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Influence of Seasonal Variation and Growth Conditions on Seed Germination of Ebolo (*Crassocephalum crepidioides* and *Crassocephalum rubens*) Vegetables

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ABSTRACT

Background and Objective: *Crassocephalum crepidioides* and *C. rubens* are plants indigenous to tropical Africa. They are important orphan crops that are highly nutritious but are still mainly harvested from the wild. One major challenge that limits the cultivation of these crops is the high degree of seed dormancy, which makes it difficult to propagate through seeds. This study aimed to investigate the effects of growth conditions, media, and seasonal variation on the seed germination capacity of *C. crepidioides* and *C. rubens*. **Materials and Methods:** *Crassocephalum crepidioides* and *C. rubens* seeds were cultivated in the greenhouse across two growing seasons: Winter and summer. Seed germination tests were conducted using two different growth media: Filter paper and half-strength Murashige and Skoog (½MS) medium. Seeds were incubated at varying temperatures (21 and 25°C), light intensities (30, 80 µmol/m^2/s), in the dark, and long-day photoperiod (16 hrs of light/8 hrs of darkness). **Results:** Both species exhibited a high degree of seed dormancy in the dark, but light and temperature promoted germination, with light having a stronger effect on seed germination of *C. rubens*. Germination was faster on filter paper for both species compared to ½MS medium. Notably, *C. rubens* seeds harvested in the winter exhibited higher dormancy than *C. crepidioides*, while summer-harvested *C. crepidioides* seeds showed increased dormancy compared to *C. rubens*. **Conclusion:** Overall, *C. crepidioides* exhibited higher dormancy compared to *C. rubens* and required light and temperature to break out of dormancy. Improved seed germination was observed on filter paper, while seasonal variation influenced the dormancy level in *Crassocephalum* seeds.

KEYWORDS

Dormancy, ebolo, germination, underutilized crops, seasonal variations

INTRODUCTION

Crassocephalum crepidioides and *C. rubens* are underutilized, traditional leafy vegetables indigenous to tropical Africa and widely distributed across the tropical and sub-tropical regions of the world. They belong to the plant family Asteraceae and are annuals that grow rapidly and thrive well in marginal

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conditions[1]. Both species are highly nutritious and are used as leaf vegetables and medicinal plants in Sub-Saharan Africa and Asia[2,3]. Despite their importance as a nutritious food source, *Crassocephalum* species are not commonly cultivated, but are primarily collected from the wild. One of the key challenges limiting their cultivation is a high degree of seed dormancy, which makes propagation through seeds difficult. *Crassocephalum* seeds have been established to require light for germination[4,5]. Adedeji-Badmus *et al.*[5] reported that *C. crepidioides* seeds have a higher dormancy depth than *C. rubens* seeds, which was linked to a higher abscisic acid (ABA) level in *C. crepidioides* seeds at harvest. The role of ABA and Gibberellins (GA) in seed dormancy has been established. While ABA regulates seed dormancy and maintenance positively, GA promotes seed germination[6,7]. De novo synthesis of ABA during seed development and maturation plays a significant role in seed dormancy and germination[8]. Seed dormancy appears at the end of the seed maturation, where the cell cycle ceases, molecular dependence from the mother plant disappears, dehydration occurs, storage products are synthesized, and ABA is accumulated[9]. The ABA is the major internal physiological factor that induces seed dormancy[10]. It induces primary dormancy, which is an adaptive trait in seeds to prevent vivipary, and after seed dispersal, delays and spreads germination over time[11,12]. The level of ABA at maturity influences the seed dormancy level.

