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Yam Tuber Dormancy and Sprouting: The Role of Concentration Dynamics of Endogenous Gibberellic Acid

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Abstract
The role of endogenous gibberellic acid (GA_3) in the regulation of yam (*Dioscorea spp.*) tuber dormancy was investigated by determining the changes in the endogenous GA_3 levels during natural dormancy progression. Two *Dioscorea rotundata* cultivars ('Pona' and 'Labreko') and one *Dioscorea alata* cultivar ('CRI-Ahoɔdenfoɔ') used in these studies have varying dormancy duration. Endogenous GA_3 levels determined for the yam tubers ranged from 1.53 – 3.05 mg/g dw and 1.23 – 1.58 mg/g dw for 'Pona'; 1.53 – 3.40 mg/g dw and 1.25–1.57 mg/g dw for 'Labreko'; 1.48 – 3.62 mg/g dw and 1.28 – 1.60 mg/g dw for 'CRI-Ahoɔdenfoɔ', respectively, for the outer and inner portions. 'Pona' and 'Labreko' had dormancy break at 60 days after harvest (DAH), but at 90 DAH for 'CRI-Ahoɔdenfoɔ'. Generally, GA_3 levels increased from harvest to the maximum at 30 DAH, then declined to the minimum at 60 DAH before finally increasing again at 90 DAH for the outer portions of the yam tuber. For the inner portions of the tuber, GA_3 levels rather declined significantly to the minimum at 30 DAH, increased at 60 DAH and then decreased again at 90 DAH. GA_3 levels in the outer portions of the tubers increased by 84-122%, 65-77% and 61-65%, respectively, in 'CRI-Ahoɔdenfoɔ', 'Labreko' and 'Pona', but decreased in the inner portions by 19-23%, 24-26% and 26-28%. Essentially, higher amounts of endogenous gibberellins in yam tubers induced longer dormancy duration whereas lower amounts were indicative of dormancy termination and subsequent initiation of sprouting.

Keywords: *Dioscorea spp*., Yam tubers, Endogenous gibberellic acid, Dormancy, Sprouting

Dormance et germination du tubercule d'igname: le rôle de la dynamique de concentration de l'acide gibbérellique endogène

Résumé
Le rôle de l'acide gibbérellique endogène (GA3) dans la régulation de la dormance du tubercule de l'igname (Dioscorea spp.) a été étudié en déterminant les changements dans les niveaux endogènes de GA3 au cours de la progression naturelle de la dormance. Deux cultivars de Dioscorea rotundata (« Pona » et « Labreko ») et un cultivar de Dioscorea alata (« CRI-Ahoɔdenfoɔ ») utilisés dans ces études ont une durée de dormance variable. Les teneurs endogènes en AG3 déterminées pour les tubercules de igname variaient de 1,53 à 3,05 mg/g dw et

de 1,23 à 1,58 mg/g dw pour « Pona »; 1,53 – 3,40 mg/g dw et 1,25–1,57 mg/g dw pour « Labreko »; 1,48 – 3,62 mg/g dw et 1,28 – 1,60 mg/g dw pour « CRI-Ahoɔdenfoɔ », respectivement, pour les parties externe et intérieure. 'Pona' et 'Labreko' avaient une pause de dormance à 60 jours après la récolte (DAH), mais à 90 DAH pour 'CRI-Ahoɔdenfoɔ'. En général, les niveaux de GA3 ont augmenté à partir de la récolte jusqu'au maximum à 30 DAH, puis ont diminué au minimum à 60 DAH avant de finalement augmenter à nouveau à 90 DAH pour les parties extérieures du tubercule de igname. Pour les parties internes du tubercule, les niveaux de GA3 ont plutôt diminué de manière significative au minimum à 30 DAH, ont augmenté à 60 DAH, puis ont diminué à nouveau à 90 DAH. Les niveaux de GA3 dans les parties extérieures des tubercules ont augmenté de 84-122%, 65-77% et 61-65%, respectivement, dans 'CRI-Ahoɔdenfoɔ', 'Labreko' et 'Pona', mais ont diminué dans les parties internes de 19-23%, 24-26% et 26-28%. Essentiellement, des quantités plus élevées de gibbérellines endogènes dans les tubercules d'igname ont induit une durée de dormance plus longue, tandis que des quantités plus faibles indiquaient la fin de la dormance et l'initiation ultérieure de la germination.

