Drought effects on root and tuber production: A meta-analysis

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This is the author's manuscript of the article published in final edited form as:
Daryanto, S., Wang, L., & Jacinthe, P. A. (2016). Drought effects on root and tuber production: A meta-analysis. Agricultural Water Management, 176, 122-131. http://dx.doi.org/10.1016/j.agwat.2016.05.019

Abstract

Roots and tubers such as potatoes and cassava rank within the top six among the world's most important food crops, yet the extent to which their global production has been adversely affected by drought remains unclear. Greater uncertainties exist on how drought effects co-vary with: 1) root and tuber species, 2) soil texture, 3) agro-ecological region, and 4) drought timing. It is often assumed that potato is drought-sensitive whereas cassava and sweet potato are resistant to drought. To address these uncertainties, we collected literature data between 1980 and 2015 that reported monoculture root and tuber yield responses to drought under field conditions, and analyzed this large data set using meta-analysis techniques. Our results showed that the amount of water reduction was positively related with yield reduction, but the extent of the impact varied with root or tuber species and the phenological phase during which drought occurred. In contrast to common assumptions regarding drought resistance of certain root and tuber crops, we found that yield reduction was similar between potato and species thought to be drought-resistant such as cassava and sweet potato. Here we suggest that drought-resistance in cassava and sweet potato could be more related to survival rather than yield. All roots or tubers crops, however, experienced greater yield reduction when drought struck during the tuberization period compared to during their vegetative phase. The effect of soil texture on yield reduction was less obvious, and similarly we did not find any significant effects of region (and related climatic factors) on neither yield reduction nor drought sensitivity. Our study provides useful information that could inform agricultural planning, and influence the direction of research for improving the productivity and the resilience of these under-utilized crops in the drought-prone regions of the world.

Keywords: drought, potato, sweet potato, cassava, root, tuber

1. Introduction

According to the FAO definition (FAO, 1994), roots and tubers are plants that produce starchy roots, tubers, rhizomes, corms and stems commonly consumed as human food, animal feed, and as manufactured food products. There are six major root and/or tuber (i.e., root/tuber) crops: potato, cassava, sweet potato, yam, taro, and yautia (Table 1), some of them are important cash and food crops particularly for resource-limited farmers in Asia, Africa, Latin America, and the Caribbean (Okogbenin et al., 2013). Yam and cassava, for example account for a sizable portion of the daily calorie intake for people in West Africa (Asiedu and Sartie, 2010).

Root/tuber crops have much potential in terms of water use efficiency (WUE) and nutrient content compared to other food crops. Potatoes, for example, produce more dry matter and protein per hectare than major cereal crops (Birch et al., 2012). They also have higher water productivity than cereals, and are considered among the most energy productive crops, producing 5,600 kcal per cubic meter of water, compared to 3860 in maize, 2300 in wheat, and 2000 in rice (Birch et al., 2012; Monneveux et al., 2013). Similarly, sweet potatoes figure among the major crops that produce the most human-edible energy, as much as 194 MJ ha^{-1} day^{-1} (Mukhopadhyay et al., 2011). Other root/tuber crops such as taro (seven known species mostly originated from Asia), yautia (40 species mostly from the American continent), and yam (600 species of different origins) (Asiedu and Sartie, 2010; Degras, 1993) also have significant energy values and variable nutritional properties, including dietary fiber, vitamin C, and carotenoids (Asiedu and Sartie, 2010; Degras, 1993).

While drought has been considered a major constraint to root/tuber crop production, research on drought tolerance in potato only started between 1960 and 1980, compared to cereal crops which have been extensively studied in that regard since the early 1900's (Monneveux et al., 2013). Consequently, our knowledge regarding: (i) drought tolerance of roots and tubers, and underlying physiological mechanisms, as well as (ii) agronomic practices and water-saving techniques (e.g., mulching, no-till) (Monneveux et al., 2013), is still limited compared to other staples such as cereals and legumes despite the earlier cultivation of roots and tubers (i.e., >10,000 years for taro) (Lebot, 2009). Compared to roots and tubers, there has been two and four times more studies examining the effects of drought on legumes and cereal production, respectively. Yet several climate models have predicted a much stronger impact of climate change on potato production than on cereal production (Monneveux et al., 2013; Tubiello et al., 2002). Potato production in various low latitude regions, for example, is expected to decrease between 18-32% without shift in planting date and varieties as opposed to 9-18% if such mitigation strategies are adopted (Monneveux et al., 2013). Given the significance of root/tuber crops to food security in various regions of the world and the uncertainties regarding the global climate, there is a need for greater understanding of the resilience of root/tuber species to water stress and how different root/tuber species respond to drought (e.g., changes in timing and intensity of water stress).

Meta-analysis is a powerful statistical tool that can be used to summarize results from numerous independent experiments on drought while accounting for variability across experiments (Hedges et al., 1999). By synthesizing the results of field experiments investigating drought effects on root/tuber production in different regions, this study aims to provide a quantitative summary of the factors that either amplify or minimize production loss associated with droughts. We aim to answer the following questions: 1) to what extent factors such as root/tuber species, soil texture, and climatic region contribute to variations in drought-induced yield reduction, and 2) how can the information gained from the analysis of these factors be used to minimize the impact of drought on root/tuber production? Specifically, we are interested in quantitatively assess the yield reduction of generally assumed drought-resistant root crops (i.e., cassava and sweet potato) (Onwoume and Charles, 1994) and comparing their response to that of the more drought-sensitive species (i.e., potato) (Monneveux et al., 2013). While anecdotal evidence suggest that cassava and sweet potato are widely grown and continue to expand in drought-affected regions, and can remain profitable in areas with annual rainfall as low as 500 mm (Hahn, 1977; Onwoume and Charles, 1994), the data that support the extent of yield reduction due to drought for both of these crops are still lacking. The results of this study could thus lead to the formulation of better agricultural practices by considering the aforementioned factors to increase the resilience of roots/tuber production systems in the drought-prone regions of the world.