Seed dormancy and germination capacity can be significantly influenced by growth conditions and environmental variations during plant growth and development, and at harvest[13]. Environmental cues such as temperature, photoperiod, and drought stress can influence the germination characteristics of seeds during their development, maturation, and after dispersal. These factors may also affect the conditions under which dormancy is released[14,15]. Numerous studies have investigated how day length, light quality, temperature, water availability, and nutrients influence the level of dormancy in many species[16-18]. The duration of day length during the final stages of seed maturation can affect seed behaviour[19]. Some species may exhibit higher germination capacity when grown under short day conditions[20,21]. While day length had no significant impact on seed performance of some species[22,23]. Additionally, light quality during seed maturation has a direct effect on seed dormancy[13]. The maternal light environment during seed development plays a crucial role in determining seed weight, germinability, and longevity[22]. Temperature during seed development and maturation also influences seed germination or dormancy in many species[16,23-28]. Seeds developed at warmer temperatures are generally less dormant at maturity compared to those developed at cooler temperatures[13,16,23,27,29,30].

Crassocephalum plants grow in various regions across the world and have the potential to serve as an important food crop. A major limitation of their commercial cultivation is the high degree of dormancy and low germination capacity of their seeds. The ecological conditions in which the mother plants grow can influence the dormancy level and germination capacity of *Crassocephalum* seeds. Thus, the present investigation examined the effect of environmental conditions and seasonal variation on seed dormancy and germination capacity of *Crassocephalum* seeds.

MATERIALS AND METHODS

Study area and duration: The greenhouse experiment was conducted at the Technical University of Munich (TUM) School of Life Sciences Plant Facilities in Freising, Germany (48°24'N, 11°45'E). The experiment took place over two years, during the winter of 2018/19 and the summer of 2020.

Plant material and growth conditions in the soil: *Crassocephalum crepidioides* accession Ile-Ife (*C.C.*Ile-Ife) and *C. rubens* accession Mali (*c.r.*Mali) were previously described by Rozhon *et al.*[31] and Schramm *et al.*[32]. For soil cultivation, soil substrate C700 with Cocopor® (Stender AG, Schermbeck, Germany) was used. *Crassocephalum crepidioides* and *C. rubens* plants were grown in the greenhouse at two different seasons (winter and summer). Seeds were harvested during the 2018/19 winter and

2020 summer periods. Plants were initially cultivated in growth chambers (Bright Boy, CLF Plant Climatics, Wertingen), equipped with Philips Master TLD 58W/840 light bulbs. The standard growth conditions were a temperature of 25±2°C and cycles of 16 hrs of white light and 8 hrs of darkness, with an intensity of 80 μmol m^{-2} s^{-1}. Plants were germinated and pre-grown in small pots, filled with soil substrate, in the growth chambers for 3-4 weeks, using the conditions above, and then transferred to larger pots in the greenhouse. In the greenhouse, the plants were grown at a temperature of 20±2°C, 50% relative humidity with artificial lightning (80-100 μmol m^{-2} s^{-1} for 12 hrs) in winter and 25±3°C, 50% relative humidity without artificial lightning during the summer in Freising, Germany (48°24'N, 11°45'E). Watering was done with tap water; no additional fertilizer was added.

Germination experiments: *Crassocephalum seeds* were sterilized using 75% commercial bleach solution containing 0.01% Triton X-100. The bleach solution was added to the seeds and then gently shaken on the bench for 20 min. Seeds were then rinsed three times with deionized water in a sterile hood and transferred to either wet filter paper (Roth, Karlsruhe, Germany) or half-strength Murashige and Skoog (½MS) medium (Duchefa, Haarlem, Netherlands). Seeds from the mother plants grown at the same time and in the same conditions were used. The seeds were incubated at different temperature regimes (21 and 25°C), light intensities (30, 80 μmol m^{-2} s^{-1}), in the dark, and long-day photoperiod (16 hrs of light/ 8 hrs of darkness). Germination was assessed by the emergence of the radicle from the seed coat.

