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A hidden mechanism of forest loss under climate change: The role of drought in eliminating forest regeneration at the edge of its distribution

Ella Pozner [a], Peleg Bar-On [a], Stav Livne-Luzon [a], Uri Moran [a], Mor Tsamir-Rimon [a], Efrat Dener [a], Efrat Schwartz [b], Eyal Rotenberg [b], Fyodor Tatarinov [b], Yakir Preisler [b], Nitai Zecharia [c], Yagil Osem [d], Dan Yakir [b], Tamir Klein [a,*]

[a] *Plant & Environmental Sciences Department, Weizmann Institute of Science, Rehovot, Israel*
[b] *Earth and Planetary Science Department, Weizmann Institute of Science, Rehovot, Israel*
[c] *KKL Forest Service, Israel*
[d] *ARO Volcani, Rishon Lezion 7505101, Israel*

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ABSTRACT

The ongoing global warming and associated drying are shaping the fate of forests worldwide. While processes of tree mortality are visible and studied, a decrease in forest regeneration is mostly overlooked, although equally deleterious. Populations at the edge of tree species distribution areas are at higher risk and are hence hotspots for species extinctions.

Here we use a semi-arid pine forest growing at the timberline edge of forest existence as a model for forest survival under warming and drying conditions. Seedling recruitment, including seed germination, seedling survivorship, and multiyear seedling growth, were measured along six consecutive years. To pinpoint the role of drought, we designed a field experiment, manipulating stand density at three levels and grazing regimes.

Seed germination was high across all studied plots, but seedling survivorship and multiyear seedling growth were near-zero. Stand density and grazing exclusion positively affected germination. Seedling survivorship was higher in wetter years. Multiyear seedling growth was stunted by grazing, and seedling height was distributed differently across different stand densities.

Our data indicate that seedling survivorship during the first dry season acts as a bottleneck for forest existence at the dry and hot edge of current forest distribution. We also quantified the roles of other stressors such as shading, and highlighted the eliminating role of grazing on multiyear seedling growth. Forest regeneration should be more closely monitored in sensitive populations, as climate change-driven forest loss can happen even without mature tree mortality.

1. Introduction

In the current era of climate change, global warming trends modify the climate system leading to precipitation regime changes and extreme climatic events. Predictions point to harsher, longer, and more frequent climatic disturbances, including consecutive drought episodes (IPCC Climate change, 2014; IPCC Climate Change, 2021). For the past decades, a wide range of studies shows a significant climate signal on natural ecosystems globally (Parmesan and Yohe, 2003; Walther et al., 2005; Allen et al., 2015; Seidl et al., 2017). The effects of such changes include changes in biodiversity, transition of dominant species, and changes in species distribution, including range expansion on the one hand and species' extinctions on the other hand (Parmesan and Yohe, 2003; Walther et al., 2005; Petit et al., 2008; Lindner et al., 2010; Scheffers et al., 2016). Generally, the vulnerability of a population to extinction depends on its adaptive potential and the rate of changes required to track the changing environment (Bürger and Lynch, 1995; Williams et al., 2008). At the current climate trend, the responses of many populations in large areas of the globe are likely to be inadequate to counter the rate and magnitude of climate change (Savolainen et al., 2004; Savolainen et al., 2007; Loarie et al., 2009; Lindner et al., 2010; Kuparinen et al., 2010; Hoffmann and Sgrò, 2011; Lindner et al., 2014; McDowell et al., 2020).

Among terrestrial ecosystems, forests play a crucial role in shaping

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* Corresponding author.
E-mail address: tamir.klein@weizmann.ac.il (T. Klein).

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the global water and carbon cycles. Currently, many forests are shaped by the ongoing warming, CO_2 rising and the water limitations associated with droughts (Allen et al., 2010; IPCC Climate change, 2014; Klein and Hartmann, 2018; McDowell et al., 2020). Comprehensive analysis shows that these drivers continue to cause forest loss, including tree mortality and disturbance to forest dynamics (recruitment and growth; Lindner et al., 2014; McDowell et al., 2020). Considering that forests develop slowly and that trees are long-lived and immobile organisms, it is unclear whether their adaptations would be sufficient to buffer the changes (Lindner et al., 2010; Hoffmann and Sgrò, 2011). Genetic variability, distribution shifts, new colonization and human-assisted translocation can all increase the endurance of trees to environmental changes (Hoffmann and Sgrò, 2011). The probability of a population to reach a suitable habitat with the proper climatic conditions depends essentially on demographic factors (Loarie et al., 2009; Hoffmann and Sgrò, 2011), that represent the prerequisites allowing an organism to counter changing conditions (Williams et al., 2008; McDowell et al., 2020).

Extirpation of a tree population is a relevant outcome, considering the evidence of increasing tree mortality and increasing disturbances in forests worldwide. Even in water-abundant areas, no forest is immune to climatic changes, with drought playing a major role in forest decline (Allen et al., 2010; Allen et al., 2015; Anderegg et al., 2015; Seidl et al., 2017; Brodribb et al., 2020; McDowell et al., 2020). Moreover, drought effects are linked with multiple stressors from biotic and abiotic agents (Niinemets and Valladares, 2006; Allen et al., 2010; Seidl et al., 2017; Lindner et al., 2014; Anderegg et al., 2015; Seidl et al., 2017). While drought-induced tree mortality has been documented and studied in numerous studies, little is known on the role of forest regeneration in limiting forest sustainability under warming and drying conditions. Adaptation plays a fundamental role within the ontogenetic steps of an individual tree and between trees. During its maturation, tree performance is projected not only for its own survival, but also for the capability of supporting the next generation – whether by a suitable seed quality, long-distance dispersal, high genetic variation, or by creating a suitable microclimatic conditions. To ensure the sustainability of a forest, the two parallel processes of adequate growth of mature trees and the ability to recruit the next generation of trees are required (Keeble, 1988; Oliver and Larson, 1996; Bell et al., 2014).

The process by which an individual is added to the population is defined as seedling recruitment. Forest regeneration can be regarded as sufficient to ensure forest sustainability if new recruits can replace dead and old trees. Seedling recruitment consists of three basic steps: (i) seed germination, (ii) seedling survivorship, and (iii) multiyear seedling growth (Eriksson and Ehrlén, 2008). Generally, the recruitment of a new generation into an existing forest requires the transition of the seedling from one step to the next. Considering the vulnerability of these steps in an individual life period, the mortality rate of seedlings is claimed to be high (Eriksson and Ehrlén, 2008; McDowell et al., 2020). Chronic droughts, continuous warming and their cascading effects are predicted to result in recruitment limitations (McDowell et al., 2020). For example, *Pinus ponderosa* recruitment failure is related to the climatic variation of dry periods that was preceded by a decline in seedling survivorship (League and Veblen, 2006; Kolb et al., 2020). Seedling survivorship and growth performance of Mediterranean pine species were shown to be significantly reduced with future drought scenarios (Matías et al., 2017). Nevertheless, dry lowland Mediterranean species, among them *Pinus halepensis*, the most abundant Mediterranean pine, demonstrated higher drought tolerance (Mauri et al., 2016; Bonari et al., 2021). Although warm and dry bioclimatic regions promote tolerant species, rapid changes and extreme climatic events such as heatwaves are predicted to increase the aridity of these regions, like low elevation regions in the Mediterranean region (Diffenbaugh et al., 2007; IPCC Climate change, 2014; Spinoni et al., 2018). Life under these developing conditions becomes nearly impossible for sustainable tree populations, often defined as the edge of species distributions (Osem et al., 2009; Voltas et al., 2018; Patsiou et al., 2020). These marginal populations encounter more considerable evolutionary challenges with small adaptive capacity and migration potential on the one hand, and higher exposure to stress factors on the other hand (Watkinson and Sutherland, 1995; Aitken et al., 2008; Lindner et al., 2010; Alberto et al., 2013; Bussotti et al., 2015).

