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Research Article

SHADE-INDUCED PHENOTYPIC PLASTICITY AND ITS IMPACT ON THE ECONOMIC TRAITS OF PATCHOULI, *POGOSTEMON CABLIN* (BLANCO) BENTH., A HIGH-VALUE AROMATIC CROP

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Abstract: The study was conducted to assess the patchouli crop responses to varying light intensities: full-sunlight (open-condition), 30% shade, and 50% shade. It showed notable variations in growth, development, essential oil yield, and chemical composition between full-sunlight and partial-shade conditions. Plants grown in 50% shade exhibited significant increases in height (113.83 cm), inter-nodal length (8.81 cm), leaf area (59.17 cm^2), petiole length (3.78 cm), and width (3.44 mm) compared to open conditions. However, reductions in branches/plant (14.26), fresh weight (152.95 g), dry weight (29.64 g), leaf thickness (117.57 µm), number of trichomes (13.14 no./mm^2), number of oil glands (10.14 no./mm^2), and oil content (0.98%) were observed in 50% shade plants compared to open conditions. Anatomical modifications like bundle sheath extensions (BSEs) were present in 30% and 50% of shade-grown plants but absent in open-condition-grown plants.

Keywords: bundle sheath extensions (BSEs), oil glands, patchouli, phenotypic plasticity, shade stress.

Introduction

Shade affects a variety of developmental, physiological, and phenological traits in many plants. Increased shoot length via inter-node elongation, petiole growth, leaf position alteration, increased apical dominance, decreased tillering or branching, earlier flowering and a higher leaf area to biomass ratio [EVANS & POORTER, 2001]. The shade avoidance syndrome is defined by these characteristic alterations taken together. The physiological and developmental mechanisms behind this syndrome, which involve photoreceptors and phytohormones, are thoroughly described by [BALLARÉ & PIERIK, 2017]. A common feature of sun–shade adaptation changes in leaf anatomy. Sun leaves are smaller, have more leaf mass per area, are thicker, and have a larger palisade/spongy parenchyma ratio than shade leaves, and also have a higher stomatal density [TERASHIMA & al. 2006]. On the other hand, their stomata are noticeably smaller than those of shade leaves [BRESINSKY & al. 2008]. Besides these morpho-anatomical differences, sun and shade leaves have significant physiological characteristics. The photosynthetic light saturation rate is much higher in sun leaves than in shade leaves, as is the light compensation point, light saturation irradiance, and chlorophyll a/b ratio [MENDES & al. 2001]. Shade leaves, on the other hand, have more chlorophyll content per leaf dry mass and area, as well as a larger nitrogen allocation to light-harvesting complexes [NIINEMETS, 2010]. Furthermore, photoprotection based on non-photochemical quenching

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(NPQ), which relies on the violaxanthin cycle and the plastidic protein PsbS, is significantly enhanced in sun leaves [NIYOGI & TRUONG, 2013]. Sun and shade leaves differ in size, shape, and number of chloroplasts, in addition to structural morpho-anatomical and physiological characteristics. The size of the chloroplasts in sun leaves is smaller, and the thylakoid/grana ratio is lower than in shade leaves [BRESINSKY & al. 2008]. On the other hand, bundle sheath extensions (BSEs) confer plasticity in leaf structure and function in response to low irradiance levels and may act as a hub connecting leaf structure, photosynthetic performance, and water supply and demand [BARBOSA & al. 2018].

Patchouli (*Pogostemon cablin* (Blanco) Benth.) is an aromatic herbaceous plant that belongs to the Lamiaceae family. Because of its strong fixative characteristics, its oil is employed as a "base" substance in the fragrance industry. It is utilized as a flavoring agent in a variety of foods and also has a variety of medical benefits. It is an effective under-crop in areca nut and coconut orchards. It could also be accomplished by planting appropriate shade trees. The plant prefers partial shade but can also be grown in full-sun conditions. In horticultural crops, phenotypic plasticity can be used to boost productivity [LANDE, 2009], and it is an important concern for breeders grappling with the genetic association between important morphological attributes [WAITT & VLEVIN, 1998]. In this context, the present detailed investigation was undertaken into shade-induced morphological and anatomical plasticity in patchouli concerning economic traits.

