



RESEARCH ARTICLE

Allelopathic potential of *Eucalyptus camaldulensis* Dehnh. on germination of obligate root-parasitic broomrape (*Orobancha cernua* Loebl.)

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ABSTRACT

In the present study, an assessment of allelopathic effect of *Eucalyptus camaldulensis* Dehnh. and its various derivatives was assessed on the germination of obligate-root and holo-parasitic weed, nodding broomrape (*Orobancha cernua* Loebl.). Optimized *in vitro* *O. cernua* germination assays were conducted under different experimental setups, to determine the allelopathic potential of sapling, leaf-litter extract, plantation-soil, distilled *Eucalyptus* oil and purified eucalyptol of *E. camaldulensis*. A considerable and varying levels of inhibitory allelopathic impact on *O. cernua* seed germination was observed with all tested materials of *E. camaldulensis*. These findings indicate the possibility to use of allelopathic potential of *E. camaldulensis* for managing the underground root parasitic-weed infestation in various agricultural crops.

Keywords: Allelopathy, Broomrape, *Eucalyptus camaldulensis*, *Orobancha cernua* and Weed management

INTRODUCTION

Eucalyptus camaldulensis Dehnh., an indigenous to Australia, is a large, fast-growing evergreen tree (Sani *et al.* 2014). Owing to its faster growth, wider eco-adaptability, higher productivity and its commercial application, various *Eucalyptus* sp. have been introduced in many countries (Davidson 1995). One of most characteristic features of *Eucalyptus* plantation is its ability to reduce the diversity and productivity of underneath crops and species in its vicinity (del Moral and Muller 1970). The suppressive effect of *Eucalyptus* is either due to its direct- or indirect-impact on ground vegetation (Bowman and Kirkpatrick 1986). The direct-impact of *Eucalyptus* has been attributed primarily due to its allelopathic effects on other plants (Turnbull 1999). The broad-spectrum negative allelopathic impact of *Eucalyptus* was reported on the growth and survival of various herbs, agronomical-crops, weeds, forest-crops, algae, microbes (*i.e.* bacteria and fungi) as well as certain avian species (Goded *et al.* 2019). However, reports of allelopathic impact of *Eucalyptus* on obligate-root and holo-parasitic weed, broomrape (*Orobancha cernua* Loebl.) are scanty.

Broomrape parasitizes the diverse-range of crops and pastures (Das *et al.* 2020). Global revenue losses of \$1.3-2.6 billion/annum have been projected

due to overwhelming damages (0-100% crop failures) owing to broomrape infestation (Ahmad *et al.* 2018). To overcome these losses, a number of control-strategies have been evaluated in the past (Cartry *et al.* 2021). However, none of the available control measures for broomrape infestation can be considered as practically viable, foolproof, effective, economical and eco-friendly. This is primarily due to broomrape hybrid traits (weed and root-parasite), achlorophyllous nature, predominant subterranean life, close proximity with host roots, exclusive uptake of host's resources *via* haustoria, growth synchronization with the specialized range of host cultivation, complex mechanisms of seed dispersal and germination, fecundity (up to 5,00,000 seeds/plant), physiological seed-dormancy, tiny seed size, eternal seeds longevity and existence of enormous seed-bank in infested fields (Das *et al.* 2020, Cartry *et al.* 2021). Thus, the only precautionary and sustainable way to effectively minimise the devastating damages caused by *Orobancha* sp. is through the use of natural product(s) having potential orobanchicidal effect. In this context, allelopathy and allelochemical(s) potential of *E. camaldulensis* needs to be evaluated.

Thus, a preliminary study was conducted to evaluate the allelopathic impact of *E. camaldulensis* sapling, leaf litter extract, plantation soil, distilled *Eucalyptus* oil and purified eucalyptol of *E. camaldulensis* on *in vitro* germination of nodding broomrape (*O. cernua*) under laboratory-conditions.

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MATERIALS AND METHODS

A study was conducted in the Plant Science laboratory, ITC Life Science and Technology Centre (LSTC), Bengaluru, Karnataka, India during October, 2022 to June, 2023. In order to conduct the study on allelopathic potential of *E. camaldulensis*: i. approximately 3 months old (30–32 cm) *E. camaldulensis* saplings (ITC clone no. 1803); ii. healthy leaf-litters from 4 years old *E. camaldulensis* tree plantation and top-layered (0–30 cm depth) soil (from the field with a history of >10 years of *E. camaldulensis* plantation) were procured from *Eucalyptus* plantation field of ITC-Paperboards and Specialty Papers Division (PSPD), Bhadrachalam at Jagannadhapuram (17.6071° N, 80.7533° E), Kothagudem district, Telangana, India. The collected *E. camaldulensis* leaves and soil sample (that was air-dried and sieved through a 2 mm mesh) were stored in tight-seal dark containers until use; iii. GR₂₄ (Catalogue#racGR24), a synthetic strigol analog, was acquired from Strigolab S.r.l., Italy; iv. *Eucalyptus* oil (EO) was sourced from Ultra International Limited, Uttar Pradesh (U.P.), India; v. GC-grade eucalyptol (Catalogue # r46090) was procured from Sigma-Aldrich (St. Louis, USA); vi. *O. cernua* seeds were collected from its mature flower spikes that feeds off the cultivated tobacco (*Nicotiana tabacum* L.) grown during 2021–22 season at Rajahmundry, India (17.0005° N, 81.8040° E). The harvested *O. cernua* seeds were stored in darkness at 25 °C until utilized.

