

# Seed Germination and Seedling Emergence of *Lysimachia mauritiana* Lam. (Primulaceae)

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## Abstract

*Lysimachia mauritiana* Lam. (Primulaceae), a biennial maritime plant, is widely distributed in East Asia, the Philippines, Micronesia, Polynesia, and the Indian Ocean. Because of this species' wide distribution in Japan, we hypothesized that it could germinate and grow even in the bare coastal areas damaged by the tsunami caused by the Great East Japan Earthquake. Thus, we aimed to evaluate the seed germination of *L. mauritiana* under different sowing depths, temperatures, and salinity soil conditions. The highest germination rate was obtained by sowing *L. mauritiana* seeds near the soil surface, with germination rate decreasing as the seeding depth increased. *Lysimachia mauritiana* germinated even at relatively low temperatures. Moreover, we found that *L. mauritiana* seeds could germinate in less than 1% salt water and in salt-accumulated soil, using soil soaked in 5% or 10% salt water. Our results therefore suggest that *L. mauritiana* seeds could germinate by sowing on the bare soil surfaces damaged by the tsunami.

**Keywords:** coastal area, germination, *Lysimachia mauritiana*, salinity, seed

## 1. Introduction

The biodiversity of coastal environments is valuable at the global scale, as these environments have high endemism rates of plant species that occur as a result of the unique environments, with strong persistence of shore winds carrying sand and salt spray that dries leaves and soil (Hassani et al., 2021; Nakajima & Yoshizaki, 2018). Plant species in coastal areas have traits adapted to coastal environments (Kumekawa et al., 2013; Ohga et al., 2013; Shiba et al., 2022; Sunami et al., 2013; Takizawa et al., 2022; Tunala et al., 2012); therefore, the conservation and sustainable use of coastal forests require close attention (Cori, 1999; Schlacher et al., 2008).

Coastal forests reduce the energy of tsunami, but they cannot completely stop the tsunami itself (Tanaka, 2009). Previous studies on the effectiveness of coastal forests (e.g., Dahdouh-Guebas et al., 2005; Danielsen et al., 2005; Dengler & Preuss, 2003; Hiraishi & Harada, 2003; Tanaka & Yagisawa, 2009) have shown that it depends on the magnitude of the tsunami, forest width, and vegetation structure (Shuto, 1987; Tanaka et al., 2007; Tanaka & Yagisawa, 2009). Coastal forests in large areas of the Tohoku and Kanto districts of Japan were destroyed by the tsunami after the Great East Japan Earthquake on March 11, 2011. The regeneration of these coastal forests is essential in the post-earthquake recovery process, and it is desirable that these forests be regenerated not only to restore coastal forests to their condition before the tsunami but also to improve them. However, salt accumulation on coastal soils continues even as waves, storm surges, tides, and currents interact with various components of the coastal environment after earthquakes. The low rainfall in coastal areas of the Tohoku and Kanto districts prevents efficient drainage of salinity from the soil, which results in poor desalination. Moreover, many areas have not yet begun succession into coastal forests, and many of them remain bare (Ono et al., 2014).

Primary succession of coastal forests typically occurs very slowly when site conditions are unfavorable to most plants, with only few unique plant species being able to thrive; therefore, selecting and sowing plant species adapted to such environments could encourage primary succession (Ito & Yoshizaki, 2013; Yoshizaki, 2011). Nevertheless, as many species exhibit genetic variations in Japan (Fujii et al., 2002; Fukuda et al., 2011a, 2011b; Hayakawa et al., 2012, 2014; Iwasaki et al., 2010, 2012; Matsumura et al., 2009; Saitou et al., 2007; Sakaguchi et al., 2017; Yamaji et al., 2007;

Yokoyama et al., 2003), the use of species from other regions could lead to genetic pollution, in which the original genes are swamped out by hybridization with introgression sources (Fischer & Matthies, 1998; Lynch et al., 1995). This would result in a loss of endemic alleles and the dominance of the introduced genotypes over coastal areas (Hufford & Mazer, 2003; Saltonstall, 2002). Therefore, plants with a wide distribution in coastal areas, including the Tohoku and Kanto districts, were considered the most effective in starting succession from bare ground.

*Lysimachia mauritiana* Lam. (Primulaceae) is a biennial maritime plant that grows to approximately 50 cm tall, with spatulate to obovate leaves, and is widely distributed in East Asia, the Philippines, Micronesia, Polynesia, and the Indian Ocean islands (Yamazaki, 1993). Its white flowers are small (Figure 1A), blooming of this species occurs with the greatest intensity in late spring and early summer, and the dehiscent fruits containing many small seeds (ca. 1 mm) are 3–5 mm in diameter (Figure 1B, 1C). In Japan, the populations of *L. mauritiana* are frequently seen in rocky places in seacoasts from north to south in the Archipelago (Yamazaki, 1993). As *L. mauritiana* germinates under saline conditions, it may be a candidate plant for seeding in the early succession period in poorly desalinated areas of the Tohoku and Kanto districts. However, the conditions for germination of this species remain unclear. Germination experiments were conducted on *L. minoricensis* J. J. Rodr., which is related species of *L. mauritiana*. Rossello and Mayol (2002) reported that seed germination of *L. minoricensis*, a Mediterranean endemic species, was not inhibited in the dark and a high germinability was recorded in most experiments, with the exception of those performed at low temperatures, indicating no highly specific requirements for seed germination. Germination requirements and rates are among the most important seed traits associated with plant fitness and are important factors in the ecology and evolution of plant life histories (Donohue, 2005; Dwyer & Erickson, 2016). Knowledge of the performance of these stages may help determine whether the species could contribute to early succession in the bare ground of Tohoku and Kanto districts. These data are essential not only for improving the recovery of coastal forests in these areas but also for determining reproductive strategies for this species.

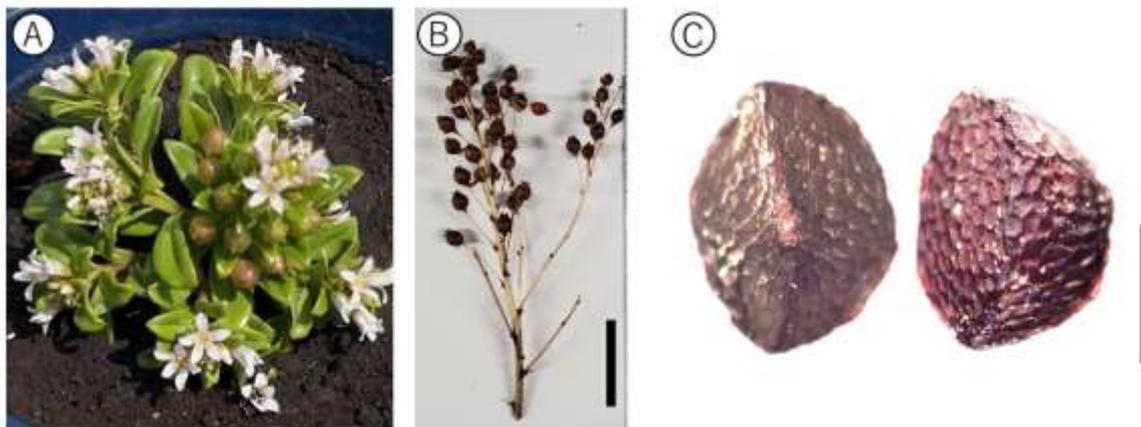


Figure 1. *Lysimachia mauritiana* Lam

(A) gross picture, (B) dehiscent fruits (bar = 30mm), (C) seed (bar = 0.5mm).