Material and methods

Study area, *methodology*, *and plant material*

The present study was conducted at the CSIR-CIMAP Research Centre in Bengaluru with three different light intensity treatments: full sunlight (50000 lux), 30% shade (35000 lux), and 50% shade (25000 lux). The sunlight intensity was measured under the canopy of the Jack fruit tree via a handheld Lux meter (LX-102); the respective PAR values are 925 µmol $s^{-1}m^{-2}$, 647.5 µmol $s^{-1}m^{-2}$, and 462.5 µmol $s^{-1}m^{-2}$, respectively. Before plantations, the selected experimental area was confirmed for constant light intensity under the trees. The patchouli cultivar CIM-Shrestha was selected for the present study and was grown under field conditions at an optimum temperature of 32±3 °C. The treatments were replicated eight times in a randomized complete block design (RCBD), and recommended doses of fertilizer and cultural practices were adopted.

Morphological, *growth*, *and yield parameters*

Plant growth and yield parameters were taken at the harvest time (after five months of plantation). The leaf and stem color of the plants were recorded by visual observations. Plant height (cm), inter-nodal length (cm), and petiole length (cm) were measured using a graduated ruler. Petiole diameter (mm) was measured using a digital caliper rule. The number of branches and leaves was counted. The leaf area was determined by using a leaf area meter (LI-COR 3100C, Nebraska, USA). Chlorophyll content was recorded by the SPAD-502 meter at the time of harvest, and mean values for each treatment were calculated. The infestation of leaf rollers was observed and recorded as the number of larvae per plant.

Anatomical observations

The leaf samples for the anatomical studies were collected fully expanded in the third node from the apical bud. Leaves were cross-sectioned freehand with a razor aid in a manual microtome and mounted with 5% glycerin for leaf thickness measurement. The thickness of the leaf blade and palisade parenchyma was measured in µm at the midrib and then at the lamina, 1 mm to its left and right. Stomatal density (mm^2) and chloroplast number in the guard cells were counted on the abaxial side using the nail polish impression method. Trichomes (non-glandular) and oil glands (glandular) were counted by staining the decolorized leaf segment with 1% Methylene blue for one minute. All the observations were taken under the light microscope (Olympus CX 31) at 40 X magnification. In all the cases, ten readings were taken five times, and the mean was calculated.

Phenotypic plasticity analysis

The phenotypic plasticity index (PI) was calculated separately for the measured plant traits such as growth and yield, leaf anatomy, chlorophyll content, and chemical compounds [GREWELL & al. 2016]. The difference between the maximum and minimum values was divided by the maximum value to produce the index. Higher PI values, which are closer to one, imply that the variable is more plastic [CHEPLICK, 1995]. The mean PI was derived by averaging the plasticity index of individual groups such as growth and yield, leaf anatomy, chlorophyll content, and chemical compounds.

Oil extraction and analysis

To evaluate the essential oil contents, dried samples of patchouli leaves were subjected to hydro distillation (2000 mL capacity flask) for 5-6 hours using a Clevenger-type apparatus. The percentage yield of oil (g/100 g) in each of the samples was calculated concerning the dry weight of the leaves. The extracted oil samples were further subjected to the identification of compounds with GC and GC-MS.

Statistical analysis

The experimental data of all observations were subjected to one-way ANOVA by SPSS (19.0) and the values of least significant differences (LSD) were set at 1% and 5%. The simple correlation coefficient between 11 characters was carried out as per the procedure suggested by SINGH & CHAUDHARY (1995). The principal component analysis (PCA) method explained by HARMAN (1976) was followed in the extraction of the components. PCA and biplot graphical display was performed using R-studio software. A PCA-based selection index was constructed using computed principal components wherein data was normalized and weights were assigned based on the PCs having an Eigenvalue greater than one.

Results

Plants ability to grow effectively is severely hampered by shading stress. For the development of aromatic crops, it is critical to understand how the patchouli plant's morpho-anatomical adaptations are formed in response to reduced light conditions. The effects of shade stress on the growth, development, and yield of the patchouli cultivar CIM-Shrestha were investigated and analyzed. The data are shown in Table 1.