Along with the multi-decadal climatic trend, other human interventions such as the use of the forest as rangeland toward grazing and land-use change have significantly affected forest dynamics for millennia. In addition, reforestation often results in massive, non-controlled plantations of high stand density that often have a high vulnerability to change (Allen et al., 2010). In turn, forest management attempts to mitigate these trajectories by reducing stand density. Thinning induces various outcomes, among them a change in the stand water balance and light penetration (Simonin et al., 2007; Vesala et al., 2005). In semi-arid sites, thinning improved the performance and resistance of remaining trees (Moreno-Gutierrez et al., 2011; Sohn et al., 2013; Sohn et al., 2016; Tsamir et al., 2019). In parallel, forest self-thinning was found to support seedling recruitment (Mast and Veblen, 1999). However, even when moderate to low stand densities show higher seedling survivorship, the interaction of subsequent droughts can suppress the recruitment process (Kolb et al., 2020). In addition, grazing regimes widely affect flora and fauna of the forest, with inconsistent effects on forest dynamics (Öllerer et al., 2019), and specifically on seedling recruitment. Modification of the recruitment process by grazing lead to pine range expansion in one case (Richardson et al., 2007), or to a continuous forest suppression in others (Chauchard et al, 2007; Connor et al, 2021). Grazing effects facilitating forest regeneration often involve reduced fire frequency (Richardson et al., 2007) and reduced competition by grasses (Chauchard et al, 2007), whereas deleterious effects involve injury to young seedlings and trampling. Ultimately, the grazing impact depends on grazing intensity, grazer type, and ecosystem type, with more negative effects in semi-arid forests (Gao and Carmel, 2020).

Studying climate change effects on forests cannot suffice with sites in temperate forests alone, and requires in-depth investigation of peripheral sites (Walther et al., 2005; Williams et al., 2008; Aitken et al., 2008; Lindner et al., 2010; Allen et al., 2010; Hoffmann and Sgrò, 2011; Alberto et al., 2013; Bussotti et al., 2015; Scheffers et al., 2016; Seidl et al., 2017; Dyderski et al., 2018; Klein and Hartmann, 2018; McDowell et al., 2020). One such site is the Yatir pine forest (Israel) at the dry timberline. At the edge of the climatic Mediterranean gradient of Israel, the Yatir forest represents a semi-arid forest system with extremely low precipitation and consequent water deficits (UNESCO, 1963; Rotenberg and Yakir, 2010; Klein et al., 2014; Preisler et al., 2019). It is located at the edge of forest existence, where processes such as natural selection of tree species are continuously affecting the population (Aitken et al., 2008; Osem et al., 2009; Schiller and Atzmon, 2009; Schiller, 2011; Kremer et al., 2012; Alberto et al; 2013; Osem et al, 2013). In this area, afforestation modified the natural flora by supporting understory vegetation, which was further subjected to a heavy grazing regime (Amir and Rechtman, 2006). In this regard, the Yatir forest is a unique case study for multiple stress agents working together (Osem et al., 2009). The effect of forest regeneration on the future of forests under climate change is still an understudied topic. Considering that Yatir forest is a marginal tree population on the dry timberline, we hypothesized that (1) germination, seedling survivorship, and seedling growth would be lower than needed for long-term forest regeneration, in turn jeopardizing the forest future as a whole. Proposing Yatir as a test case for forest management under climate change, we further hypothesized that (2) forest density reduction (thinning) and grazing exclusion could improve seedling recruitment by providing higher light and water availability to seedlings while preventing grazers' damage to seedlings. Whether this was enough to ensure the forest sustainability, is unknown to us.

2. Materials and methods

2.1. Yatir forest, site and climate

The Yatir Forest is a semi-arid planted Aleppo pine (*Pinus halepensis* Mill.) forest (Fig. 1). It is located at the northern edge of the Negev desert in Israel (31°20′49″ N; 35°03′07″ E, mean elevation of 650 m a.s.l.) and covers 3,000 ha. The forest lies at a significant transition area between two bio-climatic areas: the Sub-Desertic and the Xero-Thermo Mediterranean and is defined as an ecotone (UNESCO, 1963). The former has a semi-arid climate defined by a range of 200–250 dry days a year, and the latter has a dry-hot Mediterranean climate defined by 150–200 dry days with hot-dry summers and cool-rainy winters (UNESCO, 1963). The mean annual precipitation is 285 ± 90 mm, the mean diurnal air temperature and relative humidity are 10 °C and 65% in January and 25.8 °C and 50% in July, respectively. The forest bedrock consists of chalk and limestone (FAO classification). The soil type is shallow Aeolian-origin loess down to 20–40 cm deep that has a clay-loam texture (31% sand, 41% silt and 28% clay; bulk density of 1.65 ± 0.14 g cm^{-3}; Qubaja et al., 2020). Rock erosion created round hills with moderate slopes that have a high fraction of stoniness and surface rock cover (48% and 36.8%, respectively; Preisler et al., 2019). The belowground water table is part of the Western Mountain Aquifer of Israel, and its elevation is 300 m below the surface. Due to the unavailable belowground water table and the lack of runoff, precipitation during the wet season (November–April) and the minor re-evaporation of moisture adsorption during the dry season (May-October), fundamentally support the existence of vegetation at the site (Waisel, 1984; Schiller and Atzmon, 2009; Schiller, 2011; Qubaja et al., 2020).

Pinus halepensis is the dominant planted species of the Yatir forest, similar to other planted forest sites in Israel since it is the only native pine species in Israel and Jordan. The natural distribution of this species under sub- to thermo-Mediterranean climatic conditions consequently leads to its extensive plantation in the Yatir area, in addition to its drought resistance and pioneering characteristics (Oppenheimer1967; Schiller and Atzmon, 2009). The forest was established between 1965 and 1969 and the afforestation continues to this day. Seedlings are 1–2 years old at planting, and are irrigated during their first dry season after planting. In addition, precipitation in 1965–1969 exceeded the long-term mean. The surrounding native vegetation prior to the afforestation consisted of sparse desert fringe shrubland with dwarf shrub patches. The native flora is changes from the wide coverage of Mediterranean steppe species to sparse semi-desert Irano-Turanian species (Vogel et al., 1986). Today, the native flora creates the understory of the planted forest. The forest vegetation is subjected to moderate to heavy grazing regimes as it was prior to the afforestation for several millennia (Waisel, 1984). The common local flock consists of 150–500 sheep (*Ovis aries*) and up to 10 goats (*Capra hircus*), grazing daily during the grazing season. The grazing regimes are enforced by the foresters and are limited to up to 2500–3000 animals per day throughout the forest (i.e., 0.83–1 grazer ha^{-1} day^{-1}), for five or six months a year, depending on the annual precipitation level. In the period between February and April, the forest understory is dominated by herbaceous vegetation in parallel to the germination of the pines, resulting in a heavy grazing regime. Over the following period of April to May, the herbaceous vegetation dries as the season changes and this results in a low grazing rate. In the dry period of June to August, the flocks modify their grazing pattern and graze the herbaceous ripped seeds and woody vegetation until the end of the grazing season in July-August. In addition, the forest supports wild gazelle (*Gazella gazella*), in herds of four to six individuals, ~100 individuals in total. The forest also supports the existence and feeding habits of large rodents like the Cape hare (*Lepus capensis*) and the Indian crested porcupine (*Hystrix indica*). In addition, the forest functions as a recreation site for the local communities throughout the entire year.

2.2. Yatir thinning and grazing experiment

On relatively flat terrain of even trees' age and within ~0.5 km from the permanent research flux tower, fifteen plots of 0.5 ha were defined (70 × 70 m or 50 × 110 m), with a buffer zone of 15 m from each side of the quadrilateral to limit external impacts (Fig. S1). During 2009 the plots were thinned to form three stand density levels; five plots remained unthinned to simulate the average 300 trees ha^{-1} density level of the forest, five plots were thinned into a moderate density of 200 trees ha^{-1} and five plots were thinned into a low density of 100 trees ha^{-1}. In 2010–2011, each plot was divided into two (0.25 ha each) to examine the grazing effect; One part of the plot was fenced to exclude the entrance of grazers, and the second part remained accessible. Two parallel 30 × 4 m transects were defined in each part of the plot, facing east to west. Two permanent metal stakes fixed each transect to ensure constant measurements over the following years. Along these transects, annual measurement surveys were performed. Seedling recruitment was surveyed starting from 2015, i.e. six years following the thinning. At that time, the study plots have already reached a new steady state (Tsamir et al., 2019), and hence our results reflect long-term dynamics under the specific thinning and grazing regimes, rather than short-term dynamics affected by our manipulations.

