

Phenology-specific molecular characterization of polyamine genes in *Parthenium hysterophorus* for strategic herbicide interventions

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Abstract

Parthenium hysterophorus is a highly invasive weed that poses a serious threat to biodiversity due to its adaptability. This case study examines its vegetative and reproductive phases, focusing on phenological growth stages using the universal BBCH coding system, and the role of polyamines (PAs) in these stages. Our research identified significant polymorphisms in key enzymes involved in PAs biosynthesis, including spermidine synthase (SPDS), spermine synthase (SPMS), arginine decarboxylase (ADC), and caffeic acid O-methyltransferase (COMT), during specific growth stages. SPDS polymorphisms were more pronounced during stem elongation and flowering, while SPMS showed heightened variability primarily during flowering. Conversely, ADC and COMT exhibited increased polymorphisms during leaf development and flowering stages. These findings underscore the dynamic regulation of PA metabolism across different growth stages in *P. hysterophorus*. Drawing from these findings, we can develop targeted weed management strategies that correspond to the polymorphism patterns of vital PA biosynthetic genes. Specifically, we propose the use of broad-spectrum non-selective herbicides such as Paraquat before stem elongation, transitioning to post-stem elongation application of selective herbicides like Bromoxynil, and utilizing foliar-active translocated herbicides like glyphosate during leaf formation. These innovative strategies aim to optimize effectiveness while reducing herbicide usage by tailoring interventions to the plant's metabolic state.

Introduction

In global agriculture, effective weed management is pivotal. Among the several factors contributing to reduced crop yield, weed infestation stands out as a major hindrance. Weeds compete with crops for vital resources like moisture, nutrients, space, and sunlight, ultimately leading to decreased crop productivity (Berhan and Bekele 2021). Maintaining a weed-free environment during the critical phases of crop development automatically enhances crop yield. (Manibharathi and Vinodhini 2023; Dixit 2015). A study across 18 states in India has reported significant yield and economic losses caused by weeds, especially in soybean and groundnut crops (Gharde et al. 2018). *P. hysterophorus*, as an invasive species, poses severe ecological and agricultural threats, reducing the yield of different cereals, oilseeds, pulses, and vegetables (Table. 1). Often thriving along roadsides and in disturbed areas, it stands out as the most troublesome and noxious weed in both urban and rural landscapes (Tiawoun et al. 2024). Its rapid colonization tendencies frequently result in the displacement of native vegetation. For example, C3 and C4 plants differ in their photosynthetic pathways, with C3 plants producing a three-carbon compound as the first stable product, making them more suited to cooler, wetter climates, but less efficient in hot, dry environments due to higher photorespiration. C4 plants, on the other hand, produce a four-carbon compound, which enhances their efficiency in hot, arid conditions by minimizing photorespiration. *P. hysterophorus* demonstrates exceptional adaptability by transitioning between C4 and C3 metabolism, allowing it to thrive across a wide range of temperatures and environments (Sreekanth et al. 2023). Capable of thriving in soils with pH levels ranging from 2.5 to 10 and various soil types, it particularly favours alkaline, clay, and loam soils (Vijayakumar et al. 2023; Saravanane et al. 2023; Tang et al. 2009).

The detrimental impact of *P. hysterophorus* extends to agricultural and natural ecosystems, biodiversity, as well as human and animal health. Studies have shown significant decreases in chlorophyll and carotenoid contents of *P. hysterophorus* along FSR and M-2 roads (Khalid et al. 2017). Moreover, its photosynthetic rate declined notably along these roads, indicating the plant's adaptation to various environmental stressors. Reproducing solely through seeds, *P. hysterophorus* poses substantial challenges to primary production and health, especially in regions with over 500 mm of summer rainfall annually. Extracts from *P. hysterophorus* have been found to completely inhibit soybean and haricot bean germination, further exacerbating its impact on crop yields (Netsere and Mendesil 2012). The research underscores the alarming reduction in crop yields due to *P. hysterophorus* infestation. *P. hysterophorus*-infested sites have led to significant reductions in tomato fruit weight and growth parameters in fodder sorghum fields (Nishanthan et al. 2013; Asif et al. 2017). Beyond its agricultural impact, *P. hysterophorus* poses health hazards through allergic reactions and the spread of mature seeds, increasing the infestation area (Bashar et al. 2023). Its prolific seed production, which ranges from 5,000 to 25,000 seeds per plant (Anonymous 2003), is facilitated by unique dispersal mechanisms, further compounding the challenge of its management. In *P. hysterophorus* affected by various environmental conditions, phenological growth stages are associated with different

polyamines. Polyamines (PAs), small organic molecules, play pivotal roles in various physiological processes, including growth and stress responses in plants.

A comprehensive review of the literature underscores the multifaceted impact of PAs on biological phenomena across diverse plant genera (Jiménez-Bremont et al. 2014; Minocha et al. 2014; Majumdar et al. 2017; Masson et al. 2017). Key polyamines, including putrescine (PUT), spermidine (SPD), spermine (SPE), and the enzyme arginine decarboxylase (ADC), along with caffeic acid O-methyltransferase (COMT), have a significant impact on plant growth and stress responses. Their influence is evident through their interactions with proteins, nucleic acids, and membranes. A seminal study on rice has revealed a correlation between specific genetic variants of the *SPDS* gene and flowering time, as well as grain yield (Liu et al. 2014). Complementing genetic insights, the levels of PAs within plant tissues exhibit dynamic associations with growth stages and stress responses. Notably, during periods of rapid growth like seed germination and flower development, elevated PA levels signify their pivotal role in facilitating cell division and stem elongation (Alcázar et al. 2010).

