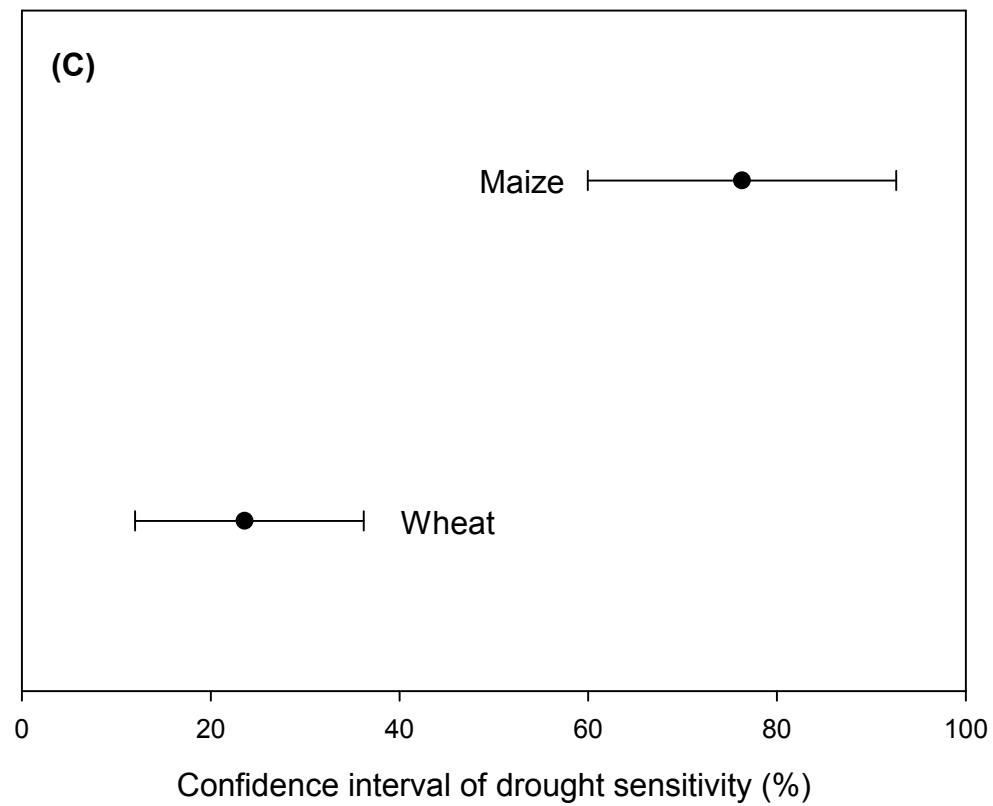
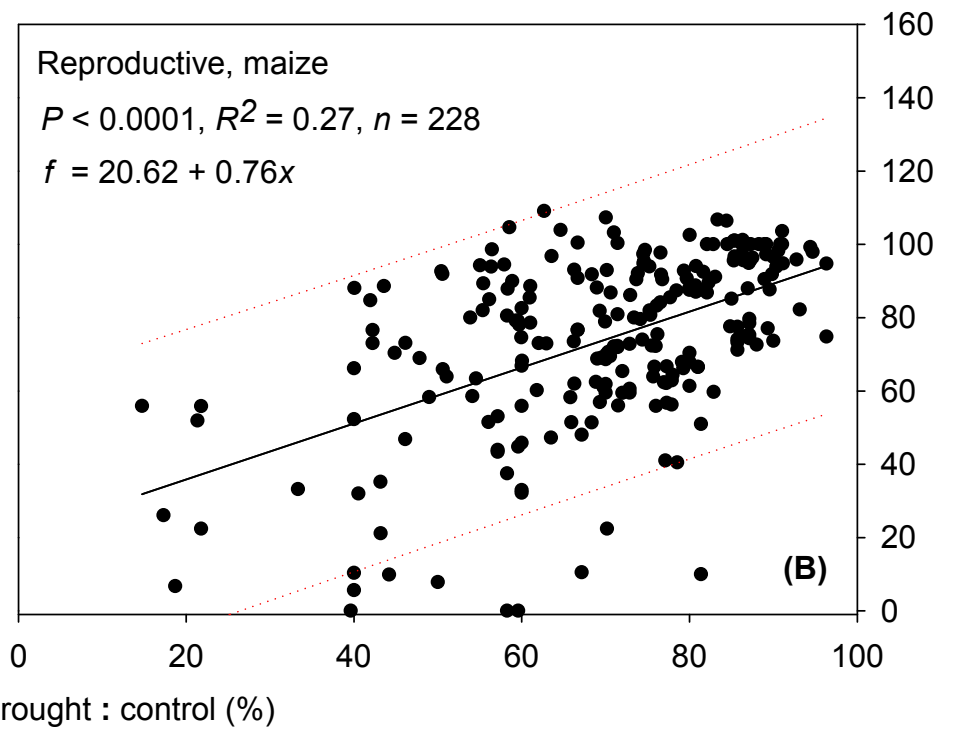