RESULTS

Response of *C. crepidioides* and *C. rubens* seeds to dormancy under varying growth conditions: Germination experiments were conducted on seeds of *C. rubens* ecotype Mali *and C. crepidioides* ecotype Ile-Ife. The seeds used have the same growth history. On ½MS medium, both species exhibited a high level of seed dormancy in the dark (Fig. 1a-b). While neither *C. crepidioides* nor *C. rubens* seeds showed any germination capacity in the dark at 21°C, *C. rubens* seeds germinated with approximately 30% efficiency at 25°C (Fig. 1a). Notably, when seeds were germinated on filter paper in the dark and at 21°C, both *C. rubens* and *C. crepidioides* seeds achieved germination efficiencies of 65 and 60%, respectively (Fig. 1c-b). Additionally, 50% germination efficiency was recorded on *C. rubens* when the temperature was increased to 25°C, however, raising the temperature to 25°C did not improve seed germination of *C. crepidioides* on filter paper (Fig. 1b). These results suggested that apart from the light requirement for the germination of *Crassocephalum* seeds, temperature and growth media also affect seed germination of *Crassocephalum*.

The effect of growth media on seed germination and dormancy of both *C. crepidioides* and *C. rubens* under light conditions revealed the interplay between light, temperature, and media and how these factors significantly influenced the germination of both *Crassocephalum* species. At 21°C and 30 μmol m^{-2} s^{-1} of light, about 40% germination was observed for *C. crepidioides* sown on filter paper as compared to 10% germination that was recorded on ½MS at 14 days after sowing (DAS; Fig. 2a). Interestingly, *C. rubens* achieved about 70% germination on ½MS compared to filter paper where about 35% germination was recorded (Fig. 2b). Keeping the light intensity constant and increasing the temperature to 25°C, seed germination significantly improved on both ½MS and filter paper for both *C. crepidioides* and *C. rubens*. *C. crepididoides* seeds had a faster germination rate on ½MS, recording 80% germination in just 6 days as compared to filter paper, where 40% germination was recorded at 6 DAS (Fig. 2c). On the contrary, *C. rubens* seeds had a faster germination rate on filter paper recording 100% germination in 5 DAS whereas, a significant reduction was observed on ½MS where 50% germination was recorded within the same period (Fig. 2d).

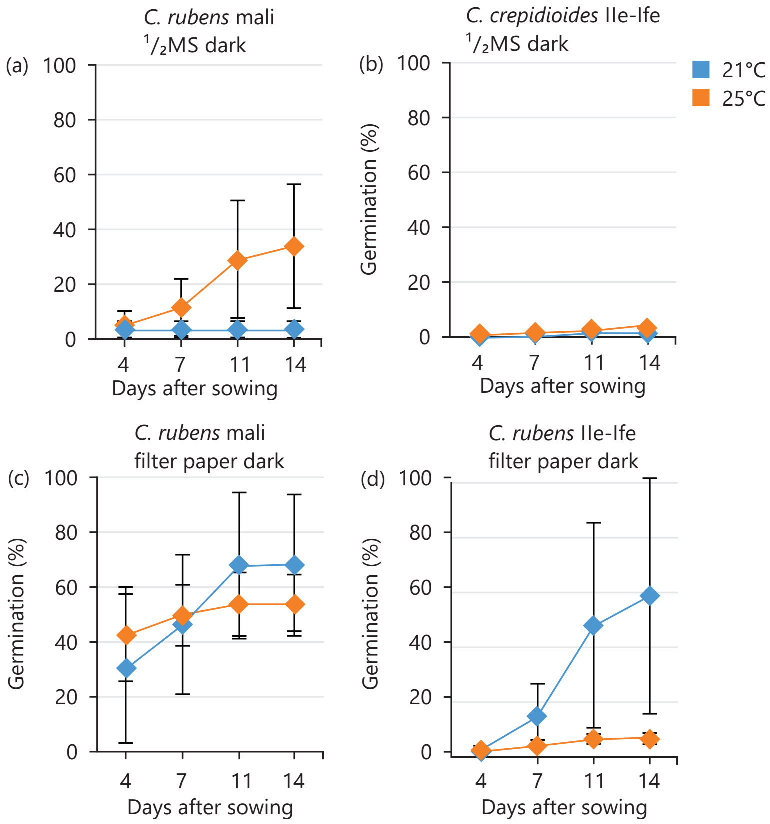

Fig. 1(a-d): Germination of *Crassocephalum* seeds on varying growth media influenced by growing temperature and photoperiod, (a-b) Germination of *C. rubens* (a) and *C. crepidioides* (b) seeds on ½MS medium and at 21 or 25°C, (c-d) Germination of *C. rubens* (c) and *C. crepidioides* (d) seeds on filter paper and at 21 or 25°C. All experiments were carried out in the dark

