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Differential Influx of Natural Plant Growth Regulators during Embryogeny in the Recalcitrant Seeds of *Syzygium cumini* (L) Skeels

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ABSTRACT

Background: The hormonal up-regulation and down-regulation in recalcitrant seeds, on the other hand, has received little research. We tested fou plant growth regulators from distinct families of phytohormones at the same time to better understand their differential input from maternal tissues to growing *Syzygium cumini* seeds.

Methods: During April-June 2020, seeds were collected in their native habitats in the Western Ghats. Seeds were chosen at random from each treatment. The embryonic tissues of seeds were chopped up and frozen for LC-MS/MS hormonal profiling.

Result: Except for ABA, the dynamics of key plant hormones in this recalcitrant seed were identical to that of desiccation-tolerant orthodox seeds. When compared to other conventional seeds, SA was shown to accumulate at an unusually high level in mature embryonic tissues, demonstrating the highly hydrated seed's defense mechanism against fungal attack following seed shedding.

Key words: Days after anthesis, Embryogeny, LC-MS/MS, Plant growth regulators, *Syzygium cumini*.

INTRODUCTION

Syzygium cumini (L.) Skeels, often known as Jamun, Malabar plum, or Indian blackberry, is an evergreen indigenous arborescent tree belonging to the Myrtaceae family (Soh and Parnell, 2015). It's native to Nepal, Sri Lanka, Pakistan and Indonesia (IUCN, 2019) and its edible fruits are commercially used (Soh, 2017). It also has pharmacological characteristics (Swami and Kalse, 2020). The species has been designated as endangered because of issues with natural regeneration and the seeds have been described as recalcitrant, with embryos losing viability extremely soon, according to Nair *et al*. (2020).

Plant growth regulators (PGRs) are important throughout several stages of embryogenesis, including histodifferentiation, reserve storage and embryo drying. These PGRs have been reported to be up-regulated or down-regulated at various phases of embryogenesis in orthodox seeds (Farrant *et al*., 1993). Despite the absence of embryo drying, such information is not available in the desiccation-intolerant recalcitrant seeds. The very recalcitrant seed of *S. cumini* was chosen for this study to better understand the dynamics of PGRs throughout embryogenesis. It also looked at the GA/ABA antagonistic relationship in this recalcitrant seed.

MATERIALS AND METHODS

Collections

Jamun seeds were collected from natural stands in the Western Ghats, at an elevation of 150 meters above sea level in the southern Western Ghats (Latitude-8°45' and 8°47'N; Longitude -77°1' and 77°4' E). During April-June 2020, Greller *et al*. (1999). The coldest and highest temperatures were 100.4°F and 55.4°F, respectively; the relative humidity varied from 48 to 97 per cent and the maximum rainfall was 2492.04 mm (India Meteorological Department, 2020).

The flowers were tagged at anthesis in April and the fruits at maturity stages; early embryogeny (40 days after anthesis), mid-embryogeny (70 days after anthesis) and late embryogeny (95 days after anthesis) seeds were collected and the malformed/infected seeds were discarded. The seeds were surface sterilized with 1% sodium hypochlorite for 10 minutes Nakagawara *et al*. (1998). A hundred seeds from each treatment were chosen at random and the seed coat was removed. For hormonal profiling, the embryonic tissues of a hundred seeds were chopped up and frozen. The extraction of various plant growth regulators was done according to the procedure of Pan *et al*. (2008).

