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FACTORS INFLUENCING THE GERMINATION CAPACITY OF *PRIMULA PALINURI*, CLIFF-DWELLING ENDEMIC SPECIES OF SOUTHERN ITALY

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Abstract – *Primula palinuri* Petagna is a narrow-endemic plant species native to southern Italy, thriving along the Tyrrhenian coast. In this study, we compared various aspects of two populations of *P. palinuri* growing in different sites: one by the sea in the SAC Capo Palinuro (IT8050008) and the other about two kilometres inland in 'La Vaccuta,' SAC Fascia Interna di Costa degli Infreschi e della Masseta (IT8050011). Seed abundance, size, germination capability, and salt response were analysed. Seed counts and measurements were conducted using image analysis software. Germination responses were assessed at three at three alternating temperatures (6-15°C, 10-20°C, and 15-25°C) in the first experiment. Subsequently, seeds from both sites were subjected to increasing NaCl concentrations (0mM, 50mM, 100mM, 200mM, and 300mM) at 6-15°C and 10-20°C. All germination experiments took place in Petri dishes containing filter paper and distilled water. No discernible differences in capsule and seed sizes were observed between the two sampling sites. However, the study revealed that higher temperatures and elevated salt concentrations negatively affected the germination rate in both populations, particularly in seeds from the innermost site. This suggests a preference for cooler regimes and higher tolerance to saline conditions in the sea-exposed population for optimal germination. This research delved into the physiological and ecological adaptations of *P. palinuri* to its current environmental envelope, investigating how seed properties, temperature, and salinity stress influence seed germination potential. The findings provide promising insights that could significantly enhance conservation and management strategies for this species. The study aimed to compare the germination characteristics of two populations of *Primula palinuri* along the Tyrrhenian coast of southern Italy.

Keywords - vulnerable populations, cliff area, endangered and rare species, germination, adaptation.

INTRODUCTION

With approximately 6,700 species, 1371 of which are endemic (Peruzzi et al., 2014), Italy is among one of the richest countries in vascular plant species in the Mediterranean biogeographical region, a well-known global biodiversity hotspot (Myers et al., 2000; Thompson, 2005). Various factors have contributed to the country's high rate of endemism: (a) geographical position, (b) diverse bioclimatic conditions, (c) complex palaeogeographical and (d) paleoclimatic history (Blondel & Aronson, 1999; Thompson, 2001; Comes, 2004; Blasi, 2010; Casazza et al., 2016).

Primula palinuri Petagna is an endemic plant species listed since 1997 as endangered in the Red Book of Plant Species of the IUCN Red List of Threatened Plants and recognised under Annexes II/IV of the Habitats Directive (92/43/EEC) and the Bern Convention (1979). In the Campania region (Italy), *P. palinuri* is safeguarded by Regional Law No. 40 of 1994.

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P. palinuri is the only species of the *Primula* genus with a Mediterranean ecology. The other taxa are mainly found in mountainous regions on Upper Triassic/Lower Jurassic limestone and dolomite substrates (Aronne et al., 2014; Aronne et al., 2018). Geological changes and coastal retreat have played a pivotal role in delineating the current range of *P. palinuri*'s populations, with the existing stations representing remnants of larger populations that existed in the past (Ricciardi, 1973). Today, the species counts only restricted populations growing on north-facing sea cliffs along the Southern-Tyrrhenian coast of Italy (Silvestro et al., 2020; Pignatti et al., 2017). Genetic and demographic monitoring insights indicate a scarcity of young individuals over the entire areal, highlighting a lack of regeneration and establishment. This poses significant concerns for the species's long-term survival in its current habitat (De Micco & Aronne, 2012a, De Micco & Aronne, 2012b).

Vertical cliffs provide sensational opportunity to mitigate inter-specific competition, predation, fire, shrub encroachment, human activities, and effects of climatic changes in the surrounding landscape (Larson et al., 2000; De Micco & Aronne, 2012). Gathering on cliff habitats is a common strategy of rare chasmophytes with narrow ecological niches and low competition capacity (De Micco & Aronne, 2012). Such environments shape peculiar microhabitats where both early-stage and mature *P. palinuri*'s plants find the proper conditions to complete their biological cycles. Physical factors of cliff spots, such as light, temperature, water availability, and salinity, differ significantly from nearby flat areas (Aronne et al., 2018) and often play a pivotal role in determining species recruitment (Silvestro et al., 2020), representing the bottleneck for the species fitness (Del Vecchio et al., 2020). This is common in species that inhabit tightly defined habitats because of co-adaptation processes (Navarro & Guitian, 2003).