In all experiments, 50 seeds were incubated in the representative conditions and germination, defined as radicle emergence from the seed coat, was assessed at the indicated time points. Data show the mean±SD of four biological replicates.

In addition, the effect of increased light intensity from 30 to 80 μmol m^{-2} s^{-1} on the germination outcome of both *Crassocephalum* species was assessed. Keeping the temperature at 21°C, there was a significant improvement in seed germination for both *C. crepidioides* and *C. rubens* compared to results obtained under 30 μmol m^{-2} s^{-1}. *C. crepidioides* seeds recorded 60% germination on ½MS at 7 DAS as compared to filter paper where approximately 30% germination was recorded under the same condition (Fig. 2e). For *C. rubens*, 90% germination was recorded on filter paper at 7 DAS, in contrast to ½MS where 50% germination was recorded 7 DAS (Fig. 2f). When temperature was increased to 25°C, *C. crepidioides* exhibited a similar germination response on both ½MS and filter paper, recording approximately 50% germination in 7 days (Fig. 2g). In contrast, *C. rubens* had a faster germination rate on filter paper, reaching 90% germination in 5 DAS, while only approximately 20% germination was recorded on ½MS during the same period (Fig. 2h).

Investigating the influence of environmental variations during seed development on the germination of *Crassocephalum* seeds, two different seed batches from *C. crepidioides* and *C. rubens* mother plants grown either during the 2018/19 winter or the 2020 summer period were subjected to germination tests. A high level of variation was observed between the germination outcomes of the two different seed batches.

Germinating the seeds at a light intensity of 30 μmol m^{-2} s^{-1} and at 21°C, both *C. rubens* and *C. crepidioides* seeds from mother plants grown in winter were more dormant than those from mother plants grown in summer (Fig. 3a-b). This was evident with the reduced germination capacity

