Comparative plant biochemistry and soil biology of wild and cultivated cotton species

Ritika Rajendra Waghmare
Kulandaivelu Velmourougane (velicar@gmail.com)
Desouza Blaise
Lalita Rameshwar Harinkhede
Pranali Tarachand Bansod
Jimmy Bhardwaj Vaidya
Vinita P Gotmare
Yenumula Gerard Prasad

Research Article

Keywords: wild cotton species, prebreeding, basal respiration, microbial metabolic quotient, glomalin, plant defense and soil enzymes

Posted Date: January 4th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1210068/v1

Abstract

Purpose

No attempts were made to analyze the diversity in soil and plant biology of wild cotton species (WCS) and cultivated cotton species (CCS), so far. Our study aimed to understand the differences in soil biological, plant biochemistry, and defense enzyme activities among the ten WCS and four CCS.

Methods

We studied the differences in soil biology, plant biochemistry, and defense enzyme activities among the ten WCS (*Gossypium anomalum, G. aridum, G. australe, G. barbosanum, G. capitis-virides, G. davidsonii, G. raimondii, G. somalense, G. stocksii, G. thurberi*) and four CCS (*G. arboreum*, *G. herbaceum*, *G. hirsutum*, and *G. barbadense*).

Results

CCS had 11%, 2%, and 10% higher soil respiration rate, microbial biomass carbon, and microbial metabolic quotient, respectively, compared to WCS. While, WCS had 45%, 15%, and 5% higher glomalin, soil polysaccharide, proteins, respectively, compared to CCS. WCS had 45%, 13%, 8%, and 13% higher acid and alkaline phosphatase, β-glucosidase, and soil dehydrogenase activities, respectively, compared to CCS. WCS had higher carbohydrates in the shoot (40%) and root (27%), while, CCS recorded higher proteins in the shoot (13%) and root (13%). WCS had significantly higher polyphenol oxidase (4% and 15%), peroxidase (30% and 31%), and catalase (36% and 31%) activities in shoots and root tissues, respectively, compared with CCS, while, WCS had higher phenol concentrations (4%) than CCS.

Conclusion

Our study suggests that the difference in soil biological, plant biochemistry, and defense enzyme activities among the WCS and CCS can be attributed to the inherent genetic makeup, which influences consequent plant and soil attributes.

Introduction

Cotton (*Gossypium* spp.) is an important natural fibre crop, which provides fibre to the textile industries and supply oil and feed to society (Velmourougane et al. 2021). In *Gossypium*, there are 43 diploids (2n = 26 chromosomes), which have been classified into 7 genomes from A to G, and 7 tetraploids (2n = 52 chromosomes) with genome designation AD (Wendel and Grover 2015). Out of 50 *Gossypium* species, two diploids (*G. arboreum* and *G. herbaceum*) and two tetraploids (*G. hirsutum* and *G. barbadense*) are cultivated for their spinnable fibre, worldwide, and the remaining 46 are wild species (Wendel and Cronn

2003; Campbell et al. 2010). Among the cotton-growing countries of the world, India is unique in terms of cultivating all four cultivated cotton species (CCS) (*G. hirsutum*, *G. barbadense*, *G. arboreum* and *G. herbaceum*) under diversified agro-ecological system (Gotmare et al. 2000; Gotmare 2021). Globally, cotton is grown in 75 countries, and breeding superior cotton to mitigate biotic and abiotic stresses for continued yield and quality enhancement is a primary goal of the cotton research community, worldwide (Shim et al. 2018). Among the *Gossypium* species, wild cotton species (WCS) serve as a genetic reservoir of several unique traits (wider adaptation, pest and disease tolerance, and yield contributing factors), which are useful to cotton breeders for prebreeding and genetic improvement in CCS (Narayanan et al. 2014; Mammadov et al. 2018). In cotton improvement, introgressive hybridization has played a significant role in transferring fiber quality (length and strength), disease resistance (black arm, rust, wilt), insect resistance (jassids, boll weevil), drought resistance, and male sterility traits (cytoplasmic male sterility) from various wild and cultivated species (Wang et al. 2016). Further, the hybridization of cultivated plant species with wild species can also transfer beneficial traits, which can alter the composition of plant and microbial communities, potentially leading to plant and soil health (Bulgarelli et al. 2015).

Understanding the heritage of crop plants and their wild relatives has been a major focus for plant science, as it helps in crop domestication and improvement (Byrne et al. 2018). Several germplasm studies and breeding programs have shown the supremacy of wild species in enduring biotic and abiotic stresses compared to their cultivated counterparts (Byrne P et al. 2020; Hübner and Kantar 2021), although tolerance genes have conventionally been considered as negatively correlated with yield (Wise 2007). However, insufficient data on phenotypic and genotypic differences, and other genetic variations (ploidy, hybridization barrier, linkage, etc.) act as blockade in wild species utilization for crop improvement (Dempewolf et al. 2017), and a large portion of the natural variation in the wild species of cotton remain untapped (Shim et al. 2018). Though cotton-breeding program traditionally utilize phenotypic and genotypic information in selecting parents (from wild or cultivated species) for prebreeding and introgression studies, they overlook plant and soil innate attributes due to absence of data. Hence, generating information related to basic plant biochemical and soil biological traits further help breeders hasten the selection of traits of agronomic importance. However, no study has attempted to analyze the diversity in soil and plant biology of cultivated and wild cotton species, so far. Therefore, a comparative analysis was conducted to understand the differences in soil biological and plant antioxidant/defense enzyme activities among the cultivated and selected wild cotton species. Our study will provide a greater understanding of biochemical and soil biological differences between cultivated and wild cotton species, and eventually supplement the cotton database, and support cotton breeders in selecting unique traits for their crop improvement programs.

Materials And Methods

Site description and sampling

Soil and plant sampling were conducted during the pre-monsoon (February) 2021 at wild species garden, ICAR-Central Institute for Cotton Research, Panjari Farm, Nagpur (21° 02' 8" N and 79° 03' 32" E) in Central India. This farm is situated at 309 m above the mean sea level and has a mean annual rainfall of 1200

mm. The study site has a deep black Vertisol (Typic Haplusterts) classified as sub humid moist bioclimate (10.2) under Agro-ecological sub-regions of India. For our analysis, we selected ten wild (*Gossypium anomalum* (Wawra & Peyritsch), *G. aridum* (Skovsted), *G. australe* (F.Muell.), *G. barbosanum* (Phillips & D.Clement), *G. capitis-viride*s (Mauer), *G. davidsonii* (Kelogg), *G. raimondii* (Ulbrich), *G. somalense* (Hutchinson), *G. stocksii* (Mast. & Hook.), *G. thurberi* (Todaro)) cotton species (based on their economic traits) and four cultivated (*Gossypium arboreum* L., *G. herbaceum* L., *G. hirsutum* L., and *G. barbadense* L.) cotton species. The detailed description about the genome, distribution, and economic attributes of wild and cultivated cotton species used in this study is presented in Table 1. The rhizosphere soil samples were collected at 0–60 cm soil depth, while, the shoot and root samples were collected from the representative cotton species, and were labelled and transported back to the laboratory in polyethylene bags/ice boxes, and stored at 4°C before analysis.