2. Materials and methods

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) root or tuber species common name, water, stress, yield, and field, or (ii) root or tuber species common name, irrigation, deficit, yield, and field. The list of articles and geographical distribution of the study locations are provided in the Supplementary Material S1 and Supplementary Fig. S1. 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 CO_2), (iii) the reported plants were monoculture roots or tubers of potato (*Solanum tuberosum*), cassava (*Manihot* spp.), sweet potato (*Ipomoea batatas*), taro (*Colocasia esculenta*), yautia (*Xanthosoma* spp.), and yam (*Dioscorea* spp.), (iv) the articles reported crop response as yield per unit area. To minimize the impact of other agronomic factors (e.g., pests, nutrients, diseases) that might affect yield, we only included studies that examined the single effect of water reduction as these other factors were controlled during the water treatment experiments (Daryanto et al., 2015, in review).

The magnitude of yield responses was examined based on the following categorical variables: (i) root/tuber species, (ii) agro-ecosystem types (dryland and non-dryland), (iii) soil texture (fine, medium, or coarse), and (iv) drought timing (i.e., early season, mid-season, late season, mid- and late-season, and throughout season). For the purposes of meta-analysis, we established discrete levels for each variable and coded each observation accordingly. Unlike grain crops in which drought timing can be categorized based on distinct vegetative and reproductive phases (Daryanto et al., 2015, in review), for some root crops, photo-assimilates are partitioned continuously between different organs (Lebot, 2009). We therefore used the following development phases of the storage root organ to differentiate drought timing: before tuber initiation as early-season, during tuber initiation as mid-season, during tuber bulking as late-season, during the whole tuberization period as mid- and late-season, and during the entire growing period as throughout-season drought. Since we focused our analysis on the amount of water available and yield, we differentiated agro-ecosystem types based on aridity indices, which showed significant correlation with yield (Bannayan et al., 2010). We considered other environmental factors (e.g., temperature, light intensity) as the same between control and droughted condition since we only used paired study sites. Similarly, we divided soil texture into three categories (i.e., fine, medium and coarse) as each category had different water-related properties (i.e., field capacity, wilting point and water holding capacity) (Keulen and Stol, 1995). We considered clay, sandy-clay and silty-clay soils as fine texture, silt, silt-loam, silty-clay-loam, loam, sandy clay-loam and clay-loam soils as medium texture, and sand, loamy-sand, and sandy-loam soils as coarse texture (Keulen and Stol, 1995). .

The total data points before averaging were 981 from 85 studies. We averaged responses across cultivars under the same drought treatment since we were only interested in evaluating the effect of drought on crop performance at the species level (for potato, sweet potato, and taro). For cassava, yam, and yautia, we did not differentiate among species, but grouped them based on their genus name due to limited number of data. Edible yam, for example, consisted of at least nine species of *Dioscorea* sp, which were native to different regions. *D. rotundata* and *D. cayanensis* were indigenous to West Africa, while *D. alata* and *D. trifida* were Asian and American origin, respectively (Asiedu and Sartie, 2010). If the same treatment was repeated over several years or locations, the data were only averaged across the years or places if there was no significant year or location effect. After averaging, the total data points used in the meta-analysis were 352, except for soil texture which was not always mentioned in all studies. We did not differentiate among irrigation types and only recorded the amount of water applied since there have been many studies showing that the type of irrigation was not significant in comparison to the amount of water in determining yield, even in semi-arid (dryland) regions (Erdem et al., 2006; Onder et al., 2005; Sammis, 1980; Shalhevet et al., 1983; Ünlü et al., 2006). If a study reported more than one timing of drought or levels of water reduction, all observations were considered independent and included in the database. Since limited data were available for taro and yautia production, we used either single amount of water reduction or other quantitative indicators of water availability (e.g., soil moisture) reported in the corresponding article as proxy for observed water reduction (Supplementary Fig. S2).

We calculated the observed water availability ratio (i.e., the ratio between water during drought and during well-watered condition) for each categorical variable as a proxy to describe drought intensity. 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. We did not use the widely-accepted drought intensity indices (e.g., Palmer index which is more effective in determining long-term naturally occurring drought) since most of the studies were controlled experiments (i.e., comparing certain amount of irrigated conditions and irrigation reduction instead of observing natural rainfall deficiency). While we used the highest water level as control (i.e., well-watered condition), some exceptions applied where we did not incorporate water levels higher than the maximum evapotranspiration (ET) demand (if this information is provided in the paper). We took this precaution to minimize the effects of overestimating the water requirement since yield might saturate at water supply lower than the observed maximum supply (Grassini et al., 2009). This observed water reduction was then compared among categorical variable using one-way ANOVA and used to calculate drought sensitivity. We defined drought sensitivity as the relationship between observed yield reduction (i.e., the ratio between yield during drought and during well-watered condition) and observed water reduction. Since not all studies recorded the amount of water reduction, we used the subset of data that recorded both yield reduction and water reduction to construct the relationship. The exact numbers of data points (*n*) were shown in the corresponding figures. Ratio was used rather than the actual yield or amount of water to make a more robust comparison among categorical variables since some species might have lower or higher yield potential or water demand than others. Confidence interval and prediction band for each drought sensitivity relationship was calculated at the 95% confidence level using Sigmaplot 12.0 (Systat Software) when more than 20 observational data points were available and the R^2 value was greater than 0.1.

To compare the differences in observed yield reduction between each categorical variable, meta-analysis was used to construct the confidence intervals. In order to include those studies that did not adequately report sample size or standard deviation, we performed an unweighted analysis using the log response ratio (lnR) to calculate bootstrapped confidence limits 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). To improve the reliability of lnR in estimating the effect size, a simple diagnostic test using the following formula was performed:

$$\bar{x}/\mathrm{SD}\ (4\mathrm{N}^{3/2}/(1+4\mathrm{N})) \geq 3$$

where $\bar{x}$ is the mean, SD is the standard deviation and N is the sample size (Lajeunesse, 2015). Bootstrapping was then iterated 9999 times to improve the probability that confidence interval was calculated around the cumulative mean effect size for each categorical variable. The sample size (*n*) of each bootstrapping which reported the amount of water reduction was shown in its corresponding figure. The difference is considered significant if the bootstrap confidence interval did not overlap with each other. A statistical significance level of $P < 0.05$ was used.