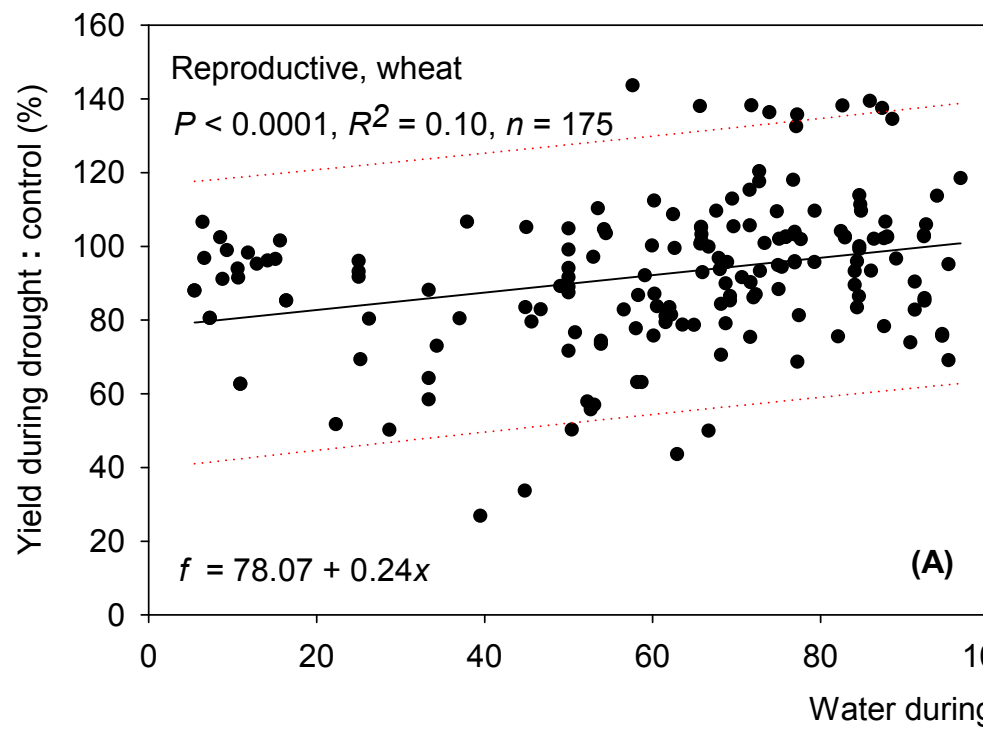
Observed water reduction (%)