O. cernua seed viability was assessed by 2,3,5-triphenyl tetrazolium chloride (TTC) method (Thorogood *et al.* 2009). Autoclaved distilled water (DW), 10 mm glass filter paper disc (GFPD; Whatman; GE Healthcare) and 47 mm filter-papers (Whatman) were used throughout the study. Prior to usage, *O. cernua* seeds underwent surface sterilization by treating them with a solution of 1% (v/v) NaOCl for duration of 2 min. Subsequently, the seeds were thoroughly rinsed with DW and left to air-dry at room temperature. Fifty surface-sterilized *O. cernua* seeds were evenly distributed on GFPD pre-treated with distilled water and placed in a petri dish lined with two layers of moistened filter paper. Each petri dish contained four GFPD with *O. cernua* seeds, which were then covered with aluminium foil and incubated at 25 °C for a period of three days. Non-viable heat-killed (HK, microwaved for 10 min) *O. cernua* seeds were taken as *negative control*. Following this, *O. cernua* seeds were soaked in a 1% TTC solution (Himedia) and then placed in a dark environment at 37 °C for 24 h. Subsequently, *O. cernua* seeds were immersed in a 0.4% (v/v) NaOCl

solution for 1 min, rinsed thoroughly with DW and examined under a compound microscope with a 4× magnification (Leica DM1000, Leica Microsystems, USA). Of note, due to dehydrogenases activity of live cells, TTC forms a red colored 1,3,5-triphenylformazan precipitate. Thereby, *O. cernua* seeds that were either stained with bright-yellow or orange colour or left unstained has been scored as viable and non-viable, respectively.

A modified laboratory scale ‘co-culture’ method was developed as described earlier (Ye *et al.* 2020) with the certain changes, wherein *O. cernua* seeds were co-cultured with *E. camaldulensis* sapling in a petri dish. Four GFPDs were placed in each 150 mm petri dish (covered with a double layer 47 mm filter-paper), with each GFPD holding around 50 surface sterilized *O. cernua* seeds. To create a suitable environment for germination, filter papers were moistened with 5 ml of DW. Sterilized vermiculite (~25 g) was added in each petri dish. One *E. camaldulensis* sapling per petri dish was planted by passing it through a hole made in peripheral frame of both petri dish container and lid and allowed to stand it vertically throughout the experiment (hereafter stated as *E. camaldulensis* conditioned seeds, ECS). Likewise, a similar treatment but without *E. camaldulensis* sapling was also used (hereafter stated as non-eucalyptus conditioned seeds, NECS). The petri dishes, sealed with parafilm and covered with aluminium-foil, were incubated at 25 °C for 7 days. Afterward, GFPD with pre-conditioned ECS and NECS (dried to eliminate excess water) were spread on fresh GFPD, transferred to a new petridish (covered with a double layer 47 mm filter-paper) and moistened with 5 ml of 10 mg / L GR₂₄ or 0.1% (v/v) acetone (*solvent control*) and further incubated at 25 °C for 3 days. Sterilised DW was added periodically to each petri dish to maintain the enough moisture throughout the germination assay. After conducting a comprehensive 10-day test, *O. cernua* seeds with an emerged radicle were scored under a compound microscope (Leica) with a 4× magnification. The calculated cumulative germination rate (CGR, in %) of *O. cernua* seeds was normalised to aforesaid average seed viability (%) determined through TTC analysis.

In vitro O. cernua seed germination assay was conducted following the methods outlined in a previous study (Louarn *et al.* 2012) with specific adjustments made. In every test conducted, four GFPDs were placed in each 150 mm petri-dish (covered with a double layer 47 mm filter paper), with each GFPD holding around 50 surface-sterilized

O. cernua seeds. Each petri dish was moistened with 5 ml of DW or corresponding test reagent. Notably in each experiment, non-viable heat HK seeds, were also included as a *negative control*. Fresh preparations of each test-reagent and its dilution were made prior to analysis in order to avoid any potential degradation of their inherent bio-actives.