3. Results and Discussion

3.1 Species effects

Our results showed no difference in yield reduction among the three major root/tuber crops - potato, cassava, and sweet potato - in response to drought (Fig. 1). These results were surprising given the considerable differences in agronomic characteristics that exist between these species (Table 2), including drought resistance and water requirements (Adeleye et al., 2010; Horton, 1988; Lebot, 2009; Talwana et al., 2009). The lack of yield difference also ran contrary to the traditional belief that potato is drought-sensitive but that cassava is drought-resistant, capable of producing under drought conditions (Onwoume and Charles, 1994). The global average yield of cassava represents only 12.5% of the crop's yield potential (Okogbenin et al., 2013) in comparison to rice yield which is almost 80% of its potential (Cassman, 1999). These facts suggest that the high production potential of cassava has not been achieved, most likely due to the sub-optimum agro-climatic conditions in which cassava is typically grown. Since cassava's root and shoot grew simultaneously (i.e., competing to each other) throughout the growing season, lower carbon (C) partitioning to the storage organ could occur as an indirect response of reduced radiation energy interception resulting from lower leaf area index (LAI) of droughted plants depending on when drought happened (El-Sharkawy, 2003; Haimeirong and Kubota, 2003). Similarly, the timing and duration of drought could change the morphology of the young root system (Pardales Jr and Esquisel, 1996), for example by developing thinner roots (i.e., increasing the ratio between root length and root weight), presumably to improve water uptake.

The number of adventitious roots also decreased during early season drought, and if such condition prolonged, it would reduce the number of adventitious roots that would differentiate into storage roots (Pardales Jr and Esquisel, 1996). It can therefore be suggested that cassava might be resistant to drought in terms of its survival, rather than in terms of its capacity to maintain high yield.

Among the anatomical characteristics that allow survival during drought is the ability of cassava plants to develop deep roots (>2 m), enabling them to extract subsoil water despite their sparse fine root system (Okogbenin et al., 2013). The stomata of cassava are particularly sensitive to vapor pressure difference; they close even before signs of water stress develop within the plant (Onwoume and Charles, 1994). At the same time, water-stressed cassava plants minimize carbon cost through cessation of osmolytes production during drought (Alves and Setter, 2004), a strategy that enables faster recovery once water becomes available. Cassava plants also form symbiotic associations with mycorrhiza, which may contribute to their ability to survive a prolonged period of drought (i.e., up to five months) (Horton, 1988). Cassava plants can also synthesize and accumulate abscisic acid during the early phase of water deficit, and this in turn results in: (i) low leaf area through limited formation of new leaves, (ii) the formation of small leaves, and (iii) leaves shedding (Alves and Setter, 2000). It has been shown that abscisic acid levels in water-stressed cassava can quickly return to normal within as little as one day after watering, resuming normal growth (Lebot, 2009). When drought lasts over an extended period, however, low leaf area will eventually lead to yield reduction (Okogbenin et al., 2013).

Our results also showed that sweet potato was more sensitive to drought compared to potato (Fig. 2), contradicting the common assumption that sweet potato is drought-resistant (Onwoume and Charles, 1994; Woolfe, 1992). We suggest that higher level of genetic development in potato compared to sweet potato could be responsible for the decrease in drought sensitivity of the former. In addition, better agricultural practices are generally adopted where potato is grown compared to sweet potato. The number of studies dedicated to a crop species can be taken as a proxy of such practices. For example Web of Science search of articles in English published between 1985 and 2015 using keywords “drip irrigation and “sweet potato” only resulted in 10 articles, but it resulted in 196 articles when replacing “sweet potato” to “potato”. The results were similar for sprinkler irrigation with one versus 96 articles found for “sweet potato” and “potato”, respectively. These factors may have contributed to the superior performance of this species (i.e., potato) that has previously been considered drought-sensitive. We acknowledge, however, that there could be some uncertainties in our determination of drought sensitivity since the amount of water required by each species cannot be confidently defined. While sweet potato might be resistant to drought in terms of its survival, it might be sensitive in terms of yield. Similar to cassava, sweet potatoes have a relative deep rooting system (0.75-0.9 m; compared to only 0.3 m for potato), which enable them to survive during drought through uptake of subsurface water pools not available to most vegetables (Mukhopadhyay et al., 2011). Supplementary irrigation for sweet potatoes, however, is highly recommended if available soil moisture is below 20% (Ravi and Indira, 1999). Irrigation at 60% moisture depletion level, for example, could increase root yield by 24% over non-irrigated sweet potatoes (Mukhopadhyay et al., 2011). The tradeoff between yield and survival is also related to the physiological and biochemical changes in the leaves. Under water deficit, stomatal resistance tends to increase to preserve leaf water content and prevent leaf senescence. Increasing stomatal resistance, however, also decrease CO_2 exchange, net photosynthetic rate and eventually yield. If droughts occur during tuber initiation and tuber bulking, these physiological processes could considerably reduce yield (Mukhopadhyay et al., 2011), explaining the yield sensitivity of sweet potato to drought. It has been further demonstrated that some drought-sensitive sweet potato cultivars did not produce yield, but were capable of surviving prolonged drought periods (Ravi and Indira, 1999).

