Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession

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Abstract

Most of the area in pine woodlands is occupied by perennial seeders that regenerate from seeds in the first winter after the fire and by annuals. Control of the germination in the regenerating vegetation after wildfire is therefore a primary ecological component of the post-fire succession in this ecosystem. The aim of the study presented here was to determine the distribution of *Pinus*, *Cistus* and other plants seeds around burned *Pinus halepensis* trees, and to measure the conditions related to seed germination in the upper soil layers in the same locations. The study was carried out in a 50-year old planted *Pinus halepensis* woodland that was burned down by a wildfire in July 1995. The variation of seedbank density was determined by collecting samples under the canopies of burned trees and in a nearby open area. Pine seedbank density decreased and that of *Cistus* and annuals increased with increasing distance from the burned trunks. Most pine seeds were present in the ash layer while those of the other plants were in the soil. *In situ* germination experiments showed that seedling density decreased with distance from the burned trunks while the proportion of pines in the seedling population increased. This was a result of seedbank variation and germination inhibition by the high pH conditions caused by the ash. The establishment of sparse pine seedling under the dead tree canopies insured their rapid development without interference by other plants and played a key role in the regeneration and stability of the pine woodland community. The concomitant mass germination of the perennial seeders in the rest of the area prevented invasion by annuals.

Introduction

Many plants in the Mediterranean pine woodlands are adapted to the effects of wildfires. This is considered to be the result of the strong selection pressure exerted on these ecosystems by humans since prehistoric times (Naveh 1990; Trabaud 1990; Archibald 1995). Three types of post-fire plant regeneration strategies were described by Keeley (1991, 1994). Firstly, most broadleaf trees and shrubs in the Mediterranean basin regenerate only by sprouting from underground plant parts (Trabaud 1987). These obligate sprouters maintain their location in the habitat throughout the burning cycles. Their population dynamics are not affected much by the wildfire events. Other facultative sprouters regenerate by germination of seeds as well as by sprouting. Among these there are shrubs and peren-

nial grasses. They not only maintain the positions they occupied before the fire, but take advantage of the special conditions that prevail after fire and spread by establishing new seedlings. The third group is comprised of obligate seeders that are killed by fire and regenerate only by germination from the large seedbanks that accumulate between fires. These species germinate in large masses during the first winter following the fire event as a response to the heat and other fire-related signals (Keeley & Fotheringham 1997).

Wildfires expose the soil surface to direct sunlight, remove layers of decaying organic matter that may contain various allelopathic compounds, and release nutrient minerals in the upper soil layers (Bond & van Wilgen 1996). Thus, the post-fire conditions are conducive for seedling establishment. The mass germination of seeders helps them to compete with an-

nuals, especially grasses, that also germinate in greater proportions under these special conditions.

Aleppo pines (*Pinus halepensis* Miller) that build the native pine woodlands of the east Mediterranean basin are subjected to wildfires periodically (Trabaud et al. 1985; Naveh 1990; Kazanis & Arianoutsou 1996). This tree is an obligate seeder species that does not regenerate vegetatively after fire. Between fires it builds up a large seedbank in semi closed serotinous cones at the treetops. As a result of the dry and warm conditions during the fire, the cones open and release the accumulated seeds. This seed rain starts during the fire and may continue for a few days (Rundel 1981; Lamont et al. 1993; Saracino et al. 1997).

Other seeder species that appear in great numbers after wildfires in east Mediterranean woodlands belong to the genus *Cistus*. A large proportion of the seeds of these plants has a hard seedcoat that is impenetrable to water, and thus prevent germination. Heating of the seeds during the fire cracks the seedcoat and induces germination (Thanos & Georghiou 1988; Thanos et al. 1992). The seedbank of the *Cistus*, as those of annuals, is stored in the upper layers of the soil, and some of it is lost during the fire. Still, massive germination of *Cistus* takes place in the first winter after the fire (Troumbis & Trabaud 1986; Thanos & Georghiou 1988; Ferrandis et al. 1996).