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Statistical analysis

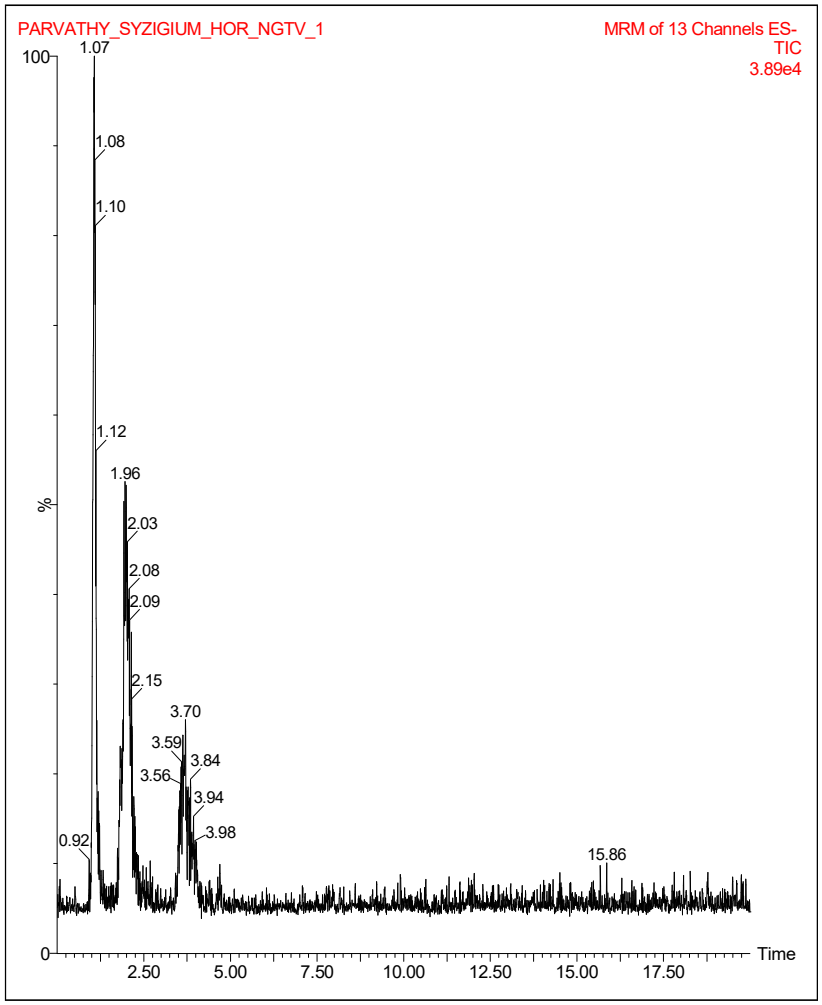
Data presented correspond to means ± standard error. Analysis of variance, DMRT were carried out with SPSS, version 11.5 software. All treatments consisted of three replicates.

Results and Discussion

PGRs belonging to different classes of phytohormones were assayed simultaneously in the embryonic tissues of *S. cumini* and the results are summarized in Table (1). Significant variation ($p<0.01$) was observed in the levels of hormones during embryogeny and certain hormones were found to be up-regulated or down-regulated at different stages of embryogeny in this recalcitrant seed.

Auxins

The two natural forms of auxins; IAA and IBA were assayed in the embryonic tissues during the embryogeny and IAA was found to be the predominant form of auxins in this recalcitrant seed. The young embryonic tissue (Chromatogram 1) had an elevated IAA content (51.53 ng g^{-1}fw) probably supplied by the maternal tissues and it got accumulated (67.82 ng g^{-1}fw) in the embryonic tissues of mid-embryogeny (Chromatogram 3) and then declined to 40.71 ng g^{-1}fw in the late embryogeny (Chromatogram 5). IBA also showed a characteristic curve like IAA but with lower levels. This indicates the significance of these auxins during embryo differentiation in this recalcitrant seed. The significance of elevated levels of IAA and IBA in the histodifferentiation process has already been reported (Valpuesta *et al*., 1989) and is also essential for the development of bipolar symmetry of the embryo (Wijers and Jurgens, 2005). The subsequent decline of IAA and IBA in the late embryogeny stage indicates that these auxins do not appear to be involved in reserve accumulation in the cotyledonary tissues. The dynamics of both IAA and IBA during embryogeny were strikingly similar to that reported for other desiccation-sensitive recalcitrant species (Farrant *et al*., 1993) and desiccation-tolerant orthodox seeds (Pharis and King, 1985; Reinecke and Bandurski, 1987).