To cope with such ecological selection processes, *P. palinuri* developed specific adaptive strategies, including morphoanatomical modifications to regulate water relations, protect against high radiation levels, and defend against biotic factors (Aronne & De Micco, 2004; Stachowicz, 2001; Padilla & Pugnaire, 2007). These adaptations allowed the species to colonise and thrive in such a narrow environmental envelope, shaping community structure and dynamics (Baraloto et al., 2005). The research conducted by Strumia et al. (2020) highlights that *P. palinuri* cannot resume germination with increasing saline concentrations, and seawater completely inhibits the germination of its seeds. These findings add salinity to other environmental factors previously identified as significant constraints for the germination of *P. palinuri* seeds, such as exposure to direct light and soil type (Aronne et al., 2018). This evidence underscores the importance of considering a range of environmental factors, including salinity, in fully understanding the germination of *P. palinuri* seeds, and provides further insights into the biology and ecology of this threatened species. In this study, we examined whether different expositions to temperature and salt concentrations, reflecting the proximity/distance to the sea of two populations of *Primula palinuri*, introduced different germination patterns in the species as a consequence of site-specific adaptations. Although *P. palinuri* develops highly viable seeds, with generally 85% germinating success (De Micco & Aronne, 2012), little is known about the various environmental factors and mechanisms influencing seed germination, seedling survival, and early plant development.

METHODS

Field sampling

P. palinuri seeds were collected in July 2022 from two sites within Parco Nazionale del Cilento Vallo di Diano e Alburni: Porto Palinuro and Vaccuta, Campania region, Italy. Porto Palinuro is located near the sea in the Special Area of Conservation (SAC) 'Capo Palinuro (CP) - IT8050008', while Vaccuta (VAC) is approximately 2 km innermost, in the SAC 'Fascia Interna di Costa degli Infreschi e della Masseta - IT8050011' (Fig. 1).

The two study areas are characterised by a Mediterranean climate (Daget, 1977) but with a different average annual rainfall regime of 763 mm in CP and 838 mm in VC, respectively (BIO12 Wordclim). The precipitation regime is concentrated mainly in autumn and winter, while a dry period persists from May to September (Aronne et al., 2015). The temperature pattern is also different at the two sites, with about 12.5 °C and 9 °C, respectively (BIO11 Worldclim). This climatic scheme influences water availability, moisture conditions and soil salinity in the topsoil, with significant implications for plant species' germination and survival, including *P. palinuri.*

Seed sampling for the germination test was carried out according to the protocols of Bacchetta et al. (2006). In each site, fruits (capsules) from visible healthy individuals with similar size and exposure were sampled at a distance among them of at least 50-100 m to ensure genetic variability. Individuals were sampled in July, complying with the end of the ripening period of the species (Pignatti et al., 2017). A total of eight individuals were sampled to avoid detrimental effects on *P. palinuri* populations (Bacchetta et al., 2006).

According to Bacchetta et al. (2006), samples underwent a post-maturation process of 15 days before laboratory trial to ensure uniform seed maturity levels.

Capsule and Seed Morphometric Traits

In the field, we counted the number of capsules of eight individuals per sampling site. These capsules were then delivered to the Germplasm Bank of the Botanical Garden of Rome.

The capsules were then opened to count the number of seeds contained within each capsule. Seeds were divided in two separate containers, one for each sampling site. From each container, 50 seeds were randomly selected, and their major (mm) and minor axes (mm) were measured. This process allowed us to gather data on the size of the seeds from each sampling site, providing information on seed morphology and potential variations between populations. The morphometric traits were measured using NIS-Element Br. 2.10 with images from a digital camera Nikon Digital Sight DS-U1, mounted on a stereo microscope Carl Zeiss.

Seed germination in response to different ecological factors

The germination potential of sampled seeds was tested by conducting different treatments according to the protocols of Bacchetta et al. (2006) and ISTA (2006). Before conducting any experiments, seeds were sterilised using a 5% hypochlorite bleach solution for 5 minutes according to the protocol of Magrini et al. (2019).

We conducted two germination trials to investigate: (a) the germination response of *P. palinuri* seeds to various temperature conditions and (b) the effect of different salt concentrations on seed germination with two fixed temperature range. Analyses were performed exclusively on seeds from ripe capsules.