The yield response of the other minor root/tuber species (i.e., taro, yam, and yautia) to drought is less well characterized as very few studies have examined the effects of drought on these crops. While our results showed that taro yield reduction did not differ from the major root/tuber crops, yautia showed a significantly higher yield reduction compared to potato in response to drought. Research has shown that potassium addition can improve taro and possibly yautia performance during drought by inducing better stomatal control and improving water use efficiency (Sivan et al., 1996) as both taro and yautia generally experience a decrease in stomatal conductance during drought (Mabhaudhi and Modi, 2015). While some wild relatives of taro exhibited drought tolerance characteristics, irrigation remains essential for these crops if they are grown during dry seasons or in areas with low annual rainfall (Bussell and Bonin, 1998). Irrigation water application rates higher (i.e., 150%) than the daily ET requirement is even recommended to maximize taro yield (Uyeda et al., 2011).

We were also unable to analyze the difference in drought sensitivity of yam, taro, and yautia due to the limited data available in the literature. As noted before, studies examining the effects of drought on root/tuber crops, already low in absolute number, have primarily focused on potato, sweet potato, and cassava with only scant information on other tubers such as yam and taro. Thus, as a group, root/tuber crops are insufficiently studied or under exploited despite their often so-called "potentials". Some of these potentials include their ability to produce yield under suboptimal conditions (e.g., drought; Cock, 1982) or their nutritional values. Taro, for example, has comparable nutritional value to potato (Talwana et al., 2009). Similarly, sweet potato outranks most "energy food" in terms of the vitamins, minerals, dietary fiber, and protein that it also provides (Mukhopadhyay et al., 2011). Along the same line, one may also note the case of yam. Although the extent of drought sensitivity and yield reduction of yams is unknown due to a paucity of experimental data, yam mayt exhibit considerable drought tolerance given some of the xerophytic features observed in the young plants, traits that are rarely found in other crops. After surviving a dry period, the new yam plants emerge with considerable vine length expansion (sometimes exceeding two meters) without forming new leaves. These vines, which initially obtain moisture and nutrients from the parent tuber, are also covered with a waxy bloom that reduces moisture loss as the plant continues to develop (Asiedu and Sartie, 2010).

3.2 Phenological effects

Similar to the findings reported in previous studies (Monneveux et al., 2013; Okogbenin et al., 2013; Onwoume and Charles, 1994), our results indicated that root/tuber crops generally experienced greater yield loss when droughts occur during tuber initiation (mid-season drought) and during tuber enlargement or bulking (late-season drought) than during their vegetative growth (early-season drought) (Fig. 3). Water stress for up to two months during the vegetative growth only delays normal growth in cassava, and the plant can resume growth once water becomes available (Lebot, 2009). Significant differences exist, however, between sweet potato and potato with regard to the leaf-level response of these crops to water stress. Sweet potato leaves wilt permanently at a much lower water potential (-1.3 MPa; Ravi and Indira, 1999) than potato leaves (-0.6 and -1.0 MPa in young and mature leaves, respectively; Levy et al., 2013) . Subsequent water stress during tuber bulking leads to malformation of tubers in potatoes, as well as to reduction in the number and size of the tubers (Monneveux et al., 2013). Both cassava and sweet potato are particularly sensitive to drought during storage root initiation, a period that typically occurs 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). Since very little initiation of storage roots occurs after seven weeks, the final number of tubers is virtually determined by this critical period (Onwoume and Charles, 1994). With the remaining period after tuber initiation is devoted to tuber enlargement, it is unsurprising that we did not find any difference in sensitivity between mid- and late-season droughts (Fig. 4). Water stress during late-season drought usually induces lignification of storage roots in sweet potato which later impede their growth (Ravi and Indira, 1999).

Although potatoes, sweet potatoes, and taros are highly sensitive to water deficit after planting (Lebot, 2009; Monneveux et al., 2013), our analysis did not capture this response since, in most studies, good emergence and early growth are typically allowed in order to study the effect of drought treatments in subsequent physiological phases. Yam is probably the only species within the root/tuber group with reported high drought-tolerance shortly after planting. As the young plant is devoid of leaves (and therefore has very low transpiration), it can tap most of its early moisture needs from the ‘mother’ tuber (Lebot, 2009). If moisture stress continues, however, tuberization can be delayed, negatively impacting yield (Lebot, 2009). While yams can survive in areas with low annual rainfall (i.e., between 500-700 mm), higher amount of water (approximately 1500 mm) during the total growth cycle is required to ensure high yield (Lebot, 2009).

3.3 Effects of agro-ecological region

We found that yield responses and sensitivities to drought were similar across eco-regions (i.e., dryland vs non-dryland) (Figs. 5 & 6). The lack of significant differences between the yield of tubers in the dryland and the non-dryland region is intriguing given the low relative humidity and high temperature of dryland regions which increase the potential evapotranspiration demand. While the underlying mechanisms could be complex, a recent study by Vicente-Serrano et al. (2013) suggested that the sensitivity of land biomes to drought was likely to be determined by the persistence of the water deficit (i.e., the drought time-scale). Research at the global biome level indicated that plants of humid regions, while having low tolerance to drought, also had fast recovery to water stress (Vicente-Serrano et al., 2013). Since our study focused on examining short-term drought experiments, we suggested that plant recovery could contribute to root/tuber crop resilience to drought. The center of origin of potato, sweet potato, and cassava were thought to be around Central and South America (Bradshaw and Ramsay, 2009; Nassar et al., 2007; Srisuwan et al., 2006) and rapid plant recovery could contribute, to some extent, to the robustness of yield across contrasting agro-climatic regions. At cellular level, the ability of potatoes to increase their WUE with partial closure of stomata (Liu et al., 2005), for example, could be responsible for their relative production resilience. At mild water deficit, photosynthesis decreases less rapidly than stomatal conductance (Liu et al., 2005), enabling potato to maintain the flow of assimilates to storage organs at lower evapotranspiration rate. Identifying the mechanisms of plant response to drought, including improving WUE in other root/tuber crops, opens the possibility of using water saving techniques to optimize the use of irrigation water. This opportunity is also available for other species (e.g., yam) in which cultivars with varying degree of drought tolerance have been identified in Asia and Africa (Lebot, 2009). In African drylands, yams are deliberately planted during the beginning of the dry season due to their resistance to drought (Lebot, 2009). Yams can survive in areas with annual rainfall as low as 500 mm (e.g., in south Madagascar) although yield potentials are low in these regions (Lebot, 2009).