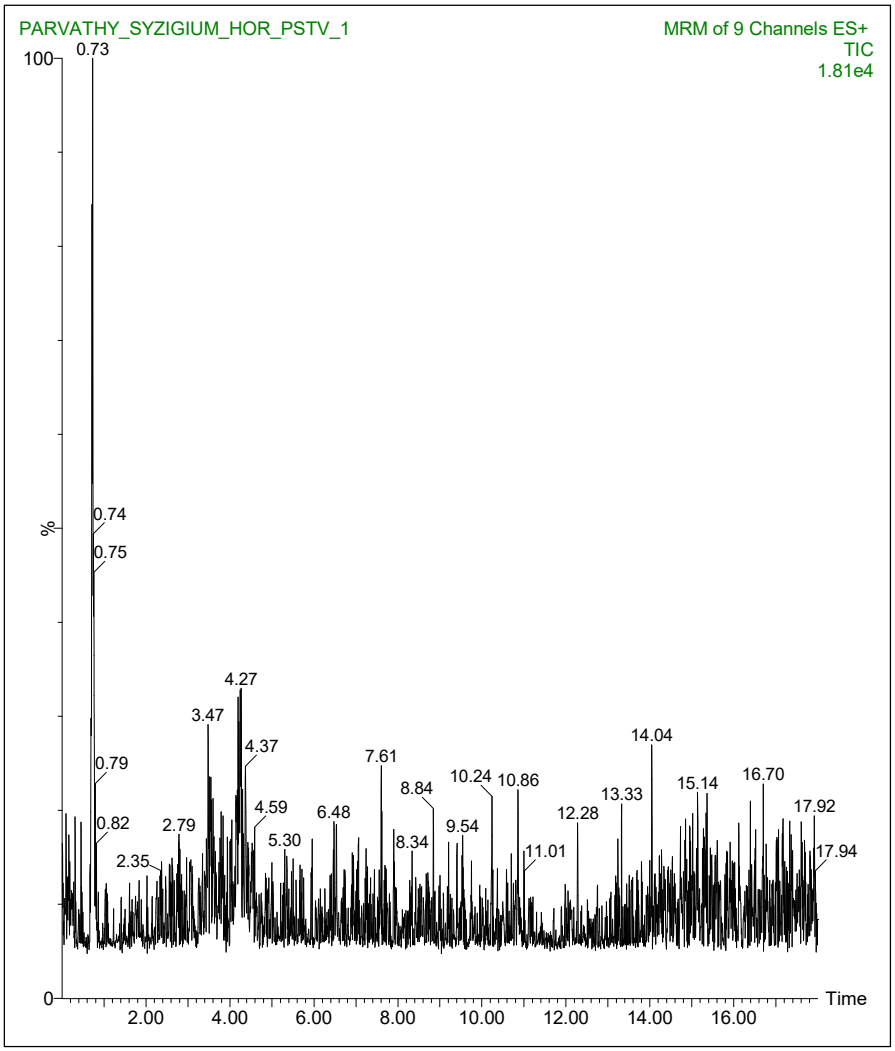
Chromatogram 1: Simultaneous analysis of hormones in the embryonic tissues of *S. cumini* during early embryogeny.
In negative mode (ES-) - Salicylic acid, IAA, IBA, JA, benzene adenine, ABA, GA-7, GA-4, GA-3, epibrassinolide.

Gibberellins

Three principal forms of gibberellins; GA_3, GA_4 and GA_7 were assayed during the embryogeny and it was found that GA_4 was the only predominant form during all stages of embryo development whereas GA_3 and GA_7 were found in insignificant levels. However, GA_3 is reported to be the predominant form of gibberellins in many orthodox and recalcitrant species (Farrant *et al*., 1993; Romero-Rodriguez *et al*., 2018). The young embryo had a lower level of GA_4 (29.7 ng g^{-1}fw) during early embryogeny (Chromatogram 1) but a sharp rise could be observed in the embryogenic tissue (172.86 ng g^{-1}fw) during mid-embryogeny (Chromatogram 3) and then a sharp decline in the late embryogeny (65.22 ng g^{-1}fw) (Chromatogram 5). The faster influx of GA_4 from the maternal tissues to the developing embryos indicates the significance of the histodifferentiation process. The dynamics of GA_4 were very similar to that of IAA and were found to be a common character shared by both orthodox and recalcitrant seeds (Farrant *et al*., 1993). The embryonic tissue of mature recalcitrant seed maintained a relatively high level of GA_4 compared to orthodox seeds which are considered as an adaptation in recalcitrant embryos to antagonize ABA and to carry out quicker germination without any dormancy as seen in orthodox seeds (Romero-Rodriguez *et al*., 2018; Vishal and Kumar, 2018; Zhang, 2007; Farrant *et al*., 1993, Musatenko *et al*., 1995).