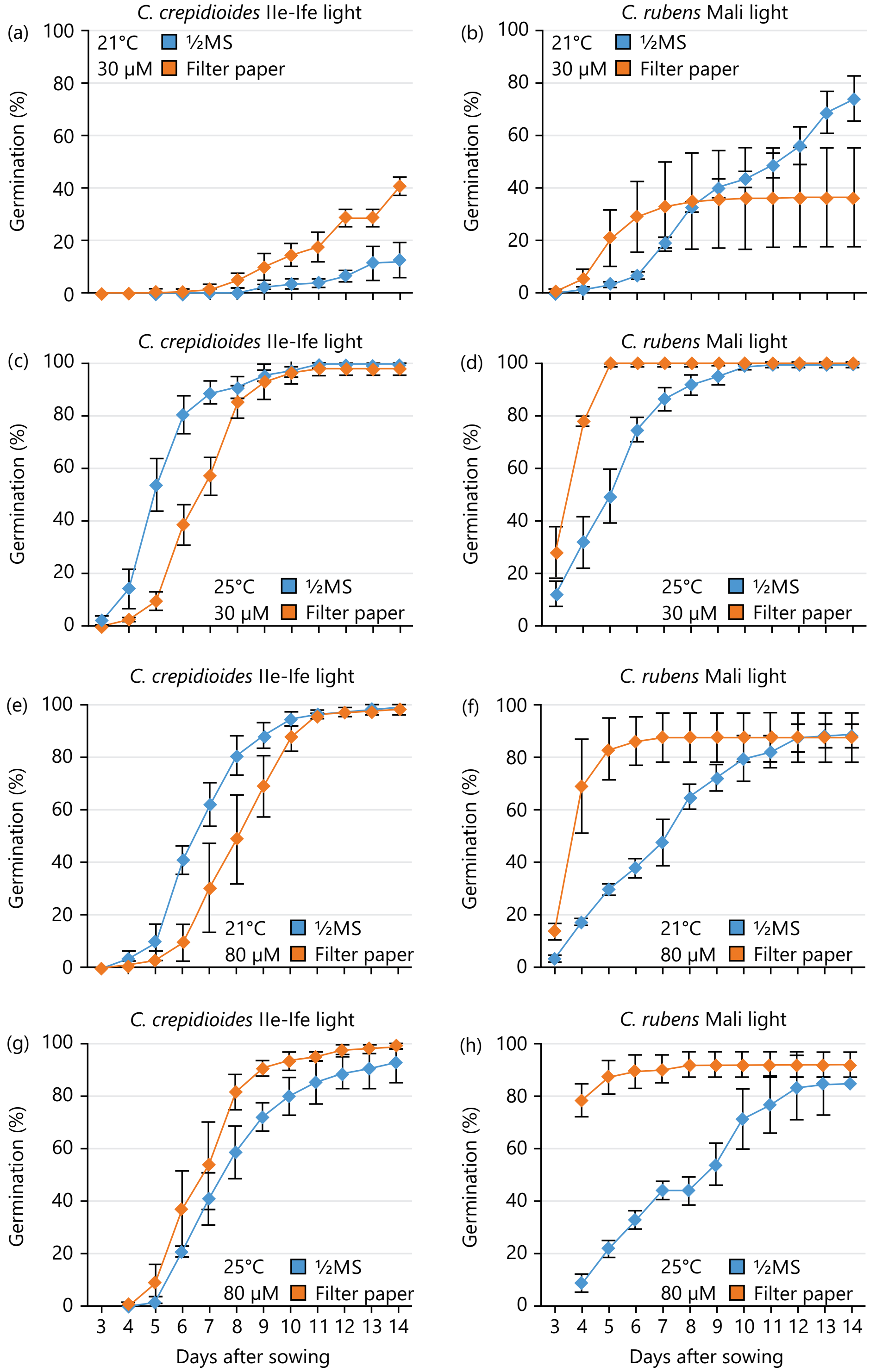

Fig. 2(a-h): Germination of *Crassocephalum* seeds is influenced by germinating media, (a-h) Germination of *C. crepidioides* and *C. rubens* seeds on filer paper and ½MS medium at different temperatures (21 and 25°C) and light intensities (30 and 80 μmol/m^2/s), (a) Germination of *C. crepidioides* seeds at 21°C and 30 μmol m^{-2} s^{-1}, (b) Germination of *C. rubens* seeds at 21°C and 30 μmol m^{-2} s^{-1}es, (c) Germination of *C. crepidioides* seeds at 25°C and 30 μmol m^{-2} s^{-1}, (d) Germination of *C. rubens* seeds at 25°C and 30 μmol m^{-2} s^{-1}, (e) Germination of *C. crepidioides* seeds at 21°C and 80 μmol m^{-2} s^{-1}, (f) Germination of *C. rubens* seeds at 21°C and 80 μmol m^{-2} s^{-1}, (g) Germination of *C. crepidioides* seeds at 25°C and 80 μmol m^{-2} s^{-1} and (h) Germination of *C. rubens* seeds at 25°C and 80 μmol m^{-2} s^{-1}

In all experiments, 50 seeds were incubated in the representative conditions and for the indicated periods, and germination, defined as radicle emergence from the seed coat, was assessed. Data shown are mean±SD of four biological replicates.