Mots-clés: Dioscorea spp., dormance, acide gibbérellique endogène, germination, tubercules d'igname

Introduction

Gibberellins (GAs), the plant hormone represented by a multiple of related molecules, regulate major aspects of plant growth and development (Binenbaum, Weinstain, & Shani, 2018; Daviere & Achard, 2013). The major bioactive gibberellins are GA_1, GA_3, GA_4 and Ga_7 (Asrar, 2009; Hedden & Sponsel, 2015). Notwithstanding, gibberellic acid (GA_3) has the most extensive application worldwide in basic research and agriculture, demonstrating its enormous economic value (Jiang & Asami, 2018). GA_3 produces diverse responses in higher plants, including root and shoot elongation, flowering, fruit growth and seed germination (Brückner, 1992; MacMillan, 1997). Over the years, GA_3 has been used to regulate dormancy in yam (Girardin et al., 1998; Hamadina & Craufurd, 2015; Tschannen *et al.,* 2003) and potato (Muchiri *et al.,* 2015; Muthoni *et al.,* 2014; Suttle, 2004). Unlike potato for which much is understood about the control of its dormancy (Aksenova *et al.,* 2013; Bisognin, Manrique-Carpintero, & Douches, 2018; Sonnewald & Sonnewald, 2013), the mechanism underlying yam tuber dormancy and how artificial regulation is achieved is still rudimentary (Hamadina and Craufurd, 2015; Ile *et al.,* 2006).

Exogenous GA application has been found to induce breaking of dormancy to enhance seed germination and sprouting in many plants. On the contrary, GA rather induces dormancy in some plants species (Kim et al., 2005). The effect of exogenously applied GA_3 on yam tuber dormancy and sprouting has been extensively investigated, and reported that generally high concentrations of this plant hormone can considerably extend dormancy period in yam tubers Ile *et al*., 2006 (Hamadina and Craufurd, 2015; Shiwachi *et al,* 2013; ; Girardin et al., 1998). However, similar attention has not been extended to endogenous GA_3 with respect to how it influences dormancy and sprouting in yam tubers although endogenous GAs have been implicated in the tuber dormancy mechanism in water yam (Park *et al.,* 2003) and Chinese yam (Kim et al., 2005). Endogenous GAs are indicated to undergo concentration changes during the storage period to influence the

duration of dormancy. Therefore, the aim of this study was to investigate the comparative levels of endogenous GA_3 in white yam (*Dioscorea rotundata*) and water yam (*Dioscorea alata*) cultivars during natural dormancy progression over storage as well as the effect of the plant hormone on tuber dormancy and sprouting to facilitate generating deeper insights into the mechanisms and variety-specific differences.

Materials and Methods

Plant materials generation and storage

Two *D. rotundata* cultivars ('Pona' and 'Labreko') and one *D. alata* cultivar ('CRI-Ahoɔdenfoɔ') were planted under standard field conditions and managed with recommended agronomic practices at the Fumesua station of CSIR-Crops Research Institute, Kumasi, Ghana. The yam tubers were planted on 24th March, 2017 and harvested on 22nd November, 2017 and stored in a barn for up to 90 days. The average minimum and maximum temperatures for the storage barn over the storage period were 23.5^{o}C and 30.1^{o}C, respectively, while the average minimum and maximum relative humidity values were 54.0% and 88.5%, respectively.

Sample preparation

Sampling of yam tubers to determine GA_3 levels was done at harvest and then regularly every 30 days until the 90th day of storage. Five yam tubers were randomly picked for the respective cultivars at these specific storage points. The tubers were washed under a running tap, air dried at room temperature and cut into three regions - head, middle and tail. The skin (periderm) was peeled off, and about 1cm deep into the flesh around the tuber regions was cut out to represent the outer portion, while the remaining part formed the inner portion of the tuber. A representative sample was obtained by pooling respective regions of the five tubers according to Karp and Lilley (2009). The representative outer and inner portions of the three regions were freeze dried, pulverized and stored at -40 ^{o}C until analysis.

