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HERITABILITY ANALYSIS OF PUTATIVE DROUGHT ADAPTATION TRAITS IN SWEETPOTATO

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ABSTRACT

Drought stress is a constraint to sweetpotato (*Ipomoea batatas* L. (Lam)) production in many parts of Sub-Saharan Africa. In this region, crop farming is predominantly rain fed; therefore, breeding for drought tolerance is appropriate for addressing low sweetpotato productivity since the crop is largely produced by resource-limited farmers. As part of developing drought tolerant genotypes in Uganda, this study aimed at determining the nature of genetic control and heritability associated with selected drought adaptation traits. Ten randomly chosen clones from each family were evaluated for three traits; tuber yield, crop vigour and canopy cover as well as five traits (leaf senescence, leaf rolling, leaf retention, SPAD readings and root vertical pulling) at 80% field capacity and under no watering conditions for three weeks in a glasshouse. Diallel analysis revealed significant effects for both GCA and SCA, indicating both additive and non-additive gene actions were present. Baker's ratio was large in most traits (>0.50), indicating predominance of additive effects. Heritability coefficients were high in most traits (>0.50), indicating that genetic gains can be achieved by conventional breeding. The predominance of additive genetic control realised in this study implies that use of small numbers of parents with suitable GCA effects is most appropriate for drought tolerance improvement in sweetpotato.

Key Words: Combining ability, diallel, *Ipomoea batatas*

RÉSUMÉ

La sécheresse constitue une contrainte importante à la production de la patate douce (*Ipomoea batatas* L. (Lam)) dans beaucoup de parties de l'Afrique sub Saharienne. Dans cette région, l'agriculture est à predominance pluviale, ainsi, l'amélioration pour la tolérance à la sécheresse est appropriée pour adresser la faible productivité de la patate douce d'autant plus que la culture est largement produite par les fermiers à resources limitées. Comme contribution au développement des genotypes tolerant la sécheresse en Ouganda, cette étude a pour but de déterminer la nature de l'heritabilié et le contrôle génétique associés aux traits d'adaptation à la sécheresse. En suite, dix clones aléatoirement choisis dans chaque famille étaient évalués au champs pendant dix huit semaines pour trois traits dont le rendement en tubercules, la vigueur de la plante et la couverture de la canopée ainsi que cinq traits (la senescence foliaire, l'enroulement de la feuille, la retention foliaire, ls lectures du SPAD et l'attrait de la racine verticale) à 80% de la capacité au champ et sans régime de conditions d'arrosage pendant trois semaines dans une serre). L'analyse Diallèle a révélé des effets significatifs pour le GCA et SCA, indicant la présence des actions additives et non additives de gènes. Le rapport de Baker était large dans laplupart des traits (>0.50), indicant la prédominance des effets addidifs. Les coefficients d'heritabilité étaient élevés dans la plupart des traits (>0.50), montrant que des gains génétiques peuvent être acquis par l'amélioration conventionnelle. La prédominance du contrôle génétique additif réalisé dans cette étude implique que l'utilisation d'un petit nombre de parents avec effets GCA appropriés est la plus indiquée pour l'amélioration de la tolérance à la sécheresse dans la patate douce.

Mots Clés: Combininaison d'aptitude, diallèle, *Ipomoea batatas*

INTRODUCTION

Sweetpotato (*Ipomoea batatas* L. (Lam)) production in Sub-Saharan Africa is compromised by drought stress (Yanggen and Nagujja, 2006; Gibson *et al*., 2008). Drought stress related effects have restricted Ugandan sweetpotato farmers to local landraces that are resilient to water stress (Yanggen and Nagujja, 2006). Landraces have long growing cycles and low yields, and this is partly responsible for the persistent national low yields despite the increasing sweetpotato acreage (Gibson *et al*., 2008; FAOSTAT, 2011). Although other constraints to sweetpotato production in Uganda have been given attention (Mukasa *et al*., 2003), drought stress has not been attended to significantly (Yanggen and Nagujja, 2006; Gibson *et al*., 2008). To unlock the role of sweetpotato in livelihood improvement in Uganda, developing drought tolerant sweetpotato varieties for the resource constrained farmers that produce the bulk of the crop is very important and a sustainable solution. Already, development of such genetically tailored genotypes for resource limited farmers amidst the changing environment characterised by excess droughts is to embrace food security in such communities (Apse *et al*., 1999; Condon *et al*., 2004; Salinger *et al*., 2005; Fuglie *et al*., 2007; Borlaug, 2007; Tuberosa, 2011).

