Determining Empty Seed Formation and Germination Rates Induced by Leptoglossus occidentalis (Heidemann) in Coniferous Species in Turkiye Forests

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Abstract

In recent years, low germination rates have been a problem in the seeds of various coniferous species in Turkiye, particularly Turkish red pine (*Pinus brutia*) and black pine (*Pinus nigra*), which are commonly used species for afforestation activities. The increase in low germination rates corresponds to the spread of *Leptoglossus occidentalis* in coniferous forests, suggesting an investigation of potential correlation between the spread of this insect and the empty seed formation and germination rates. This study aimed to investigate the main causes of empty seeds and low germination rates induced by *Leptoglossus occidentalis* (Heidemann) in coniferous species in Turkiye. In the study, sample cones from various coniferous species including Fir (*Abies* spp.), Stone pine (*Pinus pinea*), Turkish red pine (*Pinus brutia*), Spruce (*Picea orientalis*), Cedar (*Cedrus libani*), Maritime pine (*Pinus pinaster*), Black pine (*Pinus nigra*) and Scots pine (*Pinus sylvestris*) were collected based on their geographical distribution, and then their seeds were extracted. The 1000-seed weights were determined for each species, followed by germination tests conducted under controlled conditions. Statistical analysis revealed significant variations in germination rates among species. Among the eight species examined, Scots pine (*Pinus sylvestris*) had the highest germination rate at 37.9%, while fir (*Abies* spp) had the lowest rate at 0.4%. Further statistical analysis revealed variations in germination rates based on aspects, with generally higher rates observed in sunny aspects. The results indicated that *Leptoglossus occidentalis* caused a significant decrease in seed germination ranging from 60–99% in coniferous species. Additionally, reductions in 1000-seed weights ranging from 19–81% were observed in the species, except Scots pine. The findings highlight widespread germination issues in seeds of majority of the coniferous tree in Turkiye. As a result, it was found that *L. occidentalis* significantly contributes to empty seed formation and lower germination rates in coniferous forests. Therefore, it is essential to develop strategies to protect and conserve seed resources to mitigate any negative impacts on forest resources.

1. Introduction

Invasive insects like *Leptoglossus occidentalis* pose an economic threat to forests and seed orchards. They damage natural forests and seed orchards, reducing the quality and quantity of seeds availability for afforestation activities. *L. occidentalis* is known for destroying the seeds of coniferous trees and has been found to harm 48 different species (Werner, 2011; Cranshaw, 2014). In coniferous forest in Turkiye, a significant reduction in sapling production has been observed in recent years is due to low germination rates of coniferous species' seeds. It is estimated that the germination rates have dropped from 60%-80% to only 10% which is mainly caused by the spread of *L. occidentalis* in coniferous forests, leading to the production of empty seeds. This insect affects forest health by depleting seed resources, reducing genetic diversity, and inhibiting natural regeneration and sapling growth (Parlak, 2017). Without implementing effective strategies to combat *L. occidentalis*, forest regeneration in natural forests will inevitably suffer from this damages. Additionally, the loss of seeds caused by this insect may hinder the establishment of young trees in natural environments, posing even a long-term threat to sustainability of forests (İpekdal et al., 2019).

L. occidentalis is likely to compromise the health of seed stands and orchards of coniferous tree species, impeding natural regeneration success, and potentially causing issues in sapling production by reducing seed yield (Oğuzoğlu and Avcı, 2020). This insect feeds on cones and seeds, leading to the premature dropping of newly formed cones and loss of seeds (Koerber, 1963; Hedlin et al., 1981; Cibrian-Tovar et al., 1986; Strong, 2006; Santini, 2009). It has been also identified as a threat to all conifer species in Europe and natural regeneration in pines (Sanchez et al., 2013; Lesieur et al., 2014). Thriving in favorable climatic conditions and lacking natural predators, it spreads rapidly, inflicting damage on natural coniferous forests and posing a significant threat to their natural regeneration (Roversi et al., 2011; Tamburini et al., 2012; Bracalini et al., 2013; Lesieur et al., 2014). Previous researches have shown that *L. occidentalis* significantly affects seed germination and natural rejuvenation by feeding on mature seeds (Farinha et al., 2017). It has been reported that *L. occidentalis* causes damage various coniferous species and potentially impact natural regeneration of host species (Rabitsch and Heiss, 2005; Tamburini et al., 2012; Lesieur et al., 2014; Loewe-Munoz et al., 2021). It is estimated that single *L. occidentalis* can damage 310 seeds in a one season (Bates and Borden, 2005). Particularly in pine species, the insect pierces the endosperm of the seed with its long proboscis, showing a preference for newly formed cones, and can reduce seed germination by up to 80% and seed loss may increase by up to 50% in natural stands (Gobbi and Lencioni, 2009). Its damages lead to the shedding of young cones, reduction in seed quantity, or significant depletion of seed reserves by hindering germination (Bates et al., 2001; Bates et al., 2002b). The decrease in seed resources resulting from insect damage disrupts natural rejuvenation efforts and sapling production in coniferous species (Parlak, 2017).

Most sap-sucking insects, like *L. occidentalis*, belong to the order Hemiptera and possess long, needle-shaped mouthparts (Gullan and Cranston, 2012). Newly hatched nymphs typically feed on needle leaves and cone scales. After five nymphal stages, they reach adulthood in late August or early September. Adult insects continue to feed on ripe seeds until cold weather arrives, overwintering in sheltered locations. During this period, they remain in a semi-dormant state, abstaining from feeding or reproduction while surviving on their fat reserves. The insect sustains itself by extracting the endosperm from developing cones, leading to premature cone drop and failed fertilization. It is known to damage approximately 40 coniferous species and exhibits a broad feeding preference (Galli, 1992; Negron, 1994; Klass, 1995; Bates and Borden, 2005; Reid et al., 2009; Ogden, 2013; Bracalini et al., 2014; Cranshaw, 2014). Economic losses stem from both nymphs and adults consuming the endosperm portion of seeds, resulting in diminished quality and quantity (Jucker, 2008). Feeding on the endosperm induces cone abscission and inadequate fertilization (Mitchell, 2000; Bates and Borden, 2005). *L. occidentalis* feeds on the seed endosperm after the second nymphal stage (Krugman and Koerber, 1969), damaging the ovary and triggering conelet expulsion, subsequently reducing the number of viable seeds (Woods et al., 2015). Such damage can lead to substantial conelet shedding and seed losses of up to 80% (Reid et al., 2009; Resh and Carde, 2009; Bracalini et al., 2014). Even minor to moderate damage caused by insect feeding can reduce sapling formation by as much as 80% (Bates et al., 2001). Mild to moderate damage to Douglas fir seeds has been found to decrease seedling emergence by 80% (Bates, 1997). Additionally, even with mild seed damage severity, germination rates can drop to 20% in black pine (*P. nigra*) and below 30% in other tree species (Lesieur et al., 2014).

Since plant seeds contain higher levels of nutrients compared to other tissues, insects that feed on seeds exploit these resources (Gullan and Cranston, 2012). During reproductive periods, females require more nutrients for egg production than males or nymphs, obtaining this nutrition by consuming nitrogen-rich seed proteins (Bates et al., 2001). The insect inserts its sucking mouthparts directly into the seed, penetrating approximately 2 cm, releases saliva, and then proceeds to suck the softened seed. Through the absorption of oils and proteins from the seed, it can render the seed completely empty with varying degrees of damage (Kozlowski, 1972; Bates et al., 2000, 2001, 2002). A characteristic symptom of damage to mature seeds is the wilting and sponginess of the seed interior caused by insect feeding (Hedlin et al., 1981; Bates et al., 2002a). In severe cases of damage, the entire endosperm can be destroyed, resulting in the formation of empty seeds (Koerber, 1963).

During the seed maturation period, on average, adult males damage 1.4 seeds per day, while females damage 2 seeds per day (Bates et al., 2002b). These damages collectively lead to significant seed loss. It has been observed that adult females lay up to 80 eggs during the early stages of cone development and can potentially damage around 320 seeds in a season. Reports suggest that a single adult *L. occidentalis* can cause the loss of over 300 seeds, and in the absence of predators and parasitism, this damage can escalate to 434 seeds (Bates et al., 2002a; Bates and Borden, 2005). The challenge in understanding the damage caused by *L. occidentalis* lies in the fact that the insect does not damage the cell wall of the plant tissues from which it absorbs sap, resulting in no visible structural damage (Gullan and Cranston, 2012). By inserting its proboscis between the cone scales, the insect leaves no external signs of damage on the seed's surface (Reid et al., 2009; Tamburini et al., 2012; Lesieur et al., 2014a). Additionally, the insect is believed to favor the sunny upper parts of trees and is difficult to detect when viewed from below (Hedlin et al., 1981; Richardson, 2013).

In spring, adults emerge from their overwintering sites to feed, mate, and lay eggs (Ogden, 2013). Adult females lay approximately 80 eggs on needles from mid to late spring. The eggs are about 2 mm long and 1 mm wide, barrel-shaped, initially light brown, later turning dark brown (Fig. 1). The eggs hatch about 10–14 days later. The severity of damage can vary depending on the insect's developmental stages. The first generation feeds on needles and newly formed cones, then transitions to the second nymph stage after a few days. The stiletto length of second-stage nymphs increases by 2.5 times, easily reaching immature seeds in cones. The elongation of the stiletto indicates the increased need for food during this nymph stage. Damage to the ovary due to feeding, which results in cone shedding, occurs at the end of summer when nymphs feed. This phenomenon is observed in the nymphs' feeding period at the end of summer (DeBarr and Kormanik, 1975; Jucker, 2008; EPPO, 2010; Fent and Kment, 2011; Taylor et al., 2001; Pimpãp, 2014) (Fig. 1).