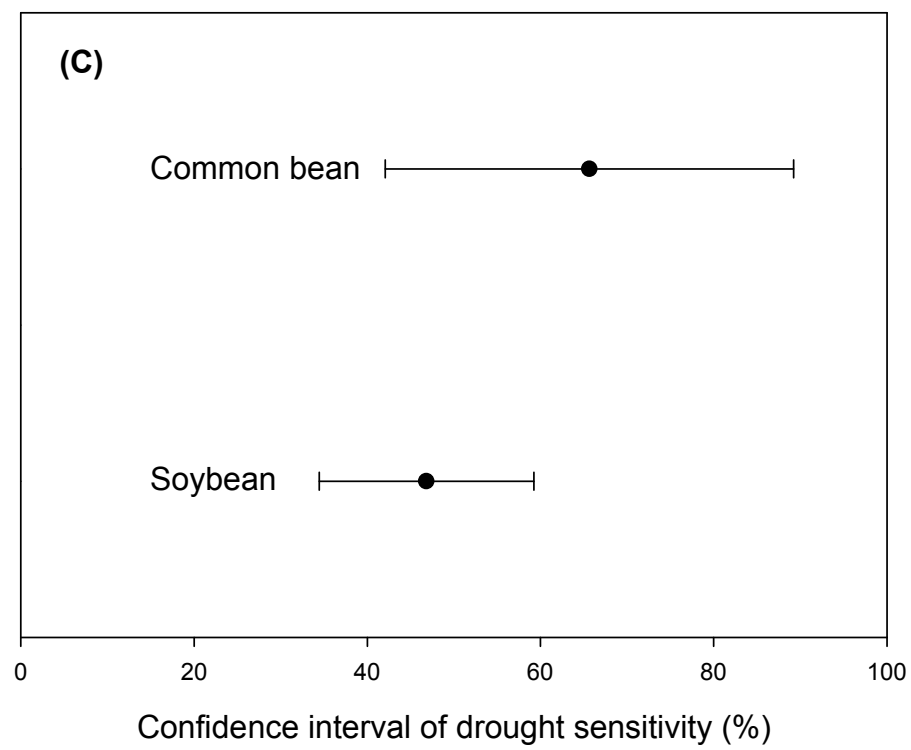
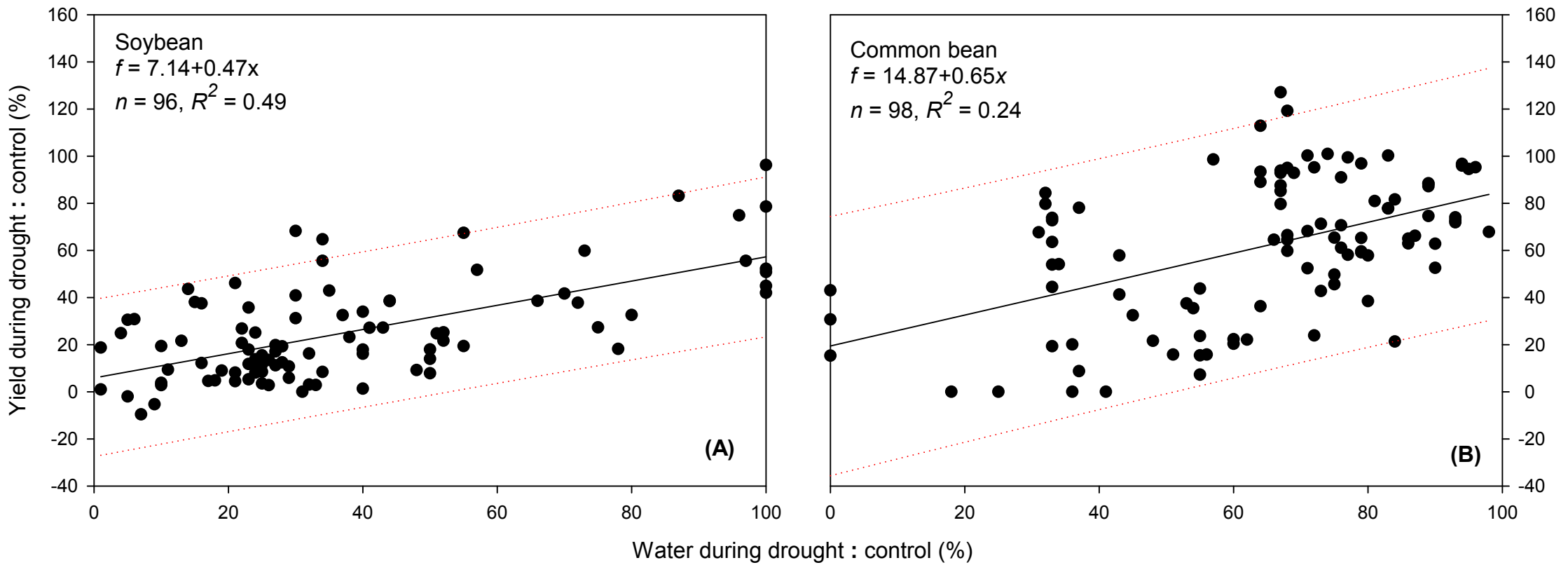
(A) Cereal $n = 757$ |●| Throughout season $n = 655$ |●| Late season $n = 262$ |●| Early season **$P < 0.05$** **(B)** Cereal $n = 690$ |●^a| Throughout season $n = 502$ |●^b| Late season $n = 182$ |●^c| Early season **$P < 0.05$** **(C)** Legume $n = 275$ |●| Throughout season $n = 290$ |●| Late season $n = 110$ |●| Early season **$P < 0.05$** **(D)** Legume $n = 273$ |●^a| Throughout season $n = 288$ |●^b| Late season $n = 93$ |●^c| Early season **$P < 0.05$** **(E)** Root/Tuber $n = 208$ |●| Throughout season $n = 109$ |●| Late season|●| Early season $n = 35$ **$P < 0.05$** **(F)** Root/Tuber $n = 193$ |●| Throughout season $n = 99$ |●| Late season $n = 18$ |●| Early season **$P > 0.05$**

