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RESEARCH ARTICLE

Allelopathy of invasive *Tithonia diversifolia* (Hemsl) A. Gray on *Pisum sativum* L. and its linkage with canopy openness in a global biodiversity hotspot

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Abstract

Allelochemicals are the secondary metabolites present in the leaves or other parts of the invasive alien plants that can either stimulate or inhibit the development of the native plants. To this end, an emerging invasive plant, i.e., *Tithonia diversifolia* from Asteraceae is inadequately explored in terms of allelopathy, especially in relation to its influence on the germination and growth of edible crops. Thus, the present study aims to study its allelopathic effect on common bioassay crop i.e., *Pisum sativum,* grown in Mizoram to help validate the 'novel weapon hypothesis (NWH). In addition, the ecological investigation was performed with respect to the canopy openness, leaf area index (LAI) and photosynthetically active radiation (PAR) as they can be inextricably linked with invasive spread and modulation of allelopathy. Results showed that with increase in the concentration of *T. diversifolia* derived fresh leaves aqueous extracts (FLE), the growth parameters (rate of seed germination, seed radicle, seed plumule and biomass) of *P. sativum* decreases, which may be ascribed to the inhibitory effect of allelochemicals. Last, the study also observed that the higher canopy openness facilitates the spread of *T. diversifolia* due to high light availability, while the lower canopy gaps restrict the growth of *T. diversifolia.* Henceforth, in control/containment perspective, the sustenance of intact canopy can sustainably manage and reduce the *T. diversifolia* infestation in agriculture systems by alleviating its field allelopathic effects on edible crops, thereby help maintain crop yield and food security.

Keywords: allelopathy; bioassay; canopy openness; edible crops; invasive alien plants; sustainable management

Introduction

In Anthropocene, ecological issues such as habitat destruction and ecological alteration can arise the introduction of invasive alien plant species into novel introduced habitats which in turn leads to biodiversity erosion, loss of ecosystem services and species extinction (1-3). Release of allelochemical *via* multiple mechanisms is one way that could affect native plants or edible crops, mediated by perturbation in physiological functions, such as growth, germination, photosynthesis, respiration, water and hormone balance of nearby edible crops (4, 5). Interestingly, allelopathy can either stimulate or inhibit the development of native plants (*Medicago sativa* L.) and agricultural crops (*Zea mays* L.) of nutritional value through the release of secondary metabolic compounds or allelochemicals (6). The allelochemicals are generally water soluble and are emitted into the environment by the process of volatilization, leaching, root exudation and decomposition of plant residues (7, 8). Invasive alien plants derived allelochemicals are produced as secondary metabolites, which remarkably modulate the chemical ecology, invasive spread and vegetation dynamics (9-11). Previous works reported that the majority of allelochemicals are found in leaves or other parts of the invasive alien plants (12). Moreover, quantification and detection of allelochemicals (minor compounds) were quite obscure due to their complex and intricate nature (12). Therefore, previous studies recommended the use of bioassay crop plants, which are more sensitive than chemical methods and are further linked with crop yield and food security (12, 13). In this respect, model bioassay crops can manifest sensitivity in terms of morphological, physiological and biochemical changes, unlike chemical quantification (13). Moreover, the elucidation of mechanism linked with allelopathy can help achieve sustainable management of this invasive alien plant.