Figure 1. Egg (left), 2nd nymph (middle) and adult stages (right) of *L. occidentalis* (S. Parlak)

The insect *L. occidentalis* causes damage to various coniferous species in Turkiye, including *Pinus sylvestris*, *Pinus nigra*, *Pinus halepensis*, *Pinus pinea*, *Picea orientalis*, *Larix decidua*, *Abies* spp., *Juniperus* spp., *Cedrus* spp., and *Pseudotsuga menziesii* (Taylor et al. 2001; Fent and Kment 2011; Tamburini et al. 2012). However, there have been no studies conducted on the sensitivity of these species (Lesieur et al., 2014). *L. occidentalis* also damages coniferous species that are not native to Turkiye, significantly affecting seed formation. While *L. occidentalis* was first identified in Turkiye in 2009 (Arslangündoğdu and Hızal, 2010), no comprehensive study has examined the extent of the damage it causes to coniferous species in the country. The feeding behavior of the insect during both the nymph and adult stages can cause significant harm to the seeds of coniferous trees. In 2010, when it arrived in Turkiye, the initial sign of damage was premature cone drop in stone pine trees. Over the following years, its population expanded and spread across the country, causing damage to various other conifer species. This damage resulted in a notable decrease in germination rates and disrupted annual production schedules in nursery studies. However, to date, no comparative analysis has been conducted on species preference and the damage caused by *L. occidentalis*. Therefore, this study aims to investigate the formation of empty seeds and germination rates resulting from *L. occidentalis* damage in naturally occurring or plantation-established coniferous species across Turkiye.

2. Materials and Methods

2.1 Material

To determine the development of empty seeds, mature cones were collected from natural coniferous species and maritime pine in sufficient quantities from the previous year. Various pieces of equipment were utilized for different stages of the study, including an automatic control seed extraction chamber for removing seeds from the cones, a temperature and humidity controlled climate cabinet (Growth chamber GC 500) for germination tests, a refrigerator for storing the extracted seeds, scales for weighing, germination petri dishes, a drying oven, and a stereo microscope for imaging any damage on the seeds. In addition, sodium hypochlorite was used as a disinfectant, blotting papers, and fungicide to prevent infections.

2.2 Method

2.2.1. Collecting pine cones and assessing their physical attributes

Location and elevation factors were considered when collecting sample cones (Table 1). The newly matured and collected cones were carefully handled to ensure they were not opened. At least 5 kg of cones were collected from each location to obtain enough seeds from Turkish red pine (*Pinus brutia*) and black pine (*Pinus nigra*) which are the most common species in Turkiye. Additionally, cones were collected from stone pine (*Pinus pinea*), Scots pine (*Pinus sylvestris*), cedar (*Cedrus libani*), fir (*Abies* spp.), spruce (*Picea orientalis*), and exotic maritime pine (*Pinus pinaster*) to study the formation of empty seeds. The number of cone collection locations was determined based on the distribution of tree species in the area. Cones were collected from various locations and elevations to cover the distribution area of each species. The location, elevation, and coordinates of the collection sites were recorded, along with information about whether the area was natural or afforested, and the proximity to the forest. Seeds were extracted from the collected cones using machines set at a temperature of + 50°C. After extraction, seeds from each location were stored in fabric bags at a temperature of + 4°C. The weight of 1.000 seeds and the germination rates of the extracted seeds were calculated to reveal the relationship between seed characteristics, germination rates, species, elevation, and aspect.

Table 1
Elevations and number of localities where cones were collected and seeds were extracted.

Species	**Number of locations (N)**	**Average Elevation (m)**
Maritime pine *(Pinus pinaster)*	27	183
Scots pine *(Pinus sylvestris)*	64	1630
Black pine *(Pinus nigra)*	104	991
Stone pine *(Pinus pinea)*	101	474
Turkish red pine *(Pinus brutia)*	259	619
Cedar *(Cedrus libani)*	35	1443
Spruce *(Picea orientalis)*	5	1567
Fir *(Abies* spp.*)*	5	1134
Total	600	

2.2.2. Germination tests and statistical analyzes

Germination tests were conducted according to ISTA (1999) rules. Four replicates of 100 seeds from each location were placed in petri dishes, and a solution of 750 ml/0.75ml of fungicide was sprayed on the seeds. A mixture of 8.6 ml of sodium hypochlorite and a liter of water was prepared and kept for 5 minutes, followed by rinsing with pure water. To protect the germinating seeds from fungal contamination, they were treated with a fungicide before being placed in petri dishes. The seed spraying was performed by using Syngenta's Maxim XL 035 FS which contains 25g/L of Fludioxonil + 10g/L of Metalaxyl-M as the active substances, and do not affect germination. The seeds were then placed on Whatman filter papers, moistened with sterilized water, and placed in petri dishes with a diameter of 9 cm. The petri dishes were placed in an incubator with a temperature of 25°C and humidity of 70%. During the germination tests, seed counts were taken every 5 days, depending on the species. The germination time was 50 days for maritime pine, 40 days for stone pine and Scots pine, and 25 days for black pine, spruce, fir, Turkish red pine, and cedar. Seeds that developed 2 mm roots were considered germinated.

Arc-sin transformations were performed on seed germination rates and other percentage values obtained based on damage categories to ensure normality. One-way analyses of variance and Duncan multiple comparison tests were conducted using the SPSS 20 statistical program. Correlation analyses were performed to explore the relationship between aspect and elevation in germination and the formation of empty seeds.

3. Results and Discussion

Seed losses can occur due to various factors, such as climatic conditions, inadequate pollination, failed seed development, and infestation by fungi and seed-feeding insects (Owens et al., 1991; Owens, 1995). Biological factors, including irregular flowering, lack of synchronous development and flowering, failed flower or embryo development, and immature seeds and fruits, can also impact seed formation. For example, newly formed conelets may be prematurely shed if fertilization is absent or insufficient. Research on stone pine pollen viability has shown that early conelet shedding is unrelated to pollination and fertilization. Insect damage can also contribute to seed losses and low germination rates. Insects feeding on seeds can consume nutritional stores and embryos, preventing germination (Boivin et al., 2019). *L. occidentalis* damages seeds by sucking the embryo and endosperm, leading to the discarding of young cones (Bracalini et al., 2013; Farinha et al., 2021). Damage to larger cones can result in empty or pathogen-infected seeds (Tamburini et al., 2012). Feeding by *L. occidentalis* on developing cones can result in the formation of visually undamaged yet empty or damaged seeds (Lesieur et al., 2014a; Bates et al., 2001). Therefore, insect damage can be detected through cone expulsion, presence of empty seeds in mature cones, and wrinkled or spongy seed endosperm. Cone set can be affected by various stresses, including climate changes, rainfall patterns, pollination, cone diseases, and abiotic factors. However, the recent decline in cone set and germination rates in Turkiye has coincided with the spread of *L. occidentalis*. Previous investigations into seed formation decline in coniferous species have not identified any abiotic factors that could explain abnormal seed decline in all species. These findings, along with logical inferences, support the thesis that *L. occidentalis* is the primary factor contributing to the formation of empty seeds. In fact, studies by İpekdal et al. (2019)d uzoğlu and Avcı (2020) have highlighted the widespread presence of this insect in Turkiye and the significant decrease in germination rates compared to previous years. The feedback received from the General Directorate of Forestry management and nursery directorates further supports these findings.

3.1. Statistical results on germination rates in coniferous species

The germination of seeds can be influenced by the amount of protein and oil consumed by the seed. This consumption is affected by damage caused by *L. occidentalis* during cone development. Even with the same degree of damage, the germination of the seeds may vary (Bates, 1997). The one-way analysis of variance was conducted to compare germination rates among different species. The results indicated a statistically significant difference in the formation of empty seeds based on species (Table 2). It can be inferred that the insect's feeding preferences vary across species when it is assume that the presence of empty seeds is due to damage caused by *L. occidentalis*. Duncan tests were performed to determine the differences in germination rates. The tests revealed that fir, stone pine, and Turkish red pine had the lowest rates, while black pine and Scots pine had higher rates (Table 3). The severity of damage caused by *L. occidentalis* varies among coniferous species. The rate of damage varies depending on the developmental stage of the seed (Krugman and Koerber, 1969). It has been noted that *Pinus engelmannii* experiences a high rate of empty seed formation due to damage caused by *L. occidentalis* during the embryo stage (Bermudes, 2012). The insect's damage to young cones increases cone drop by five times, and when it damages mature cones, it significantly reduces the percentage of viable seeds. Specific temperature thresholds are required for egg-laying and hatching, making temperature the most crucial climatic factor influencing the number of offspring. Higher numbers of offspring are produced at lower elevations (Jung et al., 2023). The extremely low germination rates observed in Turkish red pine and stone pine may be attributed to their ecological adaptation to lower elevations, where the higher number of offspring of the insect could have increased the damage.