Experiment 1: *E. camaldulensis* leaf litter extract (LLE) effect on *O. cernua* seeds germination

E. camaldulensis leaf litters were collected and washed thoroughly with DW (to remove the impurities and dirt-particles). Cleaned leaf litters were dried in a hot air incubator (Lab India Instruments Pvt. Ltd., India) at 60 °C until they become fully dehydrated. The dried leaf litter was ground using a laboratory grinder and sieved (through a 0.6 mm mesh) to achieve a fine powder (particle size ~500 μ m). The obtained leaf powder was boiled with DW [1:5 (w/v)] at 80 °C for 20 min. The resulting LLE was filtered through filter paper (Whatman No. 1) and subsequently combined with DW to attain the desired concentrations (10%, 25%, 50%, 75%, and 100%) and preserved in glass vials. *O. cernua* seeds were dispersed on a GFPD pretreated with either DW (*i.e.* NECS) or with specific aforesaid concentration of LLEs (*i.e.* ECS).

Experiment 2: *E. camaldulensis* field plantation soil effect on *O. cernua* seeds germination

The petri-dish harbouring *O. cernua* seeds were dispersed on a GFPD pretreated with DW was prefilled with ~25 g fine sieved test soil. Notably, soil sample was also collected from the demonstration / greenhouse field (with no previous history of any *Eucalyptus* plantation or broomrape infestation) of ITC-LSTC, Bengaluru (labelled as non-eucalyptus soil). Hereafter, corresponding *O. cernua* seeds that were pre-conditioned on *Eucalyptus* and non-eucalyptus soils were stated as *E. camaldulensis* soil conditioned-seeds (ESCS) and non-eucalyptus soil conditioned-seeds (NESCS), respectively. Approximately 10 ml DW was added in each petri-dish to keep the soil-moist.

Experiment 3: Eucalyptus oil (EO) effect on *O. cernua* seeds germination

O. cernua seeds were dispersed on a GFPD pretreated with either DW (*i.e.* CU) or with specific concentration of distilled EO (*i.e.* 0.01%, 0.02%, 0.03%, 0.04% and 0.05%; collectively stated as CT). Notably, various dilutions of EO were prepared in 0.02% (v/v) non-ionic surfactant, APSA-80 (Amway, India).

Experiment 4: Purified eucalyptol (EL) effect on *O. cernua* seeds germination

O. cernua seeds were dispersed on a GFPD pretreated with either DW (*i.e.* CU) or with specific concentration of purified EL (*i.e.* 0.1%, 0.25%, 0.5%, 0.75% and 1%; collectively stated as CT).

For every aforementioned trial, each petri-dish was incubated at 25 °C for 7 days. After this, GFPD with preconditioned *O. cernua* seeds were carefully blotted to eliminate any excess water or test reagent. The preconditioned *O. cernua* seeds were then spread onto fresh GFPD, kept in a new petri dish (covered with two layers of filter paper), moistened with either 5 ml of 10 mg/L GR₂₄ or 0.1% (v/v) acetone (*solvent-control*) and incubated at 25 °C for 3 days. At the end of the test period, *O. cernua* seeds were scored for its germination (*as described above*).

Each experiment was evaluated in three biological replicates (~50 seeds per measurement) and repeated twice. Results are expressed as means \pm standard deviations (SDs). Statistically significant ($p=0.05$) difference between comparative groups was analysed by Kruskal-Wallis test.

RESULTS AND DISCUSSION

Orobancha sp. germination has been considered to be a two-stage process, characterised by an independent ‘pre-conditioning’ phase, during which it becomes susceptible to natural / synthetic GS, followed by a host-dependent ‘chemical-stimulation’ phase, during which the radicle protrusion begins (Joel *et al.* 1991). As the germination-potential of *O. cernua* seed is developed during the pre-conditioning period, thereby any observed variation in its CGR resulting from the ‘test’ preconditioning media can be used to ascertain their precise influence on *O. cernua* seed germination. With this background, we investigated the allelopathic capacity of *E. camaldulensis* saplings and other allelopathy testing materials, *viz.* LLE; plantation-soil; distilled EO and purified EL as a pre-conditioning media on *in vitro* germination of *O. cernua* under prescribed assay conditions. At foremost, seed viability test of *O. cernua* seeds were quantified (~76%) by TTC method, which was used as a correction factor in normalising the CGR in all subsequent experiments.