The Asteraceae family comprises of many invasive alien plants and weeds, which are enriched with multiple allelochemicals that can perturb ecosystem functioning and agricultural productivity (14). From this family, *Tithonia diversifolia* (Hemsl.) A. Gray is an emerging invasive plant due to its aggressive growth rate and heavy seed production, especially in an Indo Burma global biodiversity hotspot of immense ecological importance (15-17). They are known to exhibit allelopathy by exerting both stimulatory and inhibitory or phytotoxic attributes which are widely described in South African, Chinese and Indian Himalayan Region (18-21). In this respect, past studies observed that the root exudates of *T. diversifolia* is known to inhibit the germination, growth and chlorophyll accumulation of tomato; however, the impacts of leaves extracts were not elucidated (22). Further, a recent study also reported that the increase in concentration of aqueous extract of the plant parts of *T. diversifolia* reduced the germination percentage, radicles and plumules length of various crops (e.g., *Z. mays*, *Glycine max* L., *Helianthus annuus* L., *Sorghum bicolor* L., *Vigna unguiculata* L. and *Eleusine indica* L.), which are inextricably linked with human dietary or nutritional requirements (23). However, *T. diversifolia* has also been used as a green manure and fertilizer for some crops (such as *Oryza sativa* L. and *Brassica oleracea* var. Brotrytis L.) in Kenya and Indonesia (24-26). There is an uncertainty about the potential use of *T. diversifolia* for agricultural crop yield, despite the positive outcomes, as the effects may be crop-specific (25). This crop-specific stimulatory and inhibitory effects in terms of *T. diversifolia* driven allelopathy warrant exploration of allelochemic studies on wide range of edible plants for concrete policy measures. Furthermore, the allelochemic potential of *T. diversifolia* was not explicitly investigated through the lens of canopy density or gaps. Therefore, the present study aimed to study allelopathy of leaves derived aqueous extract of *T. diversifolia,* the common pea i.e., *Pisum sativum* L. for elucidating effects on edible crops in agriculture systems. The rationale behind selection of *P. sativum* from Fabaceae family was its wide use as edible crops and role as model bioassay experimental plant for genetic/molecular biology, ascribed to its short life span i.e., 50-70 days (27, 28). In addition, this fast-growing crop is an essential human diet since they are enriched with protein, carbohydrates and other nutrients (29). Therefore, this leguminous plant is helpful in preventing disorders linked to deficiencies, particularly those caused by folate or selenium deficiency (30).

In India, there are numerous scientific studies on invasive plant species from Asteraceae such as *Parthenium hysterophorus* L., *Chromolaena odorata* L., *Mikania micrantha* Kunth and *Ageratum conyzoides* L, but the study and documentation on *T. diversifolia* is scant in northeast (NE) India and negligible in Mizoram, NE region despite its intense invasiveness (31- 33). In this context, *T. diversifolia* was reported to invade in the agricultural landscapes of Mizoram, causing hindrance to local farmers while harvesting their crop plants and pose a threat to the biodiversity of native plants (21). Henceforth, the present study aims to investigate the allelopathic effect of *T. diversifolia* on a common pea crop i.e., *P. sativum* grown in Mizoram with concomitant elucidation of its interrelationship with the canopy openness (the gap in the foliar portion of canopy structure), LAI (which is the total surface area of leaves per unit of ground area) and PAR (the solar radiation which serves as the primary energy source for biomass by regulating the photosynthetic rate and influencing plant growth) for control/ containment perspective. Henceforth, the study on linkage of canopy openness, LAI and PAR in an interrelated framework with spread of *T. diversifolia* and its implications on allelopathy will be in fact pioneer in Mizoram, an integral landscape of Indo Burma global biodiversity hotspot. In this sense, present study is novel as it elucidates the allelopathy of an emerging invasive alien plant on edible leguminous crop and attempt to establish an interrelationship with canopy gaps in its infested region to devise sustainable management prospects. Notably, to our knowledge, the present study is pioneer in validating the 'novel weapon hypothesis (NWH)' (34) of *T. diversifolia* by performing bioassay experiment on model leguminous plant of wide dietary intake.

Materials and methods

Study area

The present study was conducted in Aizawl which is located in the north-eastern (NE) states of India which lies between 92°3'- 92°60' E longitude and 21°58'- 24°85' N latitude and occupied 6.96 % of the total geographical area of the state (35-37) (Fig. 1). The state has the highest forest cover in percentage accounting for 85.34 % in the latest Forest Survey of India (38) report. This study area is a part of the Indo-Burma biodiversity hotspot in India (32, 39). Only 6.75 % of the geographical area of the state comes under protected area, which includes a significant number of endemic species in both flora and fauna, especially plants (40, 41).