Abscisic acid

ABA is reported to be an important plant growth regulator in preventing premature germination and desiccation tolerance acquisition in desiccation-tolerant orthodox seeds (Ali-Rachedi *et al*., 2004). The young embryonic tissue (Chromatogram 1)of this recalcitrant seed had a lower ABA content (23.04 ng g^{-1}fw) that got accumulated significantly in the embryonic tissues (88.95 ng g^{-1}fw) during mid-embryogeny (Chromatogram 3) and then declined to 51.77 ngg^{-1}fw in the mature embryonic tissues (Chromatogram 5) during late embryogeny. The initial rapid accumulation of

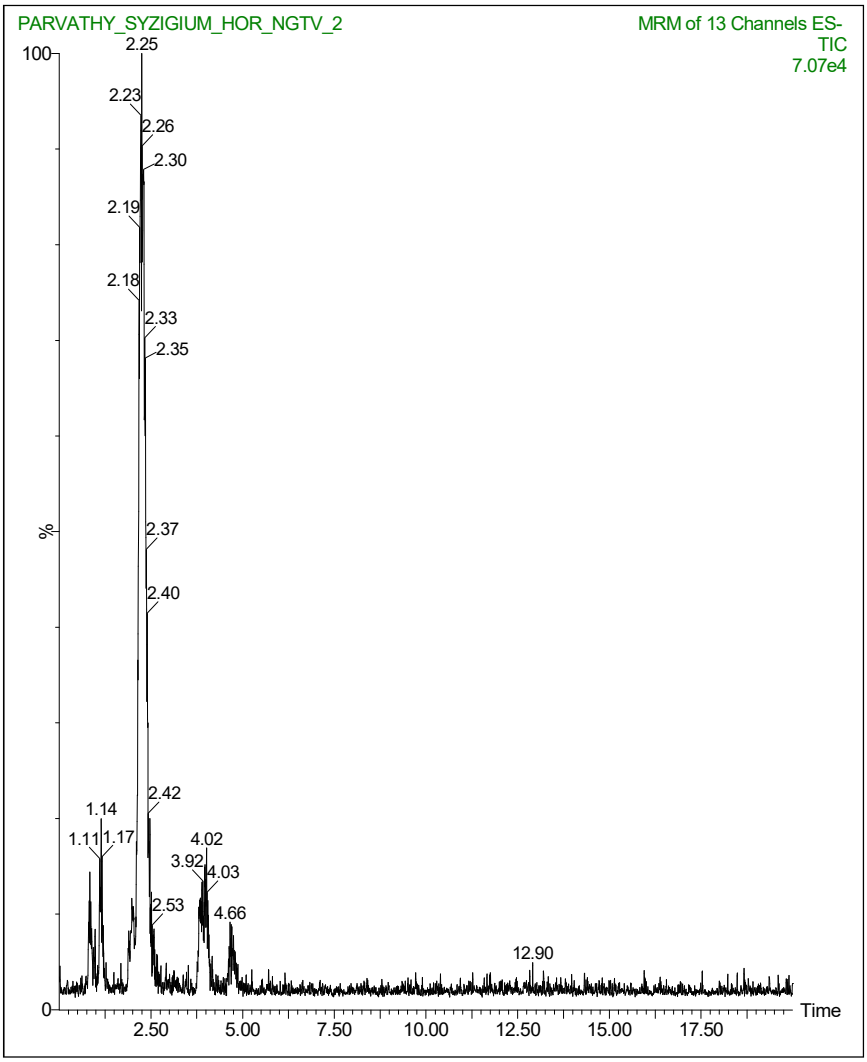


Chromatogram 2: Simultaneous analysis of hormones in the embryonic tissues of *S. cumini* during early embryogeny.
In positive mode (ES+) - ACC, Cis-jasmonate, zeatin, methyl jasmonate and trans zeatin riboside.

ABA in the mid embryogeny stage is linked with the mechanism shown by recalcitrant seeds to prevent precocious germination. However, in orthodox seeds, ABA accumulation is observed in association with the onset of embryo drying phase only and is found in insignificant levels in other stages (Farrant *et al*., 1993). The decline in ABA content to 51.77 ng g^{-1}fw and the elevated level of GA_4 in the embryonic tissues of mature seeds facilitate quicker germination in this recalcitrant seed (Farrant *et al*., 1993; Romero-Rodriguez *et al*., 2018, Gayatri *et al*., 2021).