The direct selection for tuber yields under stress conditions, in experimental fields among segregating genotypes, is a standard approach for sweetpotato breeding in Uganda. Field trials require heavy resource investments and have poor repeatability in crops like sweetpotato, which have large genotype by environment interactions (Ekanayake, 1990; Manrique and Hermann, 2000; Lebot, 2010). These factors make this breeding approach ineffective for sweetpotato drought adaptation improvement breeding programmes. Thus, it is not surprising to note that many of the newly released sweetpotato cultivars in Uganda have low drought tolerance levels (Yanggen and Nagujja, 2006; Gibson *et al.*, 2008) and this has led to their poor adoption among farmers.

Selecting genotypes for breeding programmes through assessment of their general and specific combining abilities for instance through diallel analyses gives a basis for selection of appropriate parents and their crosses as per the breeders objectives (Viana and Matta, 2003; Gnanasekaran *et al*., 2006; Saleem *et al*., 2009). In addition, efficient transmission of desirable genes from selected parents to their progeny needs firm knowledge about gene action (Falconer and Mackay, 1996). A proper selection of parents based on their combining ability and knowledge of genetic control of specific traits is helpful in designing more efficient and target oriented breeding process and helps in ensuring accumulation of desirable unfixable or fixable gene effects (Nadarajan and Gunasekaran, 2005).

In this study, using a diallel mating design Method 4, Model 1 (fixed parents) of Griffing, (1956), a set of F_1 progeny derived from five cultivars was used to determine the genetic control of selected drought adaptation traits in sweetpotato. This information is useful in building effective breeding strategies targeting drought tolerance improvement in the Ugandan sweetpotato germplasm.

MATERIALS AND METHODS

This study was done in the fields of the National Semi-Arid Resources Research Institute (NaSARRI) Serere, and Makerere University Agricultural Research Institute, Kabanyolo (MUARIK) in Uganda between 2011 and 2012. NaSARRI is a region known for drought as a major constraint to sweetpotato production (Mudiope *et al*., 2000). The field set up was supplemented with glasshouse studies repeated twice at MUARIK. Although MUARIK is not in a region documented for drought constraint to sweetpotato production, intermittent and unreliable rain seasons start and duration present a severe drought challenge to sweetpotato farmers.

Each experiment consisted of 90 clones from randomly selected 10 clones from each progeny families in a randomised complete block design (RCBD) with two replications. Each clone was planted in plots consisting of four mounds measuring 2 m x 2 m. Three vine shoot tips approximating 30 cm in length were planted in a mound. These F_1 progeny families were generated using diallel mating design Model 1, Method 4 of

Griffing, (1956) from five cultivars, which display varying drought tolerance levels in the field. These parents were:- *Munyeera* and *New Kawogo* (drought tolerant), *Semanda* and *Tanzania* (moderately drought tolerant) and *Beauregard* (highly susceptible) as per field observations. Cultivars *New Kawogo* and *Munyeera* were planted to generate data for the cross NKMU from their means since these parents were incompatible during hybridization. Planting in all fields was done one month late after onset of the main season rains to simulate drought stress during the growing cycle while in the glasshouse differential watering induced drought stress in the experiment.

In the glasshouse, the same clones as used in the field were planted in wooden boxes with soil filled to 30 cm depth in RCBD (for diallel analysis purposes mainly). Watering to 80% field capacity for 4 weeks was done to ensure full root development (Belehu, 2003), and thereafter, half of the experiment setup was subjected to watering regularly to 80% field capacity while the second half was subjected to terminal water stress treatment (no watering) for 3 weeks. Through the growing time, vines were tied upright on wire strands to prevent intertwining and setting roots on nodes, other than those planted.

Three traits namely; tuber yield, crop vigour and canopy cover were studied in the field. These traits are associated with drought tolerance in sweetpotato (Ekanayake, 1990; Yanggen and Nagujja, 2006; Andrade *et al*., 2009; Lebot, 2010). Tuber yield consisted of tubers with at least 4 cm diameter following Woolfe's (1992) description of marketable tubers.