To assess the germination capability of *P. palinuri* seeds at

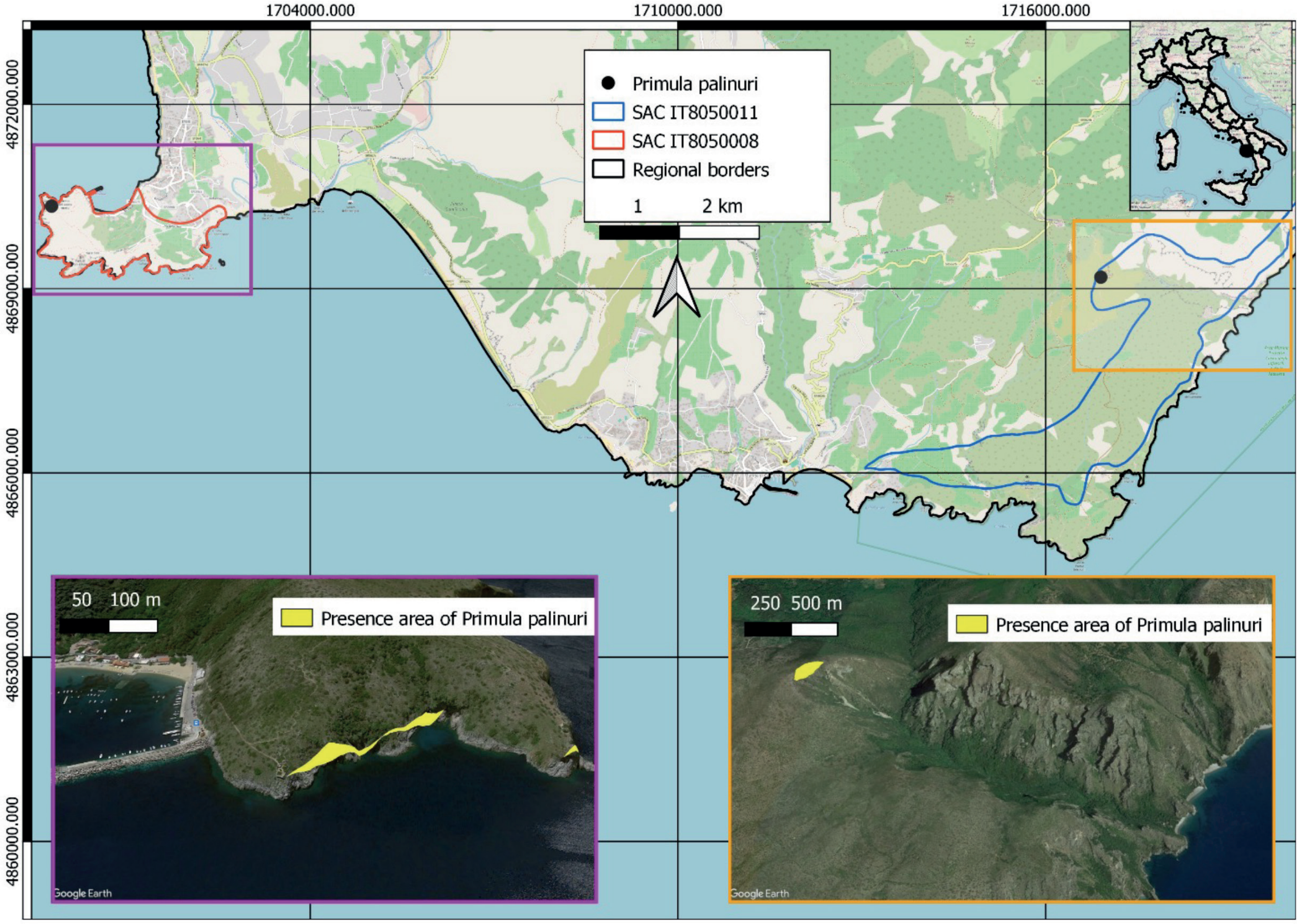

Figure 1. Distribution of P. palinuri sampling site (Capo Palinuro and Vaccuta) within Parco Nazionale del Cilento Vallo di Diano e Alburni. The points in red represent the sampling points, the lines in red represent the boundaries of the area in the Natura 2000 network. The boundaries in black are the regional boundaries.

different temperatures, we conducted experiments in germination cabinets at three temperature levels: 6-15°C (minimum), 10-20°C (average), and 15-25°C (maximum). Cabinets were programmed to alternate between 12 hours of darkness and 12 hours of light, simulating natural day-night cycles. We adjusted the cabinets so that the 12 hours of light coincided with the highest temperature level, replicating natural conditions. To simulate the effects of light on seeds, Petri dishes containing the seeds were incubated with cold white fluorescent tubes, which provided a photon flux density of ensuring an adequate light source for the germination process.