Table 2. Seed germination rates statistical test results One Way Anova

		Sum of Squares	df	Mean Square	F	Sig.
Germination	Between Groups	57893.00	7	8270.43	67.68	0.000
	Within Groups	63540.27	520	122.19		
	Total	121433.27	527			

Table 3. Germination rates Duncan tests

		Subset for alpha = 0.05		
Species	N	1	2	3
Fir *(Abies* spp.*)*	4	3.588		
Stone pine *(Pinus pinea)*	87	9.396		
Turkish red pine *(Pinus brutia)*	215	10.321		
Spruce *(Picea orientalis)*	4		22.713	
Cedar *(Cedrus libani)*	30		25.807	
Maritime pine *(Pinus pinaster)*	23		25.887	
Black pine *(Pinus nigra)*	100		28.589	28.589
Scots pine *(Pinus sylvestris)*	65			37.024
Sig.		0.145	0.223	0.053

L. occidentalis is an insect that feeds on the cones of conifers, particularly pines, and causes significant damage to pine forests. It has also been known to cause damage to other species such as *Pseudotsuga menziesii*, *Juniperus*, *Tsuga*, *Picea*, *Cedrus*, and *Calocedrus*. Studies on *Pseudotsuga menziesii* have shown that a two-week feeding period by female *L. occidentalis* during the late season can reduce seed production by 70% (Koerber, 1963; Cambell and Shea, 1990; Bates et al., 2000a, b; Lait et al., 2001; Bates, 2002; Mjøs et al., 2010). The damage rate of *Pinus echinata* in seed orchards has been reported to reach as high as 83% (EPPO, 2010), and it causes 41% damage to Douglas trees (Koerber, 1963). Controlled studies have shown that nymphs of *L. occidentalis* can reduce seed production in *Pinus strobus* by 75% (Bates et al., 2002a). Second instar nymphs have been found to feed on *Pinus echinata* cones for only four weeks, resulting in 100% cone shedding due to the destruction of the ovary. Similar damage occurs at the end of summer when the nymphs are feeding (DeBarr and Kormanik, 1975). *L. occidentalis* has been reported to cause up to 75% seed loss in annual cones of *Pinus contorta* and *Pinus monticola*

Dougl. (Bates et al., 2000; Strong et al., 2001; Bates et al., 2002b). It has also been observed to reduce seed and seedling formation by 50% in some coniferous species (Blatt, 1994; Bates et al., 2000; Bates et al., 2001). It has been found in various coniferous species such as *Pinus halepensis*, *Pinus laricio*, *P. pinea*, *P. nigra*, *Pseudotsuga menziesii* in Sicily, and *Pinus strobus*, *P. sylvestris* in northern Italy (Rice et al., 1985; Hellrigl, 2006; Maltese et al., 2009). Damage percentages reported include 26% for *Pinus monticola*, 41% for *Pseudotsuga species*, and 30% for *P. cembroides* (Mitchell, 2000; Bustamante-García et al., 2012; Gapon, 2013). Additionally, it has been found to cause 55% damage to *Pinus ponderosa* (Krugman and Koerber, 1969; Pasek and Dix, 1988). In laboratory studies, it has been reported to cause a 50% decrease in empty seed formation in Douglas and a 90% decrease in seed formation in *Pinus contorta* (Schowalter and Sexton, 1990; Strong et al., 1998). Seed loss is generally less in coniferous species such as spruce and larix compared to others (Hedlin et al., 1981; Strong et al., 2001).

3.1.1. Aspect and germination

The results indicate that there is no statistically significant difference in germination rates between the slopes (Table 4). However, according to the Tukey tests germination rate of 12.3% was observed in flat areas, while a germination rate of 25% occurred on the southern slope (Table 5). The reason for the lack of statistical difference is thought to be the wide variation in germination exhibited by seeds collected from the same slope. Further studies are necessary to uncover the reasons for the insect's preference for certain appearances.

Table 4
Anova analysis of variance for germination rates according to aspect

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	2878.68	8	359.84	1.473	.167
Within Groups	64011.68	262	244.32		
Total	66890.36	270			

Table 5
Tukey tests for germination rates according to aspects

Aspect	N	Subset for alpha = 0.05
Flat	9	12.294
East	27	15.410
Southeast	25	18.832
Northwest	33	18.930
North	33	19.182
West	32	19.212
Southwest	28	22.941
Northeast	43	23.202
South	41	25.006
Sig.		0.103

3.1.2. Slope and germination

The study analyzed the correlation between slope and germination rates, considering the potential impact of slope and sun angle on insect spread and damage (Fig. 2). The correlation analysis revealed a correlation coefficient of $R^2 = 0.9336$ for slopes ranging from 10–50%, and $R^2 = 0.7455$ for slopes ranging from 50–100% (Fig. 3). Due to the significant relationship between slope and germination, further research is necessary to investigate the feeding behavior of insects and the influence of microclimate. In a similar study conducted by Lee et al. (2023), it was discovered that slope had a strong positive effect (R^2 (??) > 0.5; $p < 0.05$) on insect dispersal.

The body temperature of insects is crucial because they are poikilotherms and highly influenced by external conditions. When temperatures are low, their activity is restricted, and they are unable to fly. It has been observed that male flowers have a higher temperature and greater heat reflection ability. Objects with higher temperatures emit more infrared radiation, which can be detected by *L. occidentalis*. Furthermore, higher temperatures lead to an increased release of volatile compounds like monoterpenes. Therefore, male flowers, with their high reflectance, high temperature, and high concentration of volatile compounds, may be more appealing to *L. occidentalis* (Kitajima et al., 2022). Previous research has shown that first-stage nymphs feed on male flowers during the spring season (Schaefer and Panizzi, 2000). Sloping areas allow both male and female flowers to receive more light and solar radiation compared to flat areas. This may help explain why sloping areas have a greater impact on insect density in terms of feeding the first nymphs and adults, rather than flat areas. Additionally, since eggs require a certain temperature for hatching (Jung et al., 2023), the slope of the area may influence the insect's preference for warmer spots on the tree for egg-laying.

3.2. Germination rates and weights of 1000 seeds of the species.

Germination rates and 1000 seed weights of different tree species were compared using the data collected prior to the insect's arrival in Turkiye. Among the species, fir seeds had the lowest germination rate at 0.4%, followed by Scots pine seeds at 37.9% and black pine seeds at 25.1%. Stone pine, which has been experiencing empty seed formation for many years, had a germination rate of 2.6%, while Turkish red pine had a rate of 3.7%. The germination rate for maritime pine, commonly used in fast-growing afforestation, was found to be 22.1%, and, it was 16.5% for spruce. These results highlight the significant variation in germination rates across different tree species (Table 6). This difference suggests that insect damage may vary depending on factors such as seed size, reproductive cycle, sensitivity of the host tree, and tree species (Bates, 1999). Studies have shown that insects are capable of distinguishing between different conifers and selecting hosts in a versatile manner. They first choose the tree, then the cone, and finally their feeding place. Robust insects tend to select trees with dense crowns and long needles. Nutritional status and cone size may also play a role in the selection process, particularly for polyphagous species like *L. occidentalis*. Additionally, irrigated and fertilized trees are more likely to be preferred by these insects (Blatt, 1997; Lesieur et al., 2014; Farinha et al., 2018a).

Table 6
Comparison of germination rates found in this study and at literature by species

	Average germination rate at (%)			
Species	literature		in this study	Decrease rate (%)
Scots pine *(Pinus sylvestris)*	Giray (1993)	96.8	37.9	61
Black pine *(Pinus nigra)*	Varol (1968)	82.0	25.1	69
Maritime pine *(Pinus pinaster)*	Marques et al. (2012); Alía et al. (1996)	80.0	22.1	72
Cedar *(Cedrus libani)*	Eler et al. (1992)	76.4	17.9	77
Spruce *(Picea orientalis)*	Erkuloğlu (1989)	66.7	16.5	75
Turkish red pine *(Pinus brutia)*	Öktem (1992)	81.6	3.7	95
Stone pine *(Pinus pinea)*	Saatçioğlu (1967)	85.0	2.6	97
Fir *(Abies spp.)*	Saatçioğlu (1967)	82.0	0.4	99

L. occidentalis not only causes damage during seed formation and development but also affects mature seeds, resulting in decreased seed germination. Research shows that seed loss due to *L. occidentalis* can exceed 70% in natural regeneration studies. It has been found that when more than one-third of the seed content is consumed, its ability to germinate is lost (Lesieur et al., 2014). Only 18% of the seeds consumed by *L. occidentalis* in a germination experiment were able to sprout (Blatt and Borden, 1998).

Certain clones of the species are preferred by *L. occidentalis* (Blatt and Borden, 1996). In a study on *Pinus contorta*, 86% of the insects were found in only 10% of the clones, indicating that certain clones were more attractive to the insects. Among conifers in the same plantation, certain species were found to be more preferred. Factors such as cone weight and temperature influence the insect's choice (Strong, 2010; Richardson, 2013; Loewe-Muñoz et al., 2019), and the insect uses infrared sensors to locate the cones (Takács et al., 2009). Comparing the results of the study with previous studies revealed significant decreases in germination rates. While Scots pine had the lowest decrease at 61%, fir species experienced up to a 99% reduction. Turkish red pine (95%) and stone pine (97%) had the highest germination losses (Table 6). A study on pine species reported that if one-third of the seed was damaged by *L. occidentalis*, germination dropped below 30%. Moderate damage resulted in germination rates below 5% (Bates et al., 2001; Lesieur et al., 2014). Even slight damage to the seed leads to failed germination (Mitchell, 2000).

The effect of elevation on 1000 seed weight and germination was determined by grouping based on elevation stage. The data revealed that seed weight and germination rates were concentrated at specific elevation levels, particularly in Turkish red pine and Scots pine (see Fig. 4). It is necessary to investigate in detail whether this difference in germination is due to insect damage or inadequate seed development depending on elevation. No significant difference in germination was observed depending on elevation in other species (Additional Table 1). The study reported that damage in high elevation species like *Pinus albicaulis* was as low as 2.1%. While the insect tends to prefer species growing at lower elevations in their natural distribution areas, it may choose species residing at higher elevations in forced conditions such as food competition or lack of sufficient cones (Anderton and Jenkins, 2001). Elevation has a strong positive effect ($r > 0.5p < 0.05$) on insect spread, and modeling indicates that the probability of spread increases when elevation is below 345 m or slope is less than 200% (Lee et al., 2023).

The study compared the weights of 1000 seeds with previous studies conducted before the insect first detected in Turkiye. It was found that, except for Scots pine, the 1000 seed weights of other species were lower than in the previous studies (Fig. 5). Only the 1000 seed weights of Scots pine were consistent with the literature data. However, the 1000 seed weights of other species showed decreases ranging from 15–75%. Turkish red pine had the smallest decrease (12%), while fir seeds had the largest decrease (75%) (Table 8). This decrease in seed weight can be attributed to damage to the endosperm and embryo. Previous studies have demonstrated that coniferous species, which serve as hosts for *L. occidentalis*, not only experience a decrease in seed germination but also a decrease in seed weight depending on the amount consumed (Lesieur et al., 2014). These studies highlight that the severity of damage varies between locations (Bustamante-García et al., 2012) and that local climatic conditions may influence the population and, consequently, the damage (Schowalter et al., 1985; Tamburini et al., 2012).