Effect of co-culturing with *E. camaldulensis* saplings on *O. cernua* seed germination

The study on the direct impact of growing *E. camaldulensis* in the vicinity of *O. cernua* (*co-culture*) recorded a CGR of ~58% (**Figure 1**). Conversely, the CGR of *O. cernua* seeds pre-conditioned in the

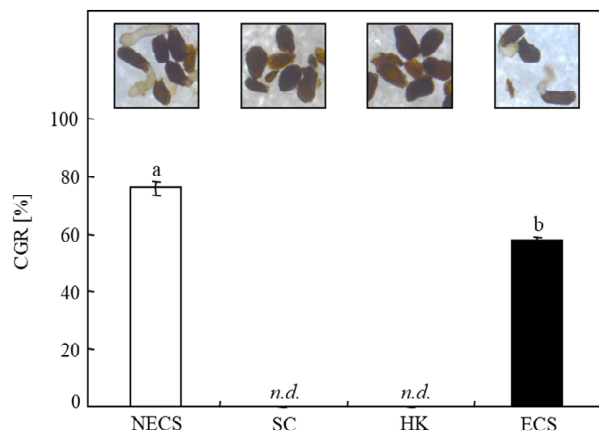


Figure 1. Allelopathic effect of *E. camaldulensis* saplings 'co-culture' on *O. cernua* seed germination

The micrographs illustrate the representative *O. cernua* seeds / germlings at the end of test-period. The bar chart depicts the base corrected CGR (%), wherein distinct letters demonstrate statistically significant variations ($p=0.05$). ECS - *E. camaldulensis* conditioned seeds, NECS - non-eucalyptus conditioned seeds, SC - solvent control, HK - heat killed, CGR - cumulative germination rate and n.d. - not detected.

absence of *E. camaldulensis* sapling (stated as NECS) was observed to be ~76% (Figure 1). Comparative studies (NECS vs ECS) revealed a prominent decline (~24%) in CGR of ECS supporting observations made with other crops (Shivanna *et al.* 1992; Lisanework and Michelsen 1993).

Effect of *E. camaldulensis* leaf litter extract (LLE) on *O. cernua* seed germination

O. cernua seeds were incubated with either distilled water (hereafter stated as CU) or with different concentrations of LLE (i.e. 10%, 25%, 50%, 75% and 100%, correspondingly abbreviated as LLE₁₀, LLE₂₅, LLE₅₀, LLE₇₅ and LLE₁₀₀ respectively; collectively stated as CT) under prescribed assay-conditions (Figure 2A). The CGR of CU was observed to be ~76% (Figure 2B). For CT, a CGR of ~72%, ~67%, ~58%, ~43% and ~41% was observed for LLE₁₀, LLE₂₅, LLE₅₀, LLE₇₅ and LLE₁₀₀, respectively (Figure 2B). Comparative analyses (CU vs CT) demonstrated a significant gradual decrease in