3.4 Effects of soil texture

Greater yield reduction has been observed for roots and tubers planted on coarse soils compared to those planted on medium-textured soils under similar levels of water reduction (Figs. 7 & 8). Differences in soil texture usually correspond to their potential production capacity, including soil water-holding capacity. Medium- and fine-textured soils usually have higher water holding capacity than coarse-textured soils and, when available water is sufficient to produce yield, plants tend to become less responsive to any reduction in irrigation. We suggest that the presence of soil water reserve might be responsible for the lack of yield difference between crops planted on fine- and medium-textured soils, but not on the coarse-textured soil. An earlier examination of the effects of soil texture on potato yield also indicated that residual soil water provided most of the required water, and that irrigation larger than 40% ET had no beneficial effect on yield on medium-textured soils, but resulted in a significant yield increase in coarse-textured soils (Martin and Miller, 1983). This trend, however, is different from legumes which generally experience greater drought-induced yield loss in medium-textured soils (Daryanto et al., 2015). While the reason for this discrepancy is unknown, differences in root structure and density might account for these observations. When water is a limiting factor, most plants usually allocate more biomass to the roots. Interestingly, a negative correlation between root biomass and tuber yield was reported for potato (Tourneux et al., 2003). Additionally, continuous potato root growth which has been observed until early senescence (Gregory and Simmonds, 1992) might also contribute to the lack of drought sensitivity. As for other root crops (e.g., cassava and sweet potato), they are able to extract water from deeper soil layers and therefore less likely to be affected by soil texture. Indeed, extensive and deep rooting systems have been shown to increase the resilience of cereal yield to drought across a range of soil texture (Daryanto et al., in review).

4. Conclusions

Contrasting with the common belief that cassava and sweet potato are resistant to drought, our results indicated that, under similar water shortage conditions, these crops experienced yield reduction comparable to drought-sensitive species. Sweet potato even showed higher sensitivity to drought compared to potato. All root/tuber species were particularly sensitive to drought during the tuberization period, and this drought sensitivity was observed across contrasting agro-eco-regions and soil texture.

Roots and tubers have so far been regarded as inferior and neglected food crops even in areas where they are staples (Horton, 1988). For several decades, studies have examined the problems and potentials of root/tuber crops production, but limited progress has been made in improving the productivity of most of these crops under drought conditions. There are numerous challenges to the development of tuber and root crops, but an intensification of research (e.g., germplasm conservation, improved cultivation methods) is a critical step toward that goal. Among the dominant root/tuber crops, yam has probably the greatest potential for development and genetic improvement in part due to its xerophytic characteristics, its ability to survive in areas with low annual rainfall, its long dormancy period, and its high nutritional content. As reviewed elsewhere for cassava (Lebot, 2009; Okogbenin et al., 2013; Prochnik et al., 2012), sweet potato (Lebot, 2009; Mukhopadhyay et al., 2011), yam (Asiedu and Sartie, 2010; Lebot, 2009), taro and yautia (Lebot, 2009; Onwoume and Charles, 1994), available technologies (e.g.,. genetic modification, improvement of cultivation and irrigation methods) could help maintain the productivity of tuber crops in the face of a changing climate, and improve food security in the drought-prone regions of the world.

Acknowledgements

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

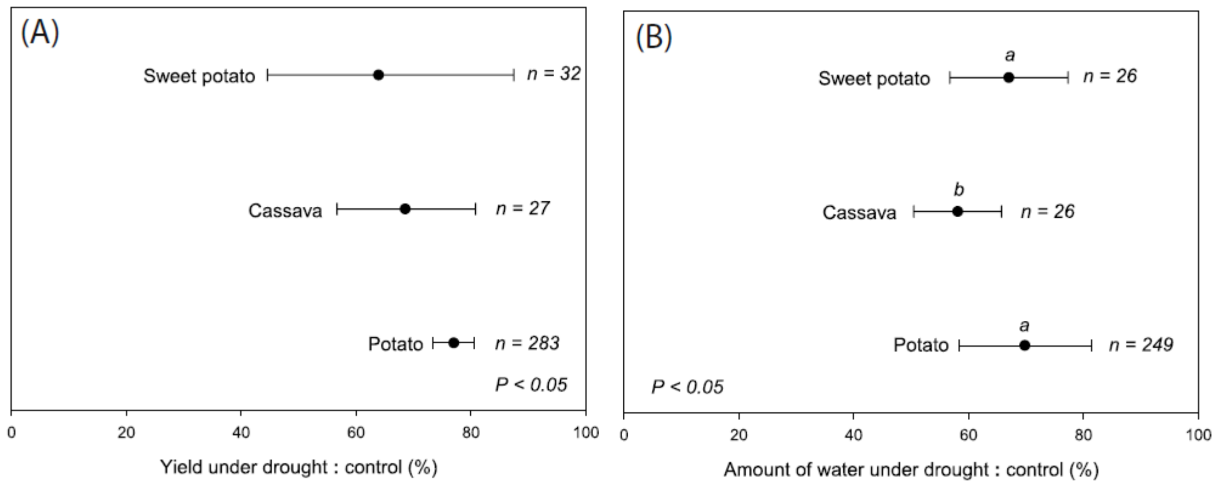

Fig. 1. Observed confidence intervals of drought-induced yield reduction for different root/tuber crops as determined by meta-analysis (A) and the corresponding water reduction for each species (B). The yield reduction is the same if the species confidence intervals overlap with each other (A). Letters *a* and *b* indicate significant difference between observed water reduction level (B). Letter *n* indicates the number of samples for each categorical variable.