Seed germination is a sensitive stage in the life cycle of plants because it plays a major role in determining the final plant fitness, and factors such as gene control, seed size, viability, depth of planting, soil moisture, and temperature influence germination and seedling emergence (Baskin & Baskin, 1985; Rajasekaran et al., 2002; Shafii & Price, 2001; Windauer et al., 2007). Temperature is the most important driving force influencing germination and seedling emergence, and its effects are the basis for models used to predict germination timing (Kamkar et al., 2008). A distance of approximately 800 km extends the coastal areas from north of Tohoku to south of Kanto district, and temperatures are very different within these areas; therefore, clarification of the temperature required for germination of *L. mauritiana* would indicate the areas adequate for sowing. In addition, the seed of *L. mauritiana* is very small (ca. 1 mm) (Figure 1C), and a shallow depth is considered the best for sowing; however, the surface layer tends to dry out in the coastal areas because of the wind, and it is not necessarily better to sow seeds at a shallower depth. However, some studies have reported that increased seeding depth reduces seedling emergence and emergence rates (Gul & Allan, 1976; Sepaskhah & Ardekani, 1978). It would be interesting to clarify whether the germination of small seeds of *L. mauritiana* could be affected by changing the planting depth in coastal areas. Therefore, the aim of this study was to elucidate and compare seed germination of *L. mauritiana* under different salinity soil conditions, temperatures, and planting depths.

## 2. Method

Seeds of *Lysimachia mauritiana* were collected from the coastal areas of Kyonan-machi, Awa-gun, Chiba Prefecture, Japan (35°06'05" N, 139°49'33" E) in September 2021. Seeds were manually separated from inflorescences, and healthy seeds were selected and placed in envelopes. Baek et al. (2021) reported that dormancy could lead to efficient germination in *L. coreana* Nakai. A temperature of approximately 5 °C is generally optimal for seed dormancy and is thus often used as a pre-chilling treatment; however, in some cases, temperatures below 5 °C are more effective (Baskin & Baskin, 1985). Therefore, the germination tests were stored in a refrigerator (MPR-312D, SANYO, Japan) at 4 °C until their use.

First, to clarify the optimal depth of seed germination for *L. mauritiana*, we used four flower pods (10 cm depth × 10 cm diameter) three-quarters full of sea sand from the seed collection site. We buried 30 seeds at depths of 0 mm (surface), 5 mm, 10 mm, and 20 mm from the surface, and added 10 mL of distilled water daily in an incubator (A5501, AS ONE, Japan) set at 25 °C. The percent germination was recorded daily for three weeks. Tukey's multiple comparison test was used to determine significant differences in germination among the different incubation periods of low temperature for all parameter means ( $p < 0.05$ ). The same trial was performed twice to verify the reproducibility of the experiment.

Second, to determine the effect of temperature on *L. mauritiana* germination, we put cotton in four petri dishes with a diameter of 15 cm and placed 30 seeds in each, adding 10 mL of distilled water daily, in incubators at four temperature regimes: 4 °C, 15 °C, 20 °C, and 25 °C (4 °C: MPR-312D, SANYO, Japan; 15 °C and 20 °C: THS-020DB, ADVANTEC, Japan; 25 °C: A5501, AS ONE, Japan). The percent germination was recorded daily for about three weeks. Tukey's multiple comparison test was used to determine significant differences in germination among different incubation periods for all parameter means ( $p < 0.05$ ). The same trial was performed twice to verify the reproducibility of the experiment.

Third, to clarify the germination ability of *L. mauritiana* in salt water, we used different concentrations (0%, 0.5%, 1%, 2%, and 3.45% [3.45%: seawater concentration]) of saline (NaCl solution). We placed cotton in five petri dishes with a diameter of 15 cm and placed 30 seeds in each, adding 10 mL of saline water daily at different concentrations in an incubator (A5501, AS ONE, Japan) set at 25 °C. The percent germination was recorded daily for about three weeks. Tukey's multiple comparison test was used to determine significant differences in germination among different incubation periods for all parameter means ( $p < 0.05$ ). The same trial was performed twice to verify the reproducibility of the experiment.

Finally, additional experiments were conducted to analyze the germination rate of *L. mauritiana* in salt-soaked soils. We submerged sea sand collected from the seed collection site in different concentrations of salt water (5% and 10%), and then removed it to create dry soils, including salts. Moreover, we used two flower pods (10 cm depth × 10 cm diameter) three-quarters full of dry soil and placed 30 seeds on the surface of each pod, adding 10 mL of distilled water daily in an incubator (A5501, AS ONE, Japan) set at 25 °C, respectively. The percent germination was recorded daily for about three weeks. Tukey's multiple comparison test was used to determine significant differences in germination among different incubation periods for all parameter means ( $p < 0.05$ ). The same trial was performed twice to verify the reproducibility of the experiment.

## 3. Results and Discussion

### 3.1 Optimal Depth of Seed Planting

Planting seeds at the right depth improves their chances of developing into hardy seedlings and increases germination rates, and the appropriate depth varies with the size and type of seeds. Previous studies have reported the effects of seed size and sowing depth on various stages of plant growth, development, and establishment (Bockstaller & Girardin, 1994; Graven & Carter, 1990; Gubbels, 2010; Hunter & Kannenberg, 1972; Nafziger, 1992; Varga et al., 2012), indicating that there is no consistent trend, but that it rather varies with species and habitat (Umeoka & Ogbonnaya, 2016). Additionally, the particle size composition of surface sediments significantly impacts seed germination (Shiono & Mochida, 2012), affecting seed entrapment, water holding capacity, and inter-space of soil particles, which in turn affects root elongation (Chambers et al., 1990, 1991). The smaller the particle size, the higher the water retention capacity and the seed germination (Yabashi et al., 1995). Kuramoto et al. (1993) reported that there was more bare land on gravelly sites than fine-grained soil sites. Considering the seeding of *L. mauritiana* in coastal areas, we herein analyzed sand collected from coastal areas. The results of the first and second trials on the depth of seed planting indicated that the highest germination rate was obtained by sowing *L. mauritiana* seeds near the soil surface layer, and the germination rate decreased as the seeding depth increased (Figure 2), suggesting that it was more effective to sow seeds of *L. mauritiana* on the soil surface than burying them in the soil. This species has buoyant capsules suitable for sea dispersal, and Kono et al. (2016) suggested that its distribution has been expanded by long-distance sea dispersal.