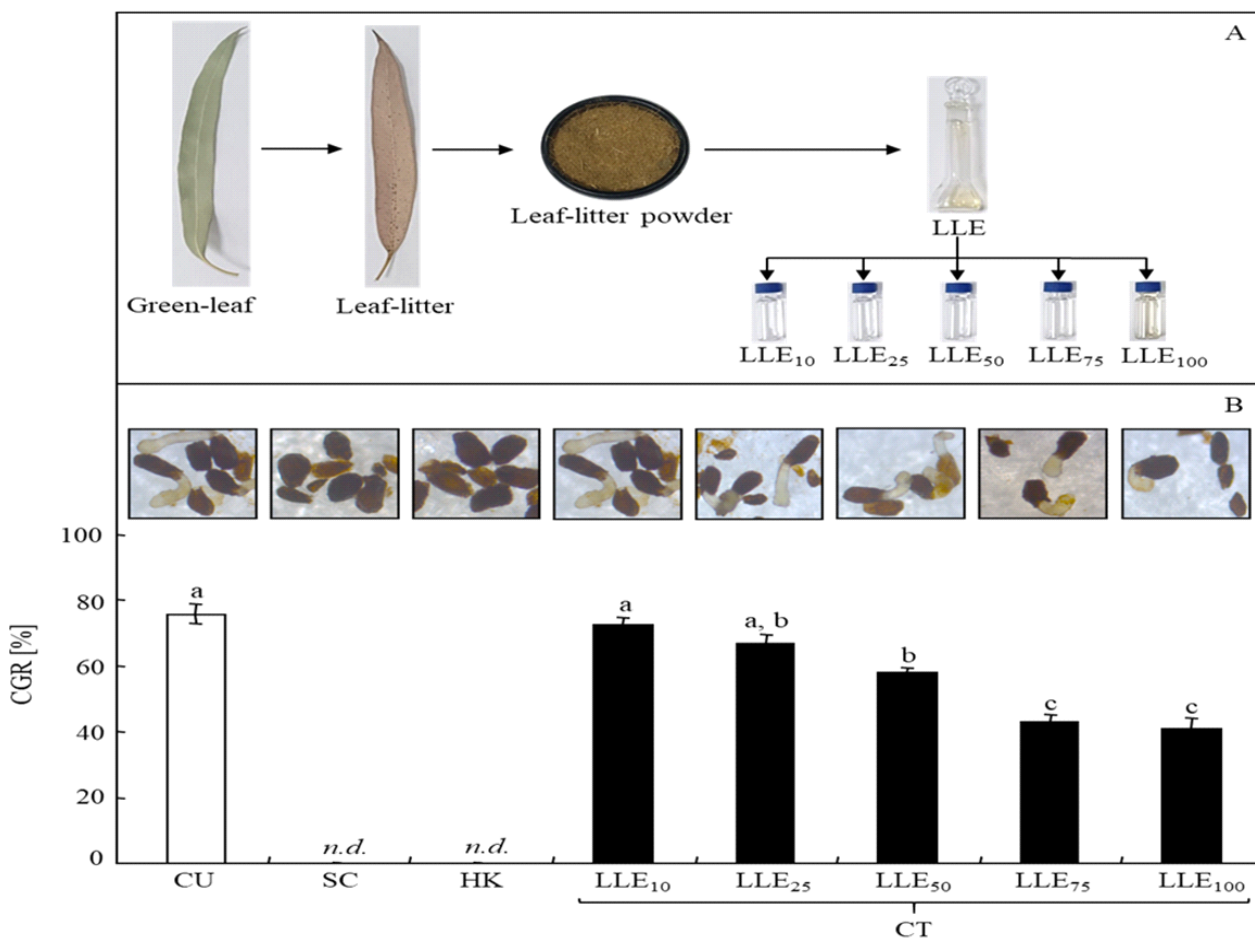


Figure 2. Allelopathic effect of *E. camaldulensis* leaf litter extract (LLE) on *O. cernua* seed germination

A. Flow chart depicts the preparation of *E. camaldulensis* LLE and its various dilutions (i.e. LLE₁₀, LLE₂₅, LLE₅₀, LLE₇₅ and LLE₁₀₀). **B.** *O. cernua* seeds were pre-conditioned either in the absence (i.e. CU) or presence (i.e. CT) of various concentration of LLEs, followed by stimulation with 10 mg/L GR₂₄ or 0.1% (v/v) Ac (i.e. SC) under specified assay conditions. The micrographs illustrate the representative *O. cernua* seeds/germlings at the end of test-period. The bar chart depicts the base-corrected CGR (%), wherein distinct letters demonstrate statistically significant variations ($p=0.05$). SC - solvent control, Ac - acetone, LLE - leaf litter extract, CU - conditioned untreated seeds, CT - conditioned treated seeds, HK - heat killed, CGR - cumulative germination rate and n.d. - not detected.

CGR of CT (~5%, 12%, and 24% at LLE₁₀, LLE₂₅ and LLE₅₀, respectively), before stabilizing at a plateau (with a corresponding decline of ~44–46% at LLE₇₅ and LLE₁₀₀). These results are in accordance with a dose-dependent inhibitory effect of *Eucalyptus* ALE on seeds/seedlings germination of different crops (Padhy *et al.* 2000), Djanaguiraman 2005, Akram *et al.* 2017, Sousa *et al.* 2018). In order to assess whether the observed inhibitory impact of LLEs display toxicity toward *O. cernua* seeds, we additionally measured the CT seeds viability. Our results demonstrated the null effect of *E. camaldulensis* LLEs on *O. cernua* seed viability at all tested concentrations (data not given here and can be obtained from authors) indicating that Ec LLEs only alters the ability of *O. cernua* seeds to germinate, without affecting their inherent viability.

Effect of *E. camaldulensis* plantation soil on *O. cernua* seed germination

The CGR of non-eucalyptus soil conditioned-seeds (NESCS) was observed to be ~72% (Figure 3). On the contrary, the CGR for *E. camaldulensis* soil conditioned-seeds (ESCS) was observed to be ~27% (Figure 3). Comparative analysis (NESCS vs ESCS) revealed a substantial decline (~63%) in CGR of ESCS. These results were also in agreement with recent findings, wherein *E. camaldulensis* infested soil has been reported to significantly reduce the

growth of *Aloe barbadensis* Mill. plantations (Singh *et al.* 2021).