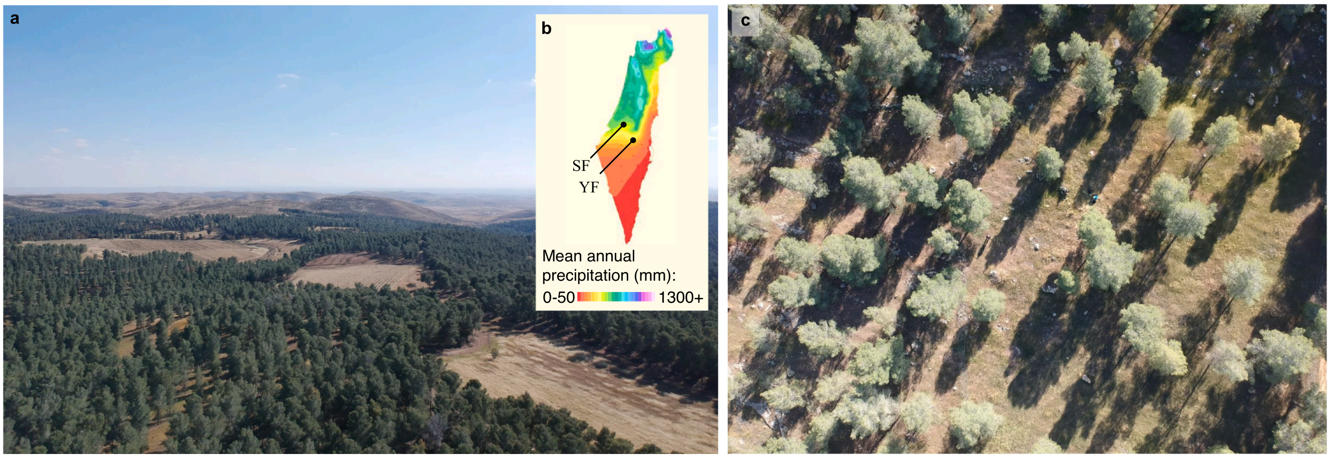

Fig. 1. Yatir Forest in May. a) Eastern view of Yatir forest from the height of 100–120 m. b) Israel climatic map with annual precipitation gradient in 1991–2020. Arrows point on the Yatir forest (YF) and Shaharia forest (SF). c) Forest plot with stand density of 200 trees ha^{-1} captured from a height of 40–50 m.

2.3. Yatir surveys of seedling recruitment

The three stages of seedling recruitment were monitored in Yatir for five years by sample count surveys normalized by hectare. The germination monitoring included counting new germinants and was performed in April throughout the plot in 2015–2016 and along the plot transects in 2018–2020. Seedling survivorship monitoring included counting surviving germinants after one summer and was performed in September throughout the plot in 2015–2018 and along transects in 2019–2020. Multiyear seedling growth monitoring included counting multiyear seedlings (seedlings that survived at least two summers) in September throughout the plot since 2015, with additional measurements of seedlings' height. To detect the annual dynamics, seedling growth and seedling height surveys were performed. The surveys included counting multiyear seedlings that reached at least 10 cm in height, categorized into four height categories of 10–14, 15–24, 25–34 and 35 + cm. Considering that seedling growth rate in Yatir is ∼10 cm year^{-1}, these height categories roughly represent the age of each seedling.

2.4. Yatir soil water monitoring layout

Soil water content (SWC, m^3 m^{-3}, EC-5 soil moisture sensor), soil water potential (SWP, kPa, MPS-6 soil water potential sensor), and soil temperature dielectric sensors were placed at depths of 20 and 25 cm belowground and were connected to an Em50 data-logger (all made by Decagon devices Inc., Pullman, WA, USA). Data loggers were programmed to record observations at 30-minute intervals. Soil water potential correction for temperature bias was calculated (Walthert and Schleppi, 2018). Sensors from each type were located under the tree canopy and at the nearest forest glade, in three stand density levels. In some cases, malfunction of sensors prevented data collection from certain stand density and canopy/glade locations (SWC at 300 trees ha^{-1} canopy; SWP and soil temperature at 300 trees ha^{-1} density glade). In addition, data were missing for the dry season at 100 trees ha^{-1} density glade.

2.5. Yatir meteorological data

Meteorological data for Yatir were collected continuously since 2000 in the Yatir forest FLUXNET micrometeorological tower situated in the center of forest (31°34′52″N, 35°05′20″E) and less than 1 km from the research site (Grünzweig et al., 2007; Rotenberg and Yakir, 2010). Data were collected according to the European methodology (Aubinet et al., 2000) and were part of the European EC sites quality assessment project (Göckede et al., 2008). The air temperature was measured at 1 m and 15 m by Rotronic HC2S3 (Bassersdorf, Switzerland). All data were stored at half-hourly steps by CR1000 datalogger (Campbell Scientific Inc., Logan, USA). Daily rainfall data were provided from 1971 to 2021by the Yatir forester standard rain station of KKL (31°20°18.1″N 35°02′03.0″E, elevation 650 m a.s.l), situated ∼1.5 km from the Yatir research site. Israel Meteorological Service (IMS) provided rainfall and air temperature data for Yatir through the Shani standard weather station (31°21′24.5″N 35°03′58.3″E, elevation 700 m a.s.l.) from 2004 to 2021. Shani station is situated ∼2.2 km from the Yatir research site. At the Shani station rainfall was recorded daily, and the air temperature was recorded every three hours. A summary of Yatir meteorological data is presented in Fig. S2.

2.6. Statistical analysis

Data Analysis was performed and visualized using R (R Core Team, 2021) and the interface R Studio (RStudio Team, 2020). We assessed the effects of the different environmental factors on seedling germination, survivorship and growth, using a set of a generalized linear mixed model (GLMMs), using the user interface Jamovi (The Jamovi project, 2021) and verified and visualized using R (R Core Team, 2021) and the interface R Studio (RStudio Team, 2020), as implemented in the package "gamlj" (Gallucci, 2021). Specifically, germination was examined as counted germinants ha^{-1}. Therefore, we analyzed the data regarding germination using negative-binomial distribution. Seedling survivorship was examined as the existence of surviving seedlings ha^{-1} and was analyzed using logistic distribution. Multiyear seedling growth was examined in two steps; the first was to ascertain the existence of multiyear seedlings ha^{-1}, which was then analyzed using logical distribution. In the second step, the multiyear growth was analyzed as counted multiyear seedlings ha^{-1} by height classes, within the plots that showed multiyear seedling's existence. As part of the multiyear seedling growth analysis, seedling height was examined as the number of seedlings ha^{-1} in different height categories. We used a nested design to generate random factors and calculate the variance partitioning of the seedling recruitment process across different treatments; the grazing treatment, height range (only in multiyear seedling analysis) and the sampling date were all nested within the density level of the plot. In all models, the grazing treatment was considered as a fixed factor, while the plot and sampling date were considered as random factors. We included the density levels, annual precipitation and annual temperature as covariates in all models. When examining the multiyear seedling growth, height range was considered as a fixed factor. Effect sizes were standardized by dividing the effect size by one SD before graphical visualization.

2.7. Shaharia forest, site and climate

The Shaharia Forest is a dry-Mediterranean planted forest dominated by Aleppo pine (*Pinus halepensis*) plantations (UNESCO, 1963; Osem et al., 2013). It is located at the Southwestern slopes of the Judean lowland region (31°59′99″N 34°83′00″E, Elevation 200 m a.s.l., 40 km northwest of Yatir) and covers 700 ha. The forest is located in the transition area between the Judaean Hills to the east and the coastal plain to the west. This area constitutes a climatic penetration area of the northern Negev and a gradient that is becoming increasingly arid from the north to the south. Similar to Yatir, the forest bedrock type is chalk covered by hardpan (calcrete) shaped as round hills with moderate slopes by rock erosion. The soil type is Aeolian- Alluvial Grumosol and dark to light Rendzina. The native flora consisted of Mediterranean dwarf shrubland and herbaceous vegetation. Today the remains constitute the forest understory as adjacent shrubland. Rain falls on chalk bedrock creates runoff that may penetrate to groundwater and aquifers or be stored in reservoirs, but most of it evaporates to the atmosphere. The Shaharia forest is characterized by 400–500 mm annual precipitation, an average maximum temperature of 27 °C, and a minimum of 15 °C (IMS, 1981–2020) (Fig. S3).