Afterwards, we conducted experiments to assess the germination capability of *P. palinuri* seeds under different salt concentrations (NaCl solution). Five fixed salt concentrations were used: 0 mM (control), 50 mM, 100 mM, 200 mM, and 300 mM, following the protocol of Ghazi N. Al-Karaki (2001). The germination cabinets were set up with the same alternating 12-hour light-dark cycle applied in the previous experiment. The Petri dishes containing the seeds were placed in the cabinets and exposed to the cold white, fluorescent tubes, providing a photon flux density of during the light period. The experiment was conducted at 10-20°C, the average temperature in which the two populations differed, and at 6-15°C, the temperature where the behaviour of the two populations is similar.

For all the germination experiments, 4 replicates of 25 seeds were set up for each site per treatment. Each replicate was placed in Petri dishes with a layer of filter paper as a substrate and distilled water. Germination was assessed daily for each sample for a total test duration of 30 days. Seeds are determined to be germinated when they have produced a visible rootlet with a length greater than 1 mm (Bacchetta et al., 2006). At the end of the germination tests, we assessed missing viability tests (cut test).

Data analysis

Poisson Generalized Linear Models (GLM) with logarithm as a link function were run to investigate potential variations in the number of seeds per capsule among the different sampled populations. To compare the size of the minor (mm) and major (mm) axes of the seeds between the two sampling sites, we estimated a Gamma GLM, with a logarithmic link function.

GLM Beta Regression Models, with a logit link function, were employed to compare the maximum germination response of seeds placed under different treatments (temperature, salt). We used a log-logistic time-to-event model to analyse germination times, focusing on cumulative proportions rather than individual times. Traits like flowering or germination, measured at intervals, are considered interval-censored due to varying observation times, making precise event timing uncertain (Onofri et al., 2018). The two-parameter log-logistic function is given by the equation:

$$f(x) = \frac{1}{1 + \exp^{(b(\log(x) - \log(e))}}$$

In the equation, the parameters 'b' and 'e' represent the slope at the inflexion point of the curve and the germination percentage at the inflexion point, respectively. The parameter 'e' then expresses the day on which 50% of all germinated seeds per treatment (T50) is reached.

All analyses were carried out using R software version 4.3.1, *drcSeedGerm* package (Onofri et al. 2018), *drc* (Ritz et al., 2016) and *betareg* (Cribari-Neto & Zeileis, 2010).

RESULTS

The estimated Poisson GLMs revealed distinctions between the two sampling sites, indicating a greater number of capsules produced per individual at the VAC sampling site, the innermost one (Fig. 2a). Conversely, the count of seeds per capsule did not exhibit variance between the two sites (p-value > 0.05; Fig. 2b).

The estimated Gamma GLMs highlighted overlapping between the confidence intervals of the major and minor axes of seeds sampled in CP and VAC (Fig. 3), indicating no significant difference between the seed morphometries of the populations (Tab.1).

The GLM Beta regression model estimated to explore maximum germination variability across the sampling sites indicates variations under the different treatments (Fig. 4).

For the minimum temperature trials, VAC and CP exhibited similarly high germination percentages (estimated at 92% and 91%). The overlap between the confidence intervals of both populations suggests no significant difference between them (Fig. 4). The 10-20°C treatment induced a higher germination percentage in CP (CI 2.5% 86% and CI 97.5% 95) compared to VAC (CI 2.5% 58% and CI 97.5% 90%) but with more pronounced confidence intervals. No estimation models were applied for the maximum temperature treatment as the seeds of both sampling sites did not germinate at all.

The time-to-event model showed that when treated at the minimum temperatures, seeds from CP sampling site take a shorter time to germinate than VAC (Tab. 2). The estimated time to reach 50% germination (parameter 'e') is 12,01 and 13,83 days, respectively. At the intermediate temperature ranges, the germination speed of CP's seeds is even more pronounced than for those from VAC with 13,24 and 17,74 days, respectively, and already in the initial stages (parameter 'b')

The Beta regression model was also estimated to explore the germination variability of target *P. palinuri's* populations

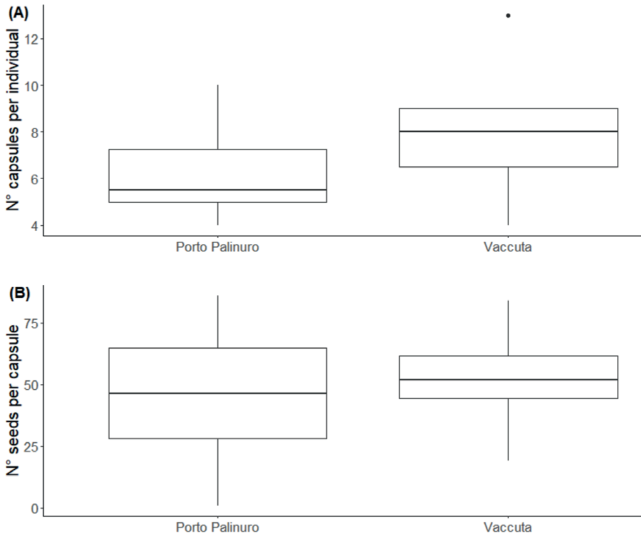

Figure 2. Boxplot of number of capsules per individual **(a)** and number of seeds per capsule **(b)** of the two-sampling site.