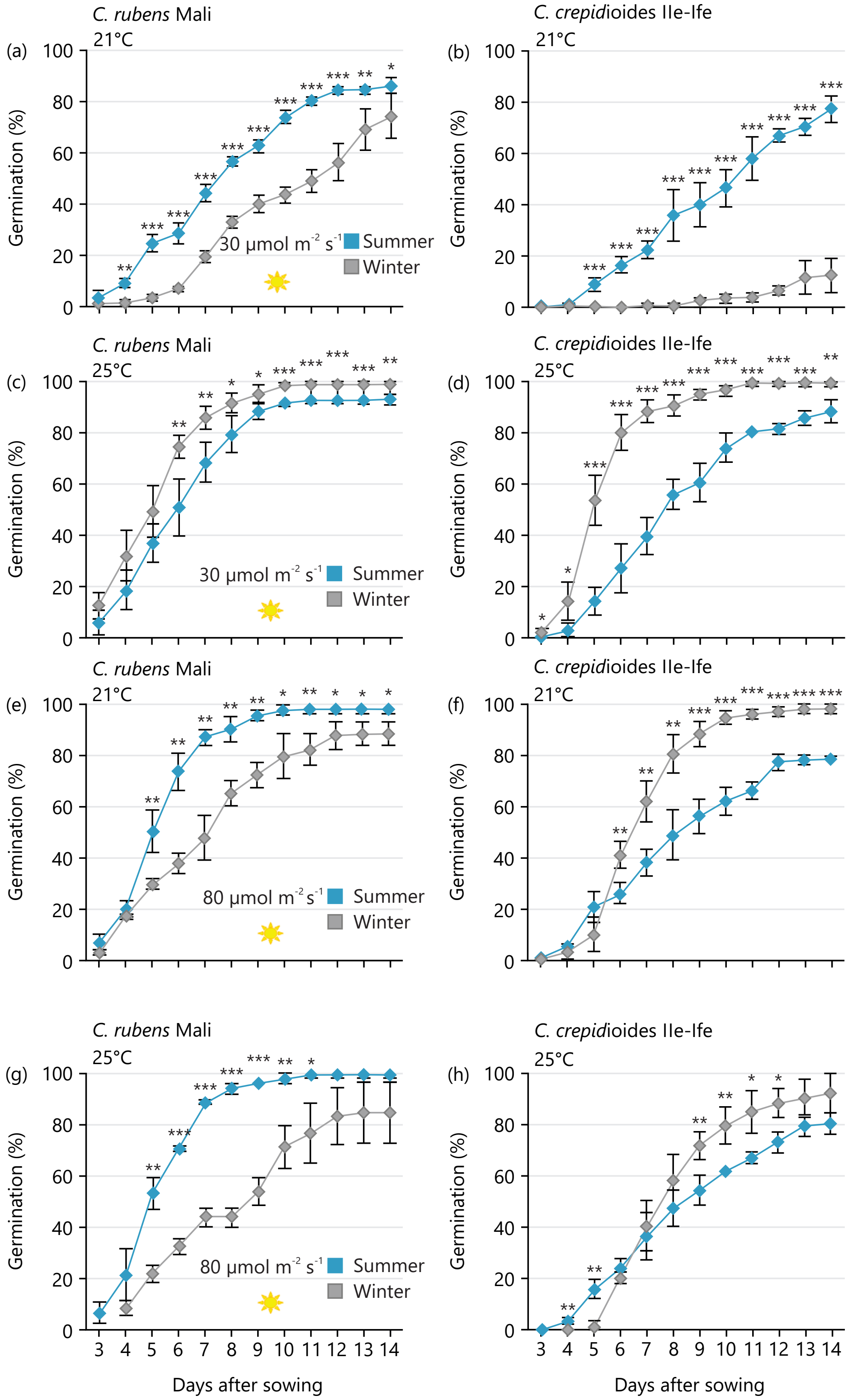

Fig. 3(a-h): Time of planting influences the dormancy level of *Crassocephalum seeds.* Germination *C. crepidioides* and *C. rubens* seeds from mother plants grown in winter or summer at different temperatures and light intensities, (a-b) Germination of *C. rubens* (a) and *C. crepidioides* (b) seeds at 30 µmol m^{-2} s^{-1} and 21°C, (c-d) Germination of *C. rubens* (c) and *C. crepidioides* (d) seeds at 30 µmol m^{-2} s^{-1} and 25°C, (e-f) Germination of *C. rubens* (e) and *C. crepidioides* (f) seeds at 80 µmol m^{-2} s^{-1} and 21°C and (g-h) Germination of *C. rubens* (g) and *C. crepidioides* (h) seeds at 80 µmol m^{-2} s^{-1} and 25°C