2.8. Shaharia experiment layout and measurements

Six plots of 2 ha each were defined in the forest, each represents a different combination of two factors; stand density and topography aspect (north and south). Grazing was excluded from all research plots. Each area consists of three to five 0.5 ha sub-plots (50 × 50 m) that constitute the measurement unit of the study (total of 27 plots). Stand density levels were thinned and defined to 100, 200 and 300 trees ha^{-1}, and each density is represented by seven to ten plots. Two parallel 30 × 4 m transects were defined in each plot. Each transect was fixed by two permanent metal stakes to ensure constant measurements. Multiyear seedling growth and height surveys in Shaharia Forest were performed in January 2009. Multiyear seedlings were counted along transects and normalized by area. Two multiyear seedlings or one of every five multiyear seedlings in each transect were sampled and measured for height (cm). Meteorological data for Shaharia were provided by the IMS from the Gat standard weather station (31°63′03″N 34°79′13″E, elevation 140 m a.s.l.). Gat station is situated ∼5 km from the Shaharia research site. At the Gat station rainfall was recorded daily, and the air temperature was recorded 3, 2 and 8 times a day in 1989–2004, 2005–2006 and 2007–2021, respectively.

3. Results

3.1. Seed germination and seedling survival in Yatir forest

Over the five years of the experiment, an increasing number of germinants was observed, peaking in 2020 (Fig. 2). In contrast, there was a non-uniform trend of the number of surviving seedlings, positively related to the annual precipitation: the wetter 2015–2016 years supported significantly higher rate of surviving seedlings, whereas drier years failed to sustain surviving seedlings (Precipitation $\chi^2_1 = 22.97$, $P < 0.001$; Fig. 2), with a mean survivorship rate of less than 0.06%. Nevertheless, the highest number of surviving seedlings was counted in 2020, evidencing no long-term effect of the consecutive dry years of 2017–2019.

3.2. The effects of stand density and grazing on seed germination and seedling survival in Yatir forest

Significantly higher numbers of germinants were generated at the higher stand densities, reaching 10,000 to 100,000 germinants ha^{-1} (Stand density $\chi^2_1 = 20.13$, $P < 0.001$; Fig. 3a). Increasing stand density induced a larger mean of germinants and surviving seedlings (Fig. 3a, pie charts). Separating this continuous trend between the two grazing treatments, we revealed a significant negative effect of the grazing on seed germination (Grazing $\chi^2_1 = 9.52$, $P < 0.01$; Fig. 3a) and a variable effect on seedling survivorship. Nonetheless, the mean survivorship rate did not exceed 10%, neither at the yearly mean rate (Fig. 2, pie charts), nor with the stand density and grazing treatments mean rate (Fig. 3a, pie charts).

3.3. Soil water content, soil water potential, and soil temperature

Overall, soil water content (SWC) increased following rain events to 0.3 and 0.4 m^3 m^{-3} in November-March and decreased below 0.2 m^3 m^{-3} in the dry season between April and October (Fig. 4a-c). SWC was higher at the low and moderate densities (100 and 200 trees ha^{-1}) than at the high density (300 trees ha^{-1}) at the forest glade (Fig. 4a). Within the low and moderate densities, SWC was lower under the canopy than at the glade during the wet season, but during the dry season, SWC under the canopy was higher at the moderate density (Fig. 4b, c). In some cases, malfunction of sensors prevented data collection from certain locations or periods (see Methods). Soil temperature curves showed a uniform trend across densities under the glade and the canopy, with the rising temperature at the end of the wet season, decreasing back at the end of the dry season (Fig. 4d). Nevertheless, temperatures were consistently 5–10 °C lower under the canopy than at glades, where high-temperature fluctuations were observed, notably during the dry season. While maintaining a high soil water potential (SWP) of close to 0 at all densities during the wet season, SWP decreased significantly at the end of the wet season (Fig. 4e). The most extreme curve was shown at the high density (300 trees ha^{-1}), reaching −6000 kPa. The low and moderate densities supported higher values of SWP, with the moderate density generally presenting lower values than the low density. Whereas the SWP at the low density under the glade showed the highest curves at the beginning and end of the dry season, the SWP under the canopy at the same density remained relatively stable during the whole year.

3.4. Multiyear seedling growth in Yatir forest and Shaharia forest, a wetter parallel

Seedlings that survived more than one year were rare, usually not more than a few dozens per ha. The numbers of these multiyear seedlings were significantly lower in the grazed plots (Grazing $\chi^2_1 = 33.05$, P

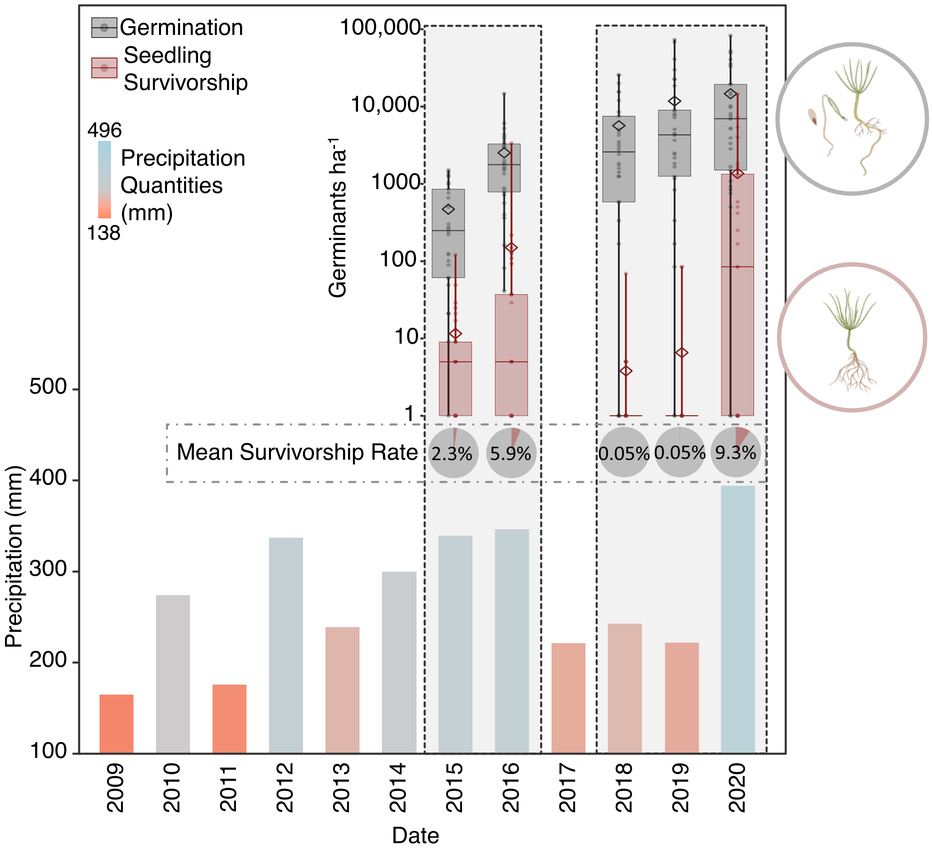

Fig. 2. Germination and seedling survivorship in Yatir forest in 2015–2020, following the thinning in 2009, in relation to annual precipitation of 2008–2021. Counted germinants and seedlings in each plot are represented as points on a semi-logarithmic scale. Grey indicates new germinants at the end of the wet season (April), and red indicates surviving seedlings at the end of the following dry season (September), and their means are represented as diamonds. Pie charts represent the mean number of new germinants (grey) and surviving seedlings (red) each year. Numbers represent the mean survivorship rate.