Gibberellic acid quantification

Gibberellic acid content was determined essentially by the method of Holbrook et al. (1961). Briefly, about 60 mg of powdered yam sample was homogenized in 100 mL absolute ethanol in triplicates to constitute three biological replicates. Two 5 mL aliquots of this solution were transferred into separate 100 mL volumetric flasks and further diluted with 5.0 mL absolute ethanol. The content of the first flask was diluted to 100 mL with 30% hydrochloric acid (sample), incubated in a water bath at 20 ± 1^{o}C for 75 minutes and the absorbance measured at 254 nm. To the second flask, 35 mL of 5% hydrochloric acid was added and further diluted to volume with deionized water (blank). The content was briefly mixed and the absorbance immediately measured at 254 nm. The blank reading was subtracted from the sample reading to obtain the gibberellic acid content of the yam sample by referencing to a calibration curve developed from standard GA_3 solutions. All chemicals used were analytical grade reagents. Quantification on a biological replicate was carried out in triplicate samples, i.e. technical replicates (Karp & Lilley, 2009), and the results presented as the mean of biological replicates ± SEM (standard error of the mean) in mg gibberellic acid/gram dry weight.

Statistical analysis

ANOVA in Minitab 18 statistical software package (Minitab, LLC, Quality Plaza, 1829 Pine Hall Road, State College, Pennsylvania 16801, USA) was used to evaluate data generated, and significant differences were reported at 95% confidence level using the Tukey's test.

Results and Discussion

Gibberellic acid levels in outer and inner portions of yam tubers

The general trends for GA_3 distribution in 'Pona', 'Labreko' and 'CRI-Ahoɔdenfoɔ' over the storage period were similar (Figures 1A, 1B and 1C). GA_3 content for 'Pona' tubers throughout the storage period ranged from 1.53 ± 0.00 – 3.05 ± 0.01 mg/g dw and 1.23 ± 0.00 – 1.58 ± 0.02 mg/g dw for the outer and inner portions, respectively. For 'Labreko', GA_3 levels ranged from 1.53 ± 0.02 – 3.40 ± 0.02 mg/g dw for the outer portions and 1.25 ± 0.00 – 1.57 ± 0.02 mg/g dw for the inner portions. 'CRI-Ahoɔdenfoɔ' had GA_3 levels ranging from 1.43 ± 0.02 – 3.62 ± 0.01 mg/g dw and 1.28 ± 0.02 – 1.60 ± 0.00 mg/g dw for the outer and inner portions, respectively.

Varietal differences in GA_3 levels for tuber regions and portions at storage

At harvest

At harvest, GA_3 was uniformly distributed along the entire length of the tuber, irrespective of the yam cultivar, except that the amounts accumulated varied for the outer and inner portions (Figures 1A, 1B and 1C). Significantly higher levels of GA_3 were recorded in the outer portion compared to the inner portion. The outer portions of the head and middle regions of 'Labreko' and 'CRI-Ahoɔdenfoɔ' contained similar levels of gibberellic acid, but 'Pona' had significantly lower content of this plant hormone (Figures 1A and 1B). However, GA_3 levels in the outer portions of the tail region were all significantly different among the yam cultivars (Figure 1C). Apparently, no significant differences in GA_3 content were registered amongst the inner portions of the yam cultivars within the three regions. While differences in the plant hormone content existed between the outer and inner portions in all regions for the three yam cultivars, the levels in the outer portions of each yam cultivar were not significantly different within the same tuber except for the tail of 'CRI-Ahoɔdenfoɔ'.