Soil biological analysis

Soil basal respiration rate (SBR) was measured following the method outlined by Anderson (1982). Soil microbial biomass carbon (MBC) was determined using the $CHCl_3$ fumigation-extraction method (Vance et al. 1987), and the MBC was calculated using the equation Biomass C = 2.64 EC (extractable carbon), where EC = (organic C in K_2SO_4 from fumigated soil) - (organic C in K_2SO_4 from unfumigated soil). The microbial metabolic quotient (qCO_2) an indicator of heterotrophic respiration was determined according to Anderson and Domsch (1986) by calculating the respiration-to-biomass ratio for the samples analyzed. The easily-extractable glomalin related soil proteins (EE-GRSP) was estimated according to Wright and Upadhyaya (1998). The total soil polysaccharides (SPS) and soil proteins (SoP) from wild and cultivated cotton species grown rhizospheric soils were quantified following the procedure outlined by Lowe (1994) and Bradford (1976), respectively.

Soil enzyme assay

The soil dehydrogenase activity (DHA) was determined by the colorimetric measurement of the reduction of 2,3,5-triphenyltetrazolium chloride to triphenylformazan according to the method of Casida et al. (1964). The activities of acid (AcP) and alkaline phosphatases (AlkP), and β-glucosidase (BG) were assayed according to Tabatabai (1982).

Plant antioxidant/defense enzymes, carbohydrates and proteins

The peroxidase (POD; EC 1.11.1.7) and polyphenol oxidase (PPO; EC 1.14.18.1) activity in the shoots and roots of wild and cultivated cotton species were determined following the method of Jennings et al. (1969).

The POD and PPO activity was determined spectrophotometrically by reading the absorbance at 470 and 546 nm, respectively, and expressed as units mg^{-1} protein min^{-1}. The catalase (CAT; EC 1.11.1.6) activity in the shoot and root samples was estimated according to the procedure outlined by Bergmeyer (1970). CAT activity was determined by reading the absorbance at 240 nm with a time scan of 0–60 s and expressed as units mg^{-1} protein min^{-1}. The L-phenylalanine ammonia lyase (PAL; EC 4.3.1.5) activity in the shoot and root samples was determined by the method described by Whetten and Sederoff (1992). The absorbance (290 nm) was measured using the upper phase and PAL activity was expressed in moles t-cinnamic acid mg^{-1} protein min^{-1}. The phenolic concentrations in the shoot/root samples were estimated using Folin-Ciocalteu reagent (Singleton et al. 1999). The intensity of the blue colour developed was measured spectrophotometrically at 660 nm. The amount of phenol in the shoot/root samples was calculated from a standard curve prepared using caffeic acid. The total phenol was expressed as milligrams of caffeic acid equivalent (CAE) gm^{-1} fresh weight. The total carbohydrate and protein content in shoot and root samples of wild and cultivated cotton species were determined by the method outlined by DuBois et al. (1956) and Lowry et al. (1951), respectively.

Statistical analysis

Experimental data in triplicate related to soil biological parameters, plant storage products, and plant antioxidant/defense enzymes were statistically analysed by one-way analysis of variance ANOVA with WASP version 2.0 (Web Agri Stat Package, Indian Council of Agricultural Research, India). Significant differences at $P \leq 0.05$, after ANOVA, were followed by single means differentiated by Tukey's honestly significant difference (HSD) test at $P \leq 0.05$. Principal component analysis was performed through XLSTAT program.

Results

Soil biological parameters

Cultivated cotton species (CCS) recorded significantly ($P < 0.05$) higher soil basal respiration rate (SBR) than wild cotton species (WCS) (Fig. 1a). Among the CCS, higher SBR was observed in *G. herbaceum* (53.81 mg CO_2 kg^{-1} soil day^{-1}) and *G. hirsutum* (53.63 mg) followed by *G. barbadense* (53.08 mg) and *G. arboreum* (51.21 mg). The percent decrease in SBR compared to *G. hirsutum* was 1% and 4.4% respectively, for *G. barbadense* and *G. arboreum*. Among the WCS, higher SBR was recorded in *G. raimondii* (48.58 mg), followed by *G. barbosanum* (48.31 mg), and the lowest SBR was observed in *G. anomalum* (44.46 mg). The percent decrease in SBR compared to *G. hirsutum* was 9.4%, 9.9%, and 17%, respectively, for *G. raimondii*, *G. barbosanum*, and *G. anomalum*. There was not much variation in soil microbial biomass C (MBC) content between CCS and WCS compared to SBR (Fig. 1b). *G. arboreum* (959 mg kg^{-1}) followed by *G. herbaceum* (916 mg kg^{-1}) recorded higher MBC among the CCS. While, among the WCS, higher MBC was recorded in *G. australe* (959 mg kg^{-1}) followed by *G. aridum* (926 mg kg^{-1}), and the lowest MBC was

recorded in *G. somalense* (845 mg kg^{-1}). A 10% increase in MBC was recorded in *G. arboreum* compared to *G. hirsutum* in CCS. While, *G. australe* and *G. aridum* recorded 10% and 6.3% increase in MBC compared with *G. hirsutum*.

The microbial metabolic quotient (qCO_2) (respiration-to-biomass ratio) an indicator of soil organic matter conversion and heterotrophic respiration was higher in CCS compared to WCS (Fig. 1c). *G. hirsutum* (0.062) and *G. barbadense* (0.061) recorded higher qCO_2 in cultivated species. In WCS, *G. thurberi* (0.058) followed by *G. capitis-virides* (0.056) recorded higher qCO_2. The lowest qCO_2 was observed in *G. anomalum* and *G. australe* (0.48). The percent decrease in qCO_2 compared to *G. hirsutum* was 21.8%, 21.7 and 13%, respectively, for *G. austral*, *G. anomalum*, *and G. arboreum*. The easily-extractable glomalin related soil proteins (EE-GRSP) (indicator of mycorrhizal colonization in plants) was significantly ($P < 0.05$) higher in WCS compared to CCS (Fig. 1d). Among WCS, higher EE-GRSP was recorded in *G. thurberi* (4.83 mg g^{-1}) and *G. aridum* (4.80 mg g^{-1}), and the lowest in *G. barbosanum* (2.30 mg g^{-1}). Among the CCS, *G. arboreum* recorded the highest EE-GRSP (4.44 mg g^{-1}), while *G. barbadense* recorded lowest EE-GRSP (1.33 mg g^{-1}). The percent increase in EE-GRSP compared to *G. hirsutum* was 262%, 260%, and 233%, respectively, for *G. thurberi*, *G. aridum* and *G. arboreum*.

WCS recorded significantly ($P < 0.05$) higher soil polysaccharide (SPS) content compared with CCS (Fig. 1e). Among the WCS, higher SPS was observed in *G. aridum* (19.1 mg g^{-1} soil) followed by *G. anomalum* (18.4 mg), and the lowest SPS was recorded in *G. barbosanum* (13.6 mg). The percent increase in SPS compared to *G. hirsutum* was 32% and 27%, respectively, for *G. aridum* and *G. anomalum*. Among the CCS, higher SPS was recorded in *G. herbaceum* (15.7 mg), followed by *G. hirsutum* (14.4 mg), and the lowest SPS was observed in *G. barbadense* (10.4 mg). WCS recorded significantly ($P < 0.05$) higher soil protein (SoP) content compared with CCS (Fig. 1f). Among the WCS, higher SoP was observed in *G. aridum* (2.49 mg g^{-1} soil) followed by *G. stocksii* (1.88 mg), and the lowest SoP was recorded in *G. capitis-virides* (1.54 mg). The percent increase in SoP compared with *G. hirsutum* was 57% and 18%, respectively, for *G. aridum* and *G. stocksii*. Among the CCS, higher SoP was recorded in *G. herbaceum* (1.99 mg), followed by *G. barbadense* (1.66 mg), and the lowest SoP was observed in *G. hirsutum* (1.58 mg).