Effect of Eucalyptus oil (EO) as a pre-conditioning media on *O. cernua* seed germination

The evaluation of the impact of EO on *in vitro* germination of *O. cernua* seeds pre-conditioned either in DW (stated as CU) or different concentration of EO (*i.e.* 0.01%, 0.02%, 0.03%, 0.04% and 0.05%, correspondingly abbreviated as EO_{0.01}, EO_{0.02}, EO_{0.03}, EO_{0.04} and EO_{0.05}, respectively; hereafter collectively stated as CT) resulted in CGR of CU to be ~76% (Figure 4). Regarding CT, a CGR of ~14%, ~8%, ~5%, 0% and 0% was observed for EO_{0.01}, EO_{0.02}, EO_{0.03}, EO_{0.04} and EO_{0.05}, respectively (Figure 5). Comparative analyses (CU vs CT) demonstrated a significant gradual decrease in CGR of CT (~81%, ~90% and ~93% at EO_{0.01}, EO_{0.02} and EO_{0.03} respectively), before stabilizing at a plateau of complete inhibition (*i.e.* 100% inhibition at EO_{0.04} and EO_{0.05}). These results confirmed the dose-dependent inhibition by EO (from *E. camaldulensis* as well as *E. citriodora* and *E. tereticornis*) of the germination of *P. hysterophorus* (Chaturvedi *et al.* 2012). Notably, no effect on *O. cernua* seed viability was observed at lower concentration of EO (*i.e.* EO_{0.01}, EO_{0.02} and EO_{0.03}; Data not given here and can be obtained from authors). Overall, these results demonstrated EO exclusively inhibited *O. cernua* seed germination, without having any impact on its viability.

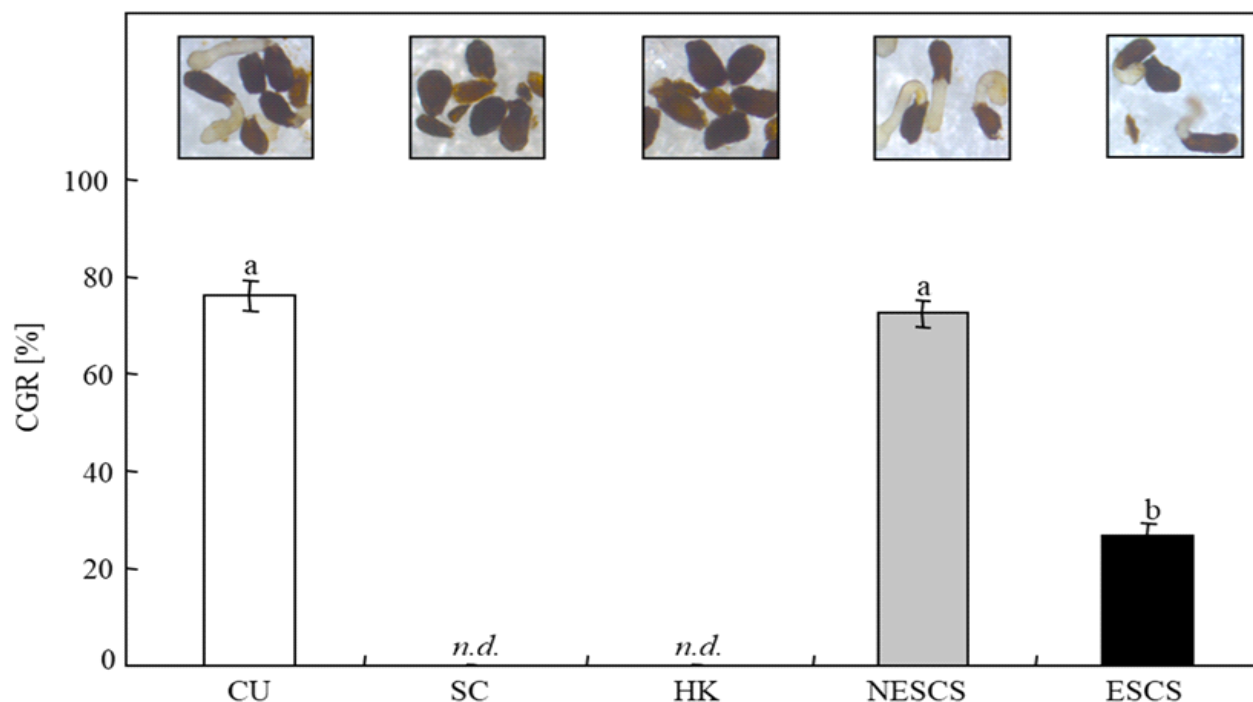


Figure 3. Allelopathic effect of *E. camaldulensis* field plantation soil on *O. cernua* seed germination

The micrographs illustrate the representative *O. cernua* seeds/germlings at the end of test period. The bar-chart depicts the base corrected CGR (%), wherein distinct letters demonstrate statistically significant variations ($p=0.05$). NESCS - non-eucalyptus soil conditioned seeds, ESCS - *E. camaldulensis* soil conditioned seeds, SC - solvent control, HK - heat killed, CGR - cumulative germination rate and *n.d.* - not detected.