Morphological, growth, and yield traits

Patchouli plants exhibited significant variability in morphological traits under different light intensity regimes that were observed and recorded. The leaf color was dark green and the young shoot was green in color in 30% (Figure 1b) and 50% (Figure 1c) shade grown patchouli, whereas it was green-yellowish in leaf color and purple in young shoots in plants that were grown under open conditions (Figure 1a). Significant increases in shoot length (113.83 cm), inter-node (3.78 cm), and petiole (3.78 cm), as well as leaf area (59.17 cm^2), while a drastic reduction in the number of branches (14.26), leaves (96.62), total fresh weight (152.95 g), dry weight (29.64 g), oil content (0.98%) and oil yield (0.30 g) per plant were recorded in the 50%

shade grown plants compared to open-condition grown patchouli plants. However, there is no significant variation noticed in the patchouli plants between the 30% shade grown and open–condition-grown plants in terms of oil content (1.97% and 2.04%, respectively) and oil yield (1.67 g and 1.89 g, respectively).

Leaf anatomical traits and SPAD chlorophyll content

Significant leaf anatomical plasticity was detected in the plants grown under different light environmental conditions. The leaf thickness was drastically reduced with increasing shade conditions. It was observed in the 50% shade (Figure 1f) grown plants (117.57 μm) followed by 30% shade (Figure 1e) grown plants (216.00 μm) compared to open condition grown (Figure 1d) plants (239.14 μm), while the thickness of palisade parenchyma tissue was also decreased in the patchouli plants grown under 50% shade (26.28 μm) followed by 30% shade (46.21 μm) compared to open condition grown (Figure 1d) plants (56.86 μm). Furthermore, the number of stomata (12.43 no./mm^2), trichomes (13.14 no./mm^2), and oil glands (10.14 no./mm^2) was found to be very low in 50% shade (Figure 1l) grown patchouli plants compared to 30% shade (Figure 1k) grown and open condition (Figure 1j) grown plants, whereas the number of chloroplasts per stomatal guard cell was found to be highest in 50% shade (13.71 no./stomata). Interestingly, major anatomical modifications such as bundle sheath extensions (BSEs) were detected in the leaf petiole of 50% (Figure 1i) and 30% of shade-grown plants (Figure 1h). Moreover, the BSEs were not found in the patchouli plants grown in open condition (Figure 1g). Furthermore, the chlorophyll content was highest in patchouli plants grown in 50% shade (46.96), 30% shade (43.03), and open conditions (40.43).

Chemical composition of patchouli essential oil

The chemical composition was analyzed, and the major chemical constituents of the oil, such as patchouli alcohol (patchoulol), α-Bulnesene (δ-guaiene), and β-Caryophyllene were considered. Of these, the compound β-Caryophyllene was recorded at the highest (3.54%) in 50% shade grown plants, followed by open-condition grown plants (3.13%), compared to 30% shade grown (2.94%) patchouli plants. However, the patchouli alcohol percentage was found to be the lowest (42.44%) in 50% shade-grown plants when compared to open-condition (47.72%) and 30% shade-grown plants (45.21%). There was no significant variation in α-Bulnesene between treatments, such as 12.28%, 11.59%, and 11.41% in open-condition, 30%, and 50% shade-grown plants, respectively.

Phenotypic plasticity index

The plasticity index showed variable values between the four analyzed groups, viz., growth and yield, leaf anatomy, chlorophyll content, and chemical compounds of the oil under two different shade levels. Box plots (Figure 2) comprising these groups exhibited the highest PI for growth and yield traits (0.56) followed by leaf anatomical traits (0.51), and the lowest for the chemical component traits (0.11) and chlorophyll content (0.14) in the 50% shade-grown plants. In the 30% shade, plants also exhibited phenotypic plasticity, but they had the lowest PI of all the analyzed traits, such as 0.20 for leaf anatomical traits, 0.18 for growth and yield traits, 0.06 for chlorophyll content, and 0.05 for chemical components.