Furthermore, PAs emerge as crucial components in plant stress responses, with environmental challenges such as drought, salinity, and temperature fluctuations inducing an increase in PA levels. This surge in PAs is proposed to fortify plants against stress by stabilizing cellular structures, safeguarding membranes, and orchestrating gene expression (Gill and Tuteja 2010). The preliminary work in this case study was conducted on *P. hysterophorus* using the BBCH coding system, with modifications tailored to the growth nature of *P. hysterophorus*. Both vegetative and reproductive growth stages were targeted, and herbicide recommendations were made for optimal timing, considering their role in herbicide selection. In this context, the present study has correlated the polymorphism of PA metabolism genes, including *SPDS*, *ADC*, *SPMS*, and *COMT*, with observed phenological growth stages of *P. hysterophorus*. Through a phenological growth stage-wise PA intervention-based management strategy, valuable insights can be gained for the application and recommendation of herbicides.

Polyamines (PAs) in plant physiology and stress response

PAs, arising from cellular metabolism, are small aliphatic nitrogenous bases. Despite not being classified as hormones, they play vital roles in numerous physiological processes in plants. PAs influence embryogenesis, organogenesis, reproductive development, leaf senescence, and fruit maturity, intricately modulating growth, development, and the plant's response to various abiotic stressors. PAs such as PUT, SPD, and SPE play essential roles in conferring abiotic stress tolerance, particularly against salinity, in plants. These organic compounds feature multiple amino groups ($-NH_2$), crucial for cell growth, proliferation, and differentiation. (Chen et al. 2019; Bano et al. 2020). PAs also enhance medicinal plant productivity and the production of natural products. *SPMS* and *SPDS* promote seed germination, while *SPMS* aids stress tolerance, and *SPDS* supports cell growth (Childs et al. 2017; Mustafavi et al. 2018). Their functions encompass maintaining membrane integrity, regulating gene expression for osmotic solute synthesis, reducing reactive oxygen species (ROS) production, and controlling ion accumulation, ultimately leading to enhanced plant growth, increased enzyme activity, and decreased membrane lipid peroxidation under stress conditions (Swarna et al. 2024).

According to the findings of Qin et al. (2023), the expression of genes related to PA metabolism was influenced by climatic variations, specifically cold stresses. The upregulation of genes involved in PA synthesis (*SPDS*, *SPMS* and *ADC*) suggests an increased demand for PAs under cold conditions, possibly to mitigate the stress effects. Conversely, the downregulation of the gene encoding polyamine oxidase (PAO) implies a reduction in the degradation of PAs, potentially indicating a mechanism to maintain higher PA levels for stress tolerance. PAs play multifaceted roles in plant-pathogen interactions, exerting profound effects on both host immunity and pathogen virulence through intricate molecular mechanisms, PAs influence the dynamics of pathogen-triggered immunity and shape the strategies employed by pathogens for infection and survival (Gerlin et al. 2021). Moreover, the impact of PAs extends beyond plant-pathogen interactions to encompass plant-microbe relationships, including weed suppression.

SPD and SPE counteract acid rain effects by reducing lipid peroxidation and H₂O₂ levels in bean plants (Velikova et al. 2000). PAs such as PUT offer significant protective mechanisms that improve the tolerance level of pea plants against Cd-related toxicity (Kumar et al. 2024). PUT exhibits the potential to alleviate dicamba-induced genotoxicity in wheat seedlings through DNA stabilization and reversal of DNA methylation alterations, highlighting the need for further investigation to elucidate the precise protective mechanism of PAs against dicamba toxicity (Arslan 2020). Differential PA levels observed in susceptible and resistant biotypes of *Chenopodium album* suggest a potential role in the response to atrazine exposure (Giebel et al. 2000). Paraquat application to *Lolium multiflorum* resulted in the vulnerability of PUT, a PA, suggesting a potential role for a membrane-bound transporter in the resistance mechanism, highlighting the intricate involvement of PAs in plant physiology and stress response (Brunharo et al. 2024).

PAs levels, notably SPM, SPD and PUT, decreased significantly under drought and waterlogging stress, with drought having a greater impact. Herbicide treatment caused a slight reduction. After returning to normal irrigation, PA levels tended to increase in drought-stressed plants, while waterlogged plants continued to show decreased levels during recovery, correlating with changes in growth parameters (Katerova et al. 2024). Exogenous PUT application reduces creasing and increases rind thickness in sweet orange fruit by elevating endogenous PA levels (Hussain and Singh 2015), while heat stress influences tomato blossom metabolism, impacting PA synthesis alongside carbohydrates and proline (Alsamir et al. 2017).

Exogenous application of PAs, particularly PUT, effectively alleviates the adverse effects of water deficit on sesame plants in arid regions. PAs enhance a multitude of physiological, biochemical, and agronomic parameters, ultimately enhancing crop water productivity and yield in conditions of limited water availability (Desoky et al. 2023). Although the precise involvement of PAs in fluazifop-p-butyl (FL)-induced phytotoxicity remains ambiguous FL, a prominent graminicide, disrupts lipid metabolism in plants by inhibiting acetyl-CoA carboxylase (ACCase). FL treatment alters maize growth, impacting pigment content and enzyme activity. The dynamic fluctuations of PAs such as PUT, SPD, and SPE in response to FL underscore their critical roles in stress response and growth regulation, emphasizing the intricate interplay between FL, chlorophylls, anthocyanins, and PAs in plant-herbicide interactions and stress responses (Horbowicz et al. 2013). PAs in plants exhibit dual roles as both protectors and potential sources of cellular damage under abiotic stress. While elevated PA levels enhance plant tolerance, their catabolic production of reactive oxygen species can induce cell harm.