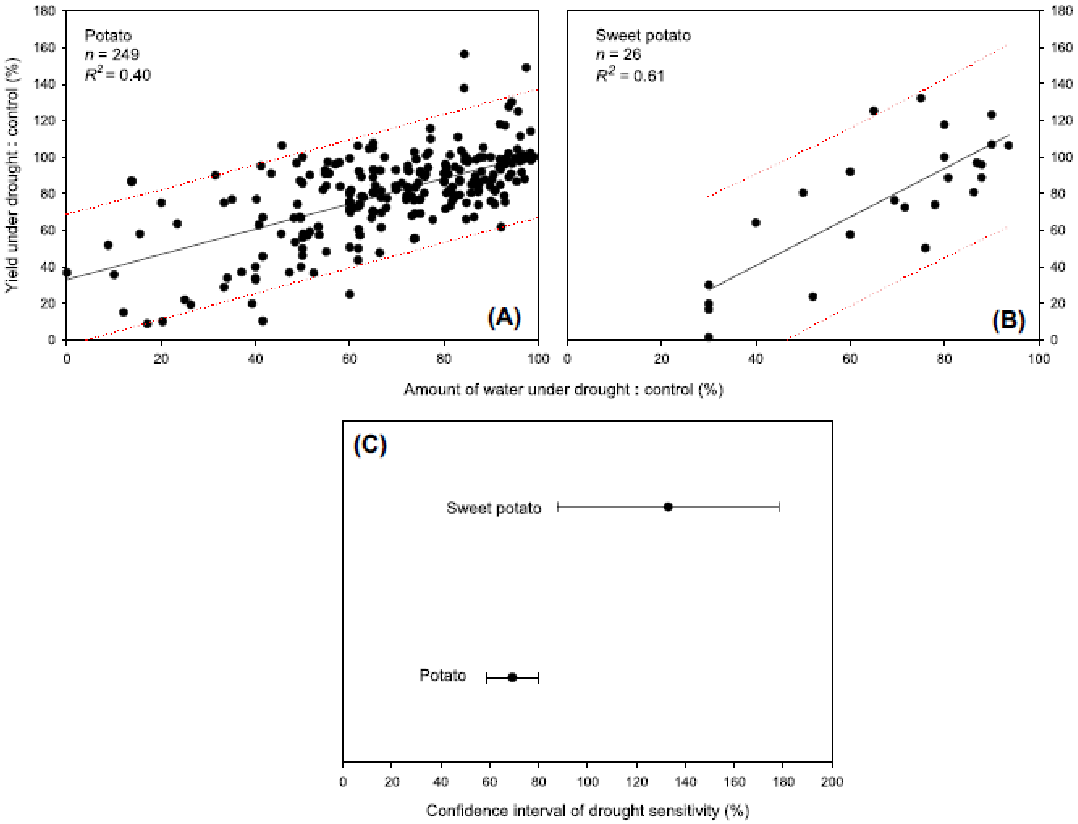

Fig. 2. Drought sensitivity (above) and confidence interval (below) of potato and sweet potato. Dotted lines indicate 95% confidence band.

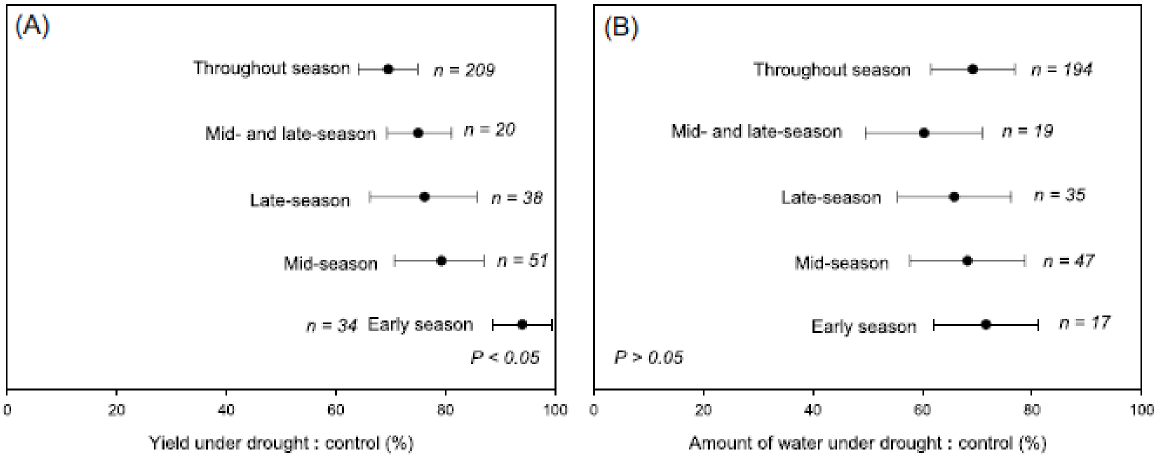

Fig. 3. Observed confidence intervals of drought-induced yield reduction of root/tuber crops as determined by meta-analysis (A) and their corresponding water reduction during different

phenological phases (B). The yield reduction is the same if the confidence intervals overlap with each other (A). Letter *n* indicates the number of samples for each category variable.