Correlation studies

The oil yield per plant in patchouli had a positive correlation with the plant height (r=0.109), inter-nodal length (r=0.141), the number of branches per plant (r=0.067), number of leaves per plant (r=0.202), leaf area (r=0.201), oil glands (r=0.315), trichomes (r=0.013), fresh weight (r =0.227), and dry weight (r=0.669), while the leaf thickness (r=-0.041) was negatively correlated with the oil yield. Concomitantly, the oil glands had a strong association with leaf area (r=0.566), leaf thickness (r=0.974), as well as trichomes (r=0.306). However, the dry weight per plant had a highly significant positive correlation with the plant height (r=0.483), the number of branches per plant (r=0.672), the number of leaves per plant (r=0.573), leaf area (r=0.562), leaf thickness, and fresh weight (r=0.606), while the inter-nodal length (r=-0.447), oil glands (r=-0.407), and trichomes (r=-0.501), were negatively correlated with the dry weight in the patchouli (Table 2).

Principal component analysis (PCA)

To analyze the pattern of relationships between traits, PCA was carried out, considering the selected 11 quantitative traits simultaneously (Table 3). Out of eleven PCs formed, only one PCs exhibited more than one Eigenvalue (3.040) and showed about 84.07% variability. Eigenvalues above one generates components with significant quantities of information about the original variations. The PC I accounted for the maximum proportion of total variability in the set of all variables studied, and the remaining components accounted for progressively less variation. PC I accounts for approximately 84.07% of the variation and is primarily contributed by leaf area (0.312), internode length (0.300), and plant height (0.292), whereas PC II (5.51) is more related to plant growth and oil yield contributing traits such as oil glands (0.354), fresh weight (0.341), plant height (0.327), internode length (0.309), leaf area (0.307), dry weight (0.303), oil yield (0.275), trichomes In addition, biplot analysis of eleven traits formed by the components PC I and PC II retained 89.58% of the original variance in the patchouli plant grown under three different conditions, *viz.*, open, 30% shade, and 50% shade. The length of arrows showed the proportion of contribution, and the direction of the arrows indicated whether the proportion was positive or negative, as shown in Figure 3.

Pest infestation

During the study period, leaf roller (*Pachyzacia stultalis*) infestation exclusively noted in 50% shade-grown patchouli, with two to five larvae per plant, resulting in the browning and drying of the affected areas.

Discussions

Plants can change their physiology and morphology in response to environmental challenges, which is reflected in their phenotypic variation. Plants that grow in low-light environments frequently undergo such changes [MARKESTEIJN & al. 2007]. The present findings showed that there are strong morpho-anatomical variations between sun and shade-grown leaves in patchouli, which match the situation in “traditional” angiosperm sun and shade leaves [GRATANI & al. 2006]. The morphological characteristics of patchouli plants grown in 50% shade showed a significant increase in leaf color, plant height, inter-nodal length, and leaf area. The improved leaf color was correlated with increased foliar chloroplast number as well as chlorophyll concentration in response to shading. A comparison of the relative levels of photosynthetic pigments in shade-growing patchouli plants revealed that chlorophyll b and carotenoids accumulate preferentially over chlorophyll a [MISRA, 1995]. To sustain the crop's normal life under shade conditions, increasing chlorophyll content is a mechanism to boost light interception. The increased chlorophyll content is to improve the effectiveness of photosynthetically active radiation (PAR) absorption, showing crop adaptability to reduced light intensity [CARTECHINI & PALLIOTTI, 1995].

Plants usually develop a higher leaf area when grown under low-light conditions. In shade-grown patchouli plants, leaf area increased while leaf number decreased as a result of a 50% increase in the shade. Several studies have shown that increasing leaf area increases net photosynthesis [SULANDJARI & al. 2005]. The plastic response of leaf area increase enables plants to maintain high performance under shading and has to constitute adaptive plasticity [EVANS & POORTER, 2001]. On the other hand, increasing the shade level, which decreases the leaf size by reducing palisade parenchyma tissue, was observed in shade-grown (30% and 50%) patchouli plants. The shade reduces the size of the plant leaf by controlling cell proliferation and expansion while also reducing the quantity and size of cells. It causes thinner leaves with thinner palisade tissues [EVANS & POORTER, 2001], resulting in a structure that hinders CO_2 dissolution and transport. Many plant species have smaller and thinner leaves as a reaction to shade stress. Changes in stomatal densities on the adaxial and abaxial surfaces reveal the anatomical plasticity of patchouli as a consequence of the cultural environment [TERASHIMA & al. 2001].