Table 8. Comparison of seed weights of different species between literature and present study

Species	1000 seeds weight (g) Literature		Present study	Decrease rate (%)
Scots pine *(Pinus sylvestris)*	Saatiçioğlu (1967)	9.6	10.6	+10
Black pine *(Pinus nigra)*	Deligöz ve Gezer, (2005)	21.8	17	-22
Maritime pine *(Pinus pinaster)*	Alía et al. (1996); Marques et al. (2012)	80.0	59.2	-26
Cedar *(Cedrus libani)*	Eler (1992)	76.4	64.8	-15
Spruce *(Picea orientalis)*	Erkuloğlu (1989)	8.0	2.9	-64
Turkish red pine *(Pinus brutia)*	Öktem (1987)	51.9	45.8	-12
Stone pine *(Pinus pinea)*	Saatçioğlu (1967)	750	529.4	-29
Abies spp	Saatçioğlu (1967)	60.6	15.0	-75

3.2.1. Formation of empty seeds in stone pine (*Pinus pinea*)

In stone pine, the average weight of 1000 seeds in cones collected from 87 localities was determined to be 529.4 g. The lowest recorded weight for 1000 seeds was 88.1 g, while the highest was 847.4 g. Interestingly, there is a noticeable increase in seed weight as elevation increases. For instance, the weight of 1000 seeds was found to be 466.1 g in the 0-250 m range, but it increased to 644.4 g in the 1000–1250 m range. This represents a 29.4% decrease in average seed weight compared to previous studies where the average weight was 750 g (Saatçioğlu, 1967; Kılcı et al., 2011). Although stone pine is known to have high germination rates, this study revealed low germination rates, suggesting that the seeds may have lost their germination feature. The highest germination rate observed in stone pine trees was 14.7%, while the average germination rate was 2.6%. In contrast, Ganatsas et al. (2008) reported an average germination rate of 88% in stone pine. Interestingly, the varying elevations did not show a clear correlation with germination rates. The lowest germination rate was recorded at 2.3% in the 750–1000 m elevation stage, whereas the highest germination rate was observed in the 0-250 m elevation range, reaching 3.3%. The statistical analysis revealed a low correlation ($R^2 = 0.1227$) (Fig. 6).

The feeding behavior of insects, larger size, and higher nutrient content of stone pine seeds contribute to increased damage. Germination rates for stone pine seeds are lower compared to those of other species, likely due to the seed insect *L. occidentalis*. Suction holes caused by *L. occidentalis* were observed on the seed shells. Farinha et al. (2021) found a strong positive correlation ($R^2 = 0.98$) between high insect densities and seed loss in stone pine trees, providing evidence for the impact of *L. occidentialis* on seed loss. It is still unknown if *L. occidentalis* is the cause of empty seeds in stone pine trees (Strong, 2006). Cone shedding in the Mediterranean Basin significantly impacts pine nut production (Bracalini et al., 2013). Major crop losses due to *L. occidentalis* were observed in stone pine trees in the Mediterranean basin. From 2011 to 2014, the rate of empty seeds increased to 50% in countries such as Portugal, Spain, Italy, and Turkiye (Mutke et al., 2014). In Italy alone, pine nut production decreased by 95% (Bates et al., 2002b). Prior to the damage caused by *L. occidentalis*, the rate of healthy seeds was 70%. However, three years after the insect was detected, this rate dropped to 6% (Innocenti and Tiberi, 2002).

Calama et al. (2020) found that the rate of damage in cones exposed to *L. occidentalis* varied between 67% and 100%. It caused a 70% loss of stone pines in the Iberian peninsula (Farinha et al., 2017). It was reported that if *L. occidentalis* damages one-year-old cones, it leads to 86% cone shedding, and if it damages two-year-old cones, it causes 100% cone shedding (Ponce-Herrero et al., 2017). Feeding during the first cone period and completed cone development can still result in a 47% decrease in seed amount (Bates et al., 2002b). Low damage severity significantly reduces seed germination (Sanchez et al., 2013).

Stone pine seeds are larger than those of other host trees (Sorensen and Miles, 1978), making them more attractive for feeding by *L. occidentalis*. Bigger seeds result in shorter feeding times for the insect, making stone pine seeds more advantageous in terms of benefit/cost (Farinha et al., 2018b). Regardless of natural stand, plantation, elevation, and aspect, Parlak (2017) found that empty seed rates in cones collected from 42 localities in stone pine areas in Turkiye varied between 14% and 98%. In Farinha et al.'s study (2018b), it was determined that the damage rate of *L. occidentalis* adults on stone pine trees was 0.014 seeds/day per individual. Examination of damaged seeds revealed that multiple insects feed from the same hole, suggesting cooperation among the insects to feed and benefit from the same feeding hole instead of drilling new holes. This feeding tactic reduces feeding time in stone pine trees and intensifies the damage severity.

In Mediterranean countries, particularly in Europe, damage from *L. occidentalis* significantly reduces the yield in natural stone pine areas by approximately 95%. In Italy, the annual production of stone pine seeds was 40 thousand tons; however, production sharply declined by 95% in 2009 due to insect damage (Bates et al., 2002b; Roversi et al., 2011). Damaged seeds wither inside and cones are discarded (Brambila, 2007). The invasive insect in Europe is considered the main factor contributing to the significant decrease in stone pine production in the Mediterranean Basin (Roversi et al., 2011; Bracalini et al., 2014). It has been observed that *L. occidentalis* consumes approximately 1/5 of mature stone pine cones every month (Farinha et al., 2017). Early sowing leads to the shedding of conalets, while late period feeding causes the formation of empty seeds and destruction of the endosperm (Mutke et al., 2015). Many of the cones damaged by *L. occidentalis* exhibit resin exudates (Bracalini et al., 2013).

3.2.2. Formation of Empty Seeds in Cedar (*Cedrus libani*)

According to Saatiçioğlu (1967) the average weight of 1000 cedar seeds to be 76.4g. Another study found the weight of 1000 seeds to be 88.0 g in seeds taken from two elevations and 10 dominant trees (Özdemir et al., 1986). In this study, the weight of 1000 seeds was found to be 15% lower compared to previous studies. The damage rate in cedar seeds was lower compared to other species. Besides, there was no significant difference in the germination rates of cedar seeds based on elevation. A low correlation was observed between elevation and germination rate, and the correlation was calculated to be very low for 1000 grain weight (Fig. 7).

The germination rates of cedar seeds have shown a significant decrease. In this study, the average germination rate was 17.9%, with the highest rate recorded at 41.7%. Previous studies on the germination percentages of cedar seeds have reported higher rates. For instance, Odabaşı (1967) found a germination rate of 75.9% in seeds collected from 15 different sources. Eler et al. (1992) determined an average germination rate of 76.4%. In this study, the germination rate recorded in this study was 76% lower compared to the average rates reported in previous studies. Furthermore, although there are limited studies, it has been determined that *L. occidentalis* also causes damage to cedar (Nemer et al., 2019).

3.2.3. Formation of empty seeds in Turkish red pine (*Pinus brutia*)

The study analyzed seeds collected from cones at 259 locations in Turkish red pine within an elevation range of 0-1500 m. The average weight of 1000 seeds in Turkish red pine was found to be 45.8 g. Previous studies reported average seed weights 51.9 g. In the current study, a seed weight loss of 12% was observed. To assess the impact of elevation on empty seed formation, germination rates were analyzed based on elevation levels. It was observed that as elevation increased, there was a corresponding increase in 1000 seed weights, but germination rates decreased by approximately half. The average germination rate from the study was determined to be 3.7%. In this study, a germination loss of 95% was observed. There was no correlation found between 1000 seed weight and elevation in Turkish red pine seeds, and a low correlation was observed between elevation and germination rate.

3.2.4. Formation of empty seeds in black pine (*Pinus nigra*)

Studies on black pine were conducted using seeds from 104 different locations. The average weight of 1000 seeds ranged from 6.4 g to 59.6 g, with an overall average of 17 g. Deligöz and Gezer (2005) found that the weight of 1000 seeds was 21.8 g in their study. Comparing these results to previous studies, a 75% reduction in seed weight was observed. In black pine, a weak correlation ($R^2 = 0.0241$) was found between 1000 seed weights and elevation (Fig. 9). The average germination rate was 25.1%. Germination rates varied depending on altitude, with rates of 19.6% and 16.1% at 0-500 m and 1500–2000 m, respectively. Rates of 24.4% and 25.4% were observed at 500–1000 m and 1000–1500 m, respectively. Kalkan et al. (2021) reported a germination rate of 13.9% for seeds damaged by *L. occidentalis*. In terms of altitude, there was no statistically significant relationship ($R^2 = 0.0401$) between germination rates. Previous studies have indicated that 25% of *P. nigra* seeds, of which more than half are consumed by *L. occidentalis*, have the potential to germinate (Lesieur et al., 2014). It has been reported that adults of *L. occidentalis* can consume between 0.7 and 1.7 seeds per day in *P. nigra*, with another study reporting a rate of 0.7 seeds per day (Lesieur et al., 2014; Farinha et al., 2018b). The insect is responsible for a 25% seed loss in black pine seed orchards and up to 70% in natural stands, with damage reaching as high as 77.4%. In *P. nigra* and *P. sylvestris*, the potential for natural regeneration is reduced by over 70%, resulting in seed yield reductions ranging from 24.2–44.2% in subsequent years. Seeds exposed to slight damage by *L. occidentalis* in black pine trees had a germination rate seven times lower than intact seeds (Lesieur et al., 2014).