The correlation between abiotic stress and foliar PAs offers promise as a potential stress marker in forest trees. PAs, including PUT, SPD and SPE, play pivotal roles in various plant functions, such as stabilizing macromolecules, scavenging radicals, acting as signalling molecules, regulating ion channels, and participating in programmed cell death. (Minocha et al. 2014). The study examined the impact of PAs, including SPE, SPD and PUT, on dill essential oil production. Notably, PUT at a concentration of 100 mg/l resulted in the highest oil yield at 3.58%. Moreover, varying concentrations of PAs exerted differential effects on oil compounds, with SPD and PUT at 50 mg/l demonstrating the most substantial influence (Zahedi and Gharneh 2023). PAs, exemplified by PUT, SPD, and SPE, are integral to plant stress responses, encompassing reactions to nutrient deficiencies and environmental pollutants (Fig. 1). Elucidating their biosynthesis and molecular pathways provides valuable insights into potential avenues for enhancing stress tolerance in plants (Pang et al. 2007).

Materials and Methods

The present study on *P. hysterophorus* phenological growth stages utilized the BBCH coding system. Polymorphisms in *SPDS*, *SPMS*, *ADC* and *COMT* genes were analysed during these stages. We evaluated these growth stages to recommend strategic herbicide interventions. *P. hysterophorus* (Accession: NIBPH-6) seeds were generously provided by ICAR - DWR, Jabalpur, MP, India and maintained at ICAR – NIBSM, Raipur, CG, India. Pot experiments were conducted at ICAR-NIBSM (21.3804° N, 81.8256° E) in 2022-23 across spring, early monsoon, and late-monsoon seasons. Each 8-inch pot contained five seeds, replicated thrice. Growth stages were analyzed using a Completely Randomized Design (CRD), and analysis of variance (ANOVA) was performed using WAPS software developed by ICAR-CCARI, Goa (Jangam et al. 2004). DNA extraction was carried out during leaf development, stem elongation, flowering, and Development of fruit, following (Saghai-Marooof et al. 1984), and quantified using Nanodrop. Gene polymorphism was assessed using PCR with primer pairs detailed in Table 2.

PCR products were visualized on agarose gel, and polymorphism information content (PIC) was calculated as per (Botstein et al.1980).

Table 1
Yield Reduction Caused by *P. hysterophorus* in Various Crops.

S.N.	Crop name	Yield reduction (%)	Reference
A. Cereals			
1	<i>Oryza sativa</i>	33–38	Bajwa et al. 2020
2	<i>Zea mays</i>	21–83	Vijayakumar et al. 2023; Safdar et al. 2015; Usman et al. 2001
3	<i>Sorghum bicolor</i>	40 to 97	Bajwa et al. 2020; Tamado et al. 2002.
4	<i>Triticum aestivum</i>	35	Khan and Aneja et al. 2016
B. Pulses			
1	<i>Cicer arietinum</i>	15	Khan and Aneja et al. 2016
2	<i>Cajanus cajan</i>	33	Safdar et al. 2016
3	<i>Vigna mungo</i>	67	
C. Oilseeds			
1	<i>Brassica campestris</i>	35	Khan and Aneja et al. 2016
2	<i>Eruca sativa</i>	55	
3	<i>Helianthus annuus</i>	52.5	
D. Vegetables			
1	<i>Abelmoschus esculentus</i>	25	Khan and Aneja et al. 2016
2	<i>Allium cepa</i>	15	
3	<i>Allium sativum</i>	7.5	
4	<i>Solanum tuberosum</i>	35	

Table 2
Primer pairs for the PCR amplification of PA metabolism genes in the present study.

Sl. No.	Target gene	Primer sequence	Reference
1.	<i>ADC</i> (F)	TTATCTGGTGCCGCTCTCTTC	Patil et al. (2021)
	<i>ADC</i> (R)	CGAGACTCAAGCACAGCAATAAG	
2.	<i>SPDS</i> (F)	CTCCGAAATCAGCCCAATGTG	
	<i>SPDS</i> (R)	ACCCCATCCAGAACAAGAACC	
3.	<i>SPMS</i> (F)	TCCTTCACTCTCCCACATTAC	
	<i>SPMS</i> (R)	CTCGCCTTCCCATCCATAGTC	
4.	<i>COMT</i> (F)	ACGTCGACATGATCATGCTC	Casassola et al. (2015)
	<i>COMT</i> (R)	ACTCGATGGCAAATGCGTTG	

Results and Discussion

Germination

At stage 0 of the BBCH code, germination occurred in pot experiments. In pots, germination happened at 22, 3, and 6 days after sowing (DAS) during spring, early monsoon, and late monsoon, respectively, with significant differences observed between spring seasons (Table 3 and Fig. 2).

Table 3 Phenological growth stages of *P. hysterophorus* in pot experiments across spring, early monsoon, and late monsoon seasons, categorized using the BBCH code. Days after sowing (DAS) indicate the progression of each stage, with significance levels ($P < 0.05$) denoted by critical differences (CD), highlighting notable variations across seasons.

Principal stage (BBCH code)	0	1	3	5-6	7	8	9
Stage	0-9	12-18	30-50	55-69	71-79	81-89	97
Phenological growth stage	Germination	Leaf development	Stem elongation	Flowering	Development of fruit	Ripening or maturity of fruit and seed	Senescence / Plant resting or dormancy
Spring (DAS)	22	25	28	111	120	149	169
Early monsoon (DAS)	3	6	27	58	70	99	142
Late monsoon (DAS)	6	15	33	80	92	119	162
CD (0.05)	6.52	3.26	4.46	24.90	5.99	6.82	12.84
	Vegetative phase			Reproductive phase			

Leaf development

The principal growth stage 1, representing leaf development, occurred at different times during different seasons in the pot experiments. Particularly, in spring, it was at 25 DAS, in late monsoon, it was at 15 DAS, and in early monsoon season, leaf development occurred at 6 DAS. Importantly, we noted a significant disparity between leaf development in each season. The

polymorphic information content (PIC) values were calculated for all four PA metabolism genes based on the number of bands amplified in the PCR during leaf development. We observed heightened polymorphisms of *ADC* during leaf development. Similarly, the *COMT* gene exhibited increased polymorphism during leaf development (Table 3, Fig. 2 and Fig. 3).