30 DAH

Significant differences existed among the three yam cultivars for GA_3 content in both outer and inner portions for all tuber regions. The outer portions along the tuber for all the yam cultivars recorded the highest content. 'CRI-Ahoɔdenfoɔ' recorded the highest of the three cultivars, with values ranging between 3.50 ± 0.00 and 3.62 ± 0.00 mg/g dw, corresponding with 84.21 – 122.06% increase from harvest values. 'Labreko' followed with 3.13 ± 0.02 – 3.40 ± 0.03 mg/g dw, while 'Pona' recorded 2.95 ± 0.03 – 3.05 ± 0.00 mg/g dw, representing an increase of 64.74 – 77.08% and 61.20 – 64.86%, respectively. This observation is consistent with the increase in endogenous gibberellin levels reported by Kim et al. (2005) for Chinese yam bulbils during storage, confirming that high level of GA_3 is essential for the dormancy of yam tubers. On the contrary, the corresponding inner portion of the tubers had GA_3 decreased to the lowest levels recorded for all the yam cultivars. 'Pona' was in the range of 1.23 ± 0.00 – 1.25 ± 0.00 mg/g dw, indicating a decrease of 25.60 – 27.64%, while 'Labreko' and 'CRI-Ahoɔdenfoɔ', respectively recorded 1.25 ± 0.00 – 1.25 ± 0.03 mg/g dw and 1.28 ± 0.03 – 1.32 ± 0.03 mg/g dw, signifying 24.00 – 25.60% and 18.94 – 22.66% reduction. This concurrent increase and decline in GA_3 levels in the outer and inner portions of the tubers, respectively, suggest that alongside biosynthesis and accumulation of gibberellic acid in the outer portions, active translocation from the inner portions could have occurred (Binenbaum et al., 2018). The work of Tal et al. (2016) corroborates our results, having observed higher accumulation of gibberellic acid in the epidermal layer compared with the inner layers, indicating that the epidermal layer