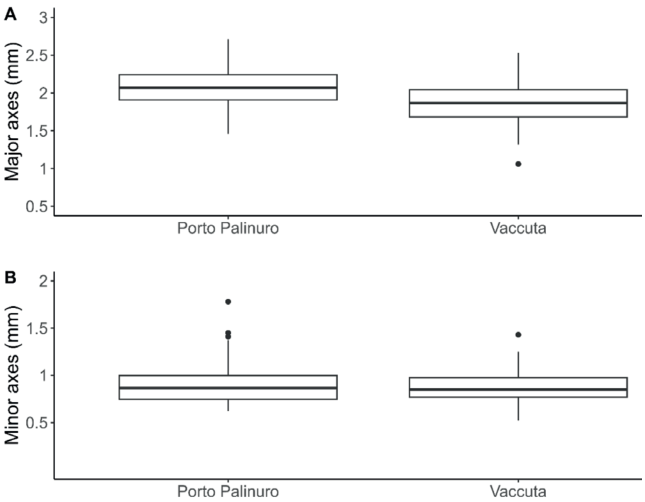

Figure 3. Boxplot of major (a) and minor axis (b) of seeds and width (c) and length (d) of the two populations of Primula palinuri

treated with different salt concentrations at 20-10°C. At 0 mM salt concentrations, seeds from both sampling sites achieved very high maximum germination (90% and 84%) (Fig. 5A).

The germination percentages began to shrink with the increase of the salt concentrations (50- and 100- mM NaCl). However, CP's seed responds better than VAC, maintaining rather high germination performances (87% or 71%), while in VAC, the percentages drastically decrease at 65% and 36% when seeds are treated with 50 mM and 100 mM, respectively. No model was estimated for 200 and 300 salt solutions because the germination was practically neil.

The time-to-event model confirmed the negative impact of salt exposure on *P. palinuri* seeds. Germination time does not consistently change when seeds from both sites are treated at 0 mM NaCl (control) but progressively slows down at increasing salt exposition (Tab. 3).

The results of the Beta regression model estimated for salt treatment at 6-15°C showed that seeds from both sampling sites exhibited notably high germination rates at 0 mM salt concentrations (95% and 94% respectively) (Fig. 5B). However, as salt concentrations increased, germination percentages gradually declined, although they remained relatively elevated compared to results obtained at temperatures of 20-10°C with salt treatment. Notably, germination was still observed at salt concentrations of 200 mM and 300 mM.

Furthermore, CP seeds demonstrated a more favourable response compared to VAC, maintaining relatively high germination rates even at salt concentrations of 200 mM and 300 mM (65% or 31%). In contrast, VAC seeds experienced a significant decrease in germination percentages at higher salt concentrations, dropping to 19% and 36% at 200 mM and 300 mM in both sampling site.

The time-to-event model confirmed the adverse effect of salt exposure at 5-16°C on *P. palinuri* seeds. Germination time remained relatively consistent when seeds from both sites were treated with 0 mM NaCl (control), but it progressively slowed down with increasing salt exposure (Fig.6).

DISCUSSION

Our results demonstrated that variations in temperature and salt tolerances among physically separated populations are

Table 1. Estimates (fourth column) of GLM for capsule and seed sizes (first column) for each sampling site (second column) and confidence intervals (2.5 third column, 97.5 fifth column).