Canopy cover and crop vigour were scored once a month starting one month after planting, and lasting up to 4 months. Crop vigour was scored with a 1-5 scale where 1 = poor, 2 = fair, 3 = good, 4 = very good and 5 = excellent. Canopy cover reflecting vine survival was scored on a scale of 1-5 too where 1= 1 to 20%, 2 = 20 to 40%, 3 = 40 to 60%, 4 = 60 to 80% and 5 represented 80 to 100% of mound area covered.

In the glasshouse, five plant drought traits, namely, chlorophyll concentrations derived using the Soil Plant Development Analysis (SPAD) instrument readings; these values are also referred to as SPAD chlorophyll meter readings (SCMR), leaf retention, leaf senescence, leaf rolling and root vertical pulling. These traits have been studied and measured based on previous drought studies of Ekanayake (1990), Andrade *et al*. (2009), Vilaro (2011) and Tuberosa (2011). Since drought adaptation traits have low heritability under non-stress conditions (Muthuramu *et al*., 2010), the data in the glasshouse were collected as differences between non-stressed and stressed plots.

Data for each site were analysed independently. Field and glasshouse data were subjected to analysis of variance (ANOVA) using GenSTAT Discovery 13th edition, prior to combining ability analysis. The parents were chosen based on their level of susceptibility to drought stress and, hence, were considered as a fixed set, in the fixed model (Model 1) (Dabholkar, 1992). Since reciprocal progenies are a problem in sweetpotato breeding (Wilson *et al*., 1989), we chose Method 4 that disregards reciprocals and uses F_1 progeny as the experimental material (Mwanga *et al*., 2002; Mihovilovich *et al*., 2000). Therefore, combining ability analysis followed Method 4, Model 1 of Griffing, (1956) diallel analysis procedures.

$$Y_{-ij} = \mu + g_i + g_j + s_{ij} + (1/bc)\, \Sigma_k \Sigma_l\, e_{ijkl}$$

Where:

Y_{-ij} is the observation recorded on ij^{th} *genotype*, m is the population mean where as g_i and g_j are the general combining ability effects of the i^{th} and j^{th} parents respectively. S*ij* is the specific combining ability of the ij^{th} cross; while e_{ijkl} is the error effect associated with the $ijkl^{th}$ observation.

Important combining ability effects were revealed through F-tests, the restrictions imposed on combining ability estimates were: $Sg_i = 0$, and $Ss_{ij} = 0$ (zero), for all GCA and SCA effects respectively. These combining ability estimates were tested for deviation from zero by using two tailed t-tests as described by Singh and Chaudhary (1977) and Dabholkar (1992).

For the traits studied, GCA and SCA estimates were considered as described in Table 1. In addition, estimates for broad and narrow sense coefficients of genetic determination (BSCGD and NSCGD), the fixed effect equivalent of broad and

TABLE 1. Classification of combining ability values for the various drought adaptation traits for sweetpotato

Trait	GCA		SCA	
Tuber yield	Desirable:	Significant, positive	Desirable:	Significant, positive
	Average:	Non-significant, positive	Average:	Non-significant, positive
	Detrimental:	Any negative	Detrimental:	Any negative
Crop vigour	Desirable:	Significant, positive	Desirable:	Significant, positive
	Average:	Non-significant, positive	Average:	Non-significant, positive
	Detrimental:	Any negative	Detrimental:	Any negative
Leaf rolling	Desirable:	Significant, negative	Desirable:	Significant, negative
	Average:	Non-significant, negative	Average:	Non-significant, negative
	Detrimental:	Any positive	Detrimental:	Any positive
Leaf retention	Desirable:	Significant, positive	Desirable:	Significant, positive
	Average:	Non-significant, positive	Average:	Non-significant, positive
	Detrimental:	Any negative	Detrimental:	Any negative
Leaf senescence	Desirable:	Significant, negative	Desirable:	Significant, negative
	Average:	Non-significant, negative	Average:	Non-significant, negative
	Detrimental:	Any positive	Detrimental:	Any positive
Chlorophyll levels	Desirable:	Significant, positive	Desirable:	Significant, positive
	Average:	Non-significant, positive	Average:	Non-significant, positive
	Detrimental:	Any negative	Detrimental:	Any negative
Root-pulling resistance	Desirable:	Significant, positive	Desirable:	Significant, positive
	Average:	Non-significant, positive	Average:	Non-significant, positive
	Detrimental:	Any negative	Detrimental:	Any negative