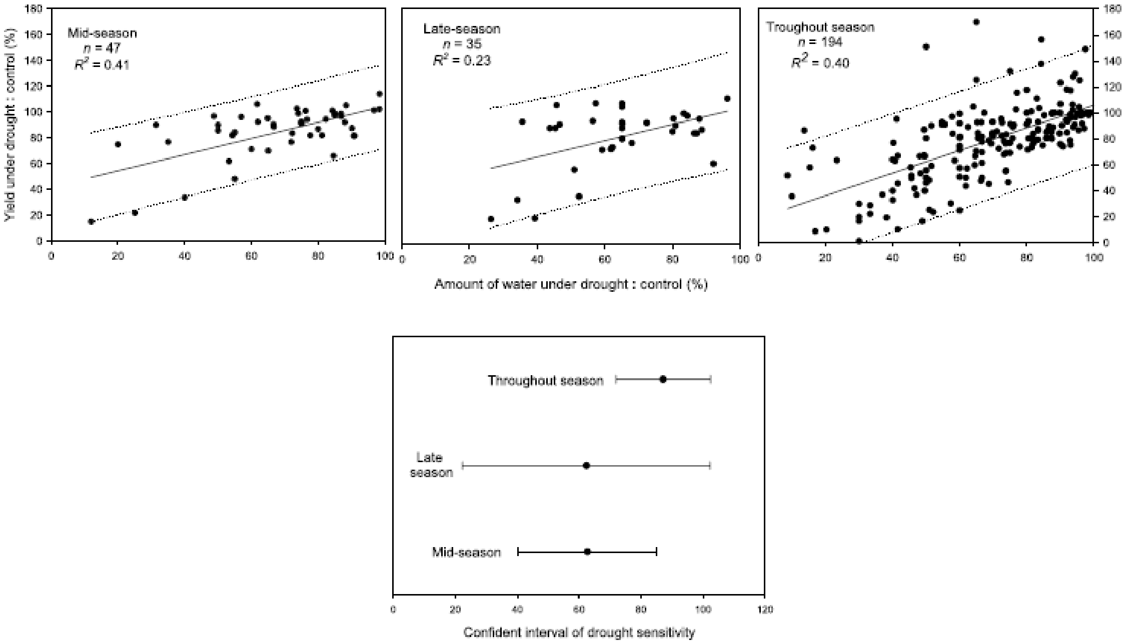

Fig. 4. Drought sensitivity (above) and confidence interval (below) of root/tuber crops during different phenological phases. Dotted lines indicate 95% prediction band.

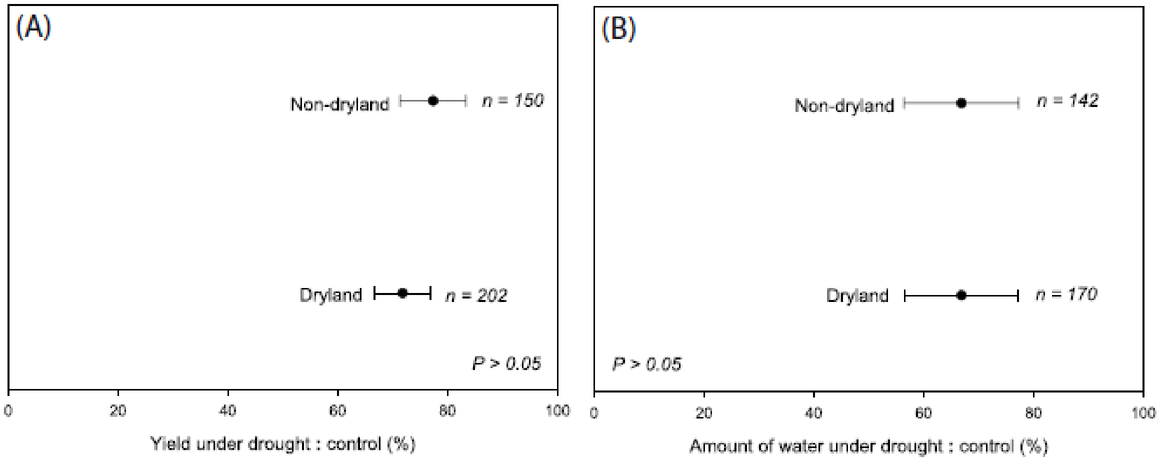

Fig. 5. Observed confidence interval of drought-induced yield reduction for root/tuber crops as determined by meta-analysis (A) and their corresponding water reduction in dryland and non-dryland regions (B). The yield reduction is the same if the confidence intervals overlap with each other (A). Letter *n* indicates the number of samples for each categorical variable.