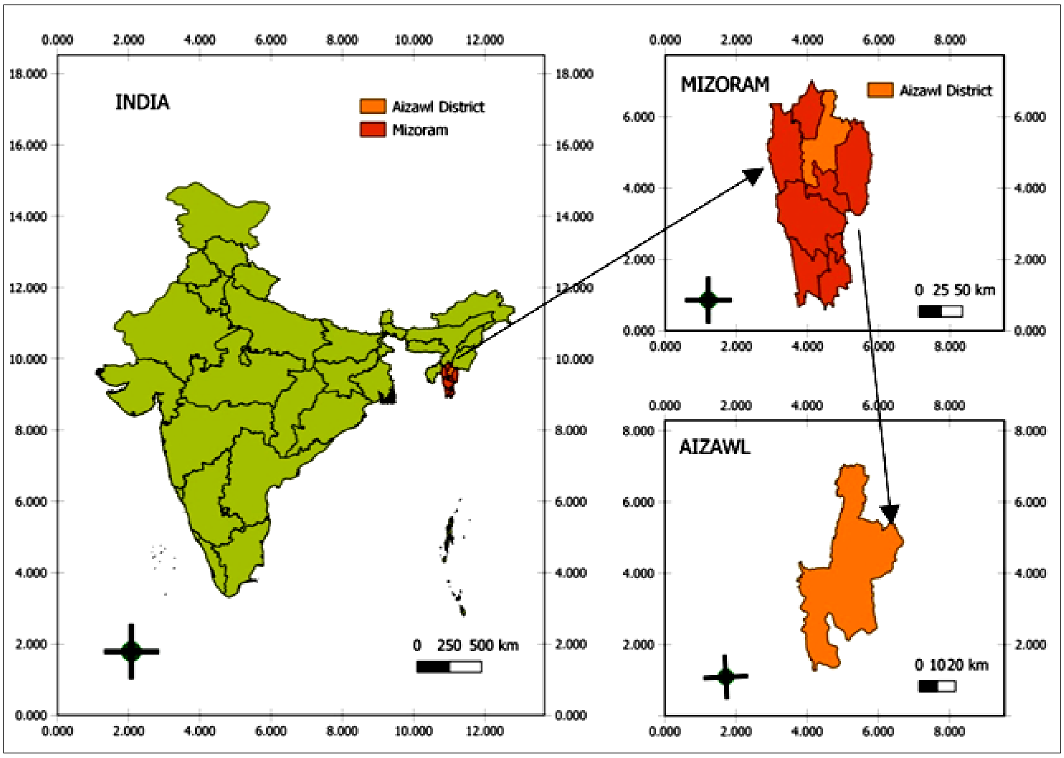

Fig. 1. Map of study area showing the sites of soil samples collection and canopy gaps related vegetation studies in NE India, an Indo Burma biodiversity hotspot region.

Collection of plant material

T. diversifolia is an invasive plant that grows in all parts of Mizoram (21). The leaves of *T. diversifolia* were collected from the roadside of invaded region and washed with clean water to remove dust. The clean fresh leaves were measured and prepared for aqueous extract using standard methodologies (42).

Preparation of FLE of *T. diversifolia*

The standard method was adapted for the preparation of aqueous leaf extract of *T. diversifolia* with slight modification (43). The freshly leaves collected from the site were cut into small chips of about 4 cm length and soaked in conical flask containing 100 mL distilled water and agitated in a rotary shaker (Rotary Flask Shaker, Scientech, Science Enterprises, Delhi, India) at 140-150 rpm for 18 hr at 27 °C. The aqueous extract was then filtered through 2 layers of filter papers (Whatman No. 41) to remove solid materials and maintained it eventually into 4 concentrations (i.e., 50 mg/L, 37.5 mg/L, 25 mg/L and 12.5 mg/L). Besides these concentrations of aqueous extracts, a control (distilled water) was used to compare the results.

Germination experiment

Ten seeds of *P. sativum* were kept in petri dishes containing 5 mL of different extract concentrations and control were added in petri dishes and covered with the filter papers. All experiments were done in triplicate. The petri dishes were covered and incubated BOD incubator, at 30 ºC for 4 days. Ten seeds of test crop i.e., *P. sativum* were randomly selected and placed in each of oven dried petri dishes (90 x 15mm) which have been lined with Whatman No. 41 filter paper. The filter paper served as an absorbent for FLE or distilled water so as to keep the seed moistened always and avoid the imposition of water stress. Twelve petri dishes were moistened with 5 mL of different extract concentrations and three petri dishes were moistened with 5 mL distilled water, which was served as the control. The petri dishes were incubated (in BOD Incubator), at 30 ºC for a period of 4 days. Emergence of 1 mm radicle was marked as the criterion for germination. The seed germination percentage, radicle length, plumule length and biomass of the test crops were measured to compare the effects of *P. sativum* based leaf extracts in comparison to control.