Soil enzyme activities

WCS recorded significantly ($P < 0.05$) higher acid phosphatase (AcP) activity compared to CCS (Fig. 2a). Among the WCS, higher AcP was observed in *G. aridum* (328.5 µg PNP g $soil^{-1}$ h^{-1}) followed by *G. anomalum* (285.3 µg), and the lowest AcP was recorded in *G. barbosanum* (170 µg). The percent increase in AcP compared to *G. hirsutum* was 133% and 103%, respectively, for *G. aridum* and *G. anomalum*. Among the CCS, higher AcP was recorded in *G. herbaceum* (164 µg), followed by *G. hirsutum* (141 µg), and the lowest AcP was observed in *G. barbadense* (112 µg). WCS recorded significantly ($P < 0.05$) higher alkaline phosphatase (AlkP) activity compared to CCS (Fig. 2b). Among the WCS, higher AlkP was observed in *G. anomalum* (800 µg PNP g $soil^{-1}$ h^{-1}) followed by *G. stocksii* (682 µg), and the lowest AlkP was recorded in *G. barbosanum* (346 µg). The percent increase in AlkP compared to *G. hirsutum* was 24% and 6%

respectively for *G. anomalum* and *G. stocksii*. Among the CCS, higher AlkP was recorded in *G. hirsutum* (644 µg), followed by *G. arboreum* (612 µg), and the lowest AlkP was observed in *G. barbadense* (336 µg).

The β-glucosidase (BG) activity as a measure of organic matter degradation and C recycling was significantly ($P < 0.05$) higher in WCS compared to CCS (Fig. 2c). Among the WCS, higher BG was observed in *G. anomalum* (419 µg PNP g soil^{-1} h^{-1}) followed by *G. australe* (406 µg), and the lowest BG was recorded in *G. barbosanum* (182 µg). The percent increase in BG compared with *G. hirsutum* was 38% and 34%, respectively, for *G. anomalum* and *G. australe*. Among the CCS, higher BG was recorded in *G. arboreum* (398 µg), followed by *G. hirsutum* (304 µg), and the lowest BG was observed in *G. barbadense* (202 µg). The dehydrogenase activity (DHA) as an indicator of microbial activity was significantly higher ($P < 0.05$) in the CCS compared to WCS (Fig. 2d). *G. hirsutum* (14.4 µg TPF g^{-1} h^{-1}) followed by *G. arboreum* (13.1 µg) recorded higher DHA in CCS, and the lowest DHA was observed in *G. barbadense* (11.9 µg). In WCS, *G. anomalum* (14.1 µg) followed *G. raimondii* (13.6 µg) recorded higher DHA, and the lowest DHA was observed in *G. barbosanum* (8.73 µg). The percent decrease in DHA compared with *G. hirsutum* was 39.5%, 38.7, and 38.3%, respectively, for *G. barbosanum*, *G. somalense*, *and G. capitis-virides*.

Plant carbohydrate and protein

Significant differences ($P < 0.05$) in the carbohydrate concentration were recorded in root and shoot tissues of WCS and CCS, however, shoot samples exhibited higher carbohydrate concentrations (Fig. 3a). Between wild and cultivated species, WCS recorded significantly ($P < 0.05$) higher carbohydrate concentration in shoot (SC) and roots (RC). Among the WCS, higher SC was observed in *G. anomalum* (97.2 mg g^{-1}) followed by *G. australe* (86.3 mg), and the lowest SC was recorded in *G. somalense* (33.7 mg). In cultivated species, higher SC was recorded in *G. hirsutum* (45.9 mg) followed by *G. arboreum* (38.7 mg), and the lowest in *G. barbadense* (32 mg). The percent increase in SC compared with *G. hirsutum* was 112% and 88%, respectively, for *G. anomalum* and *G. australe*. Among the WCS, higher root carbohydrate (RC) was recorded in *G. australe* (47.4 mg), followed by *G. aridum* (46.1 mg), and the lowest RC was observed in *G. thurberi* (20.2 mg). In cultivated species, *G. herbaceum* (35.4 mg) recorded higher RC, and the lowest was recorded in *G. barbadense* (13.3 mg). The percent increase in RC compared to *G. hirsutum* was 152%, 146%, and 89%, respectively, for *G. australe, G. aridum*, and *G. herbaceum*.

Significant differences ($P < 0.05$) in the protein concentration were recorded in root and shoot tissues of WCS and CCS, however, shoot samples exhibited higher protein concentration in the wild and cultivated species (Fig. 3b). Cultivated species recorded significantly ($P < 0.05$) higher protein content concentration in shoot (SP) and roots (RP) compared to WCS. Among the CCS, higher SP was observed in *G. herbaceum* (74.2 mg g^{-1}) followed by *G. arboreum* (66.8 mg), and the lowest SP was recorded in *G. hirsutum* (58 mg). In wild species, higher SP was recorded in *G. australe* (73.3 mg) followed by *G. anomalum* (66 mg), and the lowest in *G. capitis-virides* (35 mg). The percent increase in SP compared to *G. hirsutum* was 28%, 26%, and 15%, respectively, for *G. herbaceum, G. australe*, and *G. arboreum*. Among the CCS, higher RP was observed in *G. barbadense* (25.9 mg g^{-1}) followed by *G. herbaceum* (22.9 mg), and the lowest RP was recorded in *G. hirsutum* (20.8 mg). In wild species, higher RP was recorded in *G. anomalum* followed by *G.*

stocksii (23.8 mg) and *G. raimondii* (23.8 mg). The lowest RP was recorded in *G. capitis-virides* (13.9 mg). The percent increase in RP compared with *G. hirsutum* was 25%, 10%, 17.5, and 14.7%, respectively, for *G. barbadense, G. herbaceum, G. anomalum*, and *G. stocksii/ G. raimondii.*

Plant antioxidant/defense enzymes

WCS recorded significantly ($P < 0.05$) higher peroxidase activity (POD) in shoots and root tissues compared to CCS (Fig. 4a). Among the WCS, higher shoot POD was observed in *G. aridum* (7.54 units (U) g^{-1} protein min^{-1}) followed by *G. somalense* (4.37 U), and the lowest in *G. australe* (3.26 U). Among the CCS, higher shoot POD was observed in *G. arboreum* (3.80 U) followed by *G. hirsutum* (3.0 U), and the lowest in *G. barbadense* (2.34 U). In wild species, *G. aridum* (10.7 U) followed by *G. somalense* (8.2 U) recorded higher root POD, while, lowest activity was recorded in *G. barbosanum* (4.64 U). Among the CCS, higher root POD was observed in *G. arboreum* (6.93 U) followed by *G. hirsutum* (4.5 U), and the lowest activity in *G. barbadense* (3.53 U). The percent increase in POD in *G. aridum* and *G. arboreum* compared with *G. hirsutum* was 144% & 139% and 23% & 54%, respectively, for shoot and root tissues.