Parameters	Site	CI (2.5%) mm	Estimate (mm^3)	CI (97.5%) mm
Seed Major axis	Palinuro	2.00	2.08	2.17
Seed Major axis	Vaccuta	1.70	1.86	2.05
Seed Minor axis	Palinuro	0.85	0.91	0.96
Seed Minor axis	Vaccuta	0.77	0.88	1.03

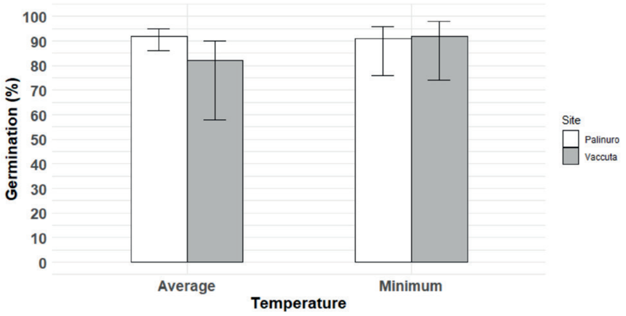

Figure 4. Estimates of maximum germination in percentage of Beta regression model for temperature regimes for each sampling site and confidence intervals. the center rapresent The model estimates, lines represent the 2.5% and 97.5% confidence intervals.

pivotal in determining *Primula palinuri*'s seed germination, rates and speed. Although the occurrence of chasmophytes depends on a complex interaction of different ecological factors, which are difficult to disentangle, our results indicate that cliff-related features are fully involved in the germination patterns and distribution of *P. palinuri*.

Lower temperatures and limited salt concentrations generated high and faster germination rates in the seeds of both studied sites. Conversely, higher temperatures and excessive salt regimes had a strong inhibitory effect, with no germination observed at the warmest (15-25 °C) and saltiest experimental conditions when temperatures were set at 10-20°C (≥ 200 mM NaCl) and a significant reduction of germination capacity and speed already at the intermediate T and salt ranges (10-20 °C; 50- and 100- mM NaCl) for VAC's seeds. CP's seeds showed higher germination rates and shorter times to reach 50% germination than those from VAC, suggesting a greater resilience to such environmental drivers related to the distance from the sea of the two sites.

Inland cliffs like VAC are likely to have cooler temperatures and lower soil salt concentrations due to the gradual decrease in marine influence and other site-level proxies, including wind intensity, altitude, topography, light radiation, and moisture, as one moves away from the coast (Del Vecchio et al., 2020). Seeds originating from the PC coastal cliff area appear to carry peculiar adaptations to tolerate greater temperature and salt conditions. *Primula palinuri* might also follow a germination pattern dependent on avoiding high temperatures, allowing germination to occur primarily during autumn (Barbi, 2008). Although these pieces of evidence are based on laboratory tests, they indicate the existence of optimal requirements for these cliffs' environmental proxies that should be further investigated to approach the species' germination niche (and recreate maximum germination performances) and mitigate both global and local disturbance effects (e.g. climate change, habitat loss) (Larson et al., 2000; Harley et al., 2006; Somero, 2010).

The two sites also differ in fruit productivity, with CP delivering significantly fewer capsules but an equivalent number of seeds. No relevant variations in seed size (major and minor axes length) were detected between the two sites' populations. Although temperature is implied in influencing morphological patterns in capsules and seeds (Mamo et al., 2006) further variables should be taken into account (e.g. altitude, sun exposure) in addition to those related to the distance to the sea to explain fruit structure modification. Comparison of *Primula palinuri* with non-Mediterranean taxa, such as species from mountain regions, should also be relevant to verify the persistence of patterns and local adaptations.

CONCLUSIONS

In this study, we investigated the germination capability of *Primula palinuri* Petagna orthodox seeds under various treatments reflecting site-specific conditions. For the first time, it was examined whether and how the distance from the sea may introduce changes in the seeds' ecophysiological responses of

Table 2. Estimates (fifth column) of time-to-event model for temperature (second column) for each sampling site (third column) and confidence intervals (2.5 fourth column, 97.5 sixth column).

Parameter	Temperature	Site	CI (2.5%)	Estimates	CI (97.5%)
B	Average	Palinuro	-9.91	-8.43	-6.95
B	Minimum	Palinuro	-9.87	-8.35	-6.83
B	Average	Vaccuta	-5.17	-4.38	-3.59
B	Minimum	Vaccuta	-11.443	-9.78	-8.12
E	Average	Palinuro	12.72	13.24	13.76
E	Minimum	Palinuro	11.55	12.01	12.48
E	Average	Vaccuta	16.35	17.74	19.13
E	Minimum	Vaccuta	13.33	13.83	14.35