We have observed that no new seedlings of either *Pinus halepensis* or *Cistus* appeared in the second or third year after the fire while the plant canopies close (Katz 1993). Daskalakou & Thanos (1996) reported the same observation in a similar ecosystem in Greece. The whole process of post-fire succession that goes through intermediate stage of shrub cover to eventual re-establishment of the woodland is based on germination during the first winter. Ne'eman et al. (1992) described the seedlings distribution pattern in a regenerating pine woodland after a wildfire on Carmel Mt., Israel. Seedling density was inversely related to distance from burned tree trunks. The proportion of *Pinus* seedlings also decreased along the same line. The causes of that pattern were not completely understood.

The aim of the study presented here was to identify the ecological factors that determine the distribution of seedlings of pines and other species at the onset of the post-fire regeneration process in this ecosystem.

Methods

The study was carried out in a 50 year old planted *Pinus halepensis* woodland that was burned down by a wildfire in July 1995. The woodland was in the Judean Mountains, Israel (35°06′ E 31°45′ N), 15 km west of the city of Jerusalem at elevation of 590 m above sea level.

The area around large burned trees was divided into three zones: Zone I – under the central half of the projected canopy area surrounding the trunk, Zone II – under the peripheral half of the projected canopy area, Zone III – in the open area among the trees immediately outside the projected canopy areas. Samples of ash (zones I and II only) and soil (0–5 cm) were collected from 10×10 cm quadrats in each zone. The ash layer in zone I was 5 cm thick and 3 cm in zone II. In zone III the ash layer was thin and could not be separated from the upper soil layer. Each ash or soil sample was spread in a 20×20 cm plastic box with drain holes, and rinsed by distilled water until the pH of the effluent was no higher than 7.8. The boxes were kept at 20 °C, 11 h light for 13 weeks to allow for germination of all viable seeds. Seedlings were counted and removed every two weeks, until no more new seedlings appeared for a month. This experiment was carried out in 10 replicates.

In situ germination experiments were carried out during the 1995–1996 winter season. Pairs of 50×50 cm plots were marked in all three zones around the trunks of 20 large, burned trees. The ash layer was removed from one plot in each pair but all the seeds that were in it were sieved out and returned to their original location. Appearance of seedlings was monitored from the beginning of the rainy season in November 1995 until next February when no more new seedlings were observed.

Ash and soil (0–1 cm and 4–5 cm depth) samples were collected every two months during the season (September 1995–March 1996) around nearby trees in the burned area, corresponding to the experimental plots. Comparable samples of the soil under the litter layer from an unburned area (500 m away) were also collected. pH was measured in the field with a portable pH meter with a FET (Field Effect Transistor) type electrode (UniFET, San Diego, California). This type of electrode can be used for measuring directly the pH of soil paste. Other ash and soil samples were enclosed in polyethylene bags and brought to the lab. Water content of the samples was determined by oven drying, and osmotic potential of the saturated paste

extracts was determined using a vapor pressure osmometer (model 550, Wescor, Logan, Utah). Water and acid extractable ion content were determined by atomic absorption spectrometry. Water retention curve of ash and soil samples was determined using pressure plates (ELE International, Inc., Lake Bluff, Illinois).

Two way analyses of variance and Tukey's multiple range tests were performed using SYSTAT 5.0 for Windows statistical package (SPSS, Inc.).

Results

The first experiment was designed in order to determine the size of the viable seedbank of the pines and other plants around large burned trees. The samples were collected before the rain season in September and included all the viable seeds present at the onset of the post-fire succession process. Germination took place under controlled conditions that were shown in preliminary experiments to be suitable for the studied plants. The ash samples were rinsed until their pH reached nontoxic level as shown by our previous data (Henig-Sever et al. 1996).