The development of bundle sheath tissue in the leaf petiole of patchouli plants has been shown to be adaptive anatomical plasticity under shade conditions. Bundle sheaths may act as flux sensors or "control centers" for leaf water transport [LEEGOOD, 2008] and bundle sheath extensions (BSEs), which connect the vascular bundle to the epidermis and so lower the resistance in the water path between the supply structures (veins) and the water vapor exits, improving hydraulic integration of the lamina. The BSEs are most typically found in minor veins, but depending on the species, they can occur in veins of any order [WYLIE, 1952]. As a result, such leaves, and thus the species that have them, are referred to as "heterobaric", as opposed to "homobaric" plants that do not have BSEs. It was reported that BSEs could play an ecological role in the leaf by influencing mechanical and physiological characteristics [TERASHIMA, 1992] and more experimental support, implying that BSEs could be adaptive traits. Concomitantly, BSEs increased in the leaves, which improved the light transmission within the leaf blade [NIKOLOPOULOS & al. 2002].

The oil yield in patchouli is mainly dependent on the number of oil glands and trichomes, leaf area, plant height, the number of branches and leaves, as well as fresh weight and dry weight. This phenotypic variation is highly influenced by the shade (50%) condition. As a result, a 50% reduction in the oil yield has been recorded in patchouli plants which were grown under the 50% shade conditions. When patchouli is grown in a plantation with more than 30% shade, the infestation of leaf roller (*Pachyzacia stultalis*) is severe, causing significant crop yield damage. During the months of October and December, the leaves are completely infested [GAHUKAR, 2018]. However, patchouli has strong insecticidal activity against lepidopteran pests, and this oil has sufficient efficacy to be considered as a component of an essential oil-based insecticide that targets lepidopteran pests [MACHIAL & al. 2010]. Trichomes are a type of morphological adaptation that protects plants by secreting chemicals to protect the leaves from insect pest [BARBOSA & al. 2018]. This clearly indicated that decreases in the number of glandular and non-glandular trichomes and oil content in the 50% shade-grown plants make them most susceptible to leaf roller infestation due to the decreases in defense mechanisms.

Table 1. Comparison of growth, yield, leaf anatomy, chlorophyll content, and oil chemical compounds in full-sunlight and shade (30% and 50%) grown patchouli plants