Stem elongation

Research investigating *P. hysterophorus* stem elongation revealed distinct phases during Spring (28 DAS), early monsoon (27 DAS), and late monsoon (33 DAS). Notably, the late monsoon phase exhibited significantly greater elongation compared to Spring and early monsoon phases. Moreover, heightened polymorphisms of *SPDS* were observed during stem elongation (Table 3, Fig. 2 and Fig. 3).

Flowering

In the present study, the principal growth stages 5 and 6 of the BBCH code denoted flowering. In our pot experiment, flowering was recorded at 111 DAS for spring, 58 DAS for early monsoon, and 80 DAS for late monsoon, with a significant difference observed in flowering among spring seasons, while no significant difference was noted between early and late monsoon periods. Additionally, heightened polymorphisms of *SPDS*, *SPMS*, and *COMT* genes were observed during the flowering stage (Table 3, Fig. 2 and Fig. 3).

Development of fruit

In the present study, the principal growth stage 7 of the BBCH code signified fruit development in *Parthenium*. Our pot experiment revealed distinct fruit development timings: 120 DAS for spring, 70 DAS for early monsoon, and 92 DAS for late monsoon, with significant differences observed among all three seasons. During the fruiting stage, only *SPDS* and *COMT* polymorphisms were detected, albeit at minimal levels, while *ADC* and *COMT* showed no polymorphism (Table 3, Fig. 2 and Fig. 3).

Ripening or maturity of fruit and seed

In the present study, the principal growth stage 8 denoted the ripening or maturity of *Parthenium* fruits. In our experiment, fruit maturity was observed at 149 DAS for spring, 99 DAS for early monsoon, and 119 DAS for late monsoon, with significant differences noted among all three seasons (Table 3 and Fig. 2).

Senescence / Plant resting or dormancy

In the pot experiment, a plant resting or dormant stage (principal growth stage 9) was observed at 169 DAS for spring, 142 DAS for early monsoon, and 162 DAS for late monsoon. Significant differences were noted between this growth stage in the early monsoon season compared to both spring and late monsoon seasons, with no significant difference observed between spring and late monsoon stages (Table 3 and Fig. 2).

Seasonal variations in BBCH growth stages of *P. hysterophorus*

Based on the BBCH code, we could represent the entire life cycle of *P. hysterophorus* starting from germination and concluding at the plant's senescence. The BBCH-scale stages, specifically stage 2 related to the emergence of side shoots and tillering, and stage 4, typically associated with the development of harvestable vegetative parts, did not align with this weed's growth pattern. Previous research, such as that by Hess et al. in 1997, delineated stage 2 as the emergence of side shoots and tillering and stage 4 as characteristic of vegetative propagation/booting in the Gramineae family of weeds. Our current investigation involving *P. hysterophorus* observed certain stages of the BBCH scale specifically stages 2 and 4 to be

inapplicable, diverging from the patterns noted in the Gramineae family. Contrary to the tillering nature observed in Gramineae, *P. hysterothorus* did not exhibit this trait in the present study. These insights from our observations contribute valuable context to the growth and developmental patterns of these weed species within the BBCH scale, extending the previous findings (Martinelli and Galasso 2011; Herraiz et al. 2015; Acosta-Quezada et al. 2016).

These findings suggest that seasonal factors play a more prominent role in influencing the growth stages of *P. hysterothorus* seed samples, highlighting the importance of considering and understanding seasonal parameters in the context of plant growth and development. An extensive investigation into sowing dates, affecting the phenological growth stages of eight common weed species in a study conducted by Hegazy et al. in 2005, indicates that seasonal factors which are inherently linked to sowing timings wield a more dominant influence on the growth stages of plants. Moreover, studies on weed ecology frequently highlight the relevance of seasonal factors in shaping weed growth dynamics. Seasonal changes in temperature, photoperiod, and moisture availability significantly impact weed germination, growth rates, and flowering times (Zimdahl 2018). This underscores the crucial significance of comprehending and accounting for seasonal parameters in understanding the growth and development dynamics of *P. hysterothorus*. In the present study, the timing of germination in *P. hysterothorus* was significantly influenced by the three seasons of seed samples despite the fluctuation in average temperature during spring (23°C), early monsoon (31°C) and late monsoon (28°C) (Anonymous 2022). This suggests that temperature variations have an impact on the germination stage of *P. hysterothorus*. Interestingly, this aligns with the findings of a previous study that in nature, the peak germination season for *A. artemisiifolia* and *C. album* is early to mid-spring, while for *A. retroflexus*, it is late spring to early summer (Baskin and Baskin 1977). Steckel et al. (2004) reported that the germination of weed seed and time of emergence are greatly affected by temperature, particularly in nine *Amaranthus* species and daily temperature fluctuations can also affect weed germination (Spitters 1989). Higher germination rates observed at high temperatures were reported on *P. hysterothorus* (Shrestha et al. 2024).

The present study indicates that leaf development took the most time during the spring season, followed by the late monsoon. The minimum time required was during the early monsoon. This suggests that in Chhattisgarh, during the early monsoon period, optimal environmental conditions are provided for fast completion of germination and early completion of leaf development stages. Previous research on *Quercus* species also noted the delay in achieving full photosynthetic capacity or leaf development during spring seasons (Morecroft et al. 2003). Leaf development is a fundamental aspect of growth in all plant species, playing a crucial role in ecological adaptability, as it is essential to perform photosynthesis, the most vital process associated with food production and overall survival (Fleming 2005).