The seedling distribution presented in Figure 1 shows that most of the viable pine seeds were included in the ash layer under the projected canopy area. The density of seeds near the trunk was larger than at the periphery of the canopy. A smaller amount of viable pine seeds, ca. 20 per m^2 was found in the soil layers, and this was not significantly different (Tukey, $P > 0.05$) from the seed density outside the canopy area. Overall, the density of pine seeds showed a decreasing trend from the burned tree trunk outwards. Seeds of *Cistus* and of the annual plants showed an inverse trend with the density among the trees being significantly larger than under the canopies. Altogether the size of the seedbank in each location was several hundred viable seeds per m^2.

The *in situ* germination experiments were carried out in order to determine what fraction of the seedbank actually produce seedlings in the field and to gauge the effect of the ash on germination under the natural conditions. The results (Figure 2) show that if the ash layer is removed but the seeds in it are left in place the seedling density has the same trend as that of overall seedbank size, as shown in the previous experiment. Pine seedling density in plots from which the ash was removed was largest near the trunks and decreased outwards, while that of *Cistus* and the annuals showed the opposite trend. The presence of ash inhibited ger-
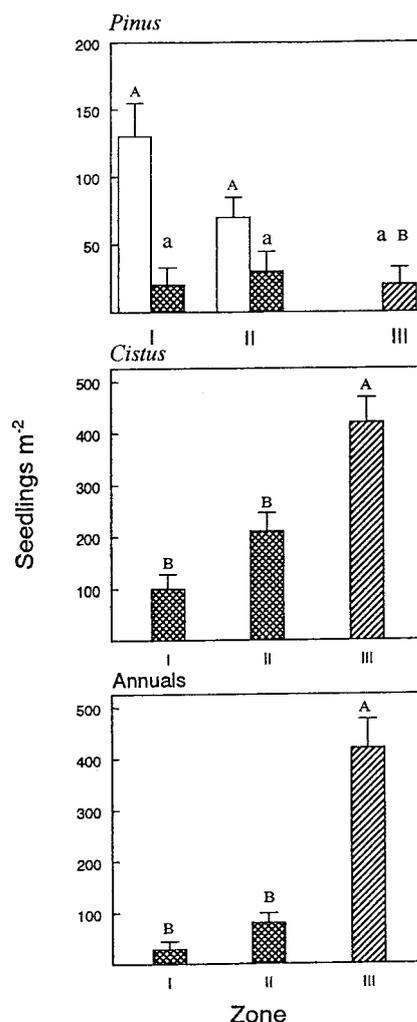

Figure 1. Seedlings of *Pinus* (top panel), *Cistus* (middle panel), and annuals (lower panel) (average ± 1 S.E. of 10 replicates) in the ash (open columns) and the soil (hatched columns) samples collected in three zones: around burned pine trees under the projected canopy area (central half – I, peripheral half – II), and in the open area among the trees (III). In zone III the ash layer was thin and could not be separated from the soil. Columns marked by the same letter do not differ significantly (Tukey, $P > 0.05$).