Cytokinins

The different forms of cytokinins; BA, tZ and tZR were assayed in the embryonic tissues during embryogeny and found that BA was the predominant form found in elevated levels in all stages of embryo development. The large influx of this PGR from the maternal tissues to the young embryo (193.23ng g^{-1}fw) was observed during the histodifferentiation stage as it is required for rapid cell divisions, embryo and endosperm formation and endosperm utilization (van Staden *et al*., 1982; Lorenzi *et al*., 1988). This level of BA was maintained till the mid-embryonic stage (Chromatogram 3) (206.01 ng g^{-1}fw) and it was followed by a decline (128 ng g^{-1}fw) after the reserve food accumulation stage (Chromatogram 5). The same trend has been reported for other desiccation-sensitive species (Farrant *et al*., 1993). Keeping a relatively high level of BA in the mature embryonic tissue at the seed shedding stage is a requirement in this recalcitrant seed to carry out faster germination without any delay (Romero-Rodriguez *et al*., 2018) and also to antagonize the ABA during germination (Wang *et al*., 2011). tZ, the next dominant cytokinins, showed lower levels in the histodifferentiation stage (Chromatogram 2) (6.9 ng g^{-1} fw) and mid-embryogeny (Chromatogram 4) (7.32 ng g^{-1} fw) but elevated (30.75 ng g^{-1} fw) after the completion of the reserve accumulation stage (Chromatogram 6). However, tZR, a

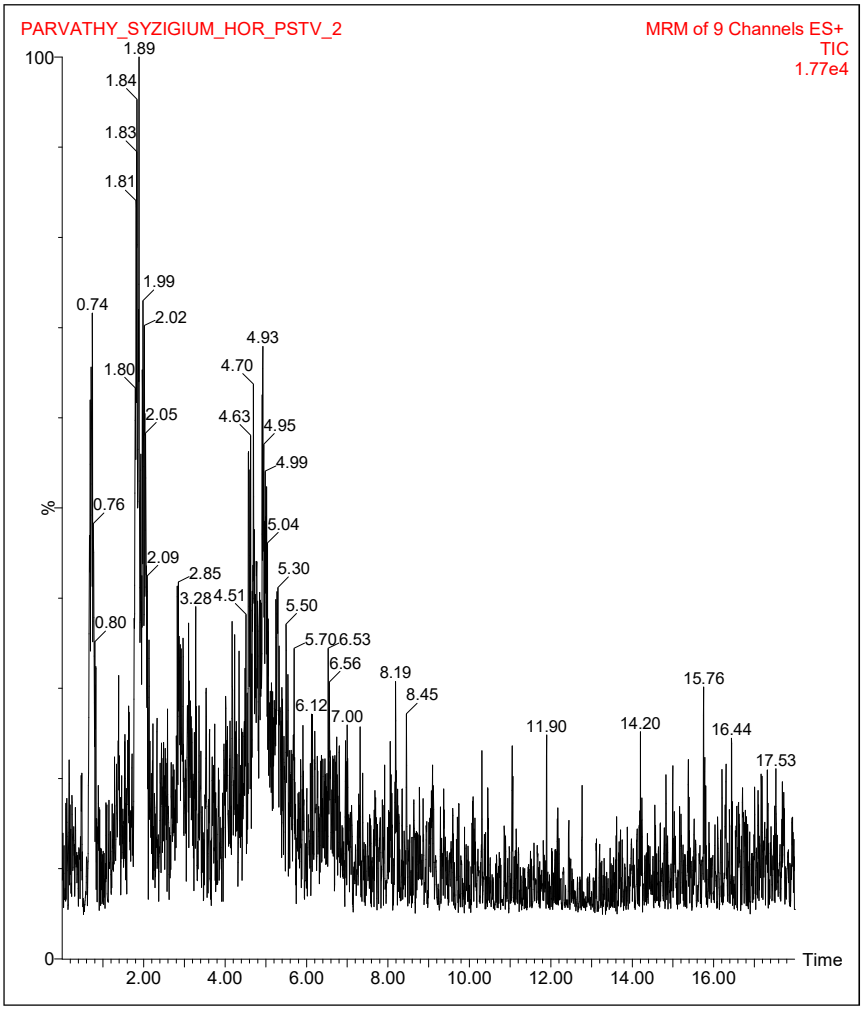


Chromatogram 3: Simultaneous analysis of hormones in the embryonic tissues of *S. cumini* during mid-embryogeny.
In negative mode (ES-): Salicylic acid, IAA, IBA, JA, benzene adenine, ABA, GA-7, GA-4, GA-3, epibrassinolide.