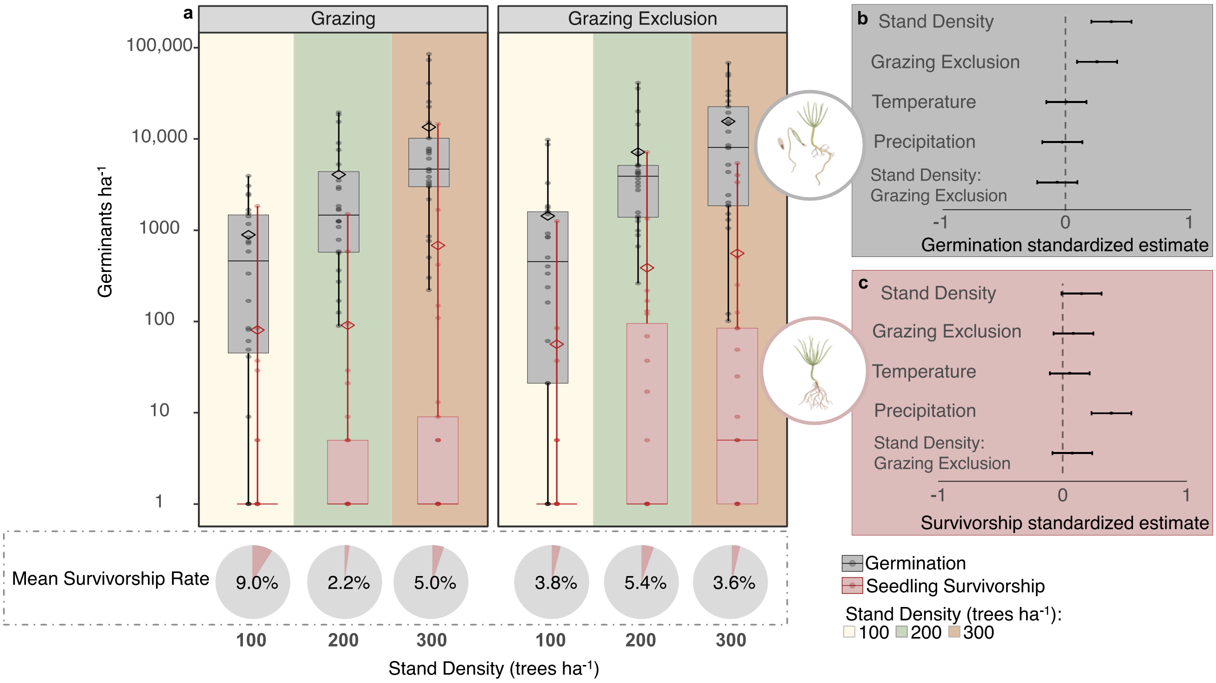

Fig. 3. Grazing and stand density effects on germination and seedling survivorship in Yatir forest in 2015–2020 (not including 2017). a) Counted germinants and seedlings in each plot are represented as points on a semi-logarithmic scale. Grey indicates new germinants at the end of the wet season (April), and red indicates surviving seedlings at the end of the following dry season (September), and their means are represented as diamonds. Pie charts represent the mean number of new germinants (grey) and surviving seedlings (red) in each density and grazing treatment. Numbers represent the mean survivorship rate. b) Forest plot showing 95% standardized confidence interval (CI) for germination standardized fixed-effects parameter estimates. c) Forest plot showing 95% standardized confidence interval for seedling survivorship standardized fixed-effects parameter estimates.

< 0.001; Fig. 5a). Higher numbers of seedlings were counted from 2015 to 2017, with top records in 2016, and decreasing in recent years. In Shaharia forest (just 40 km northwest of Yatir, yet with ~80% higher annual precipitation; see Methods), the mean of multiyear seedlings counted in a single year (2009) mounted to ~500, over an order of magnitude higher than in Yatir forest in any year. In Yatir, the effect of stand density on seedling growth was not significant (Stand density $\chi^2_1 = 1.06$, $P = 0.3$), in contrast to the previous stages of the recruitment process (above). We did not have information on seedling age, yet grouping the multiyear seedlings into height categories helped to identify long-term patterns. There was a distinct distribution in each of the stand densities, along with a significant negative effect of grazing on the number of multiyear seedlings in different height categories (Grazing; logistic distribution $\chi^2_1 = 5.39$, $P < 0.05$; negative binomial distribution $\chi^2_1 = 9.88$, $P < 0.01$; Fig. 6a). Significant multiple interactions between stand density, grazing treatments and height categories were found for Yatir plots that successfully sustained multiyear seedling growth and for the rate of the growth within them (Stand density: Grazing: Height categories; logistic distribution $\chi^2_3 = 12.81$, $P < 0.01$; negative binomial distribution $\chi^2_3 = 13.75$, $P < 0.01$; Fig. 6a). For comparison, in Shaharia, where multiyear seedling numbers were counted in the thousands, multiyear seedlings at the mid-density plots were taller and higher in numbers (Fig. 6b). The low-density plots in Shaharia had fewer, but equally tall seedlings and the high-density plots had shorter seedlings, at a number between low- and mid-density seedlings. Focusing on the grazing exclusion treatment in Yatir forest, low stand density better supported the higher seedlings. In contrast, there was a relatively stable and uniform pattern throughout the ranges in the moderate density, whereas the high-density showed higher numbers in the low range of 10–14 cm and insufficient numbers (for replacement of dead or old trees) within the higher ranges. As seen in Fig. 5, an inter-annual peak was observed in 2015–2017. The low stand density showed a relatively high number of seedlings in all ranges in 2015, then a peak, particularly in the highest range, in 2016, followed by a decrease until 2020. Despite the decrease, a considerable number of seedlings in the higher ranges were still maintained. The middle stand density also showed a 2016 peak in the higher ranges, decreasing in the following years until 2020. In contrast to the low- and middle-stand densities, the high-density peak seemed lagging in one year, with an extreme decrease in 2018, leaving a negligible number of seedlings in all ranges in the following years.

3.5. *Seedling mortality in Yatir forest*

Although not measured directly, seedling recruitment and mortality were inferred from multiyear seedling population dynamics presented in Fig. 6. For clarity, this analysis excludes the annual mass mortality of germinants (Figs. 2, 3), and relates exclusively to the multiyear seedlings. Due to the low numbers of seedlings, these changes were typically at the range of twenty seedlings ha^{-1}, either recruited (+20) or perished (−20) (Fig. S4). Over this background, a few notable recruitment events were identified, e.g. in 2016 (>100 seedlings in the 35+ cm category at the low density without grazing; and >50 seedlings in the 25–34 cm category at the high density with grazing) and in 2017 (~90 new seedlings at the high density without grazing). These recruitments probably reflect the maturation of seedlings that survived their first year during the wet years of 2015 and 2016. However, each of these events was followed by a subsequent mortality event of similar magnitude, in the drought years of 2017 and 2018.