3.2.5. Formation of empty seeds in Scots pine (*Pinus sylvestris*)

Sample cones were collected from 64 different locations in Scots pine to obtain seeds. The weight of 1000 seeds ranges from 2.6 g to 20.1 g, with an average weight of 10.6 g. Previous studies conducted by Giray (1993), Eliçin (1970), and Saatiçioğlu (1967) reported the weight of 1000 seeds as 9.2 g, 9.7 g, and 10.3 g, respectively. Gezer and Yücedağ (2006) found the average weight of 1000 seeds to be 9.6 g in their study. A noteworthy finding of this study was that the weight of 1000 seeds was discovered to be 10% higher than the average weight observed in previous studies. The correlation coefficient between 1000 seed weight and altitude in Scots pine seeds was very low ($R^2 = 0.0095$). However, there was a slight decrease in germination rates associated with higher elevations. This relationship was also observed in the correlation tests (Fig. 10), with an R^2 value of 0.1578.

In this study, the average germination rate for Scots pine was found to be 37.9%, which is higher than that of other species. Giray (1993) reported the average germination rate for Scots pine as 96.8%. The higher germination rates in Scots pine compared to other species suggest that it experiences lower insect damage. Lesieur et al. (2014) found that *P. sylvestris* seeds, with more than half of their content consumed, did not germinate at all. The damage rate of *L. occidentalis* adults in *P. sylvestris* ranged from 0.8 to 1.7 seeds per day per insect, while another study reported it as 0.8 seeds per day (Lesieur et al., 2014; Farinha et al., 2018b). In Scots pine natural areas, insect damage causes a seed loss of 70%, and sometimes up to 54% in seed orchard (Lesieur et al., 2014). Additionally, the insects cause further damage to the seeds by feeding on adult females (Bates et al., 2002b). The damage rate in *P. sylvestris* seeds provided to mating females reached 99% (Lesieur et al., 2014). In the natural distribution areas of Scots pine, it can be inferred that low winter temperatures affect the vitality of seed insects and reduce their damage, thereby contributing to higher germination rates. Another factor may be the shorter vegetation period in Scots pine growing environments due to higher altitudes, as insects prefer lower altitudes for wintering. Several studies have identified temperature, humidity, precipitation, and wind speed as the most important environmental factors influencing the survival and development of insects (Stanton, 1983; Berryman, 1986; Córdoba-Aguilar et al., 2018; Dent, 2000). Temperature plays a crucial role in the wintering site selection of many insects, while photoperiod promotes overwintering (Leather et al., 1995). A study on this subject suggests that low temperatures, especially in high-altitude mountainous regions, limit the spread of insects (Jung et al., 2023).

3.2.6. Formation of empty seeds in maritime pine (*Pinus pinaster*)

Seeds were collected from cones at 27 different locations in maritime pine trees. The average weight of 1000 seeds was determined to be 59.2 g. When compared to existing literature data, it was found that the weight of 1000 seeds decreased by an average of 26%. Additionally, there was no correlation ($R^2 = 0.0001$) between elevation and 1000 seed weight (Fig. 11).

The average germination rate was measured to be 22.1%. When compared to existing literature data, it was found that germination rates decreased by an average of 72%. The average germination rate in maritime pine varies between 82.5% (Marques et al., 2012) and 77.5% (Alía et al., 1996). Similarly, there was no correlation (R^2 = 0.0046) between elevation and germination rates. Some studies have reported that seed germination in maritime pine is hindered by *L. occidentalis* (Ribeiro et al., 2022).

3.2.7. Formation of empty seeds in spruce (*Picea orientalis*) and fir (*Abies* spp.).

The number of cones collected from areas where spruce and fir trees are found is lower compared to other species. Cones were collected from 5 locations in these areas and the seeds were removed. The average weight of 1000 spruce seeds was found to be 2.9 g. Erkuloğlu (1989) reported that the weight of 1000 seeds of eastern spruce ranged from 7.2 g to 8.9 g. Compared to previous studies, there was a 64% decrease in the weight of 1000 seeds determined in present study, while the average germination rate of spruce was 16.5%. When compared to previous studies, it was found that there was a 75% decrease in germination rates. Göktürk et al. (2019) reported in their study on spruce that the highest germination percentages ranged from 57.0–62.7%, while the lowest germination percentage was 14.1%. According to Erkuloğlu (1989), the germination percentage of spruce seeds was generally over 80%.

The weight of 1000 fir seeds was found to be 15.0 g, which was lower than the average values reported in previous studies. For example, Yüksel and Dirik (2021) found the weight of 1000 seeds of Kazdağı fir (*Abies nordmanniana* subsp. equi-trojani) to be 82.7 g. In other studies conducted on Kazdağı fır, Aslan (1982) found the weight of 1000 seeds to be 63.2 g, Velioğlu et al. (2012) reported an average of 71.8 g, and Yılmaz et al. (2011) found it to be 94.9 g. In studies on seeds of other native fır species, the weight was determined as 82.9 g in Uludağ fir (*Abies bornmulleriana*) (Turna et al., 2010). Altun (2011) reported an average 1000-seed weight of 79.0 g for three origins of Eastern Black Sea fir (*Abies nordmanniana*), while Sevik et al. (2012) found it to be 81.6 g. In present study, the weight of 1000 seeds was found to be 75% lower than that of found in previous studies. It was found that the average germination rate in fir was 0.4% in present study. When compared to data obtained from previous studies, it was determined that germination decreased by 99%. For example, in the study conducted by Yılmaz et al. (2011), germination rates in seeds taken from different origins ranged from 30–65%. The highest germination rate was 79.2% in Taurus fir. Varsamis et al. (2014) also found the highest germination rate of 91.8% in fir. Velioğlu and Arslan (2000) reported an average germination rate of 42.4% in the Eastern Black Sea fir (*Abies nordmanniana*), while Schopmeyer (1974) found average germination rates of 83% in the fir species of *Abies bornmulleriana* and *Abies nordmanniana*, respectively.

4. Conclusions

According to studies conducted on seed and germination rates, *L. occidentalis* cause significantly decreases on germination and 1000 seed weights. In recent years, sapling production has been disrupted due to low seed germination rates. Typically, 15–20 seeds are planted in a tube. To determine the severity of damage and germination rates of coniferous species, a comprehensive study was conducted on seeds distributed in Turkiye. Cones were collected from 600 locations and eight species, including natural coniferous species and maritime pine. Seeds were then extracted, and the 1000 seed weights and germination rates were determined.

There was a significant difference in the average germination rates of seeds among different species. The highest germination rates were found in Scots pine (37.9%) and black pine (25.1%), while the lowest germination rates were observed in fir (0.4%). Turkish red pine and stone pine had germination rates of 3.7% and 2.6%, respectively. The low germination rates expressed by the planting units were supported by numerical data. When comparing the data from this study with previous studies, it was found that germination rates were very low and decreased by 60% (Scots pine) to 99% (fir) depending on the species. The data obtained reveals that coniferous species seeds in natural forests are severely damaged. Similar trends were observed for 1000 seed weights, with decreases ranging from 26–81% for all species except Scots pine. Moreover, a correlation was found between slope and aspect factors and germination rates.

This study highlights the significant reduction in germination rates of coniferous species seeds in natural forests due to *L. occidentalis*. This situation will impact natural regeneration and nursery work. The success of forestry activities relies on sufficient and healthy seed resources, which should be protected from abiotic and biotic factors. In recent years, *L. occidentalis* has threatened seed resources of coniferous species in Turkiye and worldwide. Considering the insect's rate of spread, biology, and population balance, it is predicted to continue negatively affecting forest health and regeneration activities in the long-run. Thus, urgent strategies must be developed to secure, protect, and store seed resources to minimize these impacts. For example, different light and color traps, pheromones, newly developed biochemicals under the control of the insect, and studies with feeding inhibitory or repellent substances should be conducted. Systemically effective organic substances that are not harmful to human health should be developed. Biotic or abiotic factors that cause population fluctuations should be examined in detail.

Declarations

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Figures

Figure 1

Egg (left), 2nd nymph (middle) and adult stages (right) of *L. occidentalis* (S. Parlak)