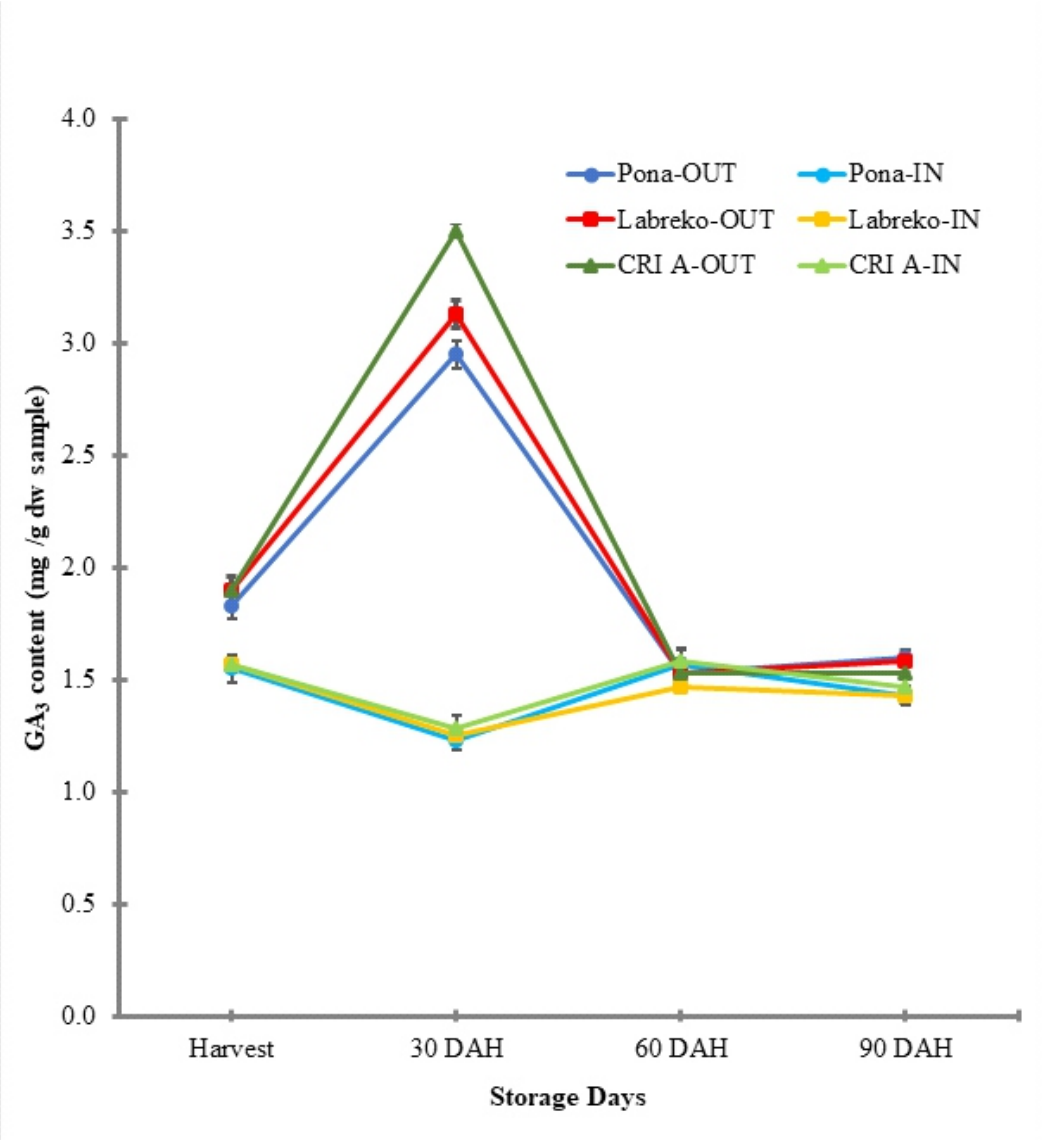

Figure 1A: GA_3 content in outer and inner portions of the head region of 'Pona', 'Labreko' and 'CRI-Ahoɔdenfoɔ' yam cultivars over storage