In all experiments, 50 seeds were plated on ½MS medium and incubated in the representative conditions and germination, defined as radicle emergence from the seed coat, was assessed and at the indicated periods. Data shown are mean±SD of four biological replicates. Statistically significant difference at $p \leq 0.05$ between seasons is shown in asterisks and was determined with one-way ANOVA with a *post-hoc* Tukey HSD test.

recorded from the seeds harvested in winter. Notably, the germination capacity of *C. crepidioides* seeds obtained during winter was considerably lower, with approximately 10% germination recorded 14 DAS (Fig. 3b).

At higher light intensity of 80 μmol m^{-2} s^{-1} or higher temperature of 25°C, the seeds were relieved of the observed dormancy (Fig. 3c-h). Interestingly, *C. crepidioides* seeds from plants grown in winter showed a higher germination capacity at higher temperatures and light levels than those from summer grown plants (Fig. 3d-f and h). In contrast, *C. rubens* seeds from mother plants grown in summer generally exhibited better germination than those from winter-grown plants. These findings are consistent regardless of the germination environment.

DISCUSSION

Ensuring food and nutritional security for a global population projected to reach approximately 10 billion by 2050 is a significant challenge. This challenge is compounded by the need to maintain crop production amid changing climatic conditions, increasing severity of abiotic and biotic stresses, and the limitations imposed by restricted agricultural land. In 2023, about 733 mL people were reported to face chronic hunger, a staggering increase from 613 mL in 2019[33]. Additionally, an estimated 2.33 billion people were classified as moderately or severely food insecure, with Africa presenting around 282 mL undernourished people[33,34]. Projections indicate that, without significant intervention, achieving zero hunger by 2030 will be extremely difficult. Many underutilized crops, which are currently grown on a small scale in hunger-prone areas, have the potential to address food and nutrient deficiencies[35]. When integrated with staple crops, these underutilized crops could play a crucial role in meeting the nutritional needs of a growing population.

Crassocephalum crepidioides and *C. rubens* are two underutilized leafy vegetables with the potential as food crops[36-39]. They are highly nutritious and have potential as vegetables and medicinal plants. However, these crops are limited in cultivation and are primarily harvested from the wild. The major constraint limiting the cultivation is high degree of seed dormancy. Light efficiently promoted germination of *C. crepidioides* and *C. rubens* seeds[5]. The effect of light on seed germination of *C. crepidioides* and *C. rubens* had already been studied, and it was reported that both species required light for germination[4,5]. Adedeji-Badmus *et al.*[5] established that *C. crepidioides* seeds are highly dormant as compared to *C. rubens.* This was due to the high amount of ABA in *C. crepidioides* seeds at harvest. The requirement of light for *C. crepidioides* surpasses that of *C. rubens*. This was evident from the germination experiment in the dark. No germination was recorded for *C. crepidioides* on ½MS media, irrespective of the temperature used, compared to *C. rubens*. A similar observation was reported by Adedeji-Badmus *et al.*[5]. Similarly, *C. crepidioides* recorded low germination on filter paper compared to *C. rubens*.