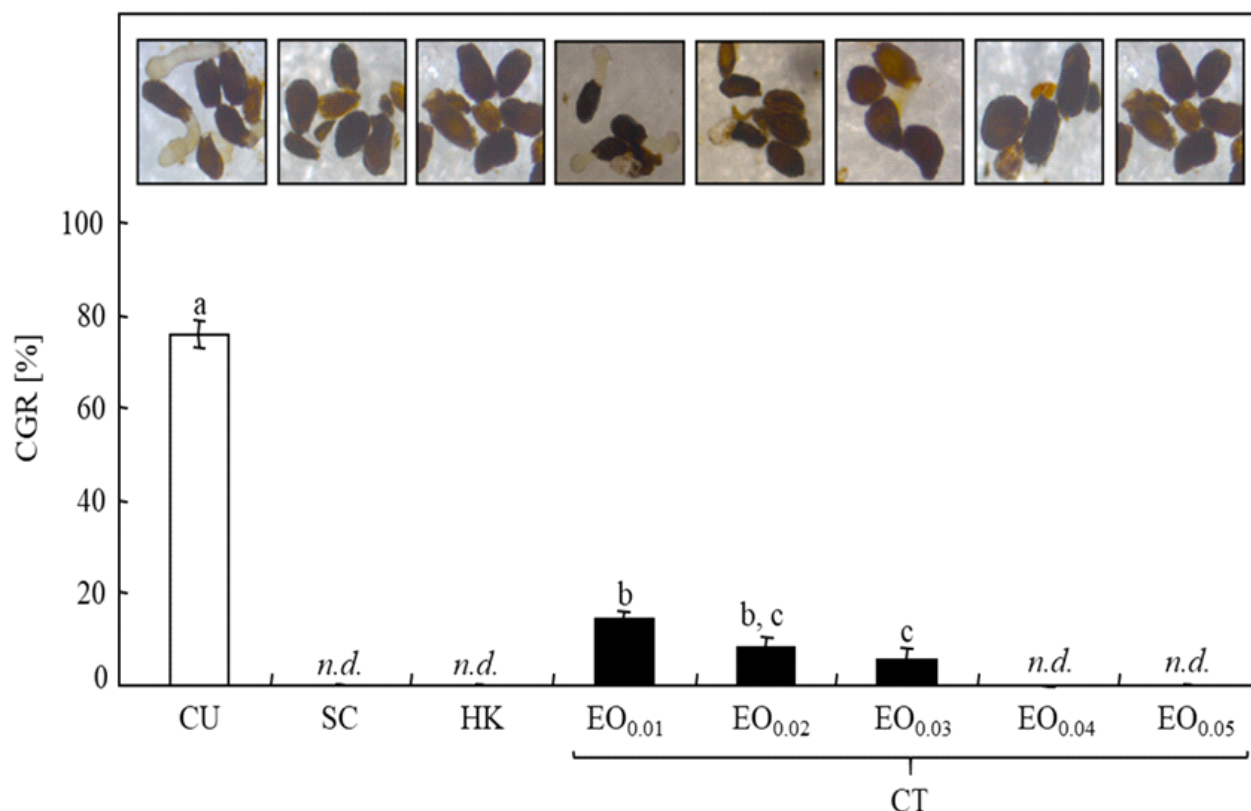


Figure 4. Allelopathic effect of Eucalyptus oil (EO) on *O. cernua* seed germination

The micrographs illustrate the representative *O. cernua* seeds / germlings at the end of test period. The bar chart depicts the base corrected CGR (%), wherein distinct letters demonstrate statistically significant variations ($p=0.05$). EO_{0.01}, EO_{0.02}, EO_{0.03}, EO_{0.04} and EO_{0.05} corresponds to EO at a concentration (v/v) of 0.01%, 0.02%, 0.03%, 0.04% and 0.05%, respectively. EO - *Eucalyptus* oil, CU - conditioned untreated seeds, CT - conditioned treated seeds, SC - solvent-control, HK - heat killed, CGR - cumulative germination rate and *n.d.* - not detected.