Significantly ($P < 0.05$) higher polyphenol oxidase activity (PPO) was recorded in WCS compared to CCS in the shoot and root tissues (Fig. 4b). *G. thurberi* (0.489 U g^{-1} protein min^{-1}) followed by *G. australe* (0.419 U) recorded higher PPO in shoot and root samples among the WCS, while, the lowest PPO in shoot and root sample was recorded in *G. capitis-virides* (0.237 U) and *G. barbosanum* (0.145 U), respectively. Among the CCS, higher shoot and root PPO were observed in *G. arboreum* (0.487 & 0.229 U) followed by *G. hirsutum* (0.319 & 0.210 U), respectively, and the lowest PPO was observed in *G. barbadense* (0.252 U) and *G. herbaceum* (0.185 U) respectively for the shoot and root samples. The percent increase in PPO in *G. thurberi*, *G. australe*, and *G. arboreum* compared with *G. hirsutum* was 54% & 31%, 55% & 38%, 53% & 9%, respectively, for shoot and root tissues.

WCS recorded significantly ($P < 0.05$) higher phenylalanine ammonia lyase activity (PAL) in the shoot as well as in root tissues compared to CCS (Fig. 4c). *G. stocksii* (28.9 moles t-cinnamic acid mg^{-1} protein h^{-1}) followed by *G. thurberi* (28 moles) recorded higher PAL in shoot sample, while, in root samples, *G. stocksii* (23 moles) followed *G. somalense* (19 moles) recorded higher PAL. Among the WCS, *G. barbosanum* recorded lesser PAL in both shoot (12.4 moles) and roots (9.9 moles). In CCS, *G. arboreum* (19.6 & 19 moles) followed by *G. hirsutum* (18.9 & 17.0 moles) recorded higher PAL, respectively, for shoot and root samples, while, *G. barbadense* recorded lower PAL in shoot (18.4 moles) and root (13.6 moles) samples. The percent increase in the PAL in *G. stocksii* and *G. arboreum* compared to *G. hirsutum* was 53% & 34% and 4% & 11%, respectively, for shoot and root tissues.

Significantly ($P < 0.05$) higher catalase activity (CAT) was recorded in WCS compared to CCS in the shoot as well as root tissues (Fig. 4d). *G. aridum* (0.589 & 0.468 U g^{-1} protein min^{-1}) followed by *G. somalense* (0.463 & 0.422 U) recorded higher CAT in shoot and root samples, respectively, while, *G. stocksii* recorded lowest CAT in shoot (0.257 U) and roots (0.212 U). Among the CCS, higher shoot and root CAT were observed in *G. arboreum* (0.287 & 0.262 U), and the lowest CAT was observed in *G. barbadense* (0.141 & 0.127 U) respectively for the shoot and root samples. The percent increase in CAT in *G. aridum* and *G.*

arboreum compared with *G. hirsutum* was 138% & 112% and 16% & 18%, respectively, for shoot and root tissues.

Both shoot and roots showed significant differences ($P < 0.05$) in the phenolic content, however, the shoot samples exhibited much higher values in the WCS and CCS (Fig. 4e). Among the WCS, the shoot phenolic concentrations were significantly higher in *G. barbosanum* (4.57 mg caffeic acid equivalent (CAE) g^{-1} fresh wt.) followed by *G. capitis-virides* (4.50 mg) and *G. anomalum* (4.41 mg), and the lowest phenol content was recorded in *G. davidsonii* (2.30 mg). In CCS, *G. herbaceum* (3.91 mg) showed the highest shoot phenolic concentration followed *G. arboreum* (3.74 mg), and lesser phenols were recorded in *G. hirsutum* (2.97 mg). There were no much differences in mean root phenolic concentrations between WCS and CCS. However, the root phenolic concentrations varied significantly ($P < 0.05$) among the species. Among the WCS, higher phenols were recorded in *G. anomalum* (2.40 mg) followed by *G. aridum* (2.08 mg), and lowest in *G. stocksii* (1.20 mg). *G. herbaceum* (2.19 mg) recorded higher root phenols in CCS, and the lowest was recorded in *G. arboreum* (1.41 mg). The percent increase in shoot phenol content in *G. barbosanum* and *G. herbaceum* compared with *G. hirsutum* was 54% & 32%. Similarly, the percent increase in root phenol content in *G. anomalum* and *G. herbaceum* compared with *G. hirsutum* was 65% & 51%.

Discussion

Presently, several *Gossypium* germplasm, including wild species and land races are conserved through national gene banks worldwide to serve as a source for introgression studies for ongoing and future crop improvement programs. However, no study has attempted to analyze the diversity in soil and plant biology of cultivated and wild cotton species, so far. Our study aimed to understand the differences in soil biological attributes and plant antioxidant and defense activities between WCS and CCS.

From our study, we found significant differences in soil, plant and microbial functional attributes between WCS and CCS (Fig. S1). CCS recorded significantly higher soil basal respiration rate and microbial biomass carbon than WCS. Since, both the CCS and WCS where grown in the similar conditions in the wild species garden, the difference in respiration rate and biomass carbon can only be attributed to plant biomass quantity and litter quality (biochemical constituents), which have favoured enhanced heterotrophic respiration in CCS compared to WCS. Higher phenolic contents in leaf and root biomass of WCS slow down the microbial growth and subsequent decomposition of biomass reducing soil CO_2 emissions.

Soil respiration is the key mechanism through which soil carbon is released into the atmosphere at a global scale, and hence it acts as an important indicator of carbon cycling in the ecosystem (Song et al. 2021), and help in the prediction of warming-related increases in soil CO_2 emissions and climate change (Davidson and Janssens 2006). However, it is still poorly understood how genotypic changes in cotton species can affect this soil respiration process. It has been proposed that soil respiration has influenced either by plant functional groups (genotypes/diversity) or through differences in nutrient concentration in the plant biomass (Dias et al. 2010). Path analysis revealed that species richness predominantly regulates soil respiration through variations in plant productivity and community structure (Xu et al. 2015), rather than differences in species composition (Dias et al. 2010). However, soil respiration is controlled by soil

temperature, soil moisture, soil aeration (Cook and Orchard 2008), soil nitrogen content (Song et al. 2021), differences in canopy structure, plant biomass, and associated litter quality (Xu et al. 2015), which influences soil physico-chemical properties (Aponte et al. 2012) and soil microbial community structure, and eventually result in soil autotrophic and heterotrophic respiration (Xu et al. 2015). In cotton, soil respiration was greatly influenced by soil water content and external irrigation, which directly affects the root respiration activity and soil CO_2 production and exchange (Yu et al. 2015). Previously, Bhattarai et al. (2006) reported low oxygen and lesser respiration can lead to lesser cotton yields on a heavy clay soil. Oxygation (irrigation of crops with aerated water, through air injection in the root zone) of cotton increased the soil oxygen content and soil respiration eventually water use efficiency, enhancing cotton plant biomass, lint yield (Chen et al. 2011).

Similarly, the microbial metabolic quotient (qCO_2) (respiration-to-biomass ratio) an indicator of soil organic matter conversion and heterotrophic respiration was higher in CCS compared to WCS, indicating faster organic matter recycling in CCS. The higher carbon recycling in CCS clearly indicates the presence of non-inhibitory substances, which favoured higher microbial activity on CCS biomass compared to WCS (higher phenolic compounds detected). The microbial metabolic quotient (MMQ) is an indicator of soil organic matter recycling (carbon cycling and heterotrophic respiration) in an ecosystem, and it's a unit of soil microbial respiration per unit of microbial biomass indicating the specific activity of soil microorganism in a given niche (Sinsabaugh et al. 2017), which is used to predict the responses of soil respiration rate to global climate change and helps in global carbon modelling (Cao et al. 2019). MMQ is greatly influenced by microbial diversity (Jiang et al. 2013), microbial biomass and respiration (Wardle 1993).