Analysis of canopy openness, LAI and PAR of *T. diversifolia* invaded sites

The method was used for the analysis of canopy openness, LAI and PAR in the present ecological investigation (44). The percentage of canopy openness was estimated in *T. diversifolia* infested area using gap light analyzer (GLA) and the hemispherical images were captured perpendicular to the ground in a skyward direction with a Skyvik Sign One 10 mm fisheye lens mounted on a smartphone. The hemispherical images were taken from ten locations (S1, S2, S3, S4, S5, S6, S7, S8, S9 and S10) to serve as a canopy gap analysis input for GLA software (Fig. 2). Using GPS (Garmin GPSMAP 64s), the geographic coordinates and elevation on the sites were recorded. The NOAA website was used to obtain the magnetic correction for the GLA configuration settings. By using a plant canopy analyzer (Integration of handheld and Software from Kaizen Imperial and Quantum Sensors from Apogee Instruments, USA), LAI and light intensity, i.e., PAR of the forest canopy were measured. The handheld device records and stores data and later extracted data using Kaizen software. Statistical analysis was done to assess their validity and significance.

Results and Discussions

Growth parameters

Seed germination

The FLE concentration of *T. diversifolia* affected the germination in the concentration dependent manner and more inhibition was noted at higher concentrations. The lowest concentration of FLE (12.5 mg/L) has shown the lowest inhibition rate of germination (20 %) while the highest concentration (50 mg/L) demonstrated the highest inhibition potential (60 %). In this respect, control set-up has lower rate of germination as compared to 12.5 mg/L concentration, which has the lowest inhibition rate among all the concentrations (Fig. 3A). This clearly showed that the FLE of *T. diversofolia* has inhibitory effects on the growth of *P. sativum* as the concentration increased. In addition, this showed that the aggressive growth of *T. diversifolia* in the agricultural land could inhibit the growth of crops to hamper productivity and hence food security.

Seedling plumule

The plumule length of *P. sativum* decreased with increasing concentrations of the treatment. Although there was a slight difference in 25 mg/L and 37.5mg/L concentration, the rest showed that the plumule length of *P. sativum* reduced with increased in the concentration (Fig. 3B). In this vein, early works observed the similar results on plumule inhibition by invasive alien plant (45). Recently, a bioassay experiment performed on other edible crops that the aqueous extracts of *T. diversifolia* negatively affected the plumule growth in *Zea mays* L., *Glycine max L.*, *Helianthus annuus L.*, *Sorghum bicolor* L., *Vigna unguiculata* L. and *Eleusine indica L.* (23).

Seedling radical

The present experiment showed that the FLE concentration inhibited the growth of radical emanating from seeds. The control plate showed the lowest inhibition rate of radicle length (i.e., 100 %) followed by 12.5 mg/L, 25 mg/L, 37.5 mg/L and 50 mg/L (Fig. 3 C). Radicle is important for absorbing water from the soil, which promotes the development of the embryonic plant (46). Since radical length is sensitive to phytotoxic compounds, the presence of allelochemicals may reduce cell division which could affect the growth of seed radical (47).

Seedling biomass

The present experiment showed that the biomass of *P. sativum* in control set-up was larger as compared to the different FLE concentration of *T. diversifolia*. The control biomass was noted to reduce by 100 % whereas the biomass reduction at different FLE concentration ranged from 67.4 % to 17.68 %. The FLE concentration of 12.5 mg/L, 25 mg/L, 37.5 mg/L and 50 mg/L observed reduction of biomass by 17.68 %, 28.73 %, 23.2 % and 67.4 % respectively (Fig. 3D). The present findings pertaining to effects on biomass was also corroborated by early results who observed that as the concentration of FLE of *T. diversifolia* on tomato plants increased, the value of fresh weight and root dry weight of tomato plants noted a significant decrease (48). Thus, from the present study it can be concluded that the concentration of FLE has remarkably affected the biomass of *P. sativum* crop.

Canopy openness, LAI and light intensity (PAR) of forest canopy cover

Forest canopy openness/gaps were analysed in ten random areas where *T. diversifolia* was highly infested to exert allelopathy. The forest canopy gaps ranged from 13.14 % to 63.64 %, which may