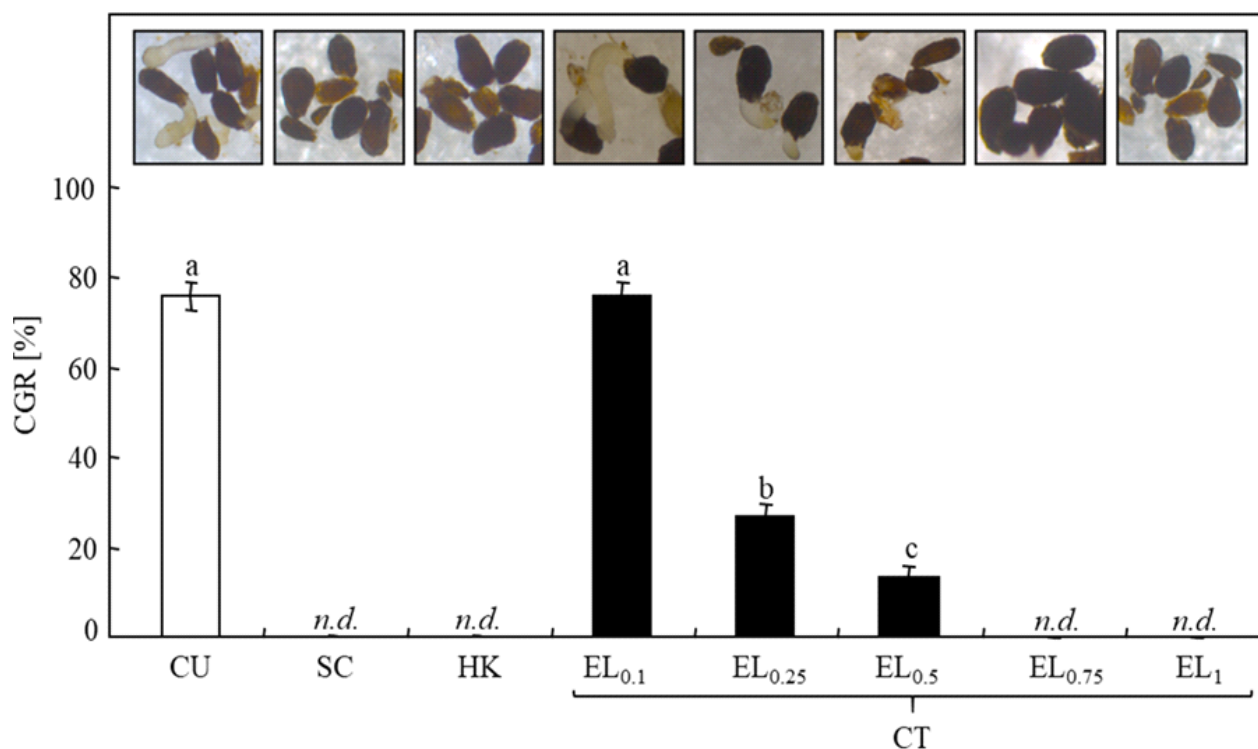


Figure 5. Allelopathic effect of purified eucalyptol (EL) on *O. cernua* seed germination

The micrographs illustrate the representative *O. cernua* seeds / germlings at the end of test period. The bar chart depicts the base corrected CGR (%), wherein distinct letters demonstrate statistically significant variations ($p=0.05$). EL_{0.1}, EL_{0.25}, EL_{0.5}, EL_{0.75} and EL₁ corresponds to EL at a concentration of 0.1%, 0.25%, 0.5%, 0.75% and 1%, respectively. EL - eucalyptol, CU - conditioned untreated seeds, CT - conditioned treated seeds, SC - solvent control, HK - heat killed, CGR - cumulative germination rate and *n.d.* - not detected.

Effect of purified eucalyptol (EL) on *O. cernua* seed germination

O. cernua seeds were incubated with either distilled water (hereafter stated as CU) or with different concentrations of EL (*i.e.* 0.1%, 0.25%, 0.5%, 0.75% and 1%, correspondingly abbreviated as EL_{0.1}, EL_{0.25}, EL_{0.5}, EL_{0.75} and EL₁ respectively; collectively stated as CT). The CGR of CU was observed to be ~76% (**Figure 5**). Regarding CT, a CGR of ~76%, ~27%, 13%, 0% and 0% was observed for EL_{0.1}, EL_{0.25}, EL_{0.5}, EL_{0.75} and EL₁ respectively (**Figure 5**). Comparative analyses (CU vs CT) demonstrated a significant gradual decrease in CGR of CT (0%, ~65% and ~82% at EL_{0.1}, EL_{0.25} and EL_{0.5}, respectively), before stabilizing at a plateau of complete inhibition (*i.e.* 100% inhibition at EL_{0.75} and EL₁). There was no impact on *O. cernua* seed viability at lower concentration of EL (*i.e.* EL_{0.1}, EL_{0.25} and EL_{0.5}; data not given here and can be obtained from authors). This study demonstrated that EL could serves a potential allelopathic agent against *O. cernua* seed germination. It is essential to identify unknown allelochemical(s) from EO through future extensive studies.

This study demonstrated the varying degree of negative allelopathic potential of *E. camaldulensis* saplings; leaf-litter extract; plantations-soil; *Eucalyptus* oil and eucalyptol on *O. cernua* seed germination indicating possibility for future screening and development of allelochemicals from *E. camaldulensis* to manage *O. cernua*.

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