Table 1: Changes in plant growth regulators during different stages of embryogeny in *S. cumini.*

Plant growth regulators (ng g^{-1}fwt)	Stages of embryogeny			Grand mean	Standard deviation
	Early (40 DAA)	Mid (70 DAA)	Late (95 DAA)		
3-Indole acetic acid (IAA)	51.53±3.81[a]	67.82±0.82[b]	40.71±0.5[c]	53.35	12.45
3-Indole butyric acid (IBA)	8.88±0.55[a]	17.28±0.34[b]	5.04±0.7[a]	10.41	5.63
Gibberellic acid 7 (GA7)		0.02±0.04[a]	0.04±0.002[a]	0.031	0.01
Gibberellic acid 4 (GA4)	29.7±2.92[a]	172.86±3.97[b]	65.22±5.45[c]	89.26	66.83
Gibberellic acid 3 (GA3)	0.27±0.011[a]	2.74±0.18[a]	0.28±0.01[a]	1.1	1.27
Zeatin trans isomer	6.9±0.41[a]	7.32±0.56[a]	30.75±0.17[b]	14.99	12.21
Trans zeatin riboside	8.84±0.17[a]	17.88±3.15[b]	5.09±0.16[c]	10.6	6.21
Benzyl aminopurine	193.23±8.48[a]	206.01±6.54[b]	128.46±2.9[c]	175.9	37.85
Abscisic acid (ABA)	23.04±0.016[a]	88.95±1.06[b]	51.77±0.52[c]	54.59	29.56
Salicylic acid (SA)	11865.57±106.98[a]	5637.94±92.42[b]	18997.85±143.12[c]	12167.12	5980.6
Jasmonic acid (JA)	0.06±0.005[a]	0.1±0.006[a]	0.12±0.006[a]	0.096	0.02
Methyl jasmonate	1.24±0.03[a]	3.55±0.18[a]	4.12±0.17[a]	2.97	1.37
Cis-jasmone	26.31±7.45[a]	46.45±0.54[b]	148.48±2.02[c]	73.75	58.79
Epibrasinolide (24 epiBL)	19±1.72[a]	20.02±0.95[a]	13.65±0.91[c]	17.55	3.35
ACC	0.48±0.06[a]	0.56±0.38[c]	1.12±0.9[b]	0.72	0.31

Values are averages of four replications with standard error; Dynamics of PGRs in seeds of Syzygium cumini during embryogeny. Mean followed by the same letter in the column are not statistically different from each other by Duncan test (ANOVA).



Chromatogram 4: Simultaneous analysis of hormones in the embryonic tissues of *S. cumini* during mid-embryogeny.
In positive mode (ES+) - ACC, Cis-jasmonate, zeatin, methyl jasmonate and trans zeatin riboside.

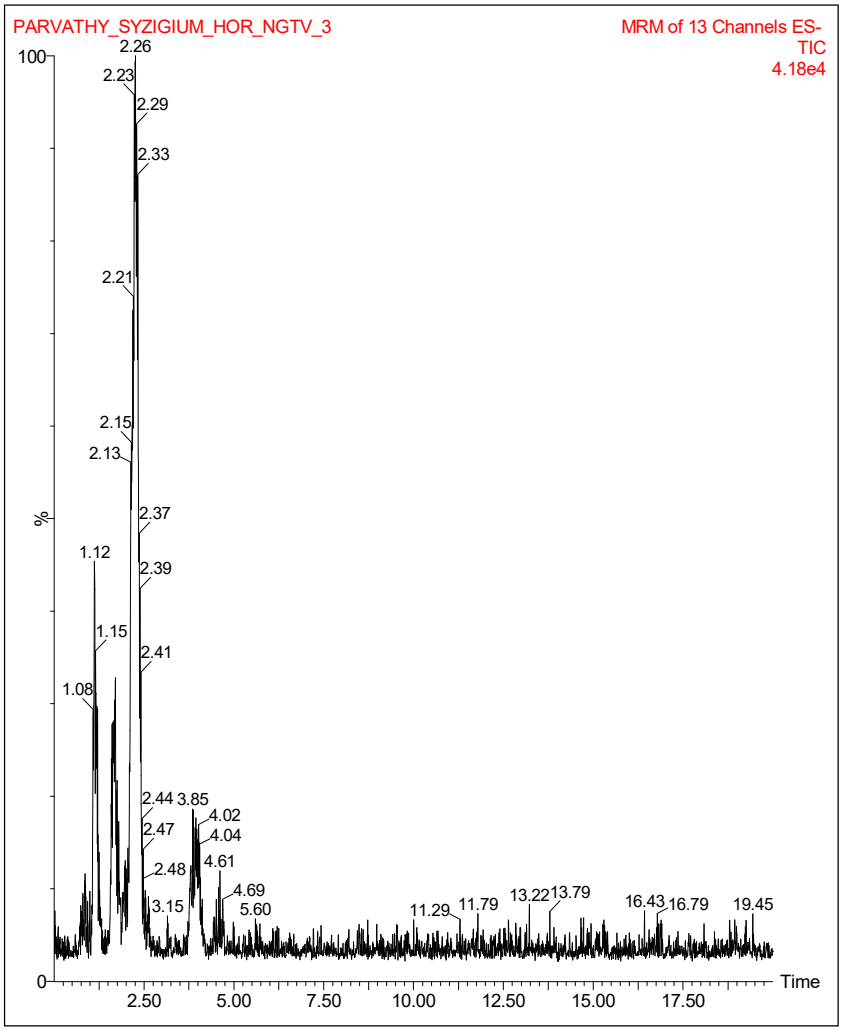
predominant form of cytokinins in other orthodox and recalcitrant seeds, was found in lower quantities during embryogeny in this seed but showed similar dynamics as that of BA.