The present case study observed that stem elongation in *P. hysterothorus* showed no significant difference between the spring and early monsoon periods. However, during the late monsoon, maximum time was required, indicating a significant difference compared to observations during spring and early monsoon. This is likely because the late monsoon period sowing of *P. hysterothorus* leads to stem elongation in the last month of July. During this period, there is excess water nearby, causing some logging situations, hence requiring maximum time compared to spring and early monsoon. In 2023, Bashar et al. reported on the allelopathic potentiality of stem extraction in *P. hysterothorus*. Prior studies underscored the positive impact of adequate rainfall during stem elongation on rice crop yield, emphasizing the detrimental consequences of inadequate precipitation on agricultural productivity (Abbas and Mayo 2021). Waterlogging during stem elongation stages exhibited a linearly diminishing correlation with wheat yield, becoming prominent ten days post-onset (Marti et al. 2015). Apart from rainfall, existing literature indicates that subjecting wheat to abbreviated photoperiods also extends the duration of stem elongation, aligning findings (González et al. 2005). Furthermore, temperature fluctuations were found to exert discernible effects on the stem elongation process (Kronenberg et al. 2021).

In the present study, the flowering of *P. hysterothorus* required the maximum duration in the spring season, with significant differences observed between the early and late monsoon periods. During the flowering stage, the average temperatures were 31°C, 27°C, and 28°C in the spring, early monsoon, and late monsoon seasons, respectively. This suggests that *P. hysterothorus* consistently flowers within the temperature range of more than 28°C requires a longer period of flowering. Opposite results have been reported earlier, with annual crop flowering and maturity observed and documented to occur

earlier in recent decades. These trends are frequently linked to warmer temperatures, particularly in the spring (Craufurd and Wheeler 2009). This valuable information on comprehending the temperature conditions conducive to flowering in *P. hysterothorus* is vital for understanding the adaptation of these plants to varying environmental conditions.

The development of fruit showed significant differences between the spring and monsoon seasons, highlighting the crucial influence of environmental factors on the plant life cycle. In the spring, fruit development took longer and often extended into the late monsoon. In contrast, the early monsoon season led to a quicker maturation process with shorter time requirements. These variations emphasize the significant impact of temperature and moisture levels on fruit development. Such findings echo those observed in studies on *Coriandrum sativum*, an herbal plant, where Nowak and Szemplinski (2014) demonstrated the significant influence of environmental factors on fruit development. Optimum tactics for weed management involve focusing efforts before the fruiting stages. Weed-free conditions between 15 and 45 DAS, as demonstrated by Duary and Hazra (2013), resulted in a significant increase in sesame yield with the critical period for weed management being 45 DAS (Justina and Thenmozhi 2024).

In the experiment, variations in fruit ripening or maturity were observed, with a longer period required during the spring season compared to early and late monsoons. This suggests that climatic changes influence ripening or maturity similar to fruit development. Previous studies on avocados have shown that environmental and climatic factors, particularly temperature, play a crucial role in various physiological processes during fruit development and ripening (Tzatzani et al. 2023).

P. hysterothorus exhibits senescence or plant resting/dormancy stages during the spring and early monsoon seasons, completing its life cycle earlier compared to the late monsoon. However, based on our hypothesis, the ideal targeted stages for weed management are identified as critical points of weed infestation, including leaf development, stem elongation, flowering, and fruiting.

Phenology-specific PA polymorphism in *P. hysterothorus* guiding herbicide intervention for effective management

The genomic characters translate the plant's survival capacity to readily adapt to new environments through various amino acids and enzymes, including PAs (Ramesh et al. 2017; Chen et al. 2019). PAs particularly not only affect stress adaptation but also play a significant role in various aspects of plant growth and development (Gonzalez et al. 2021; Tyagi et al. 2023). Generally, weed management tactics before the Economic Threshold Level (ETL) and after fruiting are not feasible when farmers' economic prospects are important. Hence, in this study, we investigated PAs Intervention targeting four phenological growth stages: Leaf development, Stem elongation, Flowering, and Development of fruit, respectively.

Leaf development stages, also observed heightened polymorphisms of *ADC* and *COMT* during leaf development and *ADC* may play an important role in the synthesis of theanine, a major compound of tea leaf (Mi et al. 2023). *ADC* is a rate-limiting enzyme responsible for the initial step of PA biosynthesis (Feng et al. 2011). *ADC* had associated earlier with stress tolerance functions in various plants, including cold stress tolerance in peaches, cucumbers and mangoes (Cao et al. 2016; Madebo et al. 2021; Bhardwaj et al. 2022), salt stress tolerance in *Lotus tenuis* (Espasandin et al. 2018). *COMT* has been reported previously to protect against a range of abiotic and biotic stresses, including temperatures (Tiryaki and Keles 2012), heavy metals (Cai et al. 2017), pathogens (Wang et al. 2018), salt (Zhang et al. 2019) and drought (Tiwari et al. 2021). During the leaf development stage, when *ADC* and *COMT* show more genetic variation, it's advised to apply foliar-active herbicides such as glyphosate (Fig. 4). However, it's crucial to recognize that *ADC* activity decreases after this phase.