Observed yield reduction (%)

Observed water reduction (%)



(A) Cereal $n = 538$ |●| Coarse $n = 893$ |●| Medium $n = 138$ |●| Fine **$P > 0.05$** **(B)** Cereal $n = 419$ |●^a| Coarse $n = 812$ |●^{a, b}| Medium $n = 103$ |●^b| Fine **$P < 0.05$** **(C)** Legume $n = 230$ |●| Coarse $n = 138$ |●| Medium $n = 290$ |●| Fine **$P < 0.05$** **(D)** Legume $n = 204$ |●| Coarse $n = 110$ |●| Medium $n = 262$ |●| Fine **$P > 0.05$** **(E)** Root/Tuber $n = 35$ |●| Fine $n = 173$ |●| Medium $n = 116$ |●| Coarse **$P < 0.05$** **(F)** Root/Tuber $n = 31$ |●| Fine $n = 153$ |●| Medium $n = 106$ |●| Coarse **$P > 0.05$** 0 20 40 60 80 100
Observed yield reduction (%)0 20 40 60 80 100
Observed water reduction (%)



(A) Cereal

$n = 515$ |—●—| Non-dryland

$n = 1159$ |—●—| Dryland

$P > 0.05$

(B) Cereal

$n = 410$ |—●^a—| Non-dryland

$n = 964$ |—●^b—| Dryland

$P < 0.05$

(C) Legume

$n = 293$ |—●—| Non-dryland

$n = 383$ |—●—| Dryland

$P > 0.05$

(D) Legume

$n = 266$ |—●^a—| Non-dryland

$n = 310$ |—●^b—| Dryland

$P < 0.05$

(E) Root/Tuber

$n = 150$ |—●—| Non-dryland

$n = 202$ |—●—| Dryland

$P > 0.05$

(F) Root/Tuber

$n = 142$ |—●—| Non-dryland

$n = 170$ |—●—| Dryland

$P > 0.05$

0 20 40 60 80 100
Observed yield reduction (%)

0 20 40 60 80 100
Observed water reduction (%)