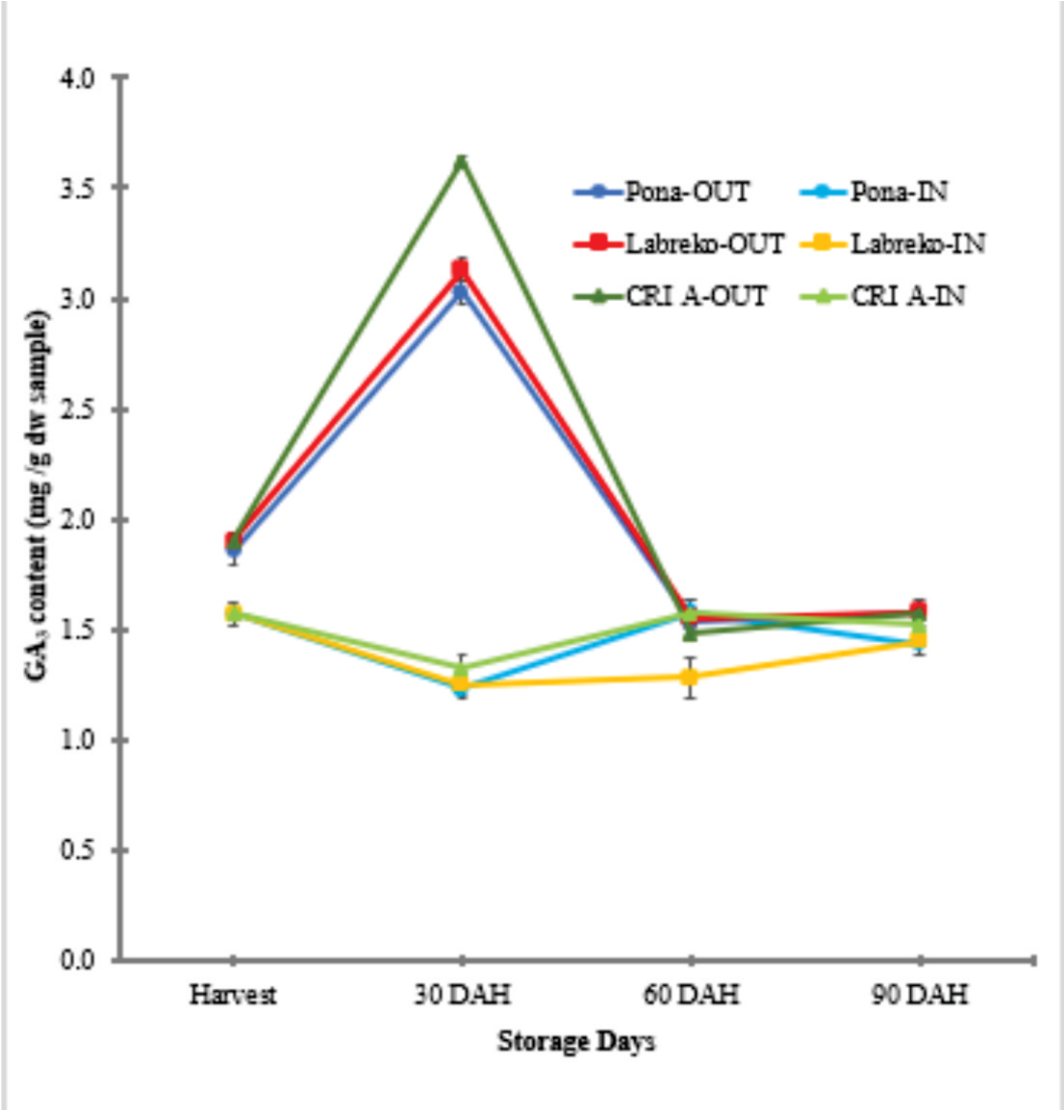

Figure 1B: GA_3 content in outer and inner portions of the middle region of 'Pona', 'Labreko' and 'CRI-Ahoɔdenfoɔ' yam cultivars over storage