Parameters	Full Sunlight	30% Shade	50% Shade	CV (%)	Phenotypic Plasticity Index (PI)	
					(30% Shade)	(50% Shade)
Growth and yield traits						
Plant height (cm)	80.71^{c}	97.50^{b}	113.83^{a}	10.06	0.20	0.29
Number of branches plant^{-1}	30.51^{a}	24.62^{b}	14.26^{c}	15.87	0.19	0.53
Number of leaves plant^{-1}	412.35^{a}	338.46^{b}	96.62^{c}	5.02	0.17	0.77
Leaf area (cm^{2})	25.83^{c}	38.45^{b}	59.17^{a}	12.73	0.48	0.56
Petiole length (cm)	1.52^{b}	1.77^{b}	3.78^{a}	13.31	0.14	0.6
Petiole width (mm)	1.59^{c}	2.31^{b}	3.44^{a}	5.88	0.31	0.54
Internode length (cm)	4.95^{c}	6.56^{b}	8.81^{a}	11.02	0.24	0.44
Fresh weight plant^{-1} (g)	266.35^{a}	271.32^{a}	152.95^{b}	6.66	0.01	0.44
Dry weight plant^{-1} (g)	92.99^{a}	85.01^{b}	29.64^{c}	8.40	0.08	0.68
Oil content plant^{-1}(%)	2.04^{a}	1.97^{a}	0.98^{b}	13.54	0.03	0.52
Oil yield plant^{-1}(g)	1.89^{a}	1.67^{a}	0.30^{b}	14.79	0.11	0.84
Leaf anatomical traits						
Leaf thickness (µm)	239.14^{a}	216.00^{b}	117.57^{c}	9.49	0.09	0.51
Cuticle thickness(µm)	6.84^{a}	5.88^{b}	3.7^{c}	13.17	0.14	0.46
Thickness of palisade parenchyma (µm)	56.86^{a}	46.21^{b}	26.28^{c}	6.77	0.18	0.53
stomatal density (number mm^{-2})	20.43^{a}	15.43^{b}	12.43^{b}	23.33	0.24	0.39
Chloroplasts number stomata^{-1}	8.43^{c}	11.71^{b}	13.71^{a}	9.67	0.38	0.38
Oil glands (number mm^{-2})	22.71^{a}	18.57^{a}	10.14^{b}	24.16	0.18	0.55
Trichomes (number mm^{-2})	68.29^{a}	51.00^{b}	13.14^{c}	14.35	0.25	0.80
SPAD Chlorophyll content						
Chlorophyll content	40.43^{c}	43.03^{b}	46.96^{a}	4.93	0.06	0.14
Chemical compounds of oil (%)						
Patchouli alcohol	47.72^{a}	45.21^{ab}	42.44^{b}	6.49	0.05	0.11
α-Bulnesene (= δ-guaiene)	12.28^{a}	11.59^{a}	11.41^{a}	10.05	0.05	0.07
β-Caryophyllene	3.13^{b}	2.94^{b}	3.54^{a}	5.13	0.06	0.17

Table 2. Correlation matrix for oil yield in patchouli

	Oil yield	Plant height	Inter-node length	No. of branches	No. of leaves	Leaf area	Leaf thickness	Oil gland	Trichomes	Fresh wt.	Dry wt.
Oil yield	1										
Plant height	0.109	1									
Inter-node length	0.141	0.994**	1								
No. of branches	0.067	0.398**	-0.388**	1							
No. of leaves	0.202	0.302**	0.305**	0.766**	1						
Leaf area	0.201	-0.329**	0.321**	-0.718**	-0.995**	1					
Leaf thickness	-0.041	-0.072	-0.131	0.559**	0.468**	0.397**	1				
Oil gland	0.315**	-0.062	-0.125	-0.623**	-0.637**	0.566**	0.974**	1			
Trichomes	0.013	-0.851**	-0.849**	-0.644**	-0.349**	0.334**	0.107	0.306**	1		
Fresh wt.	0.227*	0.952**	-0.942**	0.534**	0.342**	0.321**	0.356**	-0.064	-0.928**	1	
Dry wt.	0.669**	0.483**	-0.447**	0.672**	0.573**	0.562**	0.343**	-0.407**	-0.501**	0.606**	1

Highly significant ($p<0.001$) = **; Significant ($p<0.05$) = *

Table 3. The Eigen values, per cent variance and per cent cumulative variance for three principal components (PCs) and factor loading between PCs and traits studied in patchouli plant

Principle component	PC I	PC II	PC III
Eigen values	3.040	0.778	0.668
Proportion of variation	84.07	5.51	4.05
Cumulative proportion	84.07	89.58	93.63
Oil yield/plant	-0.315	-0.048	0.275
Plant height	0.292	-0.423	0.327
Inter-node length	0.300	-0.095	0.309
No. of branches/plant	-0.284	-0.132	-0.509
No. of leaves/plant	-0.323	-0.107	0.105
Leaf area	0.312	-0.102	0.307
Leaf thickness	-0.290	-0.468	-0.072
Oil glands	-0.261	0.672	0.354
Trichomes	-0.310	-0.164	0.125
Fresh wt.	-0.305	-0.266	0.341
Dry wt.	-0.312	-0.013	0.303