Therefore, we suggest that this species germinates immediately at the place where the seed was washed ashore by oceanic currents. However, surface soil temperature exhibits spatial variability along coastal areas, and temperature regimes on coastal areas are complex because of the interaction with the properties of the land

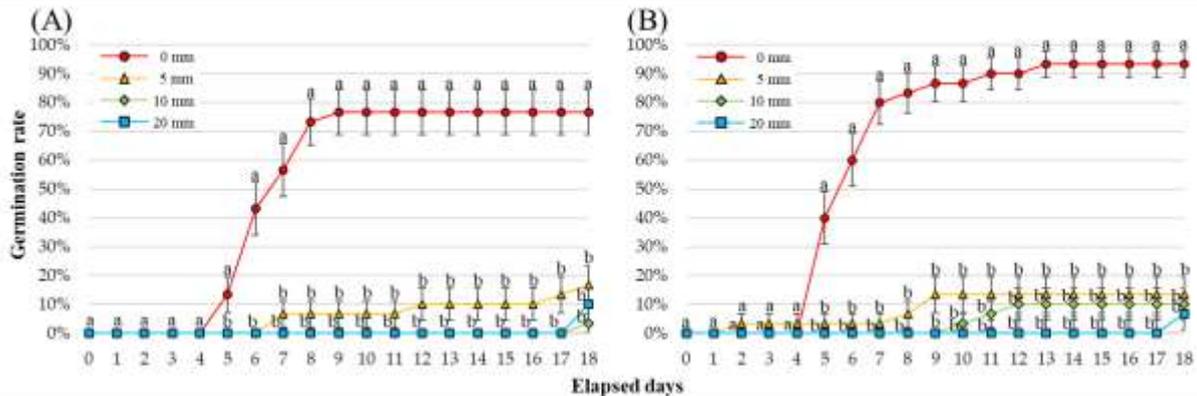


Figure 2. Cumulative seed germination rate of *Lysimachia mauritiana* versus days in different depth of planting

Each depth indicates as follows; near surface: solid circle, 5mm: solid triangle, 10mm: solid diamond, 20mm: solid square. (A) first trial, (B) second trial.

surface, atmosphere, and coastal waters and the role of hydrology in controlling daily or seasonal variations (Chen et al., 2017; Cohen et al., 2021; Huang & Li, 2017; Osland et al., 2019). Therefore, whether *L. mauritiana* has a wide optimum germination temperature was the question. In addition, soil salinization is expected to occur on the soil surface in coastal areas because of the process during which the salt in the deep soil and groundwater rises to the surface via evaporation and then accumulates in the topsoil (Marsack & Connolly, 2022). Haraguchi and Sakaki (2020) indicated that hot spots of sea salt deposition on the soil surface were observed at hollows of the ground surface, slope-facing coastal lines, or sites with an abrupt increase in height where the canopy faces the coast. Based on these facts, we analyzed the optimal germination temperature and soil salinization for germination of *L. mauritiana*.

### 3.2 Comparison of Germination Rates Under Different Temperatures

Germination rate is mainly affected by temperature because of its relationship with water absorption by seeds (Benech-Arnold et al., 2000; Batlla & Benech-Arnold, 2015). Our experiments at multiple temperature settings showed that the germination rate in *L. mauritiana* decreased with temperature, with no germination occurring at 4 °C (Figure 3).

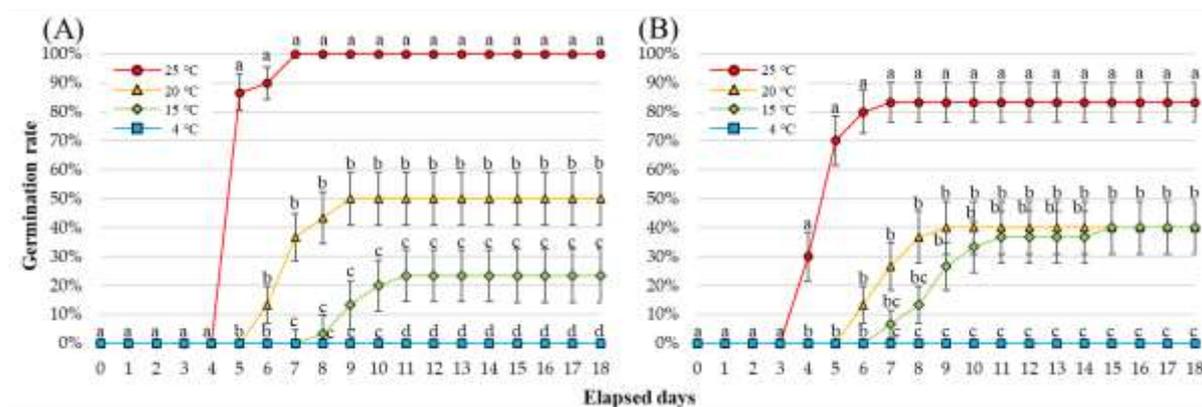


Figure 3. Cumulative seed germination rate of *Lysimachia mauritiana* versus days in different temperatures

Each temperature indicates as follows; 25 °C: solid circle, 20 °C: solid triangle, 15 °C: solid diamond, 4 °C: solid square. (A) first trial, (B) second trial.

Our previous germination study indicated that *Canavalia lineata* (Thunb.) DC. (Fabaceae) did not germinate below 20 °C, possibly explaining why this species does not spread to the Tohoku north of Kanto districts (Ishii et al., 2022). Hughes (2000) reported that a 3 °C change in mean annual temperature results in a shift in isotherms from 300 to 400

km in latitude, and our results indicated that *L. mauritiana* germinated at even lower temperatures than *C. lineata*. These results indicate that *L. mauritiana* maintains a certain germination rate even at relatively low temperatures; therefore, *L. mauritiana* could extend its distribution to the Tohoku district, which is farther north than the northern limit of *C. lineata*. In general, the base temperature for germination in field species is more than 5 °C (Lonati et al., 2009), and the optimum temperature for germination of most species adapted to cooler climates was reported to be 10–30 °C (Lonati et al., 2009; Odabaş & Mut, 2007; Schellenberg et al., 2013; Zhang et al., 2013). Interestingly, more than 30% of the seeds germinated even at 15 °C; however, it is unlikely that *L. mauritiana* is adapted to cool areas because Butler et al. (2017) indicated that the temperature for optimum germination was 10–20 °C for most annual plants adapted to cool areas, and 15–20 °C for most perennials, suggesting that *L. mauritiana* is not particularly adapted to cold climates. What is the significance of the relatively wide range of temperatures required for *L. mauritiana* germination? Brar et al. (1991) reported that adaptability and germination of seeds under a broad range of temperatures are important for early seedling emergence and establishment. McGraw et al. (2003) suggested that it could be critical for a species to germinate quickly in areas with variable rainfall patterns and amounts when competition for resources is high and the window of opportunity for growth and development is small. Sea water of coastal areas may significantly increase sodium levels in soil, thereby elevating the level of soluble salts. The soluble salt elevation could come from multiple sources such as sea spray, storm surge, and saltwater intrusion into shallow groundwater in growing areas of *L. mauritiana* on the shoreline side of the coastal forest. In this case, significant rainfall could bring an influx of salt and dilute or flush salt out of soils, whereas low rainfall would leave sodium accumulation and relatively dry conditions in the growing areas of *L. mauritiana*. Ono et al. (2014) reported that a large amount of salt remains in the coastal areas of the Tohoku and Kanto districts because of the low rainfall in these areas, indicating that the effect of salt on the germination of *L. mauritiana* needs to be clarified.