We found significantly higher glomalin-related soil proteins (GRSP- an indicator of mycorrhizal colonization in plants) in WCS compared to CCS, indicating higher mutualistic association of AMF with WCS compared to CCS. The process of domestication of WCS to CCS through introgression would have reduced the CCS dependency on AMF through modifications in root morphology, phenology, and biochemical constituents. Earlier reports on drought tolerance characteristics in most of the WCS (Kantartzi et al. 2009; Xu et al. 2013; Nazeer et al. 2014; Wang et al. 2016) corroborates our findings through the establishment of higher GRSP in WCS. Arbuscular mycorrhizal fungi (AMF) colonization of terrestrial plant roots improve host adaptability to wider environmental perturbations through the establishment of better root systems, apart from providing essential macro and micronutrients, uptake, and protection from several biotic and abiotic stresses (Brundrett and Tedersoo 2018; Kokkoris et al. 2019). However, plant species, climatic and soil variability greatly influence AMF colonization in crop plants (Sousa et al. 2018; dos Passos et al. 2021). Further, GRSP production by AMF plays a positive role in plant and soil health through the formation of soil aggregates and acts as a significant pool of organic nitrogen in soil (Wang et al. 2017). Higher glomalin content is soil was positively associated with the total carbon content in soil and found to reduce soil degradation (Gałązka et al. 2020). Plant mycorrhizal dependency depends on its root hairs length and abundance (Plenchette et al. 1983). Since, cotton has short root hairs, its dependency on mycorrhizal association is more (Damodaran et al. 2012), and is governed by mycorrhizae species and phosphorus status of the soil (Ortas and Iqbal 2019). In cotton, AMF inoculation has increased chlorophyll content, stomatal conductance, and plant growth hormones (Badda et al. 2015), apart from increasing nitrogen and

phosphorus contents in the plant tissues with subsequent reduction in fertilizer dosage and yield enhancements (Mai et al. 2019; Gao et al. 2020).

Soil enzyme activities act as in indicator of microbial activity and subsequent nutrient cycling in the ecosystem (García-Palacios et al. 2021). In our study, WCS recorded higher soil enzyme activities (phosphatases and β-glucosidase) except the DHA. The lesser DHA activity can be correlated with soil respiration, MBC, and qCO_2, where, the plant biomass quantity and litter quality determine the microbial activity and subsequent MBC and CO_2 emissions. Higher litter fall and lesser phenolics in CCS biomass were found to enhance soil respiration, MBC, and DHA compared to WCS. In spite of lesser biomass additions, higher phosphatases and β-glucosidase activities in WCS indicate efficient phosphorus and carbon cycling in WCS. Several factors, including host genome, root architecture, biochemical constituents of plant species, and soil factors modulate the microbial community structure and subsequent soil biological functions (BEZEMER et al. 2006; Philippot et al. 2013). Though differences in soil biological properties of WCS have not been studied so far, the effects of bioclimates, cropping systems, and soil types on soil physical, chemicals, and biological properties in *G. hirsutum* are well established (Velmourougane and Sahu 2013; Velmourougane et al. 2013, 2014; Blaise et al. 2021).

Nevertheless, the induction of plant antioxidant/defense enzyme activities and phenol concentrations through microbial inoculation has been studied in *G. hirsutum* (Velmourougane et al. 2017, 2019), natural occurrence of plant defense enzymes activities in WCS and CCS (*G. arboreum*, *G. herbaceum*, and *G. barbadense*) were not reported so far. WCS exhibited higher plant defense enzyme activities (POD, PPO, PAL, CAT) and phenolic compounds compared to CCS. Plants enhance their natural defense response to several biotic and abiotic stresses by induction of defense mechanisms (ElSayed et al. 2019; Li et al. 2021), which includes production and expression of several metabolites and defense enzymes, which regulates the rate of damage caused by pests and diseases (Yactayo-Chang et al. 2020). However, in our study, we found constituent expression of defense enzymes in WCS. Several WCS exhibited a wide range of tolerance against biotic (pest and diseases) and abiotic stresses (drought, salinity) (Kulkarni VN et al. 2009; Zhao et al. 2012; Miyazaki et al. 2012; Nazeer et al. 2014; Chen et al. 2015; Wendel and Grover 2015; Zhang et al. 2016; Wang et al. 2016). Our results confirm those tolerance mechanisms may be due to the expression of plant defense enzymes in WCS.

Peroxidase (POD) is a key enzyme involved in the biosynthesis of lignin and suberin (Thakker et al. 2013), and its activity in plants is induced by pathogens (Sasaki et al. 2004), and higher POD activity in plants has been correlated with the plant defense response to external stresses, which leads to lignification of plant tissues, suberization, cross-linking of glycoproteins and phenols, and phytoalexin production (Agrios 2005). Plant POD was also implicated in the inhibition of pathogens through the production of reactive oxygen species (Passardi et al. 2005). Conservation of adequate antioxidant enzymes preceding heat stress is reported to ease the leaf temperature increase in cotton (Snider et al. 2010). Polyphenol oxidase (PPO) is a key enzyme involved in catalyzes of phenols to quinones, which exhibits antimicrobial activity by several mechanisms including alkylation, reduced bioavailability of cellular proteins to the pathogen, production of reactive oxygen species (Thakker et al. 2007). Pathogen-induced PPO activity has been reported in several

plants, including monocots and dicots (Raj et al. 2006). Furthest, PPO production in plants was reported to decrease the nutritional quality of food and reducing protein digestibility by conversion of phenols to quinones (Felton et al. 1994). Phenylalanine ammonia lyase (PAL) enzyme is a key enzyme involved metabolism of aromatic amino acids (MacDonald and D'Cunha 2007), and was shown to act as defense molecules against pests and disease infestation (War et al. 2012). PAL activity is induced by signalling molecules viz., ethylene, salicylic acid, and jasmonic acid (Kim et al. 2007) and biotic and abiotic stresses (Lafuente et al. 2003). Catalase (CAT) enzyme and their isomers play a major role in the scavenging of H_2O_2 generated during photorespiration (Palma et al. 2020), and play a prominent role in lignification of vascular tissues during senescence (Rajput et al. 2021). CAT is expressed in seeds and reproductive tissues during the catabolism of fatty acids during the glyoxylate cycle in glyoxysomes. The higher CAT activity was expressed in plants during water stress (Dai et al. 2020), salinity stress (Fei et al. 2020), heat stress (Zafar et al. 2020), and pathogen infection (Anand et al. 2007).

Among the *Gossypium*, WCS serve as a genetic reservoir of diverse unique traits, which are useful for genetic improvement in CCS. Though cotton-breeding strategy largely uses phenotypic and genotypic data for parent selection and prebreeding, they overlooked plant biochemistry and soil biology attribute due to the absence of data. Further, no attempts were made to analyze the diversity in soil and plant biology of WCS and CCS, so far. Our study aimed to understand the differences in soil biological, plant biochemistry, and defense enzyme activities among the ten WCS and four CCS. Our study suggests that the difference in soil biological, plant biochemistry, and defense enzyme activities among the WCS and CCS are attributed to the inherent genetic makeup of WCS and CCS, which influences consequent plant and soil attributes. Further studies on identification of genetic mechanisms and genes involved in modulating the plant defense enzymes and nutrient cycling in WCS and CCS will help conventional and molecular breeding in cotton.