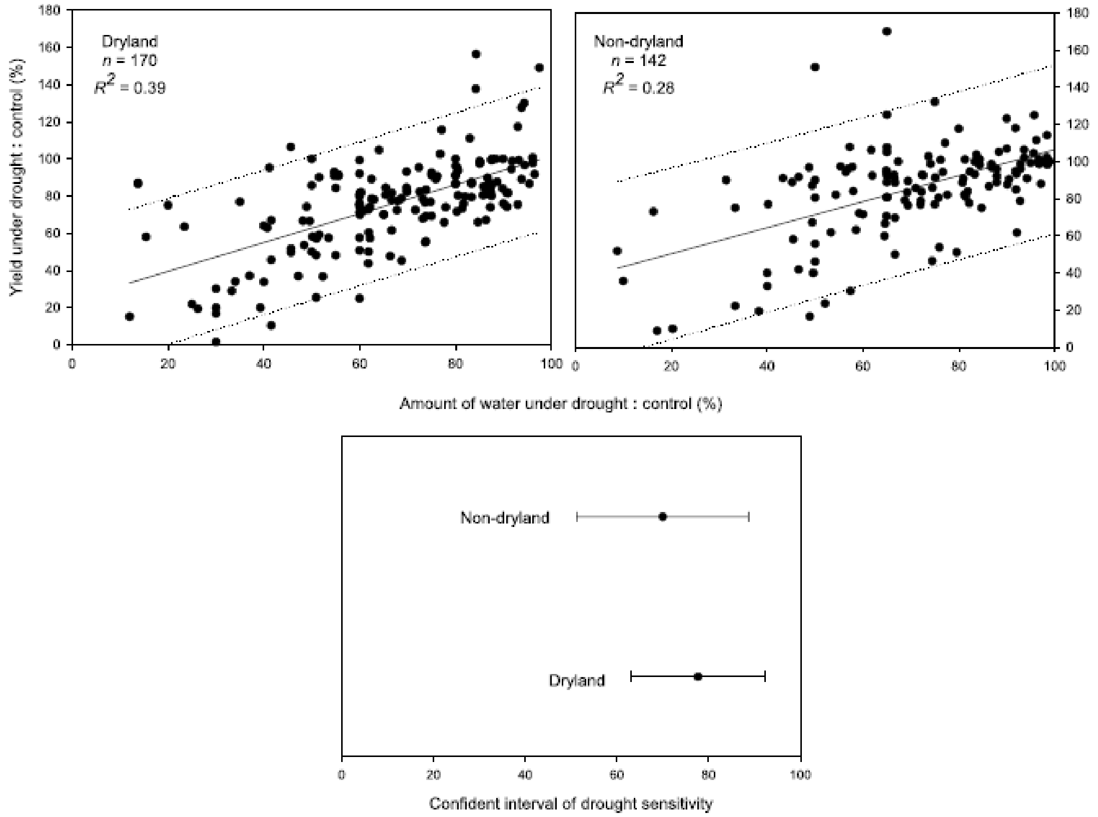

Fig. 6. Drought sensitivity (above) and confidence interval (below) of root/tuber crops in dryland and non-dryland regions. Dotted lines indicate 95% prediction band.

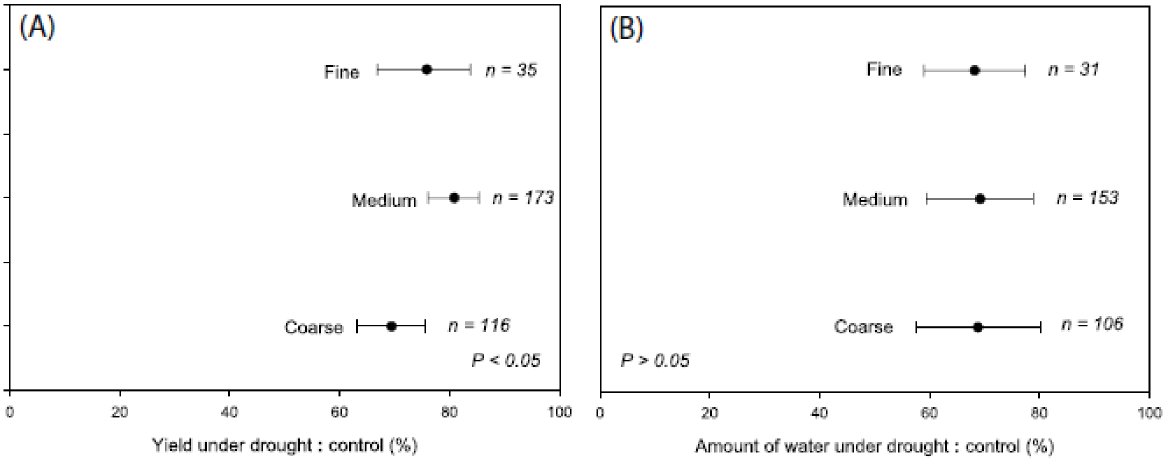

Fig. 7. Observed confidence interval of drought-induced yield reduction for root/tuber crops grown on soils of different texture as determined by meta-analysis (A) and their corresponding water reduction (B). The yield reduction is the same if the confidence intervals overlap with each other (A). Letter *n* indicates the number of samples for each categorical variable.

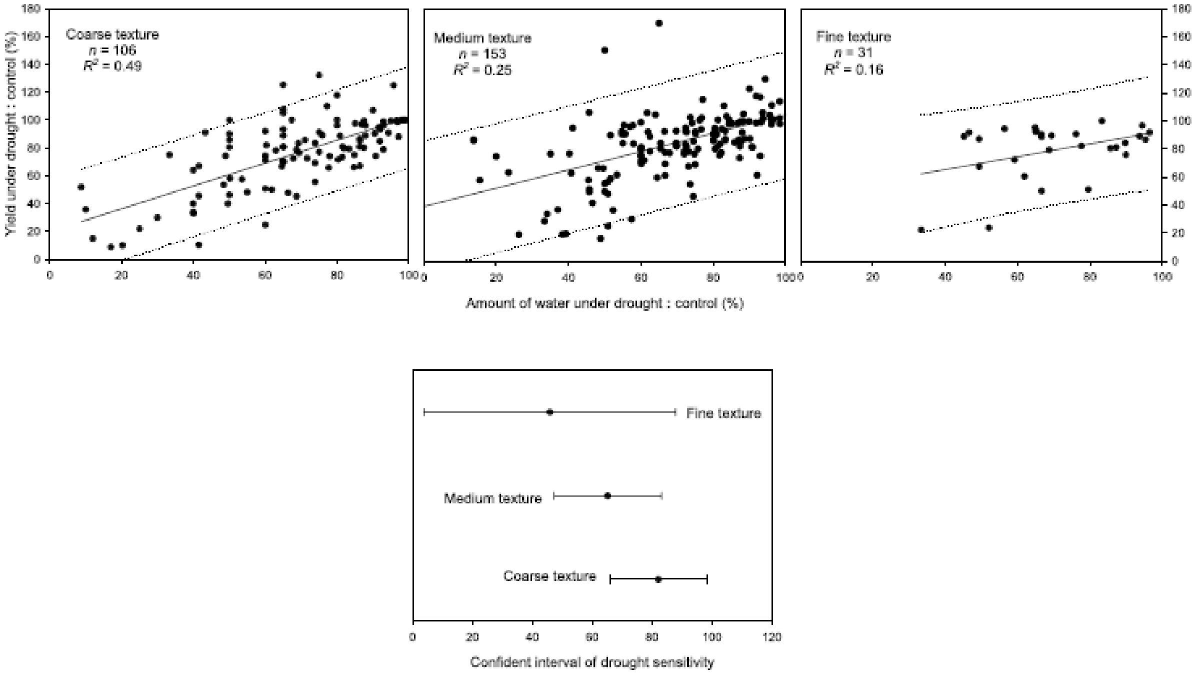

Fig. 8. Drought sensitivity (above) and confidence interval (below) of root/tuber crops grown on soils of different texture. Dotted lines indicate 95% prediction band.