Salicylic acid

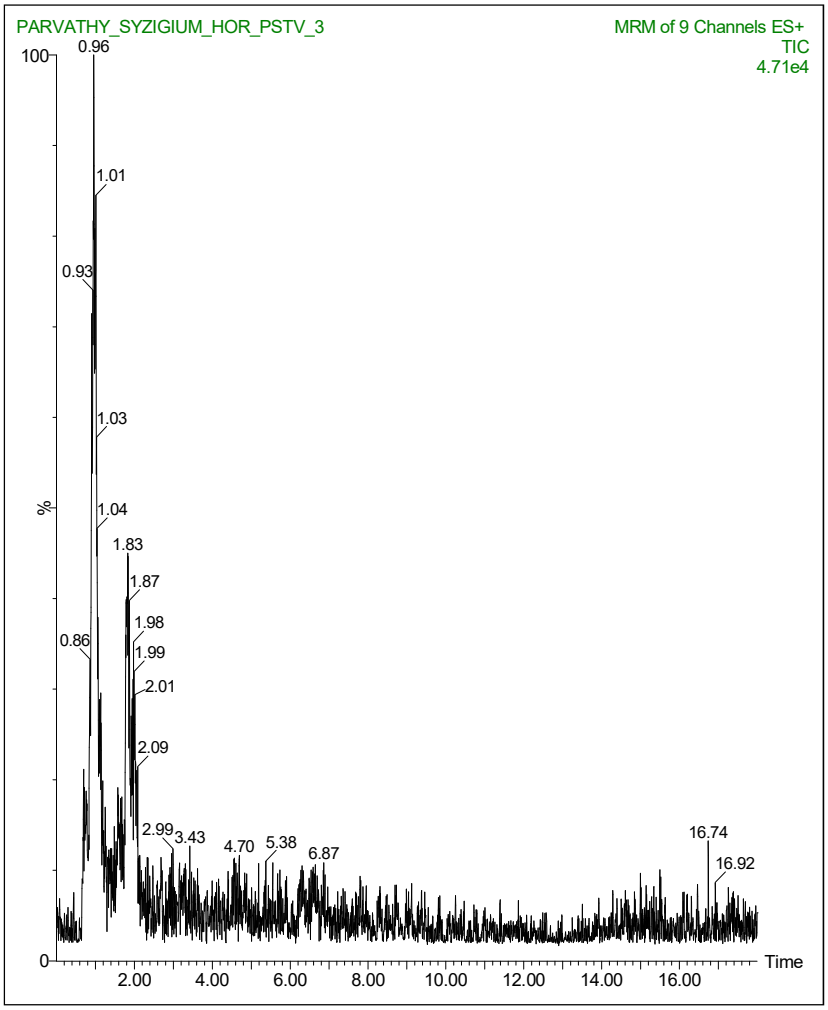
SA is a phenolic PGR known to influence seed development and seed germination processes (Mariana Rivas-San Vicente and Javier Plasencia, 2011). However, reports are contradictory suggesting that it can either inhibit or enhance seed germination (Rajjou *et al*., 2006; Xie *et al*., 2007; Ana Alonso-Ramirez *et al*., 2009). In the present study, this PGR was found in exceptionally greater quantities, ranging from 5.63 µg g^{-1}fw to 19 µg g^{-1}fw, in the embryonic tissues during embryogeny. This level of SA in seeds is higher compared to that reported in other species. In the model species, *Arabidopsis thaliana*, the basal level of SA in the leaves ranged from 0.25 µg g^{-1}fw to 1 µg g^{-1}fw (Peter *et al*. 2005). The initial huge influx of SA from the maternal tissues (11.86 µg g^{-1}fw) indicates that it might be essential for the histodifferentiation process. There was a decline in SA towards mid-embryogeny (Chromatogram 3) (5.63 µg g^{-1}fw) and then a sharp rise in late embryogeny (Chromatogram 5) (19 µg g^{-1}fw). The elevated level of this hormone is normally associated with stressful conditions (Alonso-Ramirez *et al*. 2009) but the precise role of this hormone during embryogeny is unknown. However, there are reports of cross-talk between SA with GAs and ABA during germination (Rajjou *et al*., 2006; Ana Alonso-Ramirez *et al*., 2009). Further work is needed to solve this problem.