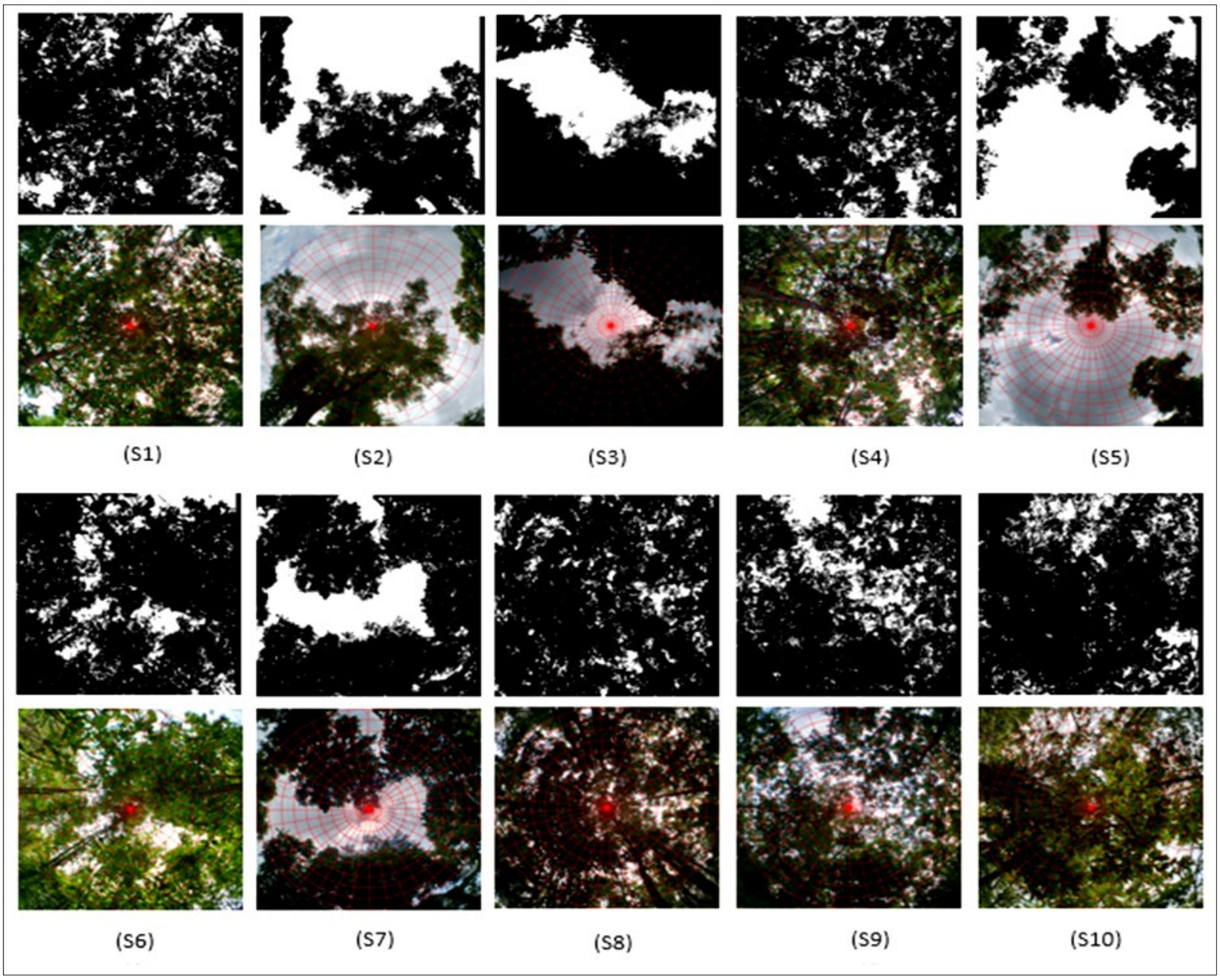

Fig. 2. Hemispherical photos taken on different plots to estimate the canopy openness on the invaded area of *T. diversifolia*. The canopy openness analyzed on GLA are shown in colour (original) and monochromatic (processed photo after adjusting) photograph.