mination of all the plants. Inhibition by the thicker layer (5 cm) in zone I (80%) was greater than that of the thinner (3 cm) layer of zone II (50%). As a result of this effect the final density of pine seedlings under the canopies was smaller than in the open area among the trees. However, the fraction of pines out of all seedlings in the sparse stands under the burned canopies was 60%. In the open area where many more *Cistus* and annual seedlings were also present this fraction was only 10%.
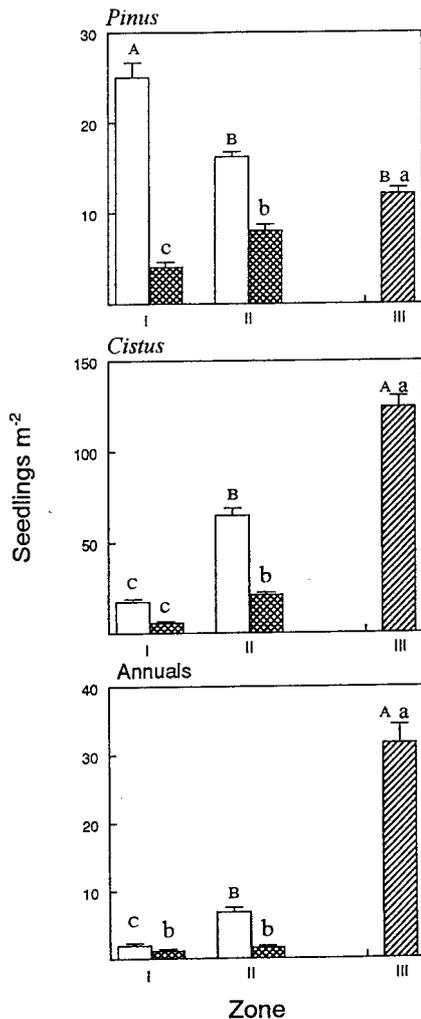
Figure 2. Seedling emergence (average ±1 S.E. of 20 replicates) in two zones around burned pine trees under the projected canopy area (central half –I, peripheral half – II), and in the open area among the trees (III). In undisturbed plots – hatched columns, and in plots from which the ash was removed and the seeds left in place – open columns. In zone III the ash layer was thin and could not be separated from the soil. Columns marked by the same letter do not differ significantly (Tukey, *p* > 0.05).

The variation of the pH and osmotic potential of the ash layer and the soil at the various zones in the burned area and unburned control plot, as a function of rainfall throughout the rainy season (September – March) is presented in Figure 3. This scale was used instead of time since in this semi-arid climate the first rains mark the beginning of the germination season. But, variability in rainfall distribution is relatively large, and germination is correlated better with accumulated rainfall than with the date. The pH of the ash

decreased somewhat during the winter, which is the only rain season, but did not decrease much below 9. Before the rains started, the pH of the upper soil layer (0–1 cm) underneath the ash was not much different from that of the soil in the unburned area. However, the first rains brought about a rapid increase in the pH of that soil layer which also remained high until the end of the season. At a deeper soil layer (4–5 cm) the rise of the pH was gradual but it did not reach the pH of the upper layer by the end of the season. Seedlings of the studied plants usually do not emerge from soil layers that are deeper than 5 cm. Among the trees, in zone III, the pH of the soil solution in the 0–1 and 4–5 cm depth was only slightly higher than in the unburned plot.

The osmotic potential of saturated paste of the various samples indicated that by January, when cumulative rain reached half the annual amount, all samples had an osmotic potential of −0.1 MPa or higher. Estimates of the osmotic potential of the undisturbed soil and ash by their natural water content and the water retention curves indicated that the osmotic potential in the field was higher than −0.15 MPa in all samples.

Chemical analyses of ash and soil samples (Table 1) showed that potassium was the only important nutrient contained in the ash at high concentration. It was washed down by the rains but did not remain soluble in the underlying soil where it was either adsorbed on to clay or leached to greater depths. Soluble phosphate content in the ash was below the detection limit, but the soil in the burned area had a higher content of this ion than the soil in the control plot. Ammonium and nitrate contents in the ash were also relatively low. Underneath the ash layer, the soil had a relatively high ammonium content that exhibited a transient increase during the winter months (data not shown). At the end of winter, when temperatures began to rise, nitrification processes brought about increase in nitrate content of the upper soil. The ash contained also large amounts of soluble calcium magnesium and sodium ions, which reacted with the rainwater to form strong bases and were eventually washed away. At the end of winter the content of these ions in the soil at the burned area was similar to that in the control plot.