### 3.3 Effect of Salt Water and Salinity Condition on Seed Germination

Seedling emergence constitutes the most critical stage in the life cycle of plants because it determines whether seedlings can survive in the local environment (Bajji et al., 2002). High soil salinity inhibits seed germination because of the low osmotic potential created around the seed, which prevents water uptake (Welbaum et al., 1990). Moreover, high concentrations of sodium and chloride ions in the soil may be toxic to seeds (Khajeh-Hosseini et al., 2003). Therefore, soil salinity seriously influences the growth of coastal plants, especially during seed germination and seedling stages. Thus, illuminating the responses to salt stress during the seed germination, post-germination, and seedling stages would be useful for sowing seeds in the coastal areas of the Tohoku and Kanto districts. Recent studies of salt stress effects on the germination of coastal trees showed that most tree species germinate or decrease their germination rate at elevated salinity levels that accompany saltwater intrusion, affecting future forest community composition (Ito & Yoshizaki, 2017, 2019; Middleton, 2016; Nakajima & Yoshizaki, 2010; Woods et al., 2020). Our study showed that seeds of *L. mauritiana* germinate in less than 1% salt water in both trials (Figure 4), suggesting that *L. mauritiana* germinates even if the salt in the soil of the tsunami-affected area is not completely removed by rainfall.

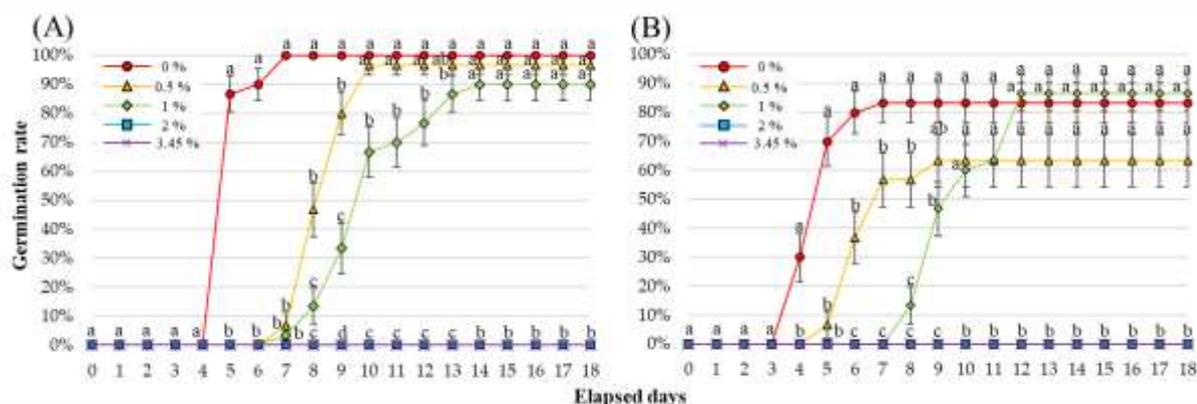


Figure 4. Cumulative seed germination rate of *Lysimachia mauritiana* versus days in different salt concentrations

Each concentration indicates as follows; 0%: solid circle, 0.5%: solid triangle, 1%: solid diamond, 2%: solid square, 3.45%: cross. (A) first trial, (B) second trial.

Also, our results indicated that germination was significantly delayed as salinity increased (Figure 4). Several studies have found that high-salinity stress retards germination and inhibits the growth of radicles and seedlings (Ito & Yoshizaki, 2017; Kandil et al., 2012; Karim et al., 1992; Mahdavi & Sanavy, 2007; Meloni et al., 2008). Therefore, we

hypothesized that *L. mauritiana* also has significant differences in germination timing with respect to salinity conditions.

Previous studies have reported that increased evapotranspiration rates and alterations in precipitation patterns in coastal areas reduce soil leaching efficiency and consequently increase salinity in the surface soil layer (Karmakar et al., 2016; Yeo, 1998), implying that analyzing the increased salt concentration in the soil is necessary. Considering the sowing of *L. mauritiana* in salt-accumulated soil, we performed germination experiments using soil soaked in 5% or 10% salt water and then dried; both experiments indicated that *L. mauritiana* could germinate by continuously adding distilled water, although germination was significantly delayed compared to that in the non-immersed soil (Figure 5). Germination of *L. mauritiana* occurred until 4 days after seeding in the control soil [0%], whereas germination occurred 6 days after seeding in both cases in the salt-accumulated soil (Figure 5). This difference in germination time was considered to correspond to the time required to lower the salt concentration of the soil by adding distilled water. Moreover, our results indicated that *L. mauritiana* has a very slow rate of germination in soils soaked in 10% salt water (Figure 5), showing that the salts in the soil could not be easily removed, and that poor desalination would prevent the germination of *L. mauritiana*.

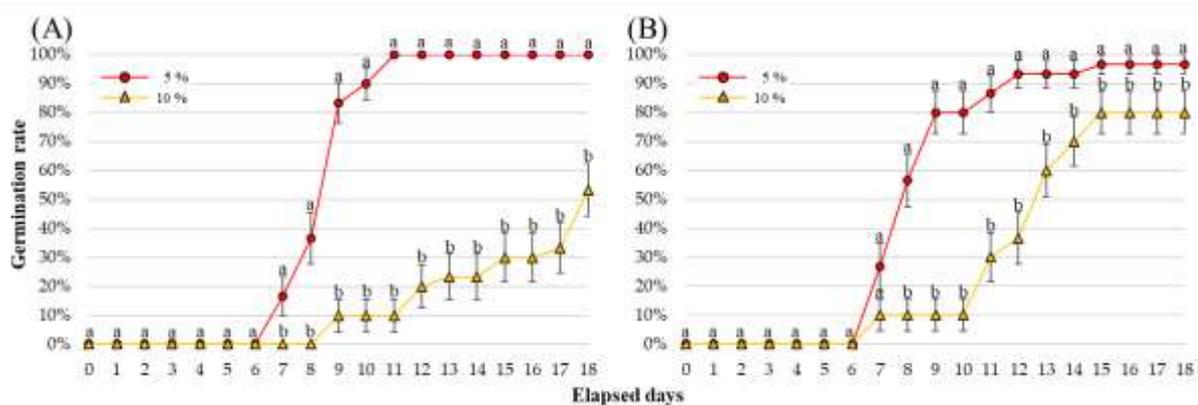


Figure 5. Cumulative seed germination rate of *Lysimachia mauritiana* versus days using soil soaked in 5% (solid circle), and 10% (solid triangle) salt water

(A) first trial, (B) second trial.