4. Discussion

4.1. *Inhibited regeneration, the “silent killer” of peripheral forests*

We presented a first-of-its-kind study of inhibited forest regeneration in a semiarid pine forest under drought and grazing. This inhibition is synthesized along the recruitment stages in Fig. 7, showing the dwindling numbers from mass germination to scarce seedling survivorship,

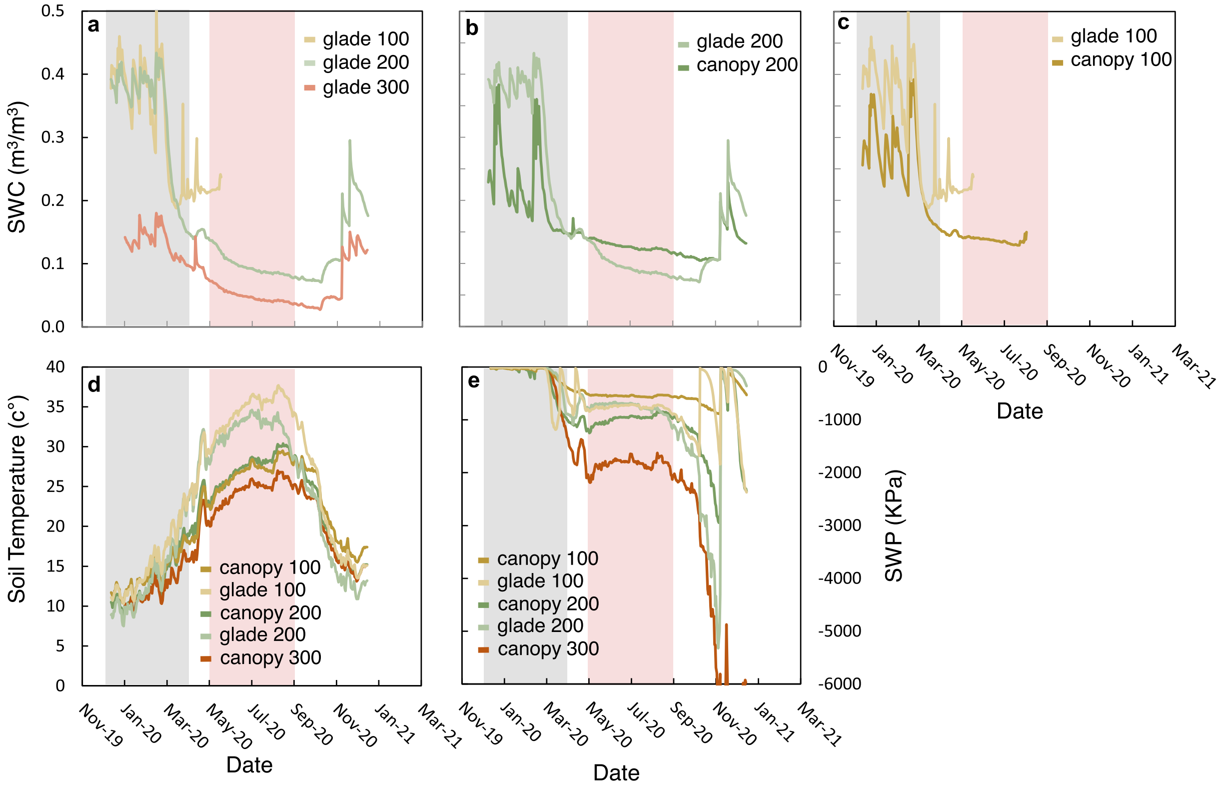

Fig. 4. Annual curves of soil water content (SWC, m^3/m^3), soil water potential (SWP, kPa), and soil temperature (°C) at different stand densities at different locations measured in depth of 20–25 cm. Grey shading marks the two months period before the measurement of germination (April). Red shading marks the two months period before the measurements of seedling survivorship and multiyear seedling growth (September). a) SWC measured at a forest glade at stand density of 100 (light yellow), 200 (light green) and 300 (light red) trees ha^{-1}. b) SWC measured at a forest glade (light green) and under the tree canopy (c, dark green) at a stand density of 200 trees ha^{-1}. c) SWC measured at a forest glade (light yellow) and under the tree canopy (dark yellow) at a stand density of 100 trees ha^{-1}. d) Soil temperature measured at a forest glade (light shades) and under a tree canopy (dark shades) at a stand density of 100 (yellow), 200 (green) and 300 (red) trees ha^{-1}. e) SWP measured under a forest glade (light shades) and below the tree canopy (dark shades) at a stand density of 100 (yellow), 200 (green) and 300 (red) trees ha^{-1}.

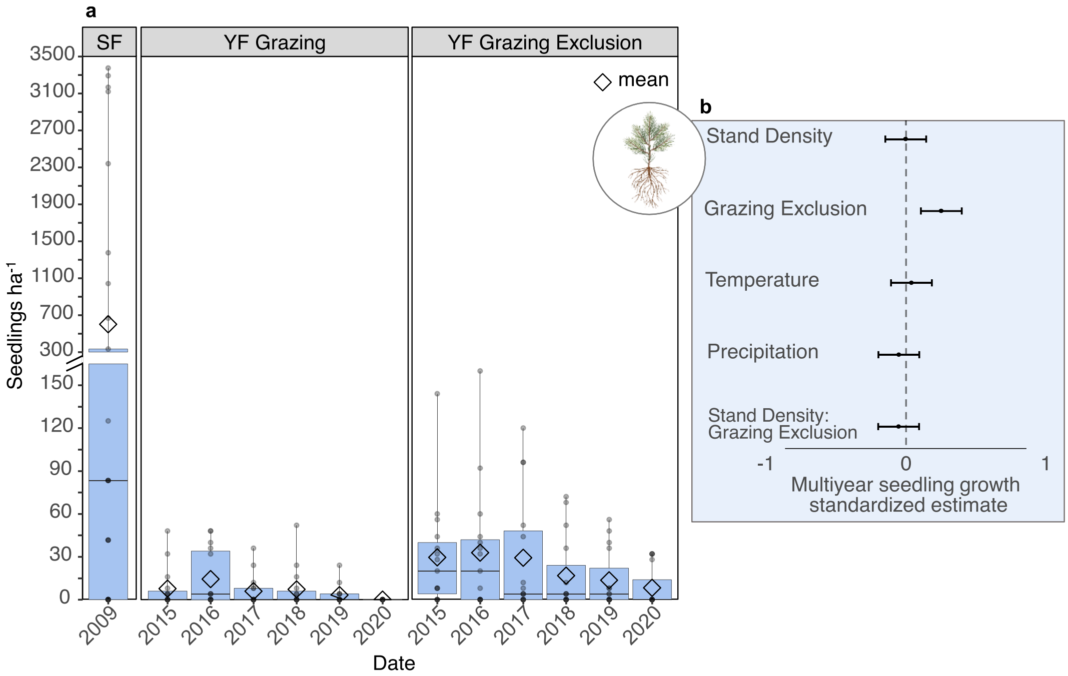

Fig. 5. Multiyear seedling growth in Yatir forest (YF) in 2015–2020 with different grazing treatments and, in Shaharia forest (SF) in 2009. Counted seedlings in each plot are represented as points on a broken y-axis scale, and their means are represented as diamonds (black). b) Forest plot showing 95% standardized confidence interval (CI) for seedling growth standardized fixed-effects parameter estimates.

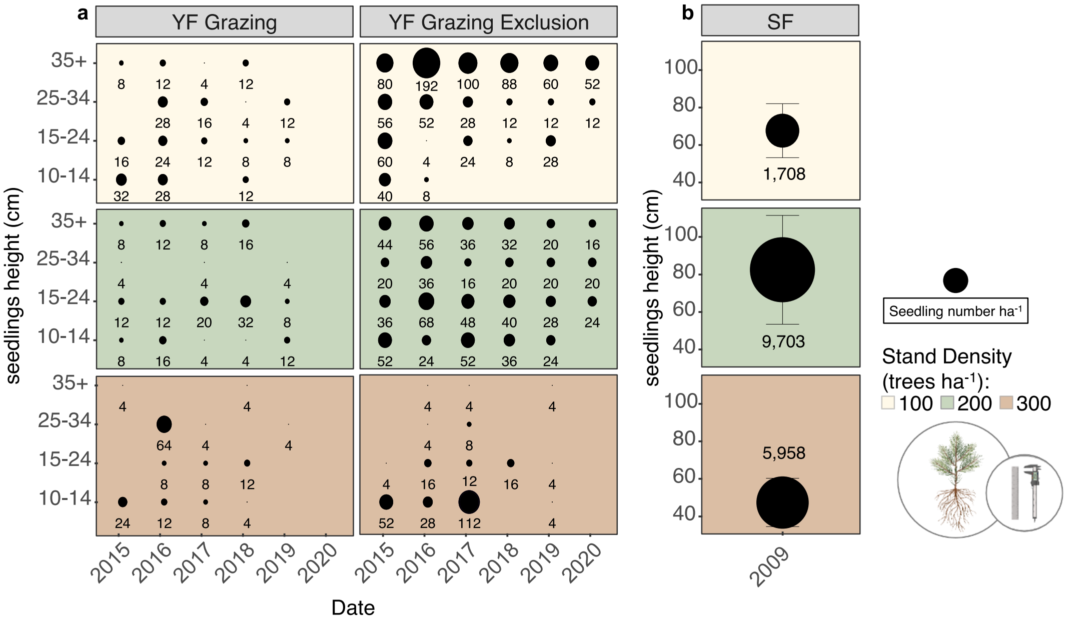

Fig. 6. Multiyear seedling numbers at different height categories in Yatir forest (YF) in 2015–2020 with different grazing treatments, and in Shaharia forest (SF) in 2009. a) Counted multiyear seedlings in each density are represented as different size points corresponding to the number of counted multiyear seedlings. b) Mean height of counted multiyear seedlings in each density is represented as different size points corresponding to the sum of counted multiyear seedlings in each density. The standard error of the mean height in SF is represented as error bars.