Discussion

Our former studies of the early stages of the post-fire succession in a natural east Mediterranean pine woodland (Ne'eman et al. 1992; Ne'eman 1997) revealed
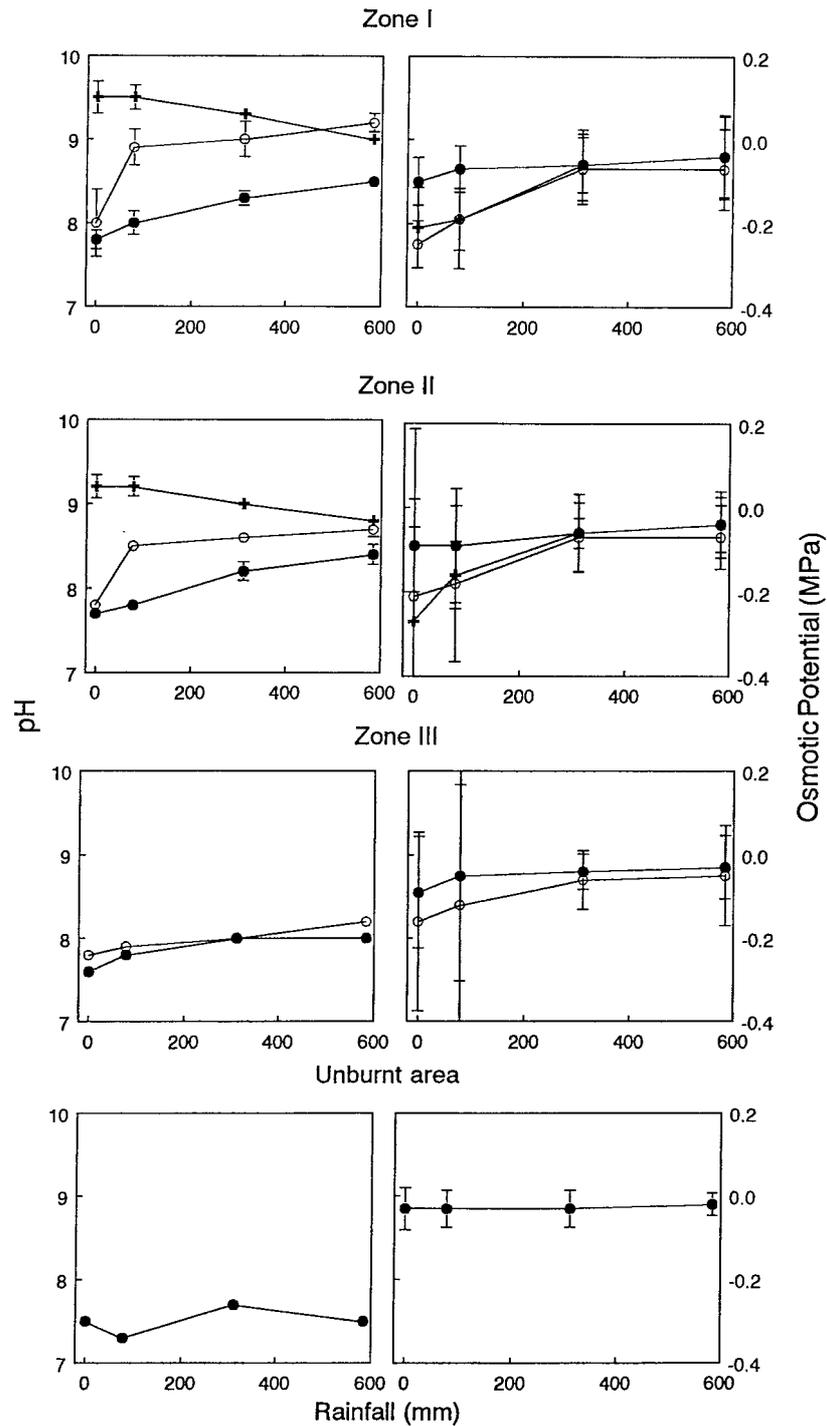
Figure 3. The variation of pH (left panel) and osmotic potential (right panel) of saturated paste of ash (crosses), and soil collected under the canopies of burned pine trees and in an unburned control area at 1 cm depth (open circles), and at 4 cm depth (closed circles), as a function of cumulative rainfall during the first winter after the fire event. Measurements were done in September and November 1995 and in January and March 1996. Data are averages ±1 S.E. of 5 replicates. Whenever the error bars were smaller than the symbols they were not shown.