Source: Based on literature for sweetpotato drought adaptation traits and improvement prospects from Ekanayake (1990); Andrade *et al.* (2009); Tuberosa (2011) and Vilaro (2011)

narrow sense heritabilities were determined for all the traits following Jacquard (1983) and Abney *et al*. (2000) as:

$$BSCGD \sim H^2 = (2\sigma^2_{gca} + \sigma^2_{sca}) / (2\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_e);$$

and $NSCGD \sim h^2 = 2\sigma^2_{gca} / (2\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_e)$

The combining ability ratio (Bakers ratio) was derived following Baker (1978) as:

$$2\sigma^2_{gca} / (2\sigma^2_{gca} + \sigma^2_{sca})$$

In these formulae, the terms are the respective variance components. Variance components for GCA and SCA were calculated using the formula $(M_{gca} - M_{sca}) / (p-2)$ following Singh and Chaudhary (1977); where M is respective mean square and p is number of parents.

RESULTS

All data, except canopy cover at all stations, tuber yield at MUARIK and crop vigour at NaSARRI were desirable for combining ability analysis; hence GCA and SCA components and heritability coefficients were determined (Table 2). Mean squares for GCA effects were highly significant (P<0.01) for all traits. The SCA effects were also significant, except for SPAD readings and crop vigour. The combining ability ratio was large for all traits (>0.50), and in some cases neared unity. Generally, heritability coefficients (BSCGD and NSCGD) for all traits were high (>0.50).

For tuber yields under drought stress, three cultivars (*Semanda* and *Munyeera* and *Beauregard*) had desirable GCAs; while *Tanzania* and *New Kawogo* displayed detrimental effects (Table 3). Only *Tanzania* and *Beauregard* had the desirable GCAs for crop vigour, with the rest of the parents (*New Kawogo, Semanda* and *Munyeera*) showing detrimental effects. Genotypes *New Kawogo* and *Munyeera* had positive significant GCA values for leaf retention; with the rest of the parents, especially *Beauregard,* showing detrimental effects. Genotypes *Tanzania* and *Beauregard* had detrimental GCA effects; while other genotypes displayed average effects for leaf rolling. Both *New Kawogo* and *Munyeera* had the best GCA effects for leaf senescence, with *Beauregard* showing average effects.

Genotypes *Tanzania* and *Semanda* displayed unfavourable GCA effects for leaf senescence. For chlorophyll levels, *New Kawogo* and *Munyeera* had desirable GCA effects; while other genotypes displayed detrimental effects. For the deep rooting trait as estimated by root-pulling resistance, genotypes *Tanzania* and *Munyeera* had desirable GCA effects; while other genotypes displayed detrimental effects.

The majority (six out of ten) of the crosses had better SCAs for tuber yield. Four crosses (TZNK, TZSE, NKSE and BEMU) displayed average effects; while two crosses (TZMU and NKBE) had desirable effects. The rest displayed detrimental effects (Table 4). BEMU displayed positive significant SCA for leaf retention with crosses TZNK, TZSE, NKSE and NKBE displaying average effects. NKBE and SEMU had desirable SCA effects for leaf rolling; while crosses NKMU and SEBE displayed positive significant SCA effects. Crosses NKSE and TZMU had negative significant SCA values for leaf senescence. No SCA effects were significant except the positive directed SEMU and TZSE for root-pulling resistance**.**

TABLE 2. GCA, SCA mean squares and heritability values for the various drought traits for sweetpotato

Source	Df	Tuber yield	Crop vigour	Leaf retention	Leaf rolling	Leaf Senescence	SPAD readings	Root-pull resistance
GCA	4	4.450**	0.016*	5.953**	0.359**	0.944**	25.086**	0.136**
SCA	5	1.236**	0.012	3.402**	0.203**	0.148*	4.738	0.045*
Error	9	0.191	0.004	0.471	0.018	0.033	1.836	0.012
Bakers ratio		0.731	0.481	0.555	0.551	0.841	0.842	0.713
BSCGD		0.953	0.815	0.933	0.959	0.957	0.909	0.904
NSCGD		0.697	0.392	0.518	0.528	0.804	0.766	0.644