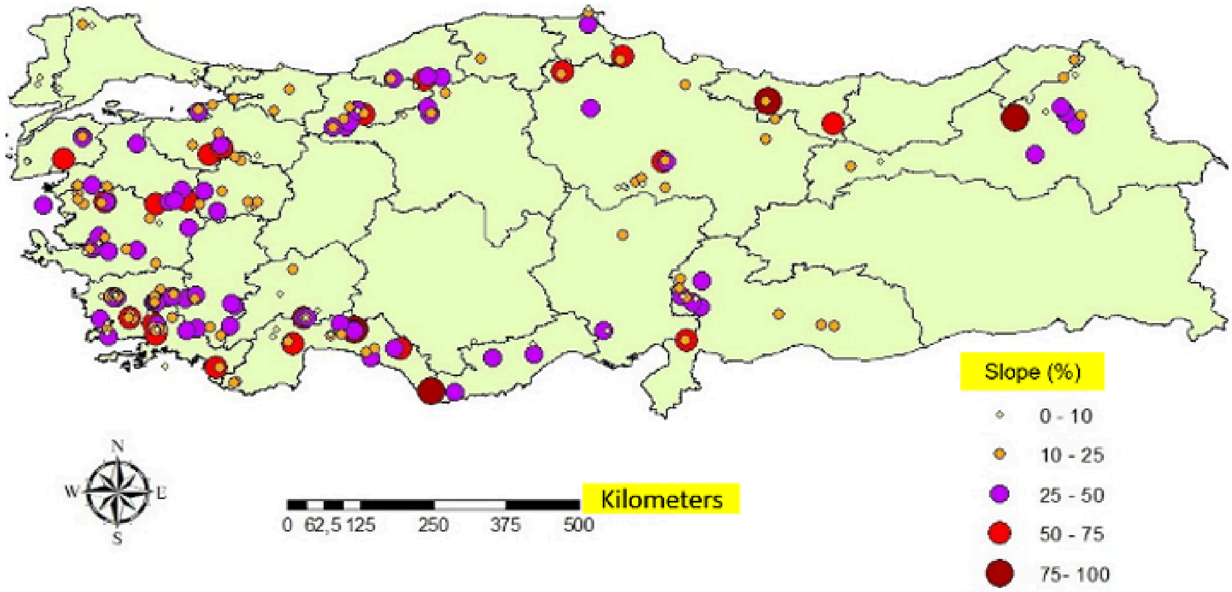

Figure 2

Distribution of germination rates according to slope

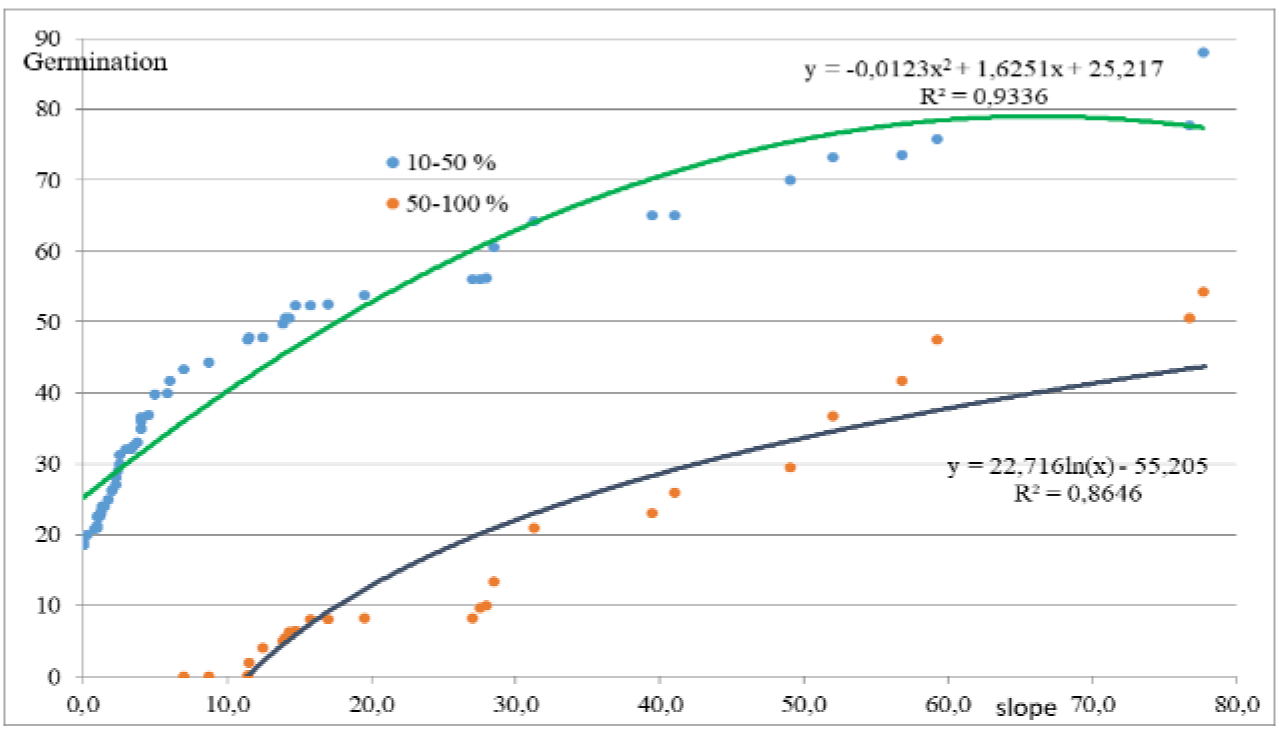

Figure 3

Correlation between slope and germination rates

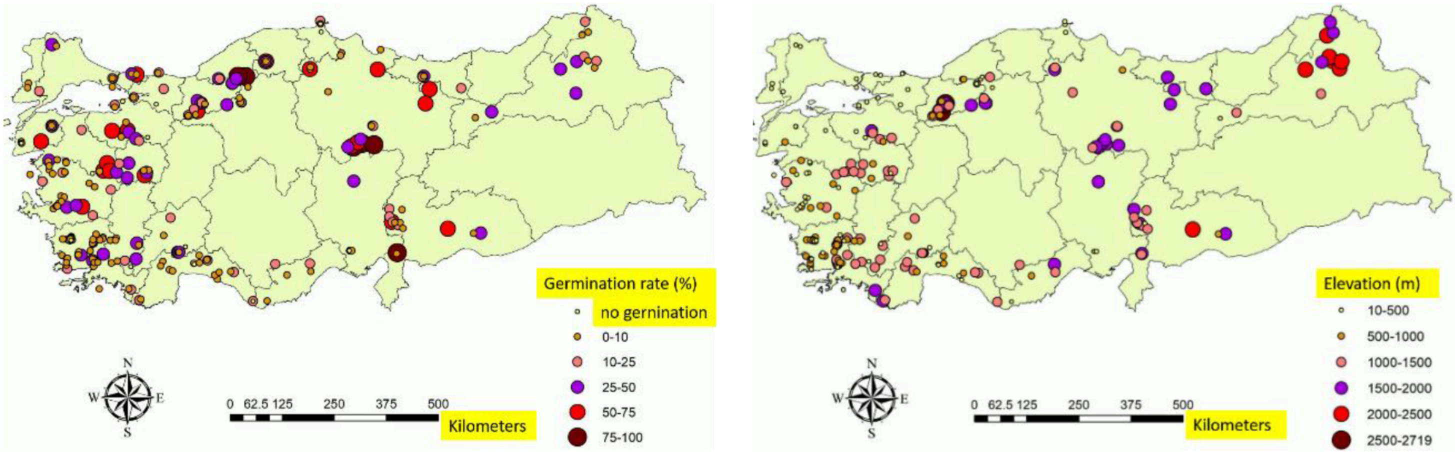

Figure 4

The distribution of germination rates in all species (left) and the distribution of germination rates based on elevation (right) (Data is represented proportionally by spot size)

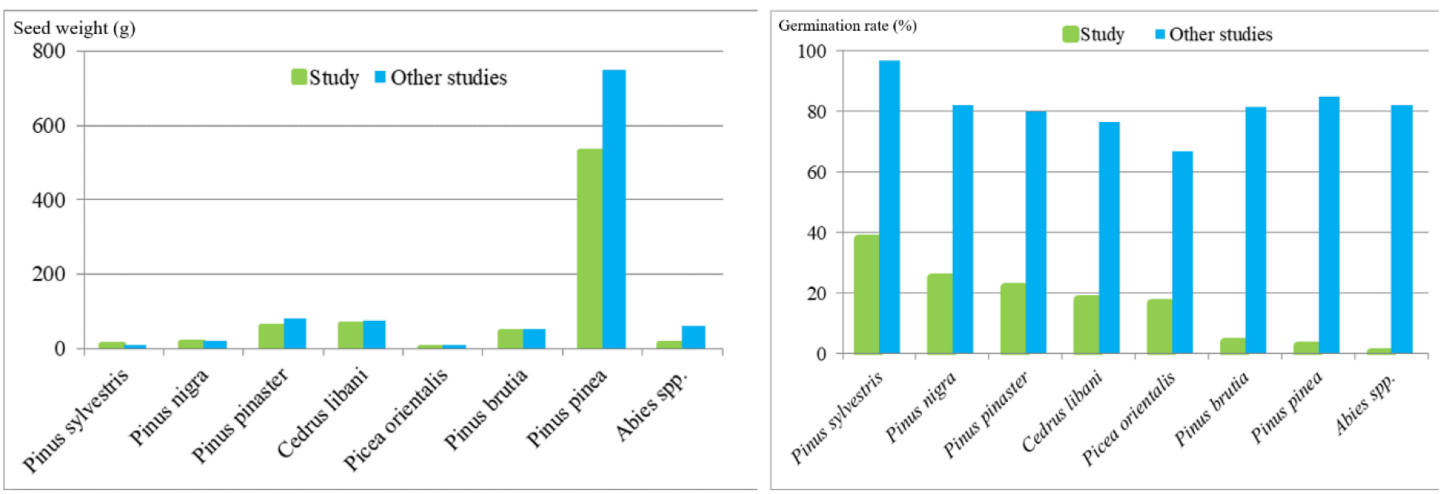

Figure 5

Comparisons of 1000 grain weights (left) and germination rates (right)