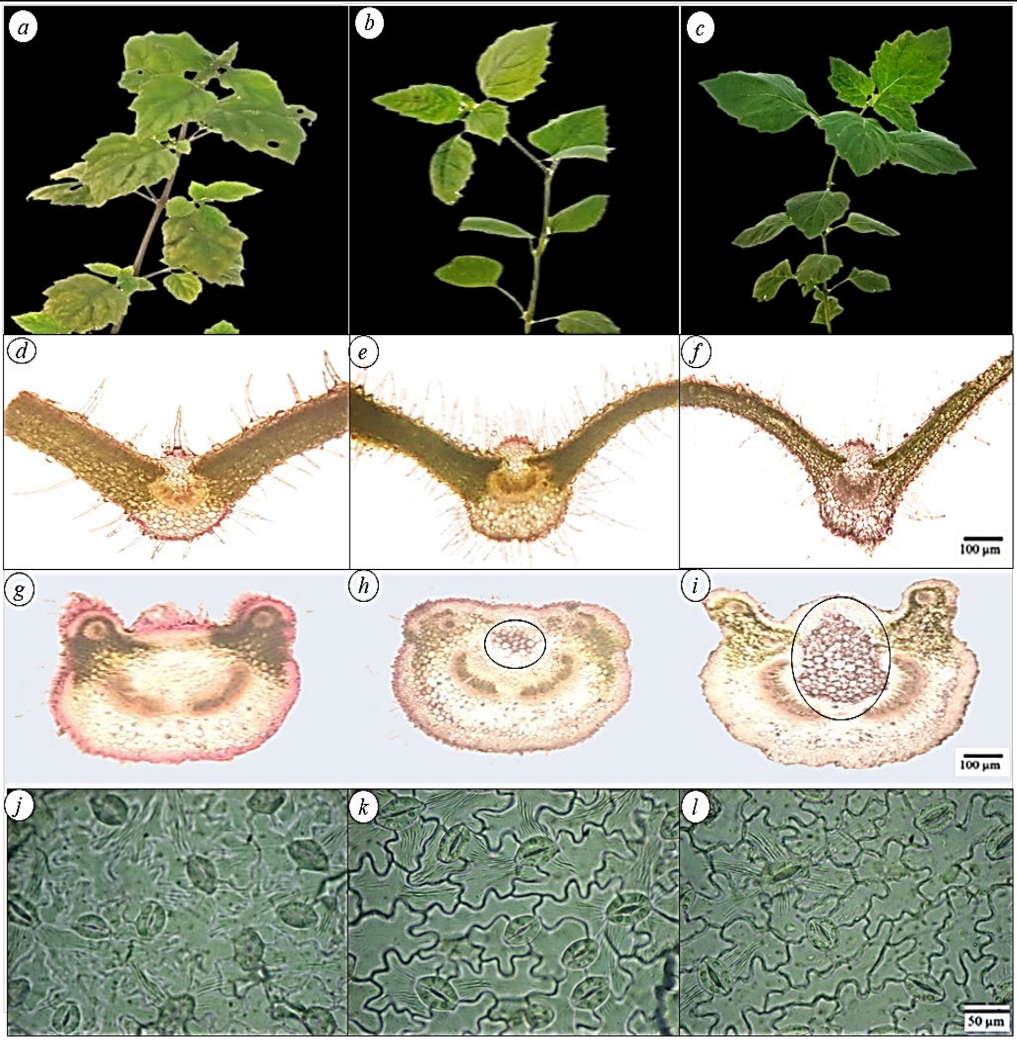

Figure 1. Plant morphology: (a) full-sunlight grown plant, (b) 30% shade grown plant and (c) 50% shade grown plant; Cross section of the leaf blade: (d) full-sunlight, (e) 30% shade, and (f) 50% shade grown plant; Cross section of the petiole: (g) full-sunlight, (h) 30% shade, and (i) 50% shade grown plant; Leaf stomatal density: (j) full-sunlight, (k) 30% shade, and (l) 50% shade grown plant. (* Circle marks show the bundle sheath extensions region in the cross section of petiole)