and on to the yet lower numbers of multiyear seedlings. The relative role of the stressors is also presented, with stand density, summer drought, and wild and livestock grazing being the major risks for the respective recruitment stages (Fig. 7). In general, vegetation in many arid and semiarid regions has been degraded by the unpredictability of dry period, and later by overgrazing (Holmgren and Scheffer, 2001). On the other hand, the scarcity of understory vegetation, grazing and intensive management in the forest mean that it is not exposed to natural fire regimes. Thus, Yatir *P. halepensis* seed dispersal is defined by drought-induced rather than fire-induced dispersal, further restricting the forest regeneration rate (Nathan and Ne'eman, 2004; Ne'eman et al., 2004). The absence of second generation trees throughout the Yatir forest raises a substantial question about the ability of a marginal forest to prevail.

Throughout the study period, germination increased, without a significant effect of the climatic conditions (Fig. 2, Fig. 3b). Not surprisingly, a significant positive effect of stand density on seedling germination showed that a higher number of trees ha^{-1} yielded a higher number of germinants (Fig. 3), presumably following high seed production in agreement with Osem et al. (2013). Furthermore, germination was affected by the grazing, where grazed plots had significantly lower germination than the un-grazed plots (Fig. 3). As Yatir is subjected to high anthropogenic impact (Osem et al., 2008), during the germination season of February to April, grazing herds (and, to a lesser extent, wild grazers like *Gazella gazella* and different rodents) fed on both herbaceous vegetation as well as the pine germinants, which were still soft to the ungulate mouth. Notwithstanding, the massive germination step, typical of *Pinus halepensis* (Ne'eman et al., 2004), still provided a fertile ground to support the next step per se. Seedling survivorship did not correspond to the observed increase in germination throughout the study period (Fig. 2); while the germination trend was sustained relatively high and uniform, the survivorship was significantly and substantially regulated by the annual precipitation. As Osem et al. (2013) showed, seed germination was unrelated to annual variation in precipitation, and was explained by the early steps of seed ripening and seed release, that are not directly linked with the short-term precipitation patterns (Nathan and Ne'eman, 2004). On the contrary, seedling survivorship represents a fundamentally sensitive phase to annual water dynamics. Indeed, changes in precipitation in the Yatir forest, as in Mediterranean forests, were suggested in the past to govern tree growth, activity, and survival (Sabaté et al., 2002; Padilla and Pugnaire, 2007; Osem et al., 2009; Klein et al., 2014; Preisler et al., 2019; Tsamir et al., 2019). We indicate that as long as the seedlings had adequate precipitation amounts, survivorship was maintained by the sufficient number of germinants provided by the previous step. For example, years with above-average annual precipitation sustained a relatively high survivorship rate, peaking in 2020 with annual precipitation of 394 mm (Fig. 2, pie charts). Inversely, survivorship was almost eliminated in dry years, independently of the massive germination rate, as presented in 2018–2019. This water deprivation pattern draws the central bottleneck for the stunted recruitment in the forest, despite the pioneering and drought resistance traits of *P. halepensis* (Oppenheimer, 1967; Ne'eman and Trabaud, 2000; Schiller and Atzmon, 2009).

Within the effect of the annual precipitation, the number of trees ha^{-1} played an intuitive role when higher germination provided a higher number of potent individuals for the next generation. Interestingly, grazing effects were not detected in the survivorship step (Fig. 3c). A suggested explanation could point to potential advantages for both grazing and grazing exclusion. Grazers consumed pine seedlings and facilitated neighbors (Padilla and Pugnaire, 2006), but in parallel, consumed the (competing) herbaceous species (Richardson et al., 2007), as shown in other studies. Therefore, removal of herbaceous competition could in fact promote the survival of seedlings that survived their first dry season. However, more research is needed to prove this hypothesis.

Multiyear seedling growth, the final recruitment step, was mainly and significantly eliminated by the grazing (Fig. 5). A similar pattern, peaking in 2016 in both grazed and ungrazed plots, was differentiated mainly by the scale of measured seedlings in each year. An *a priori* low number of multiyear seedlings set by the fundamental bottleneck, governed by precipitation dynamics, was altered into negligible numbers by the grazers. Not only that, the compensation of grazers for drier periods was previously shown to be by changing diet into woody, less preferable forage (Holechek et al., 1982; Roever et al, 2015), here suggested to have deteriorated the woody seedlings defoliation. The abovementioned potentially beneficial effect of grazing on survivorship by mitigating competition was later canceled by the long-term grazing effect on the