Similarly, in a recommendation for effectively managing weeds, it's crucial to target specific stages of leaf development with foliar herbicide applications. For instance, applying imazethapyr during the one true-leaf growth stage effectively controlled 90% of large crabgrass (*Digitaria sanguinalis*), while 95% control of red rice (weedy rice) was achieved at the three- to four-leaf stage (Klingaman et al. 1992; Avila et al. 2005). Similarly, bispyribac-sodium delivered over 97% control for barnyard grass, jungle rice, and southern crabgrass at the four-leaf stage (Chauhan and Abugho, 2012). This high level of control is

attributed to the herbicide's strong phytotoxic response during early growth stages, particularly in leaf development, reducing the need for excessive herbicide use. Glyphosate and its metabolite, amino methyl phosphonic acid, were found in grain/seeds even when applied at pre-harvest, regardless of the dosage and timing. However, the levels detected did not exceed the maximum residue limits (Kadžienė et al. 2023).

During the stem elongation stage, higher levels of *SPDS* polymorphism were reported, followed by heightened polymorphisms in *SPDS*, *SPMS*, and *COMT* during flowering stages. Soar et al. (2004) also previously reported reduced paraquat (PQ) translocation, conferring resistance-like traits in *Arctotheca calendula*. That implies a role for *SPDS* transporter in herbicide resistance apart from its roles in various physiological and developmental processes, impacting abiotic stress tolerance in plants (Kasukabe et al. 2006; Peng et al. 2023). The role of *SPDS* in PQ resistance in goosegrass and *Ralstonia* wilt resistance in eggplant has also been proved previously (Luo et al. 2019; Qiu et al. 2019). flowering stages, coinciding with environmental stresses, likely require increased lignin modifications, suggesting *COMT* polymorphism during flowering as an adaptive response. Hence, controlling this foundational phase of seed reproduction is crucial for the more effective management of *P. hysterophorus*. We recommend using broad-spectrum non-selective herbicides such as Paraquat before stem elongation (Fig. 4). Previous studies showcased resistance due to increased polymorphisms of *SPDS*.

During the fruiting stages, it's not economically beneficial to use strategies that involve PAs intervention-based management. This is because *SPMS* doesn't exhibit polymorphism. Additionally, the levels of other PAs like *SPDS* and *COMT* are very low during these stages.

Conclusion

Our pioneering research on *P. hysterophorus* has resulted in a transformative herbicide strategy that enhances efficacy while minimizing environmental impact by targeting polyamine variations at distinct growth stages. We propose using broad-spectrum, non-selective herbicides like paraquat before stem elongation when *SPDS* genetic variations are most pronounced. As the plant progresses to stem elongation and flowering, switching to selective herbicides like bromoxynil is recommended, targeting the prevalent *SPMS* genetic variations. For effective control during leaf development, foliar-active translocated herbicides like glyphosate are advised, focusing on *ADC* and *COMT* genetic variations.

By strategically aligning herbicide selection and application timing with the specific growth stages of *P. hysterophorus*, this approach should ensures optimal weed control with reduced herbicide doses. This strategy provides a practical, eco-friendly solution for farmers, addressing weed management challenges in both cultivated and non-cultivated areas. We emphasize the importance of timely herbicide application and advocate for the integration of herbicides from different chemical groups to mitigate resistance and minimize environmental impact.

Declarations

Author Contribution

LK conceptualized and designed the study and interpreted the data. AG and RM made significant contributions to data acquisition and analysis. AG and RM drafted the manuscript, while LK, KT, AD, DP, and VC provided critical revisions. All authors approved the final version for publication and agree to be accountable for all aspects of the work, ensuring that any questions regarding the accuracy or integrity of any part of the study are appropriately investigated and resolved.