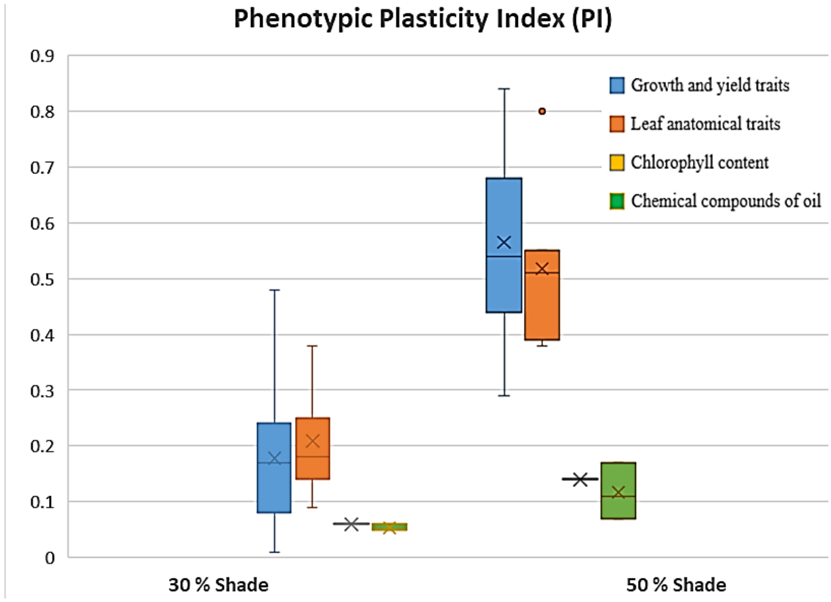

Figure 2. Box plots showing the phenotypic plasticity index (PI) distribution for each of the measured traits between 30% shade and 50% shade-grown patchouli plants

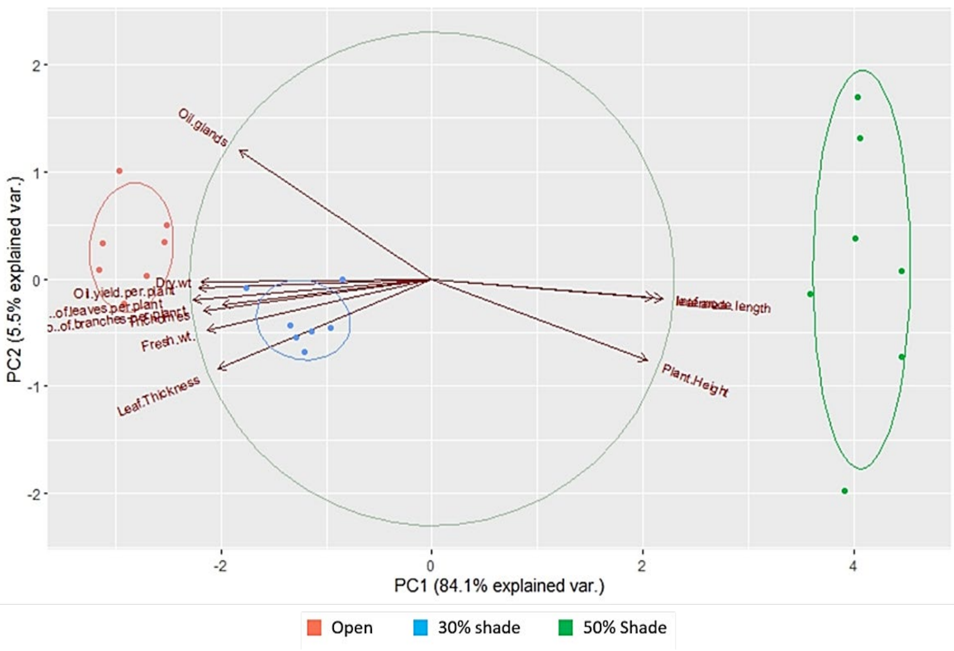

Figure 3. Biplot diagram of principal components

Conclusions

The patchouli plants when grown under more than 50% shade conditions exhibited the highest phenotypic plasticity in all the traits compared to 30% shade grown plants as well as open condition grown plants. The expression of a higher level of phenotypic plasticity in patchouli plants under shade (50%) has shown a negative impact on essential oil yield production and a positive effect on the ability to thrive under limited light intensity conditions.

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