Jasmonates

Jasmonates are a class of PGRs influencing many developmental processes such as seed germination, root growth, embryo development, fruit ripening and gravitropism (Browse and Howe, 2008; Reinbothe *et al*., 2009; Gfeller *et al*., 2010). Three forms of jasmonates; JA, meJ and CisJ were assayed in the embryonic tissues during embryogeny



Chromatogram 5: Simultaneous analysis of hormones in the embryonic tissues of *S. cumini* during late embryogeny.
In negative mode (ES-) - Salicylic acid, IAA, IBA, JA, benzene adenine, ABA, GA-7, GA-4, GA-3, epibrassinolide.



Chromatogram 6: Simultaneous analysis of hormones in the embryonic tissues of *S. cumini* during late embryogeny.
In positive mode (ES+) - ACC, Cis-jasmonate, zeatin, methyl jasmonate and trans zeatin riboside.

and found that the predominant form of jasmonates was cisJ which was found to accumulate (26.31 ng g^{-1}fw to 46.45 ng g^{-1}fw) during the histodifferentiation process (Chromatogram 2). However, a sharp rise was observed in the reserve food accumulation phase (Chromatogram 4) indicating a crucial role of this PGR in the developmental process that needs to be resolved. meJ and JA were found in insignificant levels in the embryonic tissues during embryogeny.

Brassinosteroids

Brassinosteroids are steroid PGRs involved in shoot growth, root growth, vascular differentiation and seed germination (Clouse and Sasse, 1998; Fukunda, 2004; Mussig, 2005). The predominant form of brassinosteroids, 24epi-BL was found in significant amounts in the embryonic tissues of all stages of embryogeny. It peaked during histodifferentiation (Chromatogram 1) and then declined in the reserve food accumulation stage (13.65 ng g^{-1}fw). The results indicate that this steroid PGR is equally essential for the development of the seed but its exact role is uncertain.

Conclusion

The desiccation-intolerant recalcitrant seeds of Syzygium cumini showed dynamics in PGRs during embryogeny. IAA, GA_4 and BA were found to be the predominant forms in their respective classes. These PGRs were found in elevated levels in the histodifferentiation process and declined in the subsequent reserve food accumulation phase of this recalcitrant embryo development. IAA (40.71 ng g^{-1}fw), GA_4 (65.22 ng g^{-1}fw), BA (128.46 ng g^{-1}fw), ABA (51.77 ng g^{-1}fw), SA (19 µg g^{-1}fw) and cisJ (148.48 ng g^{-1}fw) were found in higher levels in the mature embryonic tissues to facilitate quicker germination in this recalcitrant seed. Seeds exhibited GA_4/ABA antagonism with elevated GA_4 levels and lower ABA levels. The stress-induced SA was found in exceptionally high quantities in the embryonic tissues not reported elsewhere in other orthodox and recalcitrant seeds.

cisJ was the predominant jasmonate, found to increase in the embryonic tissues during all stages of development. The brassinosteroid, epiBL was also found in significant levels in this recalcitrant seed.

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Conflict of interest

All authors delare that they no conflict of interest.

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