Light and temperature promote germination of *C. crepidioides* and *C. rubens.* Low temperature (21°C) and low light I ntensity (30 μmol m^{-2} s^{-1}) significantly impact seed germination of both *C. crepidioides* and *C. rubens*. High temperature (25°C) and low light intensity (30 μmol m^{-2} s^{-1}), low temperature (21°C) and high light intensity (80 μmol m^{-2} s^{-1}); and high temperature (25°C) and high light intensity (80 μmol m^{-2} s^{-1}) significantly improved seed germination of both *C. crepidioides* and *C. rubens*. This indicates that there is an interplay of light and temperature in the seed germination of *C. crepidioides* and *C. rubens.* Adedeji-Badmus *et al.*[5] also observed a significant improvement in seed germination of *C. crepidioides* and *C. rubens* when the temperature was increased to 25°C. Yuan and Wen[4] recorded the highest germination for *C. crepidioides* at 25°C and 25 μmol m^{-2} s^{-1}.

Considering the effect of media on seed germination of *C. crepidioides* and *C. rubens*, it was observed that filter paper promoted seed germination of both species in the dark. However, under light conditions, both ½MS and filter paper promoted seed germination. Under low light (30 μmol m^{-2} s^{-1}) and low temperature

(21°C) conditions, filter paper promoted seed germination of *C. crepidioides* while ½MS media was more effective for *C. rubens*. This indicates that, in addition to light and temperature, the choice of growth media significantly influences the seed germination of these *Crassocephalum* species. At a higher temperature (25°C) and light intensity (80 μmol m^{-2} s^{-1}), ½MS improved the speed of germination in *C. crepididoides*. Conversely, for *C. rubens*, the speed of germination improved on filter paper.

Growth conditions at harvest and seasonal variation during the growth and development of plants can have a significant impact on the dormancy level and germination capacity of seeds. Therefore, it is important to assess the effect of seasonal variation and growth conditions on the seed germination capacity of *Crassocephalum* seeds. According to Baskin and Baskin[18], the environmental conditions under which seeds develop can influence seed quality. In this study, both *C. rubens* and *C. crepidioides* seeds harvested from the mother plants grown during winter were more dormant than those harvested from mother plants grown in summer. The effect of seasonal variations on seed dormancy and germination was particularly noticeable when *Crassocephalum* seeds were germinated under high temperatures or high light intensities. Specifically, *C. crepidioides* seeds from summer grown plants were more dormant than the winter-grown plants. Conversely, *C. rubens* seeds from winter-grown plants displayed a higher dormancy level than those from the summer-grown plants.

Environmental conditions during seed maturation, such as photoperiod and temperature, have a strong influence on seed dormancy and germination[14,18,40]. Temperature variation during seed set and maturation strongly affects seed dormancy[13]. Generally, lower temperatures almost always result in lower germination. Interestingly, *C. crepidioides* seeds from summer-grown plants have lower germination capacity as compared to the winter-grown plants. However, seed produced by summer-grown *C. rubens* plants tends to have a higher germination capacity.

CONCLUSION

In conclusion, there is an interplay between light, temperature, and growth media on seed germination of *C. crepidioides* and *C. rubens*. Generally, *C. crepidioides* exhibited higher dormancy compared to *C. rubens* and required light and temperature to break out of dormancy. Low temperature and low light impaired seed germination of both species. The choice of germinating media also influences the speed and rate of germination of *Crassocephalum* seeds. The ½MS significantly improved seed germination of *C. crepidioides,* while filter paper was more effective for *C. rubens*. Additionally, growth conditions and seasonal variation during maternal plant growth influenced the dormancy level in *Crassocephalum* seeds. Typically, *C. rubens* seeds harvested in winter exhibited higher dormancy than those harvested in summer, while *C. crepidioides* seeds harvested in the summer showed higher dormancy compared to the winter-harvested seeds.

SIGNIFICANCE STATEMENT

This study identified the optimal environmental conditions light, temperature, and media type required to overcome seed dormancy in *Crassocephalum crepidioides* and *C. rubens*, which could be beneficial for enhancing their cultivation and supporting efforts toward their domestication. The study will assist researchers in uncovering critical areas of seed physiology and dormancy regulation that have remained unexplored by many. Consequently, a new theory on photothermal and substrate dependent dormancy mechanisms in tropical leafy vegetables may be developed.

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