Declarations

Acknowledgments

This investigation is a part of Post-graduation thesis work of the first author (Ms. Ritika Rajendra Waghmare), who also is grateful to the Director, ICAR-Central Institute for Cotton Research (CICR), Nagpur for providing research facilities. We would like to thank Dr. Raghavendra KP, Senior Scientist, Division of Crop Improvement, ICAR-Central Institute for Cotton Research, Nagpur-440033, India for his careful review of the manuscript, as well as valuable comments and suggestions.

Authorship contribution

Conceptualization: Kulandaivelu Velmourougane; Methodology: Kulandaivelu Velmourougane; Formal analysis and investigation: Ritika Rajendra Waghmare, Kulandaivelu Velmourougane, Lalita Rameshwar Harinkhede, Pranali Tarachand Bansod, Jimmy Bhardwaj Vaidya; Writing - original draft preparation:

Kulandaivelu Velmourougane, Ritika Rajendra Waghmare; Writing - review and editing: Kulandaivelu Velmourougane, Desouza Blaise; Resources: Vinita P Gotmare, Yenumula Gerard Prasad; Supervision: Kulandaivelu Velmourougane, Desouza Blaise, Yenumula Gerard Prasad

Conflict of interest

The authors declare that they have no conflict of interest.

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Tables

Table 1 Genome, origin, distribution, and attributes of wild and cultivated cotton species used in the study

	Diploid (2n=26)			
	Species	**Genome**	**Origin (Distribution)**	**Useful Economic traits**
1	*G. herbaceum* (cultivated)	A_1	Southern Africa (Afghanistan)	Yield and Fibre traits. Resistance to jassids, white flies, thrips, aphids, and cotton leaf curl virus (Kulkarni et al. 2009)
2	*G. arboreum* (cultivated)	A_2	Indus valley, Madagascar (Indo-Burma, China and Arab)	Sturdy plant type. Resistance to jassids, white flies, aphids, cotton leaf curl virus (Kulkarni et al. 2009), thrips (Stanton et al. 1992), drought tolerant, resistance to black root rot, reniform nematodes (Kantartzi et al. 2009) and spider-mites (Miyazaki et al. 2012)
3	*G. anomalum* (wild)	B_1	Angola, Namibia (Africa)	Fibre length, strength, elongation, & fineness, fibre yield. Resistance to bollworm, aphids, bacterial blight, wilt, jassids, mites, drought tolerant, cytoplasmic male sterility (Wang et al. 2016)
4	*G. barbosanum* (wild)	B_3	Cape Verede	Bacterial blight and jassid resistance (Gotmare et al. 2000)
5	*G. capitis-viridis* (wild)	B_4	Cape Verde Islands (Cape Verede)	High fiber quality, immune to bacterial blight, resistance to *Verticillium* and *Fusarium* wilt (Chen et al. 2015)
6	*G. thurberi* (wild)	D_1	Mexico (America)	Fibre length, fineness, strength, & elongation. Resistance to bollworm, *Fusarium* Wilt, Prolific boll bearing, High Ginning Out Turn, tolerance to mild frost via defoliation, high resistance to *Verticillium dahliae* (Wendel and Grover, 2015; Zhao et al. 2012)
7	*G. davidsonii* (wild)	$D_{3\text{-}d}$	Mexico (America)	Resistance to aphids, salinity tolerance (Zhang et al. 2016)
8	*G. aridum* (wild)	D_4	Mexico (America)	Resistance to drought, high seed index, cytpoplasmic male sterility. Salinity tolerance (Xu et al. 2013). Resistance to reniform nematode (Sacks and Robinson, 2009)
9	*G. raimondii* (wild)	D_5	Peru (America)	Fibre length, strength, elongation, & fineness, resistance to bollworm, jassids, bacterial blight, high lint index, drought tolerance (Gotmare et al. 2000). Resistance to jassids (Pushpam and Raveendran, 2006)
10	*G. stocksii* (wild)	E_1	East Africa, Arabia (Arabia)	Fibre length, strength, & elongation, fibre yield, drought tolerance. Strong fibers, resistance to leaf curl virus (Nazeer et al. 2014), resistance to reniform nematode (Yik and Birchfield, 1984)
11	*G. somalense* (wild)	E_2	North-eastern Africa	Resistance to bollworm (*Helicoverpa*). Resistance to reniform nematode (Yik and Birchfield, 1984). Extra

			(Arabia)	fiber strength, resistance to Egyptian bollworm and pink bollworm, arid tolerance (Zhou et al. 2004)
12	*G. australe* (wild)	G_2	Australia	Fibre yield, high Ginning Out Turn, drought tolerance, delayed morphogenesis of Gossypol gland. Glandless-seed and glanded-plant, resistance to aphids and spider-mites (Schuster et al. 1972). Resistance to *Fusarium* and *Verticillium* wilts, drought tolerance (Chen et al. 2014)
	Tetraploid (2n=52)			
	Species	**Genome**	**Origin (Distribution)**	**Useful economic traits**
13	*G. hirsutum* (cultivated)	$(AD)_1$	Central America (America)	Yield, Fibre length, Fibre strength
14	*G. barbadense* (cultivated)	$(AD)_2$	South America (America)	Extra-long staple fibre and fibre strength. Resistance to *Verticillium* wilt (Zhang et al. 2012)

Abbreviations

WCS, wild cotton species; CCS, cultivated cotton species; SBR, soil basal respiration rate; MBC, microbial biomass carbon; *q*CO2, microbial metabolic quotient; EE-GRSP, easily-extractable glomalin-related soil proteins; SPS, total soil polysaccharides; SoP, soil proteins; DHA, soil dehydrogenase activity; AcP, acid phosphatases; AlkP, alkaline phosphatases; BG, and β-glucosidase; POD, peroxidase; PPO, polyphenol oxidase; CAT, catalase; PAL, L-phenylalanine ammonia lyase