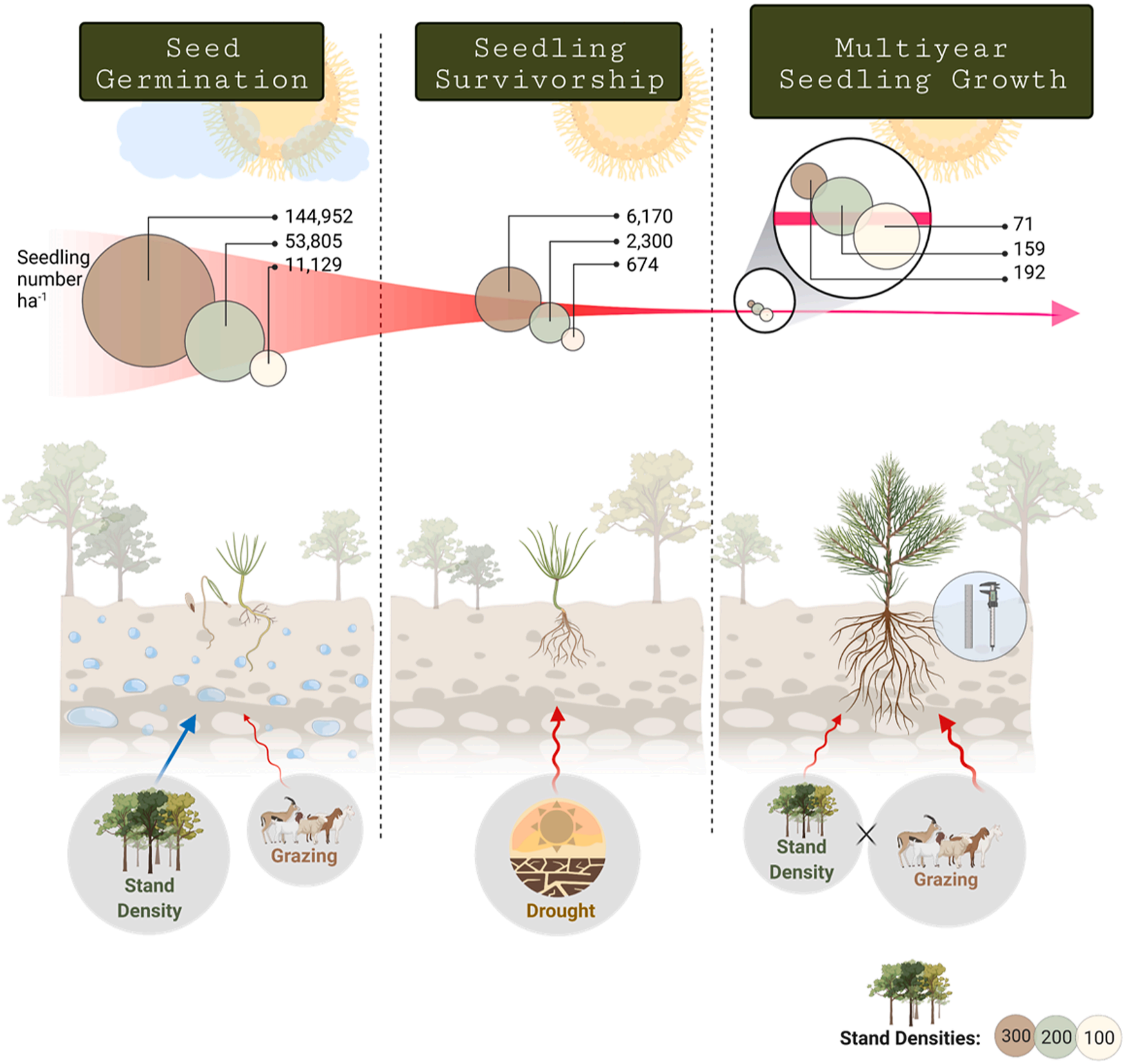

Fig. 7. The mechanisms of eliminated regeneration in a semi-arid pine forest. Numbers are means of yearly sums of all observations in 2015–2020 (not including 2017), showing the loss of seedlings along with the recruitment processes. Germination is high at the higher density forest and still significant even at low density, with grazing having a smaller effect (circle size denotes relative contribution of each factor; blue and red arrows denote positive and negative effects). Seedling survivorship is very low due to summer drought, with a smaller effect to stand density. Unlike the upstream processes, seedling growth is lower at higher stand density, and grazing effects are detrimental. Created with BioRender.com.

multiyear growth. As previously claimed for the Mediterranean climatic gradient, multiyear seedling survivorship and growth were not solely related to precipitation amounts, but to the interaction between multiple stressors (Osem et al., 2009).

In the present study, unfolding the factors' effects revealed significant multiple interactions (Fig. 6); the distribution of the counted seedlings in each height category was affected by its inter-annual dynamics, as in the 2016′s peak, within the grazing treatments and the different stand densities. In agreement with the observation that grazing regimes minimized the recruitment chances of *P. halepensis* in Israel (Osem et al., 2008), this distribution is visible under grazing exclusion. Within the grazing exclusion, the high density was limiting, as shown to maintain short and stunted seedlings. As pine seedlings are shade-intolerant (Nathan et al., 2000; Ne'eman et al., 2004), the described dwarf seedling state can be maintained for a limited time, until a local canopy opening occurs, providing higher light penetration and release of the seedling to grow further (Whitmore, 1989). At our site, we found these long-term dynamics insufficient to accomplish the recruitment process at the higher density. The moderate density had a uniform height distribution, which emphasized the consistent mild effect of this density on the recruitment process, as shown in the previous steps. Here, unlike in the germination, the low stand density provided the most beneficial conditions, in terms of growth performance and the number of multiyear seedlings. It was previously shown by Tsamir et al. (2019) that radiation level is a substantial limiting factor even in a highly lighted forest as Yatir.

4.2. Mechanisms of seedling mortality

The forest water availability is suggested to vary locally and be affected by different stress agents (Grossiord et al., 2017; Seidl et al., 2017), marking the significance of the inter-annual precipitation trends. The above led us to investigate the soil water dynamics as a valid aspect of the water balance at the site. A substantial trend of low SWC and SWP in the high stand density was detected, while the moderate and low stand densities presented relatively high SWC and SWP (Fig. 4). Simultaneously, soil temperatures decreased with increased stand density, especially in the dry season (Fig. 4d). These trends can be explained by the cumulative water consumption of the trees at 300 trees ha^{-1} (Klein et al., 2014). In accordance with previous studies, even with higher temperatures at the thinned plots that can lead to increased evapotranspiration, the total water balance was more sustainable following thinning (Simonin et al., 2007; Moreno-Gutierrez et al., 2011; Sohn et al., 2013; Tsamir et al., 2019). Findings show that seedling survivorship of *Pinus ponderosa* experiencing high temperature at the dry period, fundamentally depends on the ability of the seedlings to utilize the water by a deep developed root system and the capacity for low osmotic potentials (Kolb and Robberecht, 1996; Padilla and Pugnaire, 2007). The improved support of the multiyear seedling growth in the low-density plots agrees with the proposed preferable water balance. This evidence can point to the ability of multiyear seedlings to develop root systems that extract soil water and benefit from the improved water balance (Grossiord et al., 2017), while having a higher tolerance to the external conditions (Sohn et al., 2016). That suggestion agrees with the evidence that a relatively shallow soil layer of 20–40 cm belowground was found to be the area of the maximum fine root density, which substantially supports the population in Yatir (Klein et al., 2014).

Overall, we confirmed the first hypothesis. While seedling germination was sufficient, a significant bottleneck generated by insufficient seedling survivorship was expressed in limitation of multiyear seedlings growth, risking the future of the entire forest. Regarding the second hypothesis, we partially confirmed that reduced stand density and grazing exclusion could promote balanced and more sustainable conditions. Different recruitment steps were affected differently by stand density, and grazing exclusion was not found to be beneficial in all steps. Higher germination was supported by high stand density, contrary to better multiyear seedling growth that was supported by low to moderate stand densities. Therefore, no state could achieve optimal conditions for a regeneration process sufficient to replace dead and old trees. In prospect of these findings and the coming decades, it seems highly unlikely that even a seedling population following wet years would be able to replace aging trees, neither in number, nor in growth rate. These suggestions support the inevitable forecasts of changes in population dynamics and population extirpation, even with extensive improvement in the understanding of these processes (Brodribb et al., 2020).

4.3. Conclusions and implications for the future of marginal forests

Future global warming predictions and increased extreme climatic events generate alarming projections on the marginal *Pinus halepensis* population in this semi-arid site, as well as in others (IPCC Climate change, 2014; Dyderski et al., 2018; Voltas et al., 2018; Patsiou et al., 2020; IPCC Climate Change, 2021). The multiyear recruitment trend observed here was designed by the relative annual survivorship rate, introducing new individuals into the existing seedling pool, while eliminating others (Fig. 6). Recruitment of new individuals at the lower height ranges proceeded into the next height categories, only if local conditions permitted. The thirty-year climatic trend of Yatir (Fig. S2) typically presents droughts every 2–3 years on average. Here we identified the vulnerability of this population to extirpation, stressing the significance of the inability to endure the velocity of the climatic changes (Williams et al., 2008; Loarie et al., 2009; Lindner et al., 2010). Such predictions do not support the future existence of the pine forest in Yatir, even without an abrupt tree mortality event, as seen before (Preisler et al., 2019). Is this realm true for the unique case of Yatir forest, or can it be further generalized? On the one hand, the current and previous studies (Osem et al., 2009; Osem et al., 2013) showed that seedling recruitment in similar, yet wetter, *Pinus halepensis* forests, was sufficient to ensure its regeneration and sustainability. On the other hand, the abiotic and biotic factors that inhibited forest regeneration in Yatir (Fig. 7) are ubiquitous to many forest types, and specifically, marginal forests (Osem et al., 2009; Allen et al., 2010; McDowell et al., 2020). Evidently, even in Shaharia forest, recruitment is restricted to wet years (data not shown), and seedlings survive every year only in wetter forests (>450 mm year^{-1}). Soil moisture and temperature, solar radiation, and grazing are already limiting forest growth in many regions (Allen et al., 2010). Their interaction with the ongoing climate change could put many forests in harm's way, giving rise to non-forest land covers (Bussotti et al., 2015; Connor et al., 2021).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

The Yatir forest research station is managed by DY, and the LTER experiment is managed by TK, and was initiated together with ER and YP. The project was led by EP, with help from PBO and MTR, under the mentorship of TK. Meteorological data were archived by FT and ES. Statistical analysis was performed by EP, SLL and ED. The Shaharia forest research was led by NZ, under the mentorship of YO. The manuscript writing was led by EP, TK, and UM, with contributions from all co-authors.

Data accessibility

All data related with this paper are included in the figures and supplementary materials.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119966.

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