#### 4. Conclusion

Our study indicated that high germinability of *L. mauritiana* was recorded by sowing on the soil surface, supporting the high germination rate even in closely related species (Rossello & Mayol, 2002; Baek et al., 2021), but the germination rate of this species decreased significantly with increasing seeding depth. Alternatively, we found that *L. mauritiana* had a relatively wide range of germination temperatures and germinated under a certain salt concentration, even though the soil surface of the coastal areas tended to accumulate salt. Finally, our results suggest that *L. mauritiana* can germinate in the areas of the Tohoku and Kanto districts left bare by the tsunami after the Great East Japan Earthquake on March 11, 2011. We sincerely hope that our results will help in recovery from the tsunami damage in areas of the Tohoku and Kanto districts.

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#### References

- Baek, S. G., Im, J. H., Kwak, M. J., Park, C. H., Lee, M. H., Na, C. S., & Woo, S. Y. (2021). Non-deep physiological dormancy in seed and germination requirements of *Lysimachia coreana* Nakai. *Horticulturae*, 7(11), 490. <http://dx.doi.org/10.3390/horticulturae7110490>
- Bajji, M., Kinet, J. M., & Lutts, S. (2002). The use of the electrolyte leakage method for assessing cell membrane stability as a water stress tolerance test in durum wheat. *Plant Growth Regulation*, 36, 61-70. <https://doi.org/10.1023/A:1014732714549>
- Baskin, J. M., & Baskin, C. C. (1985). The annual dormancy cycle in buried weed seeds: a continuum. *Bioscience*, 35(8),

492-498. <https://doi.org/10.2307/1309817>

- Batlla, D., & Benech-Arnold, R. (2015). A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. *Seed Science Research*, 25(2), 147-158. <https://doi.org/10.1017/S0960258514000452>
- Benech-Arnold, R., Sánchez, R., Forcella, F., Kruk, B., & Ghersa, C. (2000). Environmental control of dormancy in weed seed banks in soil. *Field Crops Research*, 67(2), 105-122. [http://dx.doi.org/10.1016/S0378-4290\(00\)00087](http://dx.doi.org/10.1016/S0378-4290(00)00087)
- Bockstaller, C., & Girardin, P. (1994). Effects of seed size on maize growth from emergence to silking. *Maydica*, 39(3), 213-218.
- Brar, G. S., Gomez, J. F., McMichael, B. L., Matches, A. G., & Taylor, H. M. (1991). Germination of twenty forage legumes as influenced by temperature. *Agronomy Journal*, 83, 173-175. <https://doi.org/10.2134/agronj1991.00021962008300010040>
- Butler, T. J., Celen, A. E., Webb, S. L., Krstic, D. B., & Interrante, S. M. (2017). Germination in cool-season forage grasses under a range of temperatures. *Crop Science*, 57(3), 1725-1731. <http://dx.doi.org/10.2135/cropsci2015.10.0647>
- Chambers, J. C., MacMahon, J. A., & Brown, R. W. (1990). Alpine seedling establishment: the influence of disturbance type. *Ecology*, 71(4), 1323-1341. <https://doi.org/10.2307/1938270>
- Chambers, J. C., MacMahon, J. A., & Hafefner, J. H. (1991). Seed entrapment in alpine ecosystems: Effects of soil particle size and diaspore morphology. *Ecology*, 72(5), 1668-1677. <https://doi.org/10.2307/1940966>
- Chen, L., Wang, W., Li, Q. Q., Zhang, Y., Yang, S., Osland, M. J., ... Peng, C. (2017). Mangrove species' responses to winter air temperature extremes in China. *Ecosphere*, 8(6), e01865. <http://dx.doi.org/10.1002/ecs2.1865>
- Cohen, M. C. L., de Souza, A. V., Liu, K. B., Rodrigues, E., Yao, Q., Ryu, J., ... Rossetti, D. (2021). Effects of the 2017–2018 winter freeze on the northern limit of the American mangroves, Mississippi River delta plain. *Geomorphology*, 394, 107968. <https://doi.org/10.1016/j.geomorph.2021.107968>
- Cori, B. (1999). Spatial dynamics of Mediterranean coastal regions. *Journal of Coastal Conservation*, 5(2), 105-112. <https://doi.org/10.1007/BF02802747>
- Dahdouh-Guebas, F., Jayatissa, L. P., Di Nitto, D., Bosire, J. O., Lo Seen, D., & Koedam, N. (2005). How effective were mangroves as a defence against the recent tsunami? *Current Biology*, 15(12), 443-447. <https://doi.org/10.1016/j.cub.2005.06.008>
- Danielsen, F., Sorensen, M. K., Olwig, M. F., Selvam, V., Parish, F., Burgess, N. D., ... Suryadiputra, N. (2005). The Asian tsunami: A protective role for coastal vegetation. *Science*, 310(5748), 643. <https://doi.org/10.1126/science.1118387>
- Dengler, L., & Preuss, J. (2003). Mitigation lessons from the July 17, 1998 Papua New Guinea tsunami. *Pure and Applied Geophysics*, 160(10), 2001-2031. <http://dx.doi.org/10.1007/s00024-003-2417-x>
- Donohue, K. (2005). Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist*, 166, 83-92. <https://doi.org/10.1111/j.1469-8137.2005.01357.x>
- Dwyer, J. M., & Erickson, T. E. (2016). Warmer seed environments increase germination fractions in Australian winter annual plant species. *Ecosphere*, 7(10), 1-14. <https://doi.org/10.1002/ecs2.1497>
- Fischer, M., & Matthies, D. (1998). Effects of population size on performance in the rare plant *Gentianella germanica*. *Journal of Ecology*, 86(2), 195-204. <https://doi.org/10.1046/j.1365-2745.1998.00246.x>
- Fujii, N., Tomaru, N., Okuyama, K., Koike, T., Mikami, T., & Ueda, K. (2002). Chloroplast DNA phylogeography of *Fagus crenata* (Fagaceae) in Japan. *Plant Systematics and Evolution*, 232, 21-33. <https://doi.org/10.1007/s006060200024>
- Fukuda, T., Song, I. J., Ito, T., Hayakawa, H., Minamiya, Y., Kanno, A., ... Yokoyama, J. (2011a). Nucleotide sequence variations in a medicinal relative of asparagus, *Asparagus cochinchinensis* (Lour.) Merrill (Asparagaceae). *American Journal of Plant Sciences*, 2(6), 765-775. <http://dx.doi.org/10.4236/ajps.2011.26091>
- Fukuda, T., Song, I. J., Nakayama, H., Ito, T., Kanno, A., Hayakawa, H., ... Yokoyama, J. (2011b). Phylogeography of *Asparagus schoberioides* Kunth (Asparagaceae) in Japan. *American Journal of Plant Sciences*, 2(6), 781-789. <http://dx.doi.org/10.4236/ajps.2011.26093>
- Graven, L. M., & Carter, P. R. (1990). Seed size/shape and tillage system effect on corn growth and grain yield. *Journal of Production Agriculture*, 3(4), 445-452. <https://doi.org/10.2134/jpa1990.0445>