Figures

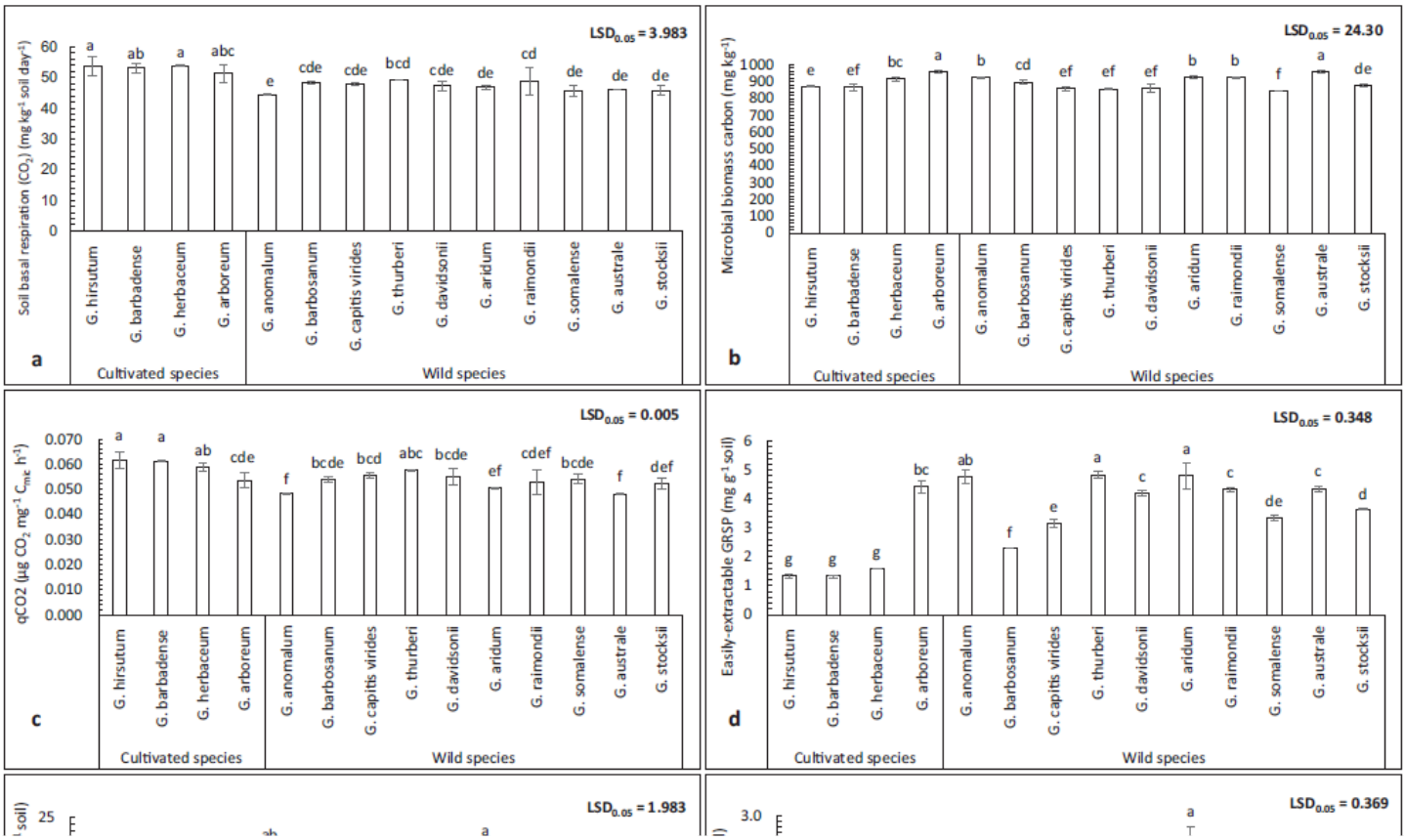

Figure 1

Soil biological activities in wild and cultivated cotton species **a**, Soil basal respiration; **b**, Soil microbial biomass carbon; **c**, Microbial metabolic quotient; **d**, Easily extractable GRSP; **e**, Soil polysaccharide; **f**, Soil proteins. Error bars indicate the standard deviation of the means from three biological replicates. Bars with different letters are statistically different according to the Tukey's honestly significant difference (HSD) test ($p < 0.01$) among wild and cultivated cotton species

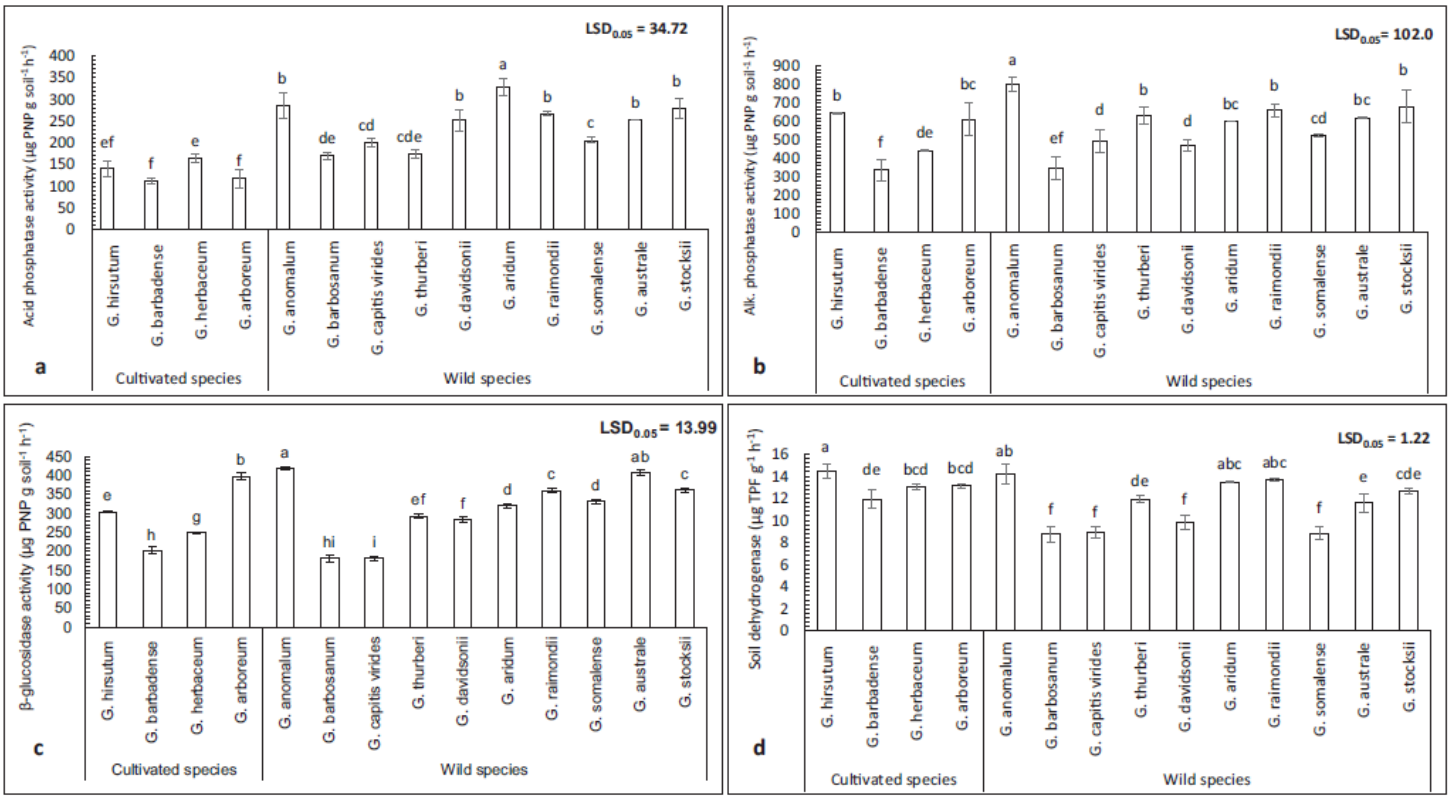

Figure 2

Soil enzyme activities in wild and cultivated cotton species **a**, Acid phosphatase activity; **b**, Soil alkaline phosphatase activity; **c**, β Glucosidase activity; **d**, Soil dehydrogenase activity. Error bars indicate the standard deviation of the means from three biological replicates. Bars with different letters are statistically different according to the Tukey's honestly significant difference (HSD) test ($p < 0.01$) among wild and cultivated cotton species