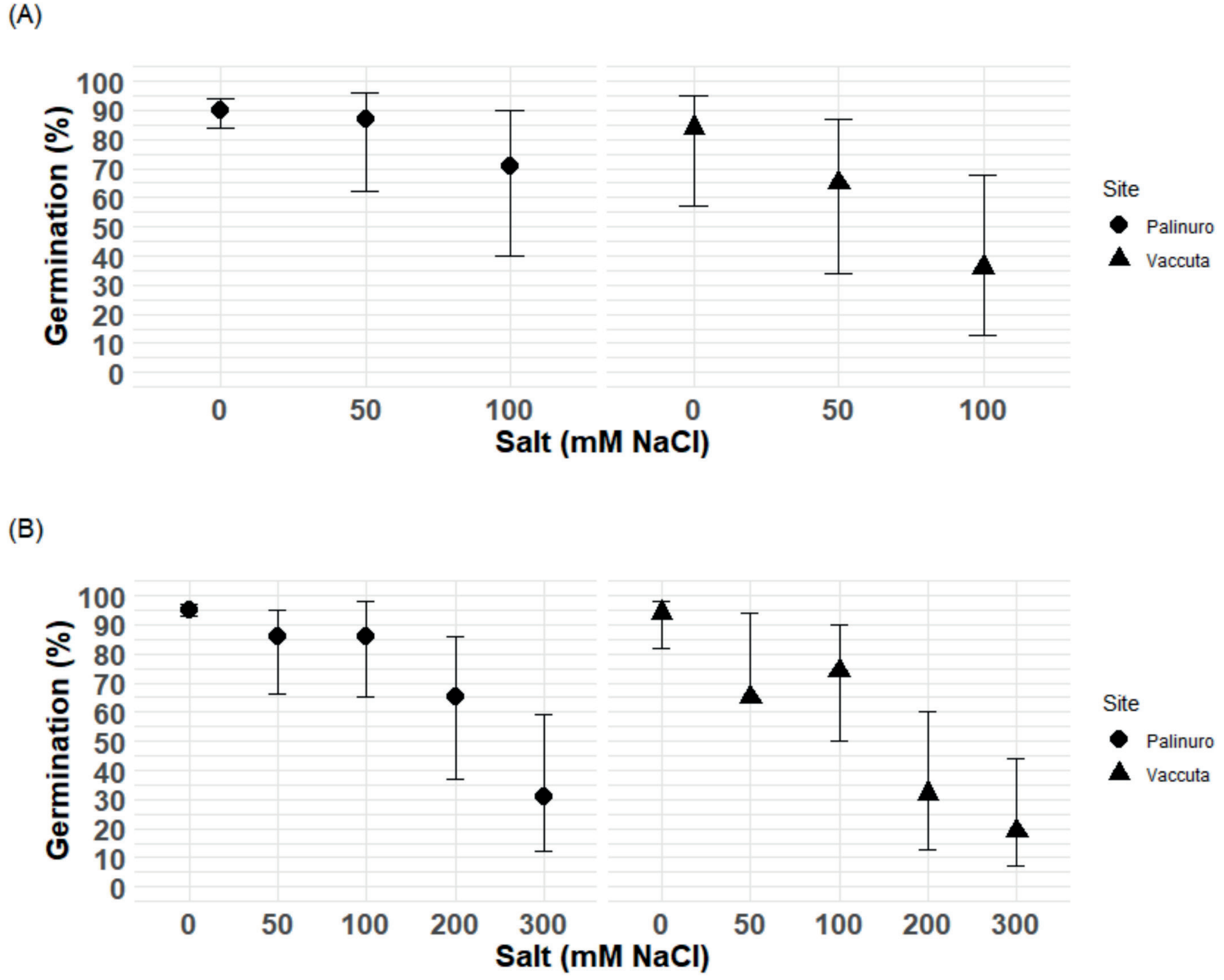

Figure 5. Estimates of maximum germination in percentage of Beta regression model for salt concentration for each sampling site and confidence intervals. the centre represents the model estimates, lines represent the 2.5% and 97.5% confidence intervals. The circle represents the Palinuro sampling site, while the triangle represents the Vaccuta sampling site. a) Experiment conducted at 20-10°C; b) Experiment conducted at 6-15°C.

the species. Temperature and salt were found to significantly impact the germination process and success, determining the capacity of the species to colonise and thrive only in certain sites. Although the environmental conditions in sea-exposed cliffs are warmer and saltier than in more internal areas. In sea proximity, excessive salinity could favour individuals which are more able to germinate under such a limited envelope, especially if combined with high temperatures. Seed size and quantity were also assessed as they are widely recognised as good indicators of seed longevity and environmental influence (Leishman et al., 2000). They revealed a slight advantage of sea-exposed populations. However, analyses did not provide conclusive explanations, requiring follow-up investigations.

Such studies can help elucidate whether the differences in germination responses result from genetic adaptation to local environments or other ecological niche processes. They can concretely contribute to identifying and anticipating the impacts of direct and indirect anthropogenic pressures (e.g. habitat destruction, climate change) against the species and support the definition of conservation and management strategies oriented to specific populations.