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Figures

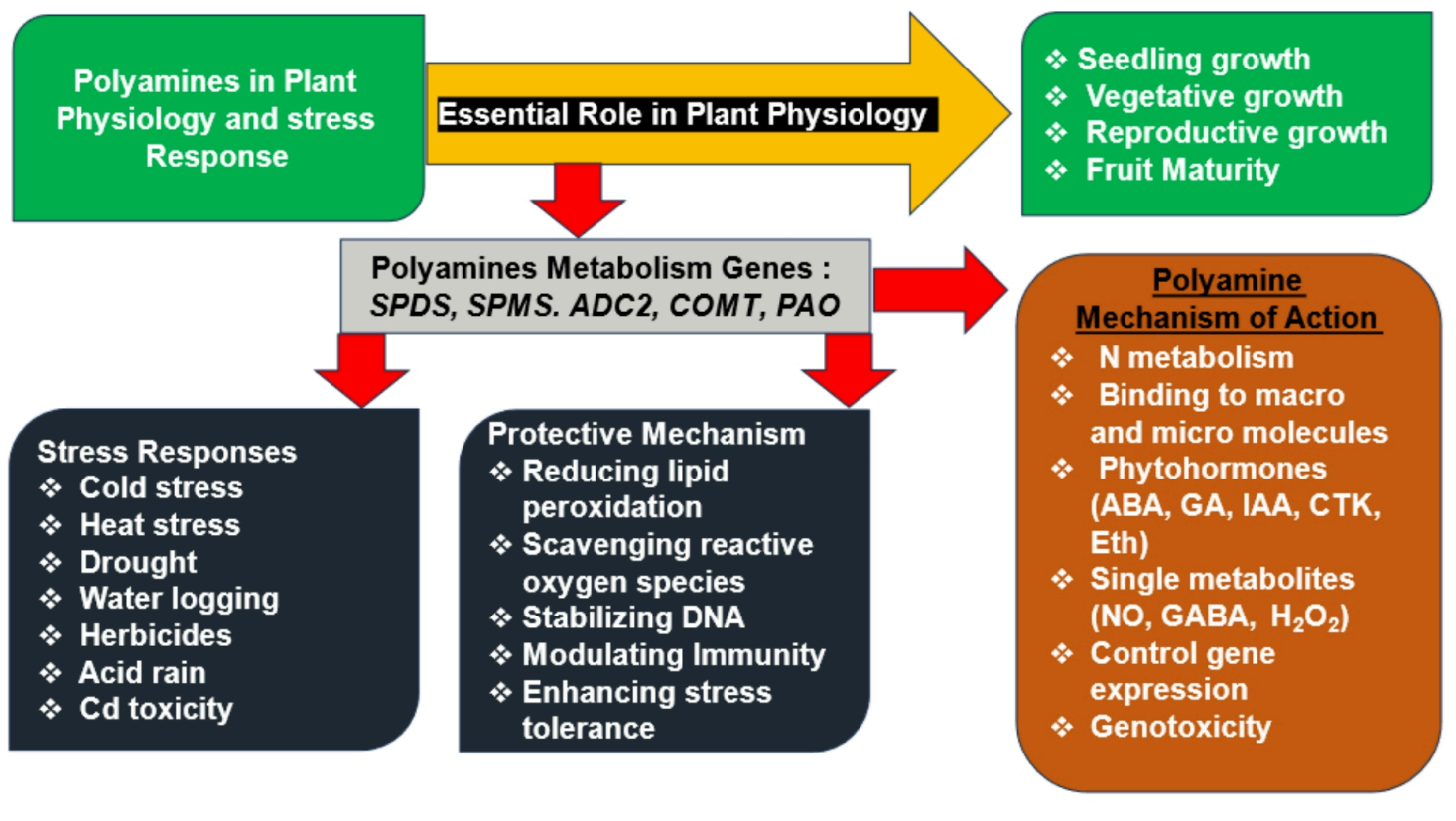


Figure 1

Interplay of PAs and Plant Physiology: A depiction highlighting the pivotal role of PAs in regulating various physiological processes crucial for plant growth and development

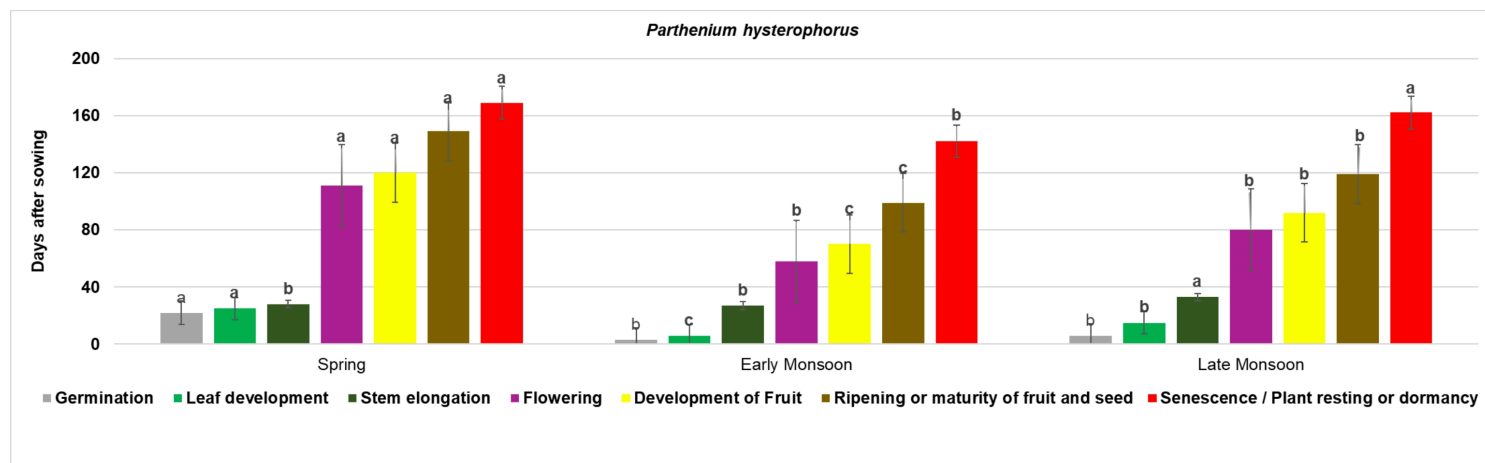
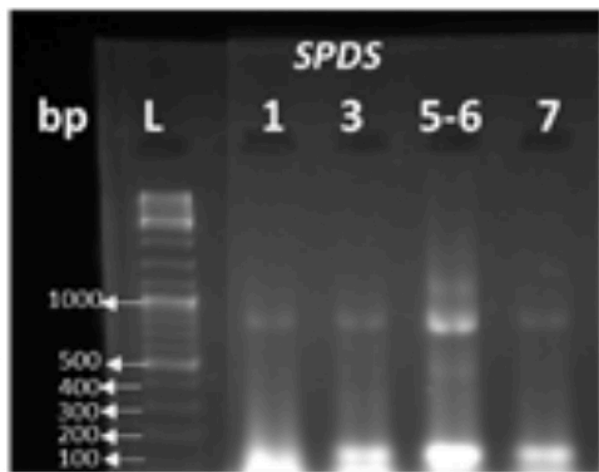
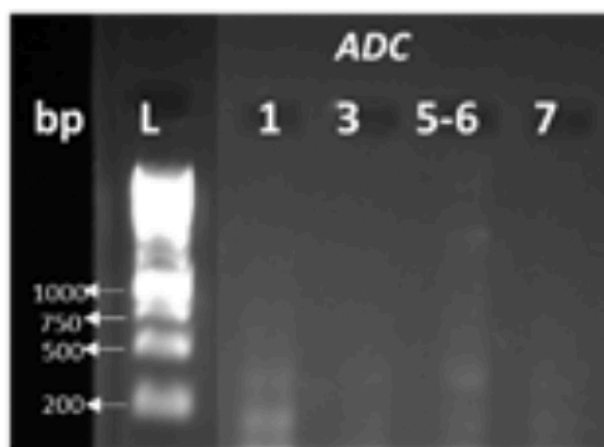