**, * significant at 1 and 5%, respectively

TABLE 3. GCA effects associated for the various drought adaptation traits for sweetpotato

Parent	Tuber yield	Crop vigour	Leaf retention	Leaf rolling	Leaf senescence	SPAD readings	Root-pull resistance
Tanzania	-0.411**	0.088**	-0.253	0.471**	0.842**	-0.804	0.163*
New Kawogo	-1.904**	-0.107**	1.313*	-0.169	-0.577**	2.649*	-0.049
Semanda	0.296**	-0.007**	-0.170	-0.062	0.217	-1.621	-0.099
Beauregard	1.094**	0.037**	-2.137**	0.193	-0.075	-3.513**	-0.274**
Munyeera	0.924**	-0.012**	1.247*	-0.432	-0.407*	3.289**	0.259**

**, * significant at 1 and 5%, respectively

TABLE 4. SCA effects associated with the various drought adaptation traits for sweetpotato

Cross	Tuber yield	Leaf rentention	Leaf rolling	Leaf senescence	Root-pull resistance
TZNK	0.455	0.125	-0.135	-0.060	0.143
TZSE	0.465	1.658	-0.075	0.087	0.307**
TZBE	-1.189*	-1.375	0.148	0.227	0.177
TZMU	1.175*	-0.405	0.065	-0.323*	-0.027
NKSE	0.0983	0.545	0.018	-0.360*	0.080
NKBE	1.348**	0.858	-0.437**	-0.100	-0.120
NKMU	-0.992*	-1.525*	0.558**	0.520**	-0.113
SEBE	-0.272	-1.805*	0.485**	0.210	0.010
SEMU	-0.292	-0.392	-0.428**	0.067**	0.207*
BEMU	0.108	2.325**	0.195	0.357*	-0.080

**, * significant at 1 and 5%, respectively

DISCUSSION

Genetic control and heritability of the drought traits. The highly significant GCA and SCA mean squares for the majority of the traits (Table 2), indicate that both additive and non-additive gene effects prevail in the genetics of these traits (Singh and Chaundry, 1977; Dabholkar, 1992). However, the high GCA to SCA (combining ability or Bakers') ratio and high narrow sense heritability (>0.50) associated with most traits (Table 2), indicate the predominance of additive genetic control (Singh, 2003; Valiollah, 2012). The closer the combining ratio is to unity, the larger the importance of additive genetic control, and hence, the greater the capacity to predict progeny performance based exclusively on GCA effects (Baker, 1978).

The significant mean squares for GCA and SCA components across all traits suggest that additive and non-additive gene actions prevail in these traits, but the relatively large combining ability ratio and narrow sense heritability (>0.50) (Table 2), indicates the predominance of GCA effects or additive genetic control in these traits. Additive variance is associated with effective response to selection (Gnanasekaran *et al.* 2006; Valiollah, 2012); hence, small numbers of parents with better GCA's should be used to generate F_1 progenies for drought tolerance evaluation. Again, since in inter-mating populations, additive genetic variance is never exhausted due to self conversion of non-additive genetic variance into additive one by fixation of heterozygote loci into homozygote ones (Falconer and Mackay, 1996), it is therefore, important to carry out inter crossing between many sweetpotato cultivars so as to fix these drought adaptation traits in desired genotypes.

General combining ability. The GCA effects of the parents and traits in this study are given and described in Tables 1 and 3, respectively. Parents *Semanda*, *Munyeera* and *Beauregard* had desirable GCA effects for tuber yield; thus are good combiners for this trait when used as a basis for drought tolerance screening. Parents *Tanzania* and *Beauregard*, displayed desirable GCA effects for crop vigour, hence are better combiners for this trait that could be important, especially for drought escape. The desirable GCA effects associated with leaf retention for cultivars *New Kawogo* and *Munyeera* indicate that these genotypes combine for increased leaf retention amidst water stress, yet the negative GCA effects of these parents for leaf senescence signifies combining for anti-leaf loss during drought. Although, it is widely believed that shedding off leaves induced by drought stress minimises water loss in plants, this behaviour is of benefit to perennial crops but not annual crops simply because such behaviour is associated with severe reduction in cumulative photosynthesis leading to poor yields (Lopez *et al.*, 1997), hence in this case, negative significant GCA and SCA effects are desirable for leaf senescence and positive significant values are desirable for leaf retention as described in Table 1.