- Gubbels, G. H. (2010). Growth of corn seedlings under low temperatures as affected by genotype, seed size, total oil, and fatty acid content of the seed. *Canadian Journal of Plant Science*, 54, 425-426. <https://cdnsiencepub.com/doi/pdf/10.4141/cjps74-065>
- Gul, A., & Allan, R. E. (1976). Stand establishment of wheat lines under different levels of water potential. *Crop Science*, 16(5), 611-615. <https://doi.org/10.2135/cropsci1976.0011183X001600050002x>
- Haraguchi, A., & Sakaki, M. (2020). Spatial distribution of sea salt deposition in a coastal *Pinus thunbergii* forest. *Water*, 12(10), 2682. <https://doi.org/10.3390/w12102682>
- Hassani, A., Azapagic, A., & Shokri, N. (2021). Global predictions of primary soil salinization under changing climate in the 21st century. *Nature Communications*, 12, 6663. <https://www.nature.com/articles/s41467-021-26907-3>
- Hayakawa, H., Barnor, M. T., Minamiya, Y., Yokoyama, J., Arakawa, R., & Fukuda, T. (2012). Nucleotide sequence variations in the Adh in a medicinal species, *Dioscorea tokoro* (Dioscoreaceae). *Environment Control in Biology*, 50(3), 223-235.
- Hayakawa, H., Asaoka, M., Shimono, Y., Kurokawa, S., Nishida, T., Ikeda, H., & Wakamatsu, T. (2014). Phylogeography based on the nrDNA ITS regions of native *Miscanthus sinensis* (Poaceae) populations in Japan. *Weed Biology and Management*, 14(4), 251-261. <https://doi.org/10.1111/wbm.12053>
- Hiraishi, T., & Harada, K. (2003). Greenbelt tsunami prevention in South-Pacific region. *Report of the Port and Airport Research Institute*, 42(2), 1-23. <https://www.pari.go.jp/search-pdf/vol042-no02-01.pdf>
- Huang, W., & Li, C. Y. (2017). Cold front driven flows through multiple inlets of Lake Pontchartrain Estuary. *Journal of Geophysical Research-Oceans*, 122(11), 8627-8645. <https://doi.org/10.1002/2017JC012977>
- Hufford, K. M., & Mazer, S. J. (2003). Plant ecotypes: Genetic differentiation in the age of ecological restoration. *Trends Ecol Evol*, 18(3), 147-155. [https://doi.org/10.1016/S0169-5347\(03\)00002-8](https://doi.org/10.1016/S0169-5347(03)00002-8)
- Hunter, R. B., & Kannenberg, L. W. (1972). Effects of seed size on emergence, grain yield, and plant height in corn. *Canadian Journal of Plant Science*, 52(2), 252-256. <https://doi.org/10.4141/cjps72-040>
- Hughes, L. (2000). Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution*, 15(2), 56-61. [https://doi.org/10.1016/S0169-5347\(99\)01764-4](https://doi.org/10.1016/S0169-5347(99)01764-4)
- Ishii, C., Shiba, M., Kumekawa, Y., & Fukuda, T. (2022). Seed germination and seedling emergence of *Canavalia lineata* (Thunb.) DC. (Fabaceae). *International Journal of Biology*, 14, 8-18. <https://doi.org/10.5539/ijb.v14n1p8>
- Ito, H., & Yoshizaki, S. (2013). Growth experiment in salt water using evergreen broad-leaved trees in coastal areas. *Japanese Society of Revegetation Technology*, 39, 117-120. (in Japanese) <https://doi.org/10.7211/jjsrt.39.117>
- Ito, H., & Yoshizaki, S. (2017). Effects of salt water immersion on seed germination of *Pinus thunbergii* Parl. and *Pinus densiflora* Sieb. et Zucc. *Journal of Japanese Society of Coastal Forest*, 16(2), 15-19. (in Japanese)
- Ito, H., & Yoshizaki, S. (2019). Effect of short-term salt water immersion on water absorption and germination of seeds in Japanese black pine (*Pinus thunbergii* Parl.). *Journal of the Japanese Society of Revegetation Technology*, 45, 260-263. (in Japanese) <https://doi.org/10.7211/jjsrt.45.260>
- Iwasaki, T., Tono, A., Aoki, K., Seo, A., & Murakami, N. (2010). Phylogeography of *Carpinus japonica* Blume and *Carpinus tschonoskii* Maxim. growing in Japanese deciduous broad-leaved forests, based on chloroplast DNA variation. *Acta Phytotaxonomica et Geobotanica*, 61, 1-20. <https://doi.org/10.18942/apg.KJ00006537150>
- Iwasaki, T., Aoki, K., Seo, A., & Murakami, N. (2012). Comparative phylogeography of four component species of deciduous broad-leaved forests in Japan based on chloroplast DNA variation. *Journal of Plant Research*, 125(2), 207-221. <https://doi.org/10.1007/s10265-011-0428-8>
- Kamkar, B., Ahmadi, M., Soltani, A., & Zeinali, E. (2008). Evaluating non-linear regression models to describe response of wheat emergence rate to temperature. *Seed Science and Biotechnology*, 2, 53-57. [http://www.globalsciencebooks.info/Online/GSBOnline/images/0812/SSB\\_2\(1&2\)/SSB\\_2\(2\)53-57o.pdf](http://www.globalsciencebooks.info/Online/GSBOnline/images/0812/SSB_2(1&2)/SSB_2(2)53-57o.pdf)
- Kandil, A. A., Sharief, A. E., & Ahmed, S. R. H. (2012). Germination and seedling growth of some chickpea cultivars (*Cicer arietinum* L.) under salinity stress. *Journal of Basic & Applied Sciences*, 8(2), 561-571. <https://doi.org/10.6000/1927-5129.2012.08.02.49>
- Karim, M. A., Utsunomiya, N., & Shigenaga, S. (1992). Effect of sodium chloride on germination and growth of hexaploid triticale at early seedling stage. *Japanese Journal of Crop Science*, 61(2), 279-284. <https://doi.org/10.1626/jcs.61.279>
- Karmakar, R., Das, I., Dutta, D., & Rakshit, A. (2016). Potential effects of climate change on soil properties: a review.