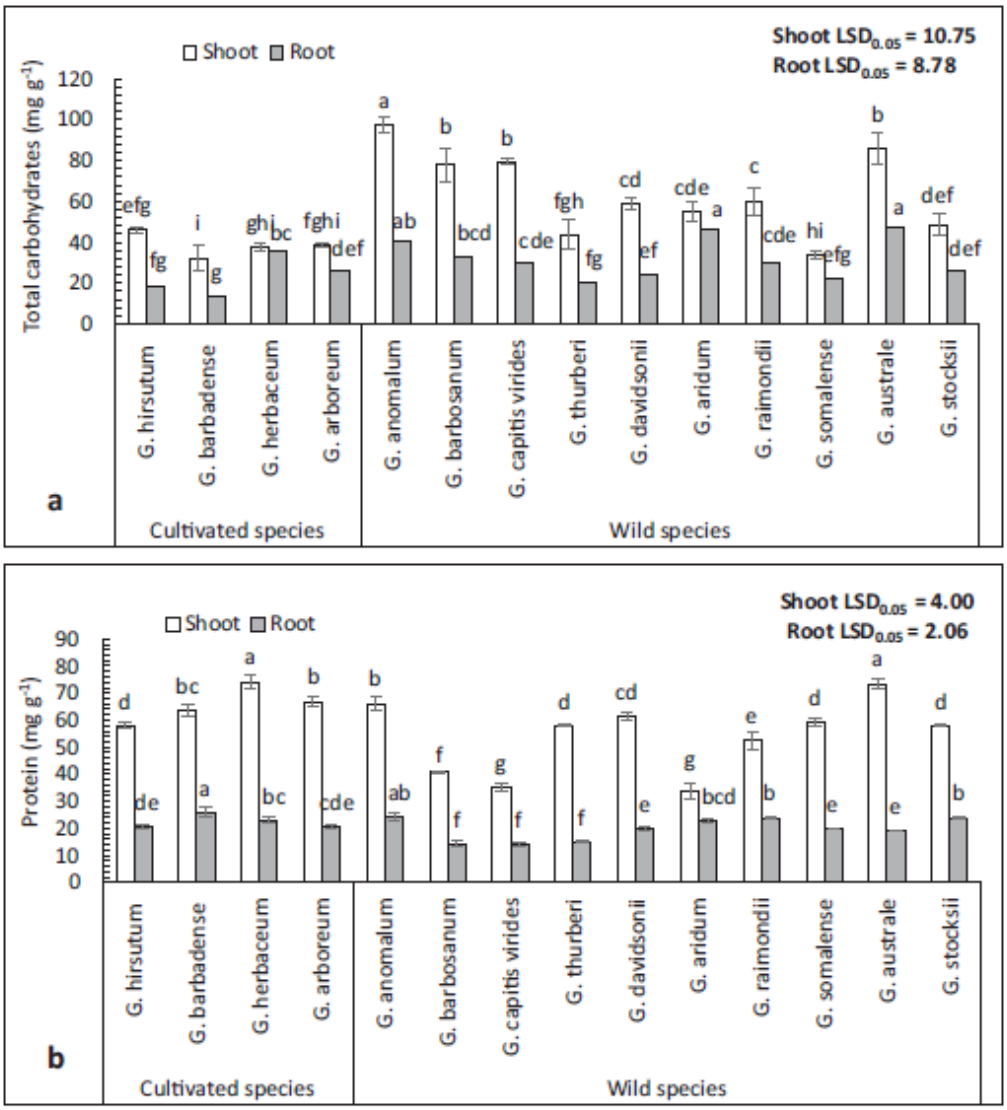

Figure 3

Total carbohydrate and protein content in shoots and roots of wild and cultivated cotton species **a**, Total carbohydrate content; **b**, Protein content. Error bars indicate the standard deviation of the means from three biological replicates. Bars with different letters are statistically different according to the Tukey's honestly significant difference (HSD) test ($p < 0.01$) among wild and cultivated cotton species

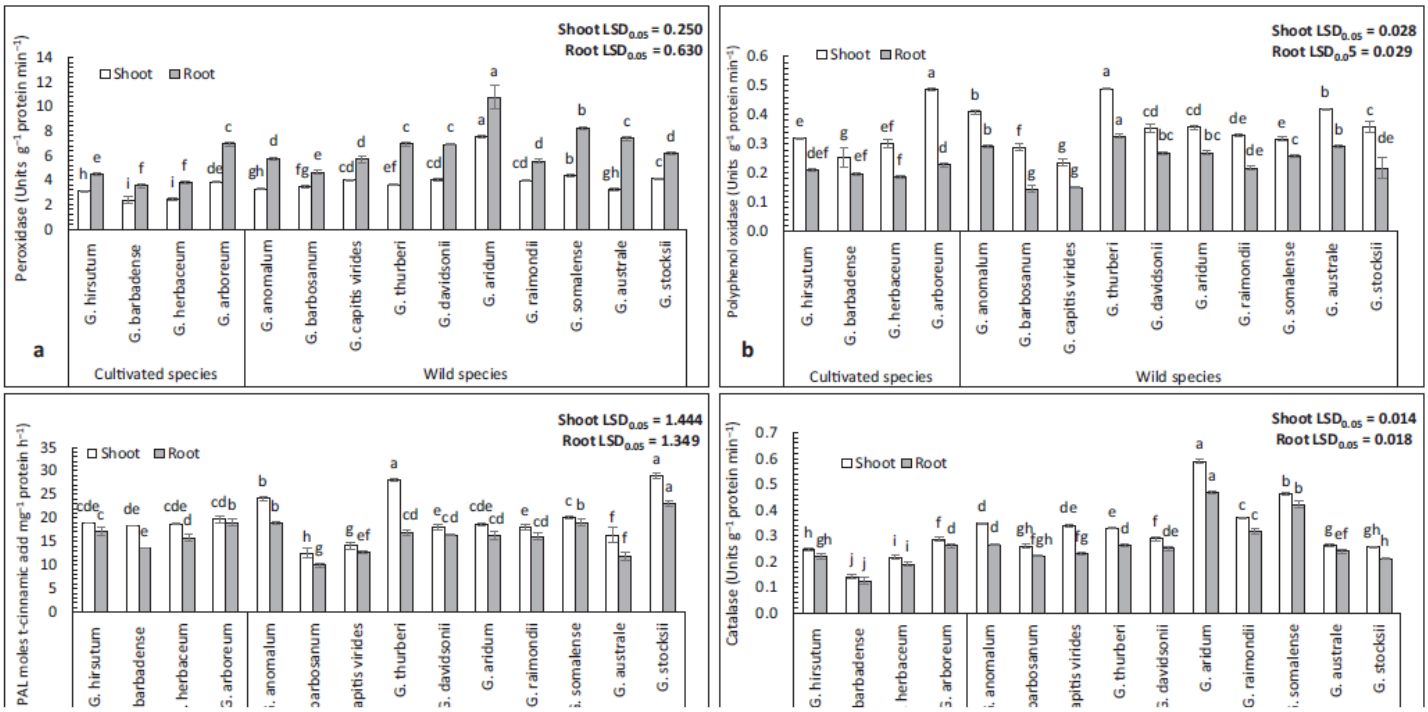

Figure 4

Plant defense and antioxidant enzyme activities in wild and cultivated cotton species **a**, Peroxidase (POD); **b**, Poly phenol oxidase (PPO); **c**, L-phenylalanine ammonia lyase (PAL); **d**, Catalase (CAT); **e**, Total phenol. Error bars indicate the standard deviation of the means from three biological replicates. Bars with different letters are statistically different according to the Tukey's honestly significant difference (HSD) test ($p < 0.01$) among wild and cultivated cotton species

Supplementary Files

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