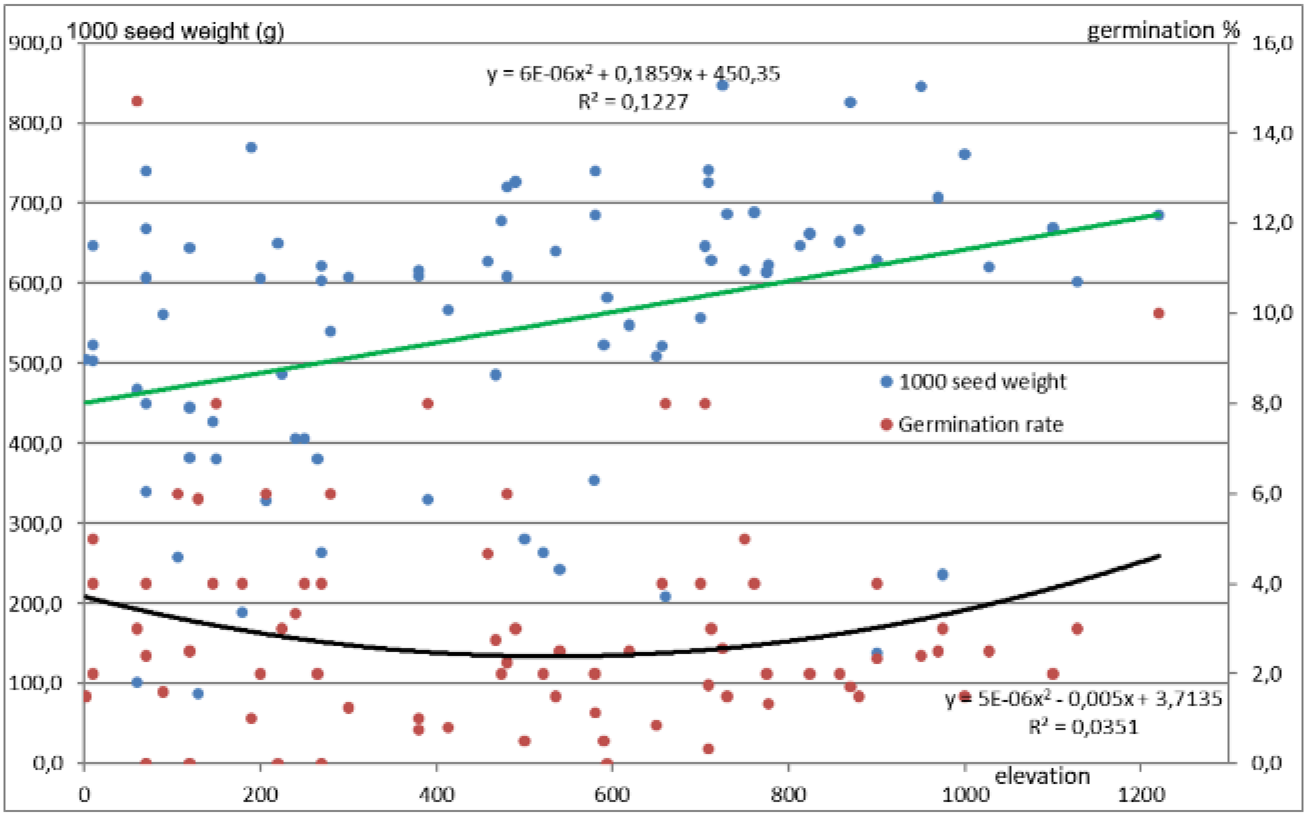

Figure 6

1000 seed weights and germination rates by elevation for stone pine

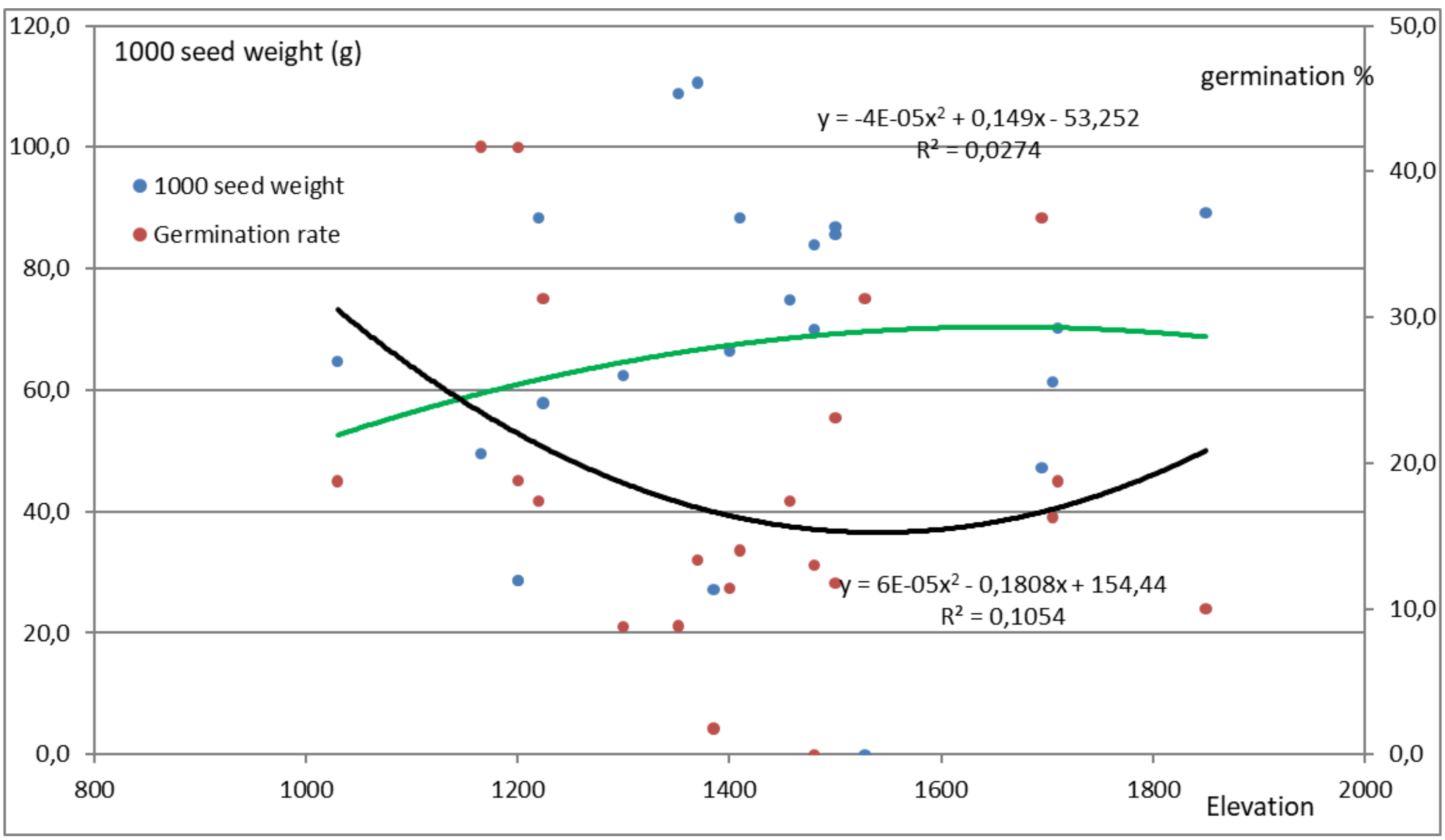

Figure 7

1000 seed weights and germination rates by elevation for cedar

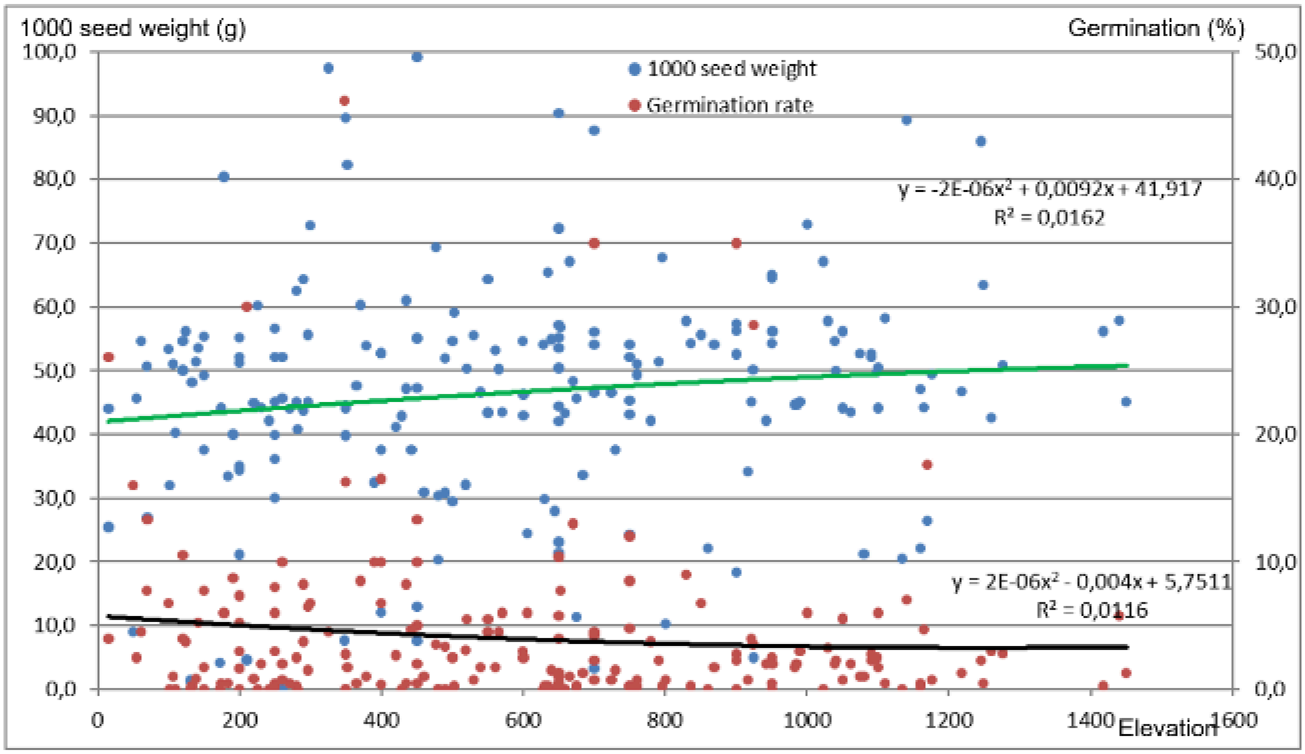

Figure 8

1000 seed weights and germination rates of Turkish red pine, categorized by elevation.