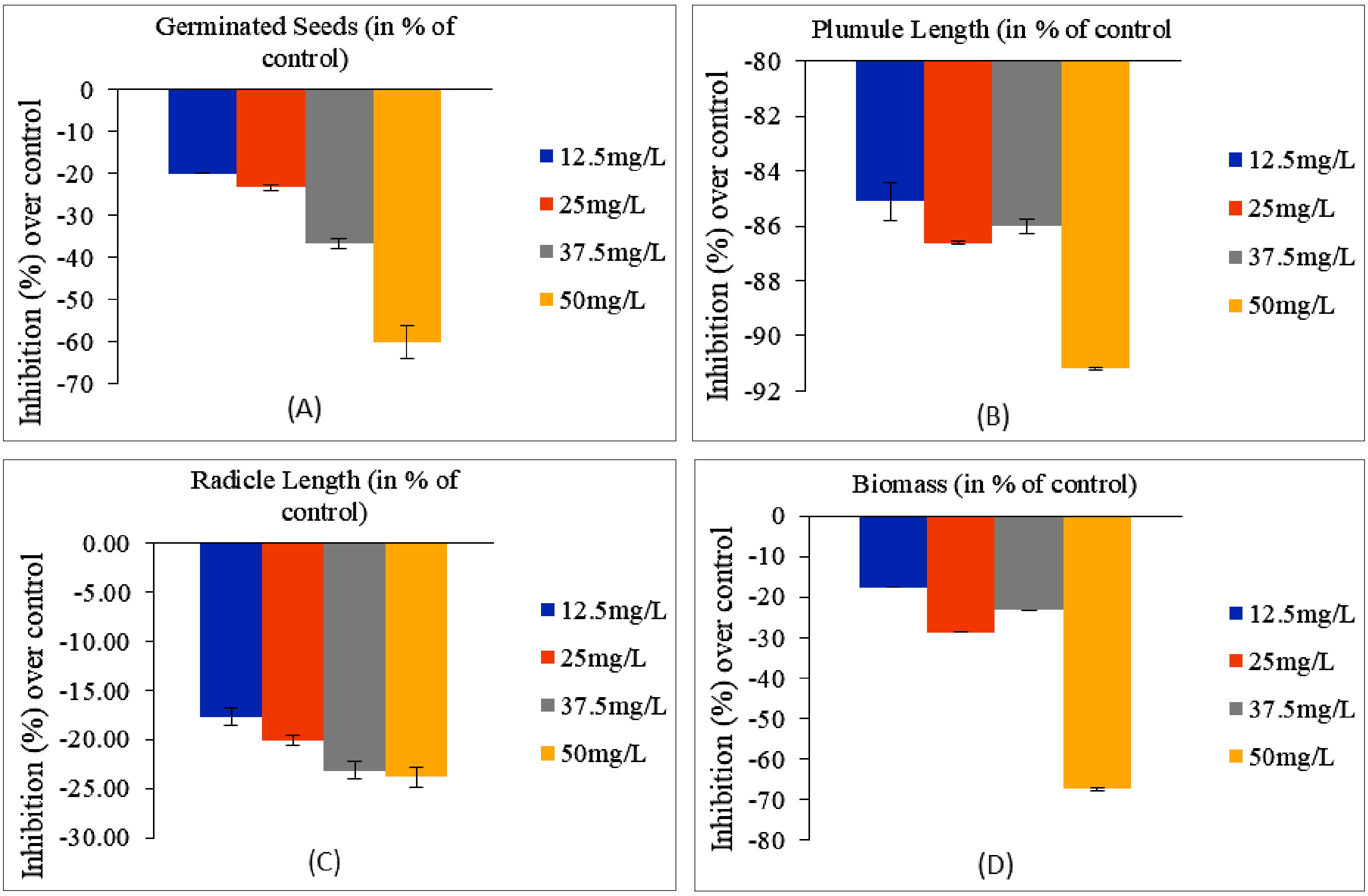

Fig. 3. Allelopathic effects of *T. diversifolia* FLE on (**A**) Seed germination, (**B**) Seed plumule, (**C**) Seed radicle and (**D**) Plant biomass of *P. sativum.*

have implications in terms of field allopathy based on the intensity of infestation. The highest canopy gap was observed at S5 (63.64 %) and the lowest at S10 (13.14 %) (Table 1). The average canopy gap of the area was 30.4 %, which has high canopy openness and less forest cover, which in turn exposes plants to solar radiation. The presence of large canopy openness allows more light to penetrate, which enhances the and proliferation of invasive alien plants, especially *T. diversifolia* (43). The solar radiation or light intensity can also be measured in terms of photosynthetic photon flux density (PPFD), which measures the photons of PAR. The incoming PAR is the direct solar radiation received from the sun and the diffused PAR is the light below the forest canopy (49). Whereas, the highest light intensity (diffused PAR) was recorded at S7, i.e., 709.67 ± 192.18 µ mol $m^{-2}s^{-1}$ and the lowest light intensity was recorded at S4, i.e., 6.00 ± 0.82 µ mol $m^{-2}s^{-1}$ (Table 1). The average light intensity of the study area recorded was 223.6 µ mol $m^{-2}s^{-1}$. The results show that the area has more sunlight due to high canopy openness, which makes it more susceptible to invasive alien species like *T. diversifolia*. The LAI measures the extent of leaf surface within an ecosystem and serves as a key variable influencing processes like photosynthesis, respiration and the interception of precipitation (50). The lowest LAI recorded was 0.10 ± 0.16 and the highest was 2.31 ± 0.93 (Table 1). The correlation analysis showed there was a positive but not a significant correlation between canopy openness and light intensity, but a negative, non-significant correlation with LAI. Similarly, light intensity has a negative and non-significant correlation with LAI (Table 2).