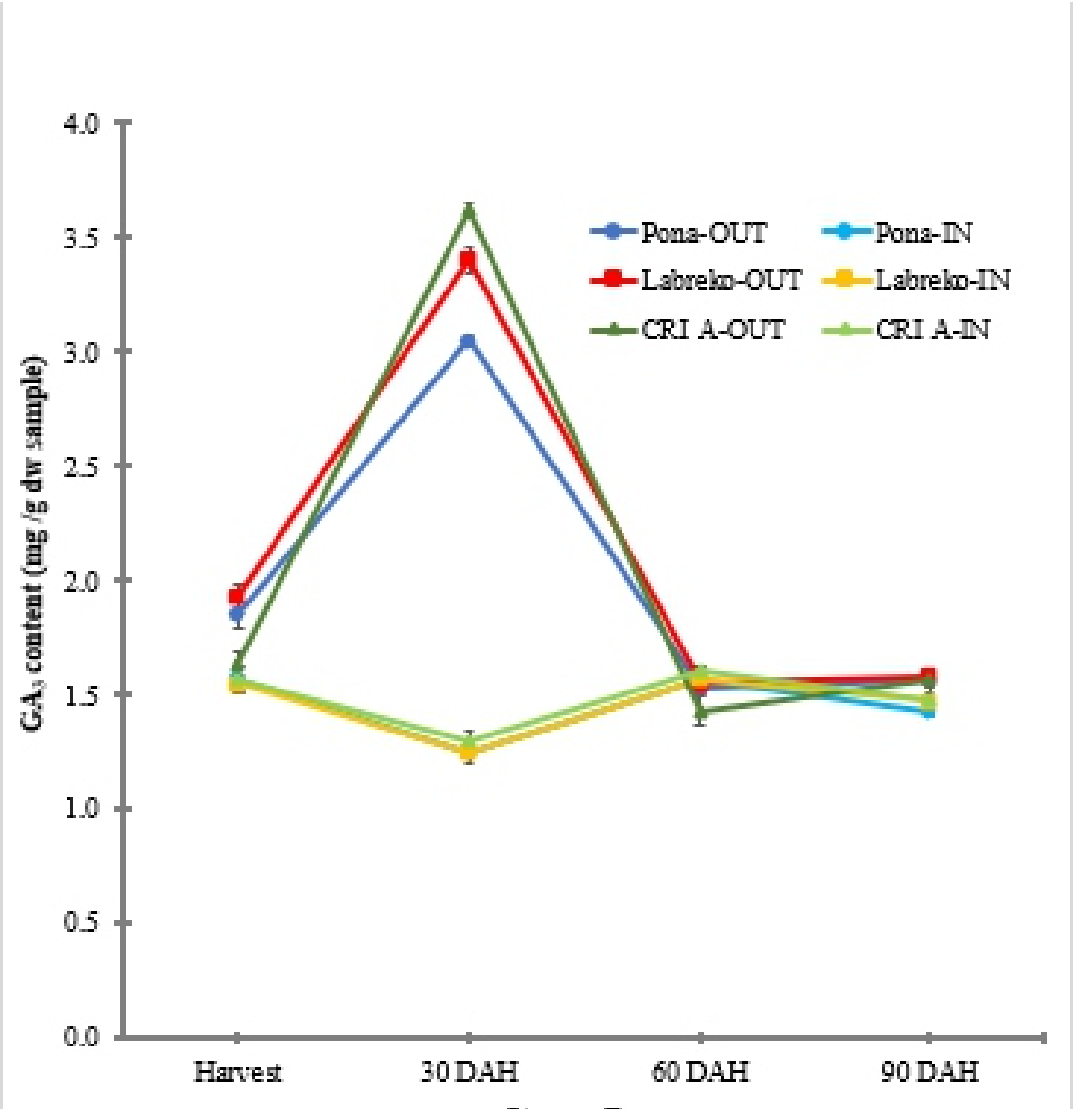

Figure 1C: GA_3 content in outer and inner portions of the tail region of 'Pona', 'Labreko' and 'CRI-Ahoɔdenfoɔ' yam cultivars over storage

imported GA_3 and trapped the molecule in the cells in an NPF3-dependent manner. Apparently, translocation of GA_3 from the inner to outer portions is to induce dormancy since sprouting is initiated by the meristematic tissue of the outer portions of yam tubers. According to Hamadina (2011) and Ile et al. (2006b), initial signs of active cell division and differentiation occur in the meristematic region of yam tubers, leading to the formation of the tuber germinating meristem. The tuber germinating meristem then develops into the shoot apical bud (foliar primordium), which eventually emerges on the surface of the tuber as an external shoot bud or sprout. Although GA_3 does not induce formation of a tuber germinating meristem, the hormone inhibits development of the tuber germinating meristem and shoot apical bud (Shiwachi et al., 2013; Ile et al., 2006). At 30 DAH, the yam tuber is said to be at the advanced stage of phase one of dormancy, marked by the presence of the tuber germinating meristem (Hamadina and Craufurd, 2015). Previous works have shown that the application of high concentrations of exogenous GA_3 during the early stages of harvest is able to largely prolong yam tuber dormancy period (Hamadina & Craufurd, 2015; Ile et al., 2006; Tschannen et al., 2003). Indeed, during early harvest stages, GA_3 applied is able to permeate the tuber epidermis to get to the meristematic tissue. However, the epidermis suberizes with age and forms a barrier which becomes difficult to permeate (Ireland & Passam, 1985). Hence, late application of GA_3 may not yield the required results (Hamadina & Craufurd, 2015). Cells in the outer layer are not suberized at harvest and so this meristematic tissue will permit GA_3 deposit for the high levels to induce dormancy. High endogenous GA_3 levels that accumulated in outer portions of all three yam cultivars at 30 DAH were essential for maintaining dormancy. At this stage, the tuber germinating meristem would have appeared and these quantities of GA_3 would delay its development into foliar primordium at the beginning of phase three of dormancy and eventual emergence as the sprout.

60 DAH

At 60 DAH, GA_3 levels in the outer portion of the yam tubers had decreased to the minimum over the storage duration for all the cultivars. Interestingly, GA_3 quantified was the same in this portion of the head region where sprouting generally originates (Figures 1A, 1B and 1C), and dormancy had broken with an onset of sprouting observed in 'Pona' and 'Labreko', but not in 'CRI-Ahoɔdenfoɔ' (Figure 2 – P60, L60 and W60). This is an apparent indication that lower levels of endogenous gibberellic acid facilitate dormancy release. Kim et al. (2005) observed a similar decrease in endogenous GAs at 60 DAH for Chinese yam. At this stage (Figure 2 – P60 and L-60), the yam tuber has completed phase three of dormancy denoting the complete development of the shoot apical bud/foliar primordium, typified by the eventual emergence of a visible sprout on the surface of the tuber (Ile et al., 2006; Shiwachi *et al.,* 2013).