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Table 3. Estimates of parameters 'b' and 'e' (fifth column) of time-to-event model for Salt concentration (second column) for each sampling site (third column) and confidence intervals (2.5 fourth column, 97.5 sixth column). The temperature was set a 10-20°C.

Parameter	Salt	Site	CI (2,5%)	Estimates	CI (97.5%)
B	0	Palinuro	-7.39	-6.28	-5.16
B	50	Palinuro	-7.88	-6.66	-5.42
B	100	Palinuro	-7.32	-5.67	-4.03
B	0	Vaccuta	-4.70	-3.95	-3.21
B	50	Vaccuta	-5.02	-3.83	-2.64
B	100	Vaccuta	-21.03	-13.73	-6.42
E	0	Palinuro	12.51	13.24	13.96
E	50	Palinuro	14.36	15.22	16.08
e	100	Palinuro	20.16	21.93	23.70
E	0	Vaccuta	13.37	14.67	15.98
E	50	Vaccuta	22.44	26.12	29.80
E	100	Vaccuta	14.45	18.95	20.46

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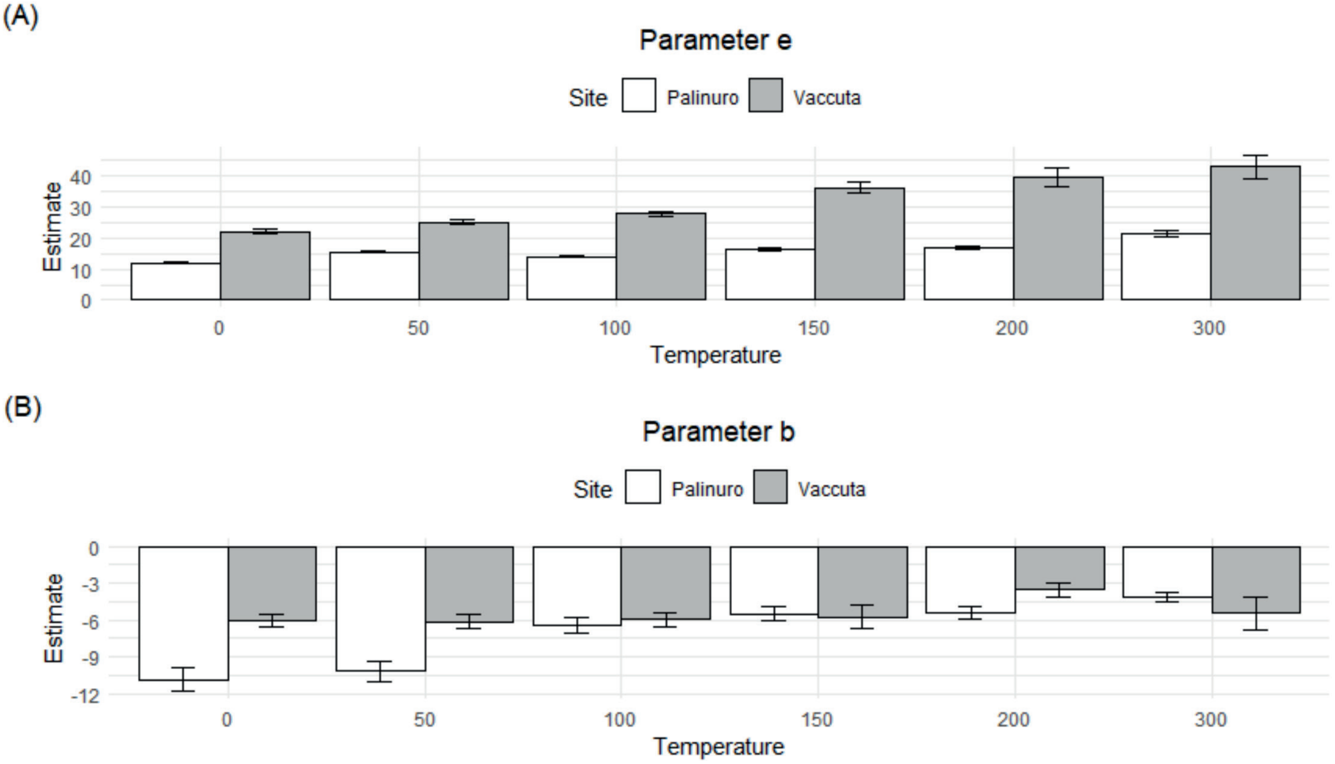

Figure 6. Estimates of parameters 'b' and 'e' of time-to-event model for Salt concentration, at 6-15°C, for each sampling and standard errors.

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