It was observed in this study that leaf margins and apexes bent downwards or upwards, with virtually no surfaces protected in contrast with the described beneficial onion-leaf like shaped rolling of leaves in cereals (Blum, 2004; 2006), whereby rolled-over surfaces are protected from photo damage and reduction in evapotranspiration rates (Richards *et al*., 2002). Thus, the leaf-rolling pattern observed in this study did not blend with dehydration avoidance benefits and could be because sweetpotato has a reticulate leaf venation. Therefore, higher scores of leaf rolling indicated susceptibility to drought than resistance or tolerance. The parent, *Tanzania,* with positive GCA effects for leaf rolling and leaf senescence, indicates drought susceptibility. Hence, parents that would yield negative and significant GCA effects would be desirable parents for drought stress tolerance since they would likely have progeny that resists leaf rolling and senescence.

Two parents (*Tanzania* and *Munyeera*) had significant and positive directed GCA effects for root vertical pulling force (Table 3), indicating that these parents can impart extensive root growth to their progenies. This feature can help in accessing moisture in lower levels of the soil during mild water stress; hence, keeping the plant bio-system operating at optimum levels. Two cultivars, *New Kawogo* and *Munyeera*, displayed highly desirable GCA effects for chlorophyll concentration, but this could be due to their inherent rich green colour instead of the actual photosynthetic capacity. This is because *Semanda* displayed a negative and non-significant GCA effect for SCMR, and *Beauregard* showed significant negative in direction GCA. This is largely unexpected since *Beauregard* and *Semanda* are known to be high root yielders and, hence, should be rich in chlorophyll to reflect a highly efficient photosynthetic apparatus. This, therefore, suggests that SPAD readings are not suitable for investigating chlorophyll changes in sweetpotato under drought stress.

Specific combining ability. The specific combining ability effects of the parents and traits in this study are given and described in Tables 1 and 4 respectively. Two crosses, NKBE and TZMU, displayed desirable SCA effects (Table 4), thus are good materials to undergo evaluation for drought tolerance if tuber yield is the selection criterion. Only cross BEMU had desirable SCA effects for leaf retention. Crosses SEMU and NKBE, showed desirable effects for leaf rolling. Crosses TZMU and NKSE, displayed the traits leaf senescence's best SCA values. Crosses TZSE and SEMU, displayed desirable SCA effects and this infers that they have excellent deep rooting ability to sustain plant functions amidst water stress, since they can access water in deep sections of the soil profile.

Parents with the best GCA effects did not necessarily produce crosses with desirable SCA effects. In cross BEMU for leaf retention, where parent *Beauregard* displayed undesirable GCA effects, both crosses TZMU and NKSE, which showed best SCA values, had only one parent with desirable GCA effects as well as crosses TZSE and SEMU for the trait root-pull resistance. Also, crosses NKBE and SEMU, which showed best SCA values for leaf rolling, had all their parents with undesirable GCA effects. This strange phenomenon which contrasted with desirable parents yielding progenies in such a fashion was also encountered previously (Shumbusha, 2011). It could be due to genome ploidy or presence of modifier genes for these traits; but again this affirms the role of additive genetic control for these traits.

CONCLUSION

Both additive and non-additive types of genetic control are responsible for the genetics of drought adaptation traits in the sweetpotato genotypes used in this study. However, additive genetic control is more predominant implying that GCA effects are more important than SCA effects. The high coefficients of heritability and importance of additive effects infers that conventional breeding can be used to improve sweetpotato for drought tolerance especially through using parents with desirable GCA effects. In this study, good combiners for respective traits were: *Semanda*, *Munyeera* and *Beauregard* for tuber yield, *Tanzania* and *Beauregard* for crop vigour, *New Kawogo* and *Munyeera* for leaf retention and leaf senescence while parents *Tanzania* and *Munyeera* were the better combiners for extensive root growth under drought stress.

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