- Science International*, 4(2), 51-73. <http://dx.doi.org/10.17311/sciintl.2016.51.73>
- Khajeh-Hosseini, M., Powell, A., & Bingham, I. (2003). The interaction between salinity stress and seed vigour during germination of soybean seeds. *Seed Science and Technology*, 31(3), 715-725. <http://dx.doi.org/10.15258/sst.2003.31.3.20>
- Kono, Y., Peng, C. I., Hoshi, Y., Yokota, M., Setoguchi, H., Lum, S. K. Y., & Oginuma, K. (2016). Intraspecific karyotype polymorphism and chromosomal evolution of *Lysimachia mauritiana* (Primulaceae) in the Ryukyu archipelago of Japan. *Cytologia*, 81(4), 431-437. <https://doi.org/10.1508/cytologia.81.431>
- Kumekawa, Y., Miyata, H., Ohga, K., Hayakawa, H., Yokoyama, J., Ito, K., ... Fukuda, T. (2013). Comparative analyses of stomatal size and density among ecotypes of *Aster hispidus* (Asteraceae). *American Journal of Plant Sciences*, 4(3), 524-527. <http://dx.doi.org/10.4236/ajps.2013.43067>
- Kuramoto, N., Inoue, K., & Washitani, I. (1993). A study of distribution of the floodplain vegetation species along stream in the middlecourse of the Tama river. *Journal of the Japanese Institute of Landscape Architecture*, 56(5), 163-168. (in Japanese)
- Lonati, M., Moot, D. J., Aceto, P., Cavallero, A., & Lucas, R. J. (2009). Thermal time requirements for germination, emergence and seedling development of adventive legume and grass species. *New Zealand Journal of Agricultural Research*, 52, 17-29. <https://doi.org/10.1080/00288230909510485>
- Lynch, M., Conery, J., & Bürger, R. (1995). Mutation accumulation and the extinction of small populations. *American Naturalist*, 146(4), 489-518. <https://www.jstor.org/stable/2462976>
- Mahdavi, B., & Sanavy, S. A. (2007). Germination and growth in grasspea (*Lathyrus sativus*) cultivars under salinity conditions. *Pakistan Journal of Biological Sciences*, 10(2), 273-379. <https://doi.org/10.3923/pjbs.2007.273.279>
- Marsack, J. M., & Connolly, B. M. (2022). Generalist herbivore response to volatile chemical induction varies along a gradient in soil salinization. *Scientific Reports*, 12, 1689. <http://dx.doi.org/10.1038/s41598-022-05764-0>
- Matsumura, S., Yokoyama, J., Fukuda, T., & Maki, M. (2009). Intraspecific differentiation of *Limonium wrightii* (Plumbaginaceae) on northwestern Pacific Islands: Rate heterogeneity in nuclear rDNA and its distance-independent geographic structure. *Molecular Phylogenetics and Evolution*, 53(3), 1032-1036. <https://doi.org/10.1016/j.ympev.2009.06.011>
- McGraw, R. L., Shockley, F. W., & Elam, T. K. (2003). Effects of temperature on germination of 10 native legume species. *Native Plants Journal*, 4, 5-9. [https://rngr.net/npn/journal/articles/effects-of-temperature-on-germination-of-10-native-legume-species/at\\_download/file](https://rngr.net/npn/journal/articles/effects-of-temperature-on-germination-of-10-native-legume-species/at_download/file)
- Meloni, D. A., Gulotta, M. R., & Martinez, C. A. (2008). Salinity tolerance in *Schinopsis quebracho* Colorado: Seed germination, growth, ion relations and metabolic responses. *Journal of Arid Environments*, 72(10), 1785-1792. <https://doi.org/10.1016/j.jaridenv.2008.05.003>
- Middleton, B. A. (2016). Effects of salinity and flooding on post-hurricane regeneration potential in coastal wetland vegetation. *American Journal of Botany*, 103(8), 1420-1435. <https://doi.org/10.3732/ajb.1600062>
- Nafziger, E. D. (1992). Seed Size Effects on yields of two corn hybrids. *Journal of Production Agriculture*, 5(4), 538-540. <https://doi.org/10.2134/jpa1992.0538>
- Nakajima, Y., & Yoshizaki, S. (2010). The comparison of tolerance to salt adhesion among 5 broad leaf trees species which grow near the coast. *Journal of the Japanese Society of Revegetation Technology*, 36, 219-222. (in Japanese) <https://doi.org/10.7211/jjsrt.36.219>
- Nakajima, Y., & Yoshizaki, S. (2018). Plant community type and site conditions of coastal forests consisting of evergreen broad-leaved tree species in warm temperate zone in south-west Japan. *Journal of the Japanese Society of Revegetation Technology*, 43(4), 596-604. (in Japanese) <https://doi.org/10.7211/jjsrt.43.596>
- Odabaş, M. S., & Mut, Z. (2007). Modeling the effect of temperature on percentage and duration of seed germination in grain legumes and cereals. *American Journal of Plant Physiology*, 2(5), 303-310. <https://dx.doi.org/10.3923/ajpp.2007.303.310>
- Ohga, K., Muroi, M., Hayakawa, H., Yokoyama, J., Ito, K., Tebayashi, S., ... Fukuda, T. (2013). Coastal adaptation of *Adenophora triphylla* (Thunb.) A. DC. var. *japonica* (Regel) H. Hara (Campanulaceae). *American Journal of Plant Sciences*, 4(3), 596-601. <http://dx.doi.org/10.4236/ajps.2013.43078>
- Ono, K., Nakamura, K., & Hirai, K. (2014). Fluctuations in the concentration of exchangeable cations in tsunami-hit