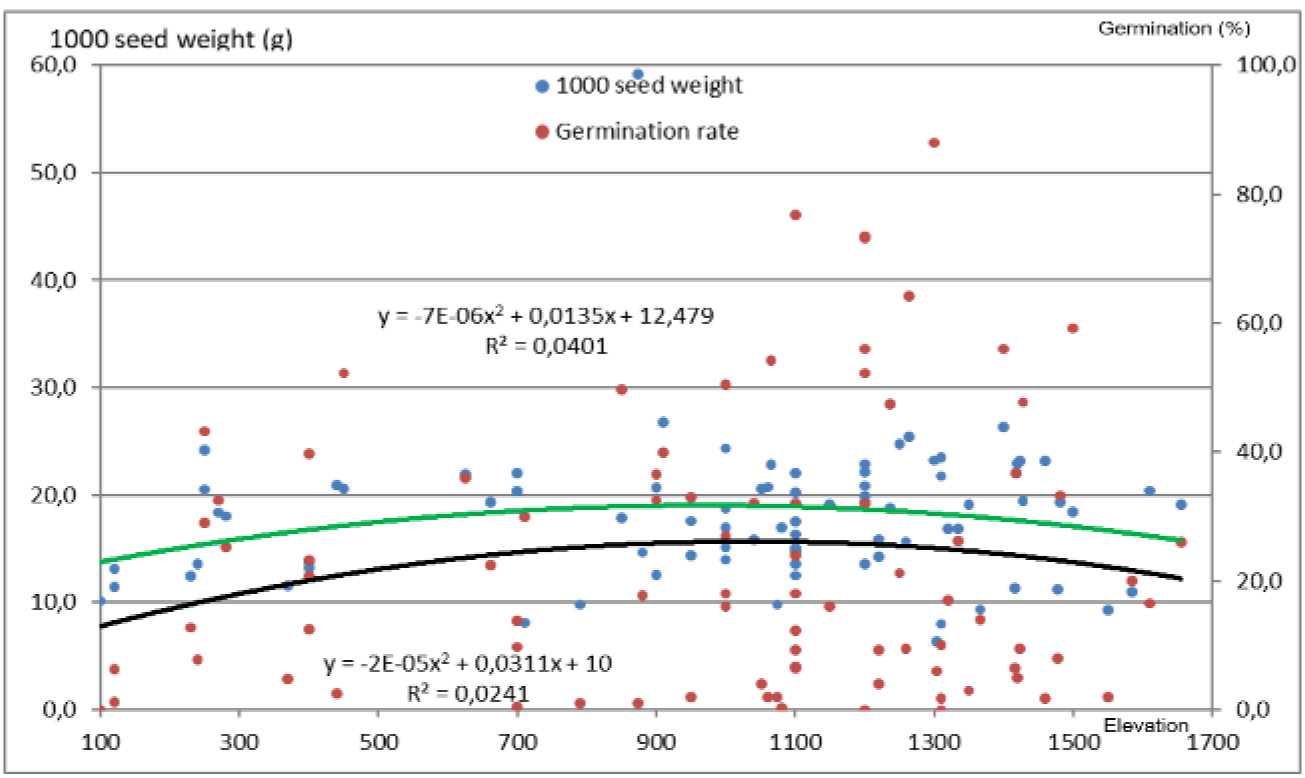

Figure 9

1000 seed weights and germination rates by elevation for black pine

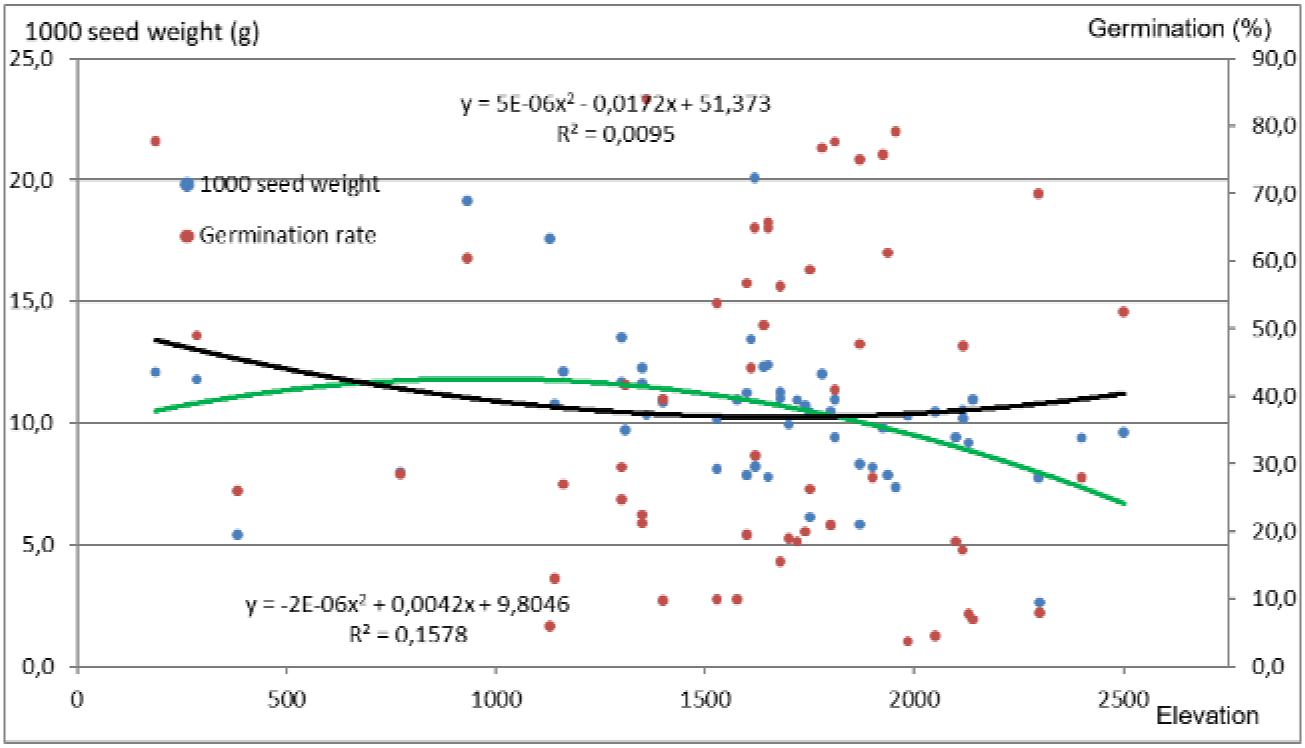

Figure 10

1000 seed weights and germination rates for Scots pine categorized by elevation

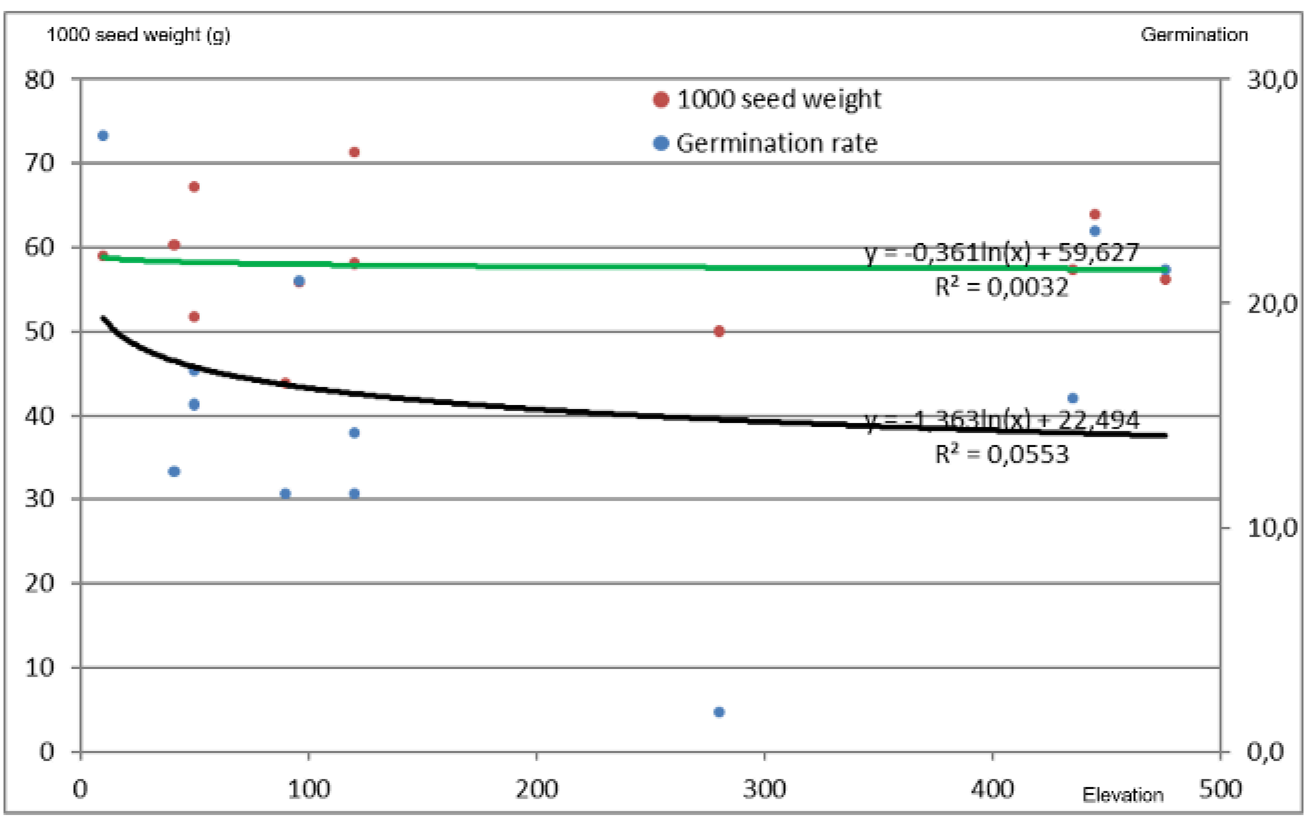

Figure 11

1000 seed weights and germination rates for maritime pine