The decline of GA_3 levels may be as a result of its deactivation and/ or possible translocation into the inner portions since a significant increase was observed in this portion of the yam tubers (Figures 1A, 1B and 1C). The inactivation of GAs provides a means to allow for a rapid reduction of biologically active GA concentration to initiate dormancy termination (Hedden & Thomas, 2012). At the break of dormancy of the *rotundata* cultivars, it was observed that twice the number of 'Pona' had sprouted compared to 'Labreko'. Gibberellic acid content of the outer portions of 'Labreko' at 30 DAH was significantly higher than that of 'Pona' and these differential levels of the hormone may explain why

Figure 2: Representative pictures of tubers of the yam cultivars 'Pona', 'Labreko' and 'CRI-Ahoɔdenfoɔ' yam cultivars during storage at natural dormancy progression**. NB:** 'Pona', 'Labreko' and 'CRI-Ahoɔdenfoɔ' are respectively represented by the letters P, L and W. The numbers 0, 30, 60 and 90 represent Harvest, 30 DAH, 60 DAH and 90 DAH, respectively.

although both are *rotundata* cultivars, more 'Pona' tubers had sprouted. Perhaps more tubers of 'Pona' were able to get to the gibberellic acid threshold levels to effect breaking of dormancy. Kim et al. (2005) asserted that larger amounts of endogenous gibberellins in yam tuber lead to a longer dormancy. The propensity to increase the amount of the hormone in the epidermal layers of yam tubers partly explains the varietal differences for dormancy duration and sprouting.

90 DAH

GA_3 levels in the outer portions of the head region of 'Pona' and 'Labreko' increased significantly at 90 DAH, but did not differ from each other. At this stage, substantial growth had taken place in the emerged shoot (Figure 2 – P90 and L90). One of the well-known functions of GA is to promote vegetative growth, including the elongation of shoots (Dilip et al., 2017; Gupta and Chakrabarty, 2013; Tanimoto, 2012; Fleet and Sun, 2005). Thus, active transport of gibberellin from the point of synthesis to shoot elongation zone is required to ensure continual shoot growth (Tanimoto, 2012). This accounts for the increase in GA_3 levels since local production and translocation of the phytohormone are essential to regulate shoot growth. GA_3 level was unchanged in the outer portion of the head region of 'CRI-Ahoɔdenfoɔ' between 60 DAH and 90 DAH. A similar observation has also been made in Chinese yam bulbils after an initial increase at 30 DAH by Kim et al. (2005). Breaking of dormancy was detected at 90 DAH for 'CRI-Ahoɔdenfoɔ' to pave way for sprouting (Figure 2 – W90). This observation suggests that although endogenous GA_3 plays a vital role in the regulation of dormancy and sprouting, other endogenous factors of varietal specificity cannot be ruled out.

Conclusions

Concentration of endogenous gibberellic acid continually changes in both the outer and inner layers along yam tubers throughout storage following harvest, and this is essential for the induction and maintenance of dormancy as well as sprouting. Endogenous GA_3 levels are significantly higher in the outer portions of the tuber relative to the inner portions as dormancy naturally progresses. Essentially, higher amounts of endogenous GA_3 in yam tubers induce longer dormancy duration, while lower amounts are required for dormancy termination and subsequent initiation of sprouting. Once dormancy is terminated and the sprouts emerge, enhanced levels of GA_3 are required for cell elongation and general growth. While GA_3 is important for regulating dormancy and sprouting, other endogenous factors of varietal specificity may also likely play vital roles in determining the natural dormancy duration in yams.

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Conflict of Interest: There is no conflict or potential conflict of interests

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