- forest soils on the northeastern Pacific Coast. *Journal of Japanese Forest Society*, 96(6), 301-307. (in Japanese) <https://doi.org/10.4005/jjfs.96.301>
- Osland, M. J., Hartmann, A. M., Day, R. H., Ross, M. S., Hall, C. T., Feher, L. C., & Vervaeke, W. C. (2019). Microclimate influences mangrove freeze damage: Implications for range expansion in response to changing macroclimate. *Estuaries and Coasts*, 42(4), 1084-1096. <https://doi.org/10.5066/P9YWSV4O>.
- Rajasekaran, L. R., Stiles, A., & Caldwell, C. D. (2002). Stand establishment in processing carrots—Effects of various temperature regimes on germination and the role of salicylates in promoting germination at low temperatures. *Canadian Journal of Plant Science*, 82(2), 443-450. <https://cdnsiencepub.com/doi/pdf/10.4141/P01-016>
- Rossello, J. A., & Mayol, M. (2002). Seed Germination and reproductive features of *Lysimachia minoricensis* (Primulaceae), a wild-extinct plant. *Annales of Botany*, 89(5), 559-562. <https://doi.org/10.1093/aob/mcf083>
- Saitou, K., Fukuda, T., Yokoyama, J., & Maki, M. (2007). Morphological and molecular (RAPD) analyses confirm the hybrid origin of the diploid grass *Calamagrostis longiseta* var. *longe-aristata* (Gramineae). *Folia Geobotanica*, 42, 63-76. <https://doi.org/10.1007/BF02835102>
- Sakaguchi, S., Horie, K., Ishikawa, N., Nagano, J. A., Yasugi, M., Kudoh, H., & Ito, M. (2017). Simultaneous evaluation of the effects of geographic, environmental and temporal isolation in ecotypic populations of *Solidago virgaurea*. *New Phytologist*, 216(4), 1268-1280. <https://doi.org/10.1111/nph.14744>
- Saltonstall, K. (2002). Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *PNAS*, 99(4), 2445-2449. <https://doi.org/10.1073/pnas.032477999>
- Schellenberg, M. P., Biligetu, B., & Wei, Y. (2013). Predicting seed germination of slender wheatgrass [*Elymus trachycaulus* (Link) Gould subsp. *trachycaulus*] using thermal and hydro time models. *Canadian Journal of Plant Science*, 93(5), 793-798. <https://doi.org/10.4141/cjps2013-028>
- Schlacher, T. A., Schoeman, D. S., Dugan, J., Lastra, M., Jones, A., Scapini, F., & McLachlan, A. (2008). Sandy beach ecosystems: key features, management challenges, climate change impacts, and sampling issues. *Marine Ecology*, 29, 70-90. <http://dx.doi.org/10.1111/j.1439-0485.2007.00204.x>
- Sepaskhah, A. R., & Ardekani, R. E. (1978). Effect of soil matric potential and seeding depth on emergence of barley. *Agronomy Journal*, 70(5), 728-731. <https://doi.org/10.2134/agronj1978.00021962007000050008x>
- Shafii, B., & Price, W. J. (2001). Estimation of cardinal temperatures in germination data analysis. *Journal of Agricultural, Biological and Environmental Statistics*, 6(3), 356-366. [10.1198/108571101317096569](https://doi.org/10.1198/108571101317096569)
- Shiba, M., Tate, T., & Fukuda, T. (2022). Leaf anatomical adaptations of *Eurya japonica* Thunb. (Pentaphylacaceae) in coastal habitats. *Journal of Plant Studies*, 11, 31-41. <https://doi.org/10.5539/jps.v11n1p10>
- Shiono, T., & Mochida, Y. (2012). Influence of grain-size distribution of sediment on vegetation, in wind-beaten bare ground, river bed and beach. *Japanese Journal of Ecology*, 62, 1-17. (in Japanese) [https://doi.org/10.18960/seitai.62.1\\_Cover1](https://doi.org/10.18960/seitai.62.1_Cover1)
- Shuto, N. (1987). The effectiveness and limit of tsunami control forests. *Coastal Engineering in Japan*, 30, 143-153. <https://doi.org/10.1080/05785634.1987.11924470>
- Sunami, T., Ohga, K., Muroi, M., Hayakawa, H., Yokoyama, J., Ito, K., ... Fukuda, T. (2013). Comparative analyses of hairless-leaf and hairy-leaf type individuals in *Aster hispidus* var. *insularis* (Asteraceae). *Journal of Plant Studies*, 2, 1-6. <http://dx.doi.org/10.5539/jps.v2n1p1>
- Takizawa, E., Tate, T., Shiba, M., Ishii, C., Yoshizaki, S., & Fukuda, T. (2022). Coastal adaptation of *Ligustrum japonicum* Thunb. (Oleaceae). *Journal of the Japanese Society of Coastal Forest*, 21, 1-8. [http://jscf.jp/journal/pdf/JSCF21\(1\)1-7.pdf](http://jscf.jp/journal/pdf/JSCF21(1)1-7.pdf)
- Tanaka, N., Sasaki, Y., Mowjood, M. I. M., & Jinadasa, K. B. S. N. (2007). Coastal vegetation structures and their functions in tsunami protection: Experience of the recent Indian Ocean tsunami. *Landscape and Ecological Engineering*, 3, 33-45. <http://dx.doi.org/10.1007/s11355-006-0013-9>
- Tanaka, N., & Yagisawa, J. (2009). Effects of tree characteristics and substrate condition on critical breaking moment of trees due to heavy flooding. *Landscape and Ecological Engineering*, 5, 59-70. <http://dx.doi.org/10.1007/s11355-008-0060-5>
- Tanaka, N. (2009). Vegetation bioshields for tsunami mitigation: review of effectiveness, limitations, construction, and sustainable management. *Landscape and Ecological Engineering*, 5, 71-79. <http://dx.doi.org/10.1007/s11355-008-0058-z>

- Tunala., Hayakawa, H., Minamiya, Y., Gale, S. W., Yokoyama, J., Arakawa, R., & Fukuda, T. (2012). Foliar adaptations in *Aster hispidus* var. *insularis* (Asteraceae). *Journal of Plant Studies*, 1(2), 19-25. <https://doi.org/10.5539/jps.v1n2p19>
- Umeoka, N., & Ogbonnaya, C. I. (2016). Effects of seed size and sowing depth on seed germination and seedling growth of *Telfairia occidentalis* (Hook F.). *International Journal of Advances in Chemical Engineering and Biological Sciences*, 3(2), 201-207. <https://doi.org/10.15242/IJACEBS.AE0916207>
- Varga, P., Berzy, T., Anda, A., & Ertsey, K. (2012). Relationship between seed harvesting method and seed physiological quality for a number of pioneer maize hybrids. *Maydica*, 57, 220-225.
- Welbaum, G. E., Tissaoui, T., & Bradford, K. J. (1990). Water relations of seed development and germination in muskmelon (*Cucumis melo* L.) III. Sensitivity of germination to water potential and abscisic acid during development. *Plant Physiology*, 92(4), 1029-1037. <https://doi.org/10.1104/pp.92.4.1029>
- Windauer, L., Altuna, A., & Arnold, B. R. (2007). Hydrotime analysis of *Lesquerella fendleriseed* germination responses to priming treatments. *Industrial Crops and Products*, 25, 70-74. <https://doi.org/10.1016/j.indcrop.2006.07.004>
- Woods, N. N., Swall, J. L., & Zinnert, J. C. (2020). Soil salinity impacts future community composition of coastal forests. *Wetlands*, 40(5), 1495-1503. <https://doi.org/10.1007/s13157-020-01304-6>
- Yabashi, S., Amemiya, Y., & Takahashi, S. (1995). Relation between size fraction component of soil and soil water retentivity especially water content in the green space irrigation. *The Technical Bulletin of Faculty of Horticulture Chiba University*, 49, 143-148. <https://opac.ll.chiba-u.jp/da/curator/900026476/KJ00004283677.pdf>
- Yamaji, H., Fukuda, T., Yokoyama, J., Pak, J. H., Zhou, C. Z., Yang, C. S., ... Maki, M. (2007). Reticulate evolution and phylogeography in *Asarum* sect. *Asiasarum* (Aristolochiaceae) documented in internal transcribed spacer sequences (ITS) of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution*, 44(2), 863-884. <https://doi.org/10.1016/j.ympev.2007.01.011>
- Yamazaki, T. (1993). *Lysimachia*. In: K. Iwatsuki, T. Yamazaki, D. E. Boufford, H. Ohba (Eds), *Flora of Japan IIIa* (pp. 80-84). Kodansha, Tokyo.
- Yeo, A. (1998). Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae*, 78(1-4), 159-174.
- Yokoyama, J., Fukuda, T., & Tsukaya, H. (2003). Morphological and molecular variation in *Mitchella undulata*, with special reference to the systematic treatment of the dwarf form from Yakushima. *Journal of Plant Research*, 116(4), 309-315. <https://doi.org/10.1007/s10265-003-0105-7>
- Yoshizaki, S. (2011). Functions of coastal forests and trees response against the tsunami. *Japanese Society of Revegetation Technology*, 37(2), 281-285. (in Japanese) <https://doi.org/10.7211/jjsrt.37.281>
- Zhang, H., McGill, C. R., Irving, L. J., Kemp, P. D., & Zhou, D. (2013). A modified thermal time model to predict germination rate of ryegrass and tall fescue at constant temperatures. *Crop Science*, 53, 240-249. <https://doi.org/10.2135/cropsci2012.02.0085>

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