Figure 2

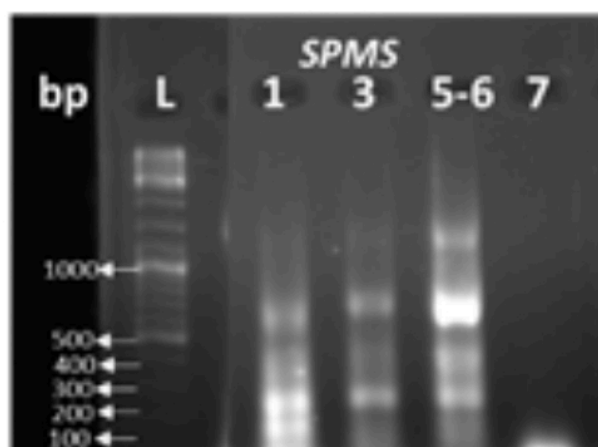
Seasonal Growth Dynamics of *P. hysterophorus*: Illustration depicting growth stages during spring, early monsoon, and late monsoon seasons. Variations in each stage are denoted by 'a', 'b', and 'c' ($P < 0.05$), emphasizing significant seasonal changes. Standard errors are represented by bar lines. For detailed analyses, refer to Table 3.



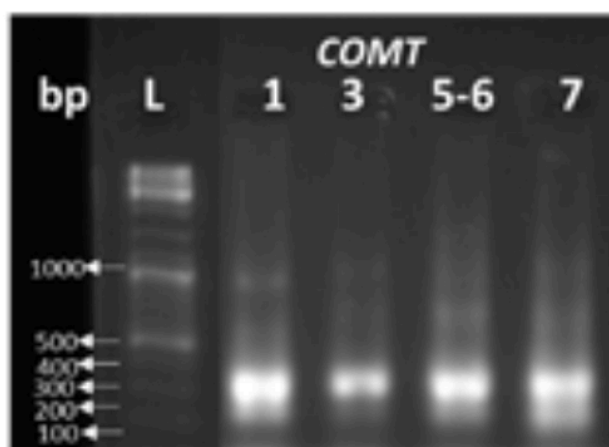
(A)



(B)



(C)



(D)

Figure 3

1.6% agarose gel electrophoresis pictures display PCR products of PA metabolism genes (a) *SPDS*, (b) *ADC*, (c) *SPMS* and (d) *COMT*. In pictures (A, C, D) Lane L features a 100 bp ladder, while (B) showcases a 1kb ladder. The remaining lanes contain products derived from 100 ng genomic DNA samples in each picture. PA polymorphism in association with the principal growth stages of *P. hysterophorus* is denoted by BBCH scale 1: Leaf development, 3: Stem elongation, 5-6: Flowering, 7: Development of fruit, in each picture

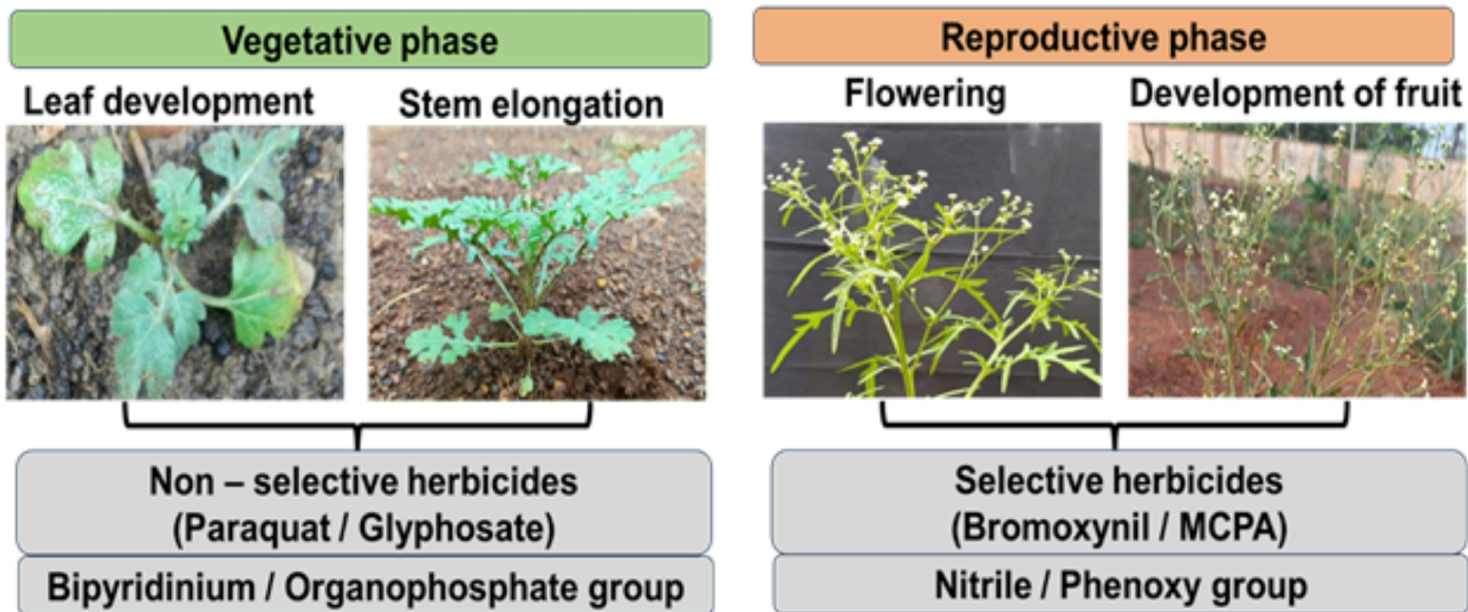


Figure 4

Herbicide Guidance Aligned with Phenological Phases and PAs Polymorphism