Conclusion

The present study confirmed that the *T. diversifolia* remarkably influenced the growth parameters such as germination, plumule, radical and biomass of *P. sativum* in a FLE concentration-dependent manner. Eventually, the results of bioassay experiment validated the NWH as an important mechanism in facilitating the success of this emerging invasive alien plant in an Indo Burma Biodiversity hotspot region. This clearly shows that the FLE of *T. diversifolia* has inhibitory allelopathic effects on selected crops, which could hamper and inhibit the nutrient absorption of the nearby crops, thereby affecting their growth, yield and food security. Thus, adequate caution should be taken by farmers in using the leaf leachates as growth enhancer or biofertilizer in agriculture systems. The vegetative indices such as canopy openness, LAI and PAR also influenced the growth of *T. diversifolia,* which in turn can modulate its allelochemic potential or field allelopathy. Present results predict that increase of canopy openness and lack of forest cover facilitates the spread of *T. diversifolia* due to adequate availability of solar radiation, impacting native plants and agricultural crops. In this sense, the effects of canopy gaps on *T. diversifolia* invasion can be site-specific. Nevertheless, these growth and development implications in terms of the canopy openness, LAI and PAR need to be directly assessed in field conditions to elucidate the explicit ecological effects on *T. diversifolia*. Therefore, in perspective of sustainable management, the sustenance of an intact canopy can reduce the *T. diversifolia* infestation in an agriculture system by alleviating its allelopathic effects on edible crops to maintain food security.

Table 2. Correlation of light intensity (PAR), LAI and canopy openness

	(Light intensity) PAR	LAI	Canopy openness
(Light intensity) PAR	1		
LAI	-0.31598	1	
Canopy openness	0.24232	-0.31194	1

*significant, **highly significant

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Authors' contributions

V carried out conceptualization, drafted manuscript, writing, data collection and analysis. PKR supervised, coordinate, reviewing, editing, ensure the completeness and accuracy of the research. STL in validation, editing and data analysis. RBS prepared material, analysed software, conception and assisted design. All authors read and approved the final manuscript.

Table 1. Analysis of canopy openness, LAI and PAR on invaded area of *T. diversifolia*

Plot	GPS coordinates (DMS)	Elevation	PAR		LAI	Canopy openness (%)
			Incoming PAR µ mol m^{-2} s^{-1}	Diffused PAR µ mol m^{-2} s^{-1}		
S1	N 23˚47'56.31" E 092˚44'02.11"	1067	67.00±1.00	21.00±9.85	2.05±0.74	16.08
S2	N23˚45'25.44" E092˚39'59.52"	686	1110.67±19.40	308.67±81.08	2.17±0.50	49.1
S3	N23˚45'31.27" E092˚40'01.35"	676	458.33±4.04	258.33±41.88	0.97±0.28	35.67
S4	N 23˚47'39.93" E 092˚44'00.90"	1139	15.00±0.00	6.00±0.82	1.54±0.23	16.63
S5	N23˚45'29.22" E092˚39'49.33"	652	250.67±1.53	178.67±7.37	0.56±0.08	63.64
S6	N 23˚47'33.97" E 092˚44'05.72"	1057	129.33±12.10	44.33±27.06	2.00±0.90	18.39
S7	N23˚45'18.61" E092˚40'20.18"	790	755.00±225.19	709.67±192.18	0.10±0.16	30.36
S8	N 23˚47'41.39" E 092˚44'59.47"	1143	29.33±2.52	20.00±6.93	0.71±0.67	13.31
S9	N23˚45'16.68" E092˚40'19.69"	793	981.00±66.02	279.67±184.86	2.31±0.93	24.43
S10	N 23˚47'33.02" E 092˚44'06.01"	1060	1158.00±75.23	409.67±320.91	2.04±1.24	13.14

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical issues: None

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