Table 1. The contents of main soluble nutrient ions (mg kg^{-1}) in the ash and upper soil layer at the beginning (September 1995) and the end (March 1996) of the first winter after the fire.

	K^+		PO_4^{3-}		NH_4^+		NO_3^-	
	IX 95	III 96	IX 95	III 96	IX 95	III 96	IX 95	III 96
Ash	1010.0	44.9	0.0	0.0	2.0	19.5	0.6	6.0
Soil zone I	53.4	17.9	86.5	97.7	73.6	52.4	3.1	58.3
Soil zone II	46.8	14.8	82.5	45.0	69.6	44.2	2.1	60.7
Soil zone III	38.2	10.5	60.1	25.2	71.5	21.5	1.4	51.4
Soil unburned	7.8	4.7	4.3	3.5	8.5	13.3	0.8	2.9

that those pine seedlings that germinate in the thick ash layer near the burned tree trunks benefit from especially luxurious conditions. Unlike the high seedling density in the burned area in general, the seedlings under the burned canopies are very sparse and include a high proportion of pines. These pine seedlings that are not inhibited by inter- or intra-specific competition are the most likely candidates to form the regenerating woodland. In order to understand the ecological mechanisms responsible for this seedling distribution we studied the effect of the ash on germination of *Pinus halepensis, Cistus* spp., and annuals (Henig-Sever et al. 1996). The pine and *Cistus* seeds were found to be only slightly less sensitive than those of the other plants to the inhibitory effect of high pH brought about by the ash. Therefore it was concluded that differential sensitivity to the high pH could not explain the observed seedling distribution.

The results reported in this article indicate that the variation in seedbank size also contribute to the differential seedling distribution. During the fire, the heat under the thick layer of litter that covers the soil underneath the canopy not only reaches higher temperatures but persists for longer time than in the open area among the trees (Bond & van Wilgen 1996). This intense heat destroys most of the *Cistus* seeds and the annual plants that accumulate in the upper soil layers. The heat does not damage the pine seeds that are released from the cones over several days after the fire. Large amounts of these viable seeds are found in the ash layer under the canopies. The branches that remain on the pine trees after fire are not dense enough to have any appreciable microclimatic effect on the area underneath.

The cations (calcium, magnesium, sodium, and potassium) are contained in the ash mostly in the form of oxides. The source of calcium and magnesium oxides are both the burned litter and the rock and soil

carbonates that undergo pyrolysis by the intense heat. These oxides dissolve in the water to form strong bases that raise the pH above 9 (Viro 1974; Rundel 1981; Giovannini et al. 1990; Soto & Diaz-Fierros 1993; Khana et al. 1994; Noble et al. 1996). The high pH conditions prevail throughout the winter and inhibit germination of all plants wherever the ash cover is thicker than 3 cm (Figures 2 and 3 and Ne'eman et al. 1993). Thus, in spite of the large amount of viable seeds that are deposited under the canopy, the seedling stand in this location is very sparse.

The osmotic potential of the soil solution does not seem to have a large effect on seedling germination in this ecosystem. By midwinter leaching of the ions by the rain and other chemical processes raise the osmotic potential above −0.2 MPa. Thanos & Skordilis (1987) and Schiller & Waisel (1989) found that this species of pine could germinate at lower water potentials. We have reported before (Henig-Sever et al. 1996) that germination of *Pinus halepensis* is not affected at all by osmotic potentials that are higher than −0.3 MPa and that of *Cistus salviifolius* can stand −0.2 MPa. Some of the annuals may be more sensitive to osmotic potential but this was never studied in detail in this east Mediterranean plant community.

Control of the germination in the regenerating pine woodland after wildfire is a primary ecological component of the post-fire succession. Most of the area covered by this plant community is occupied by perennial seeders that regenerate by germination during the first winter after the fire event and by annuals. On average, the resulting seedling stand is very dense and intense inter- as well as intra-specific competition for light takes place in the early stages of the succession (Katz 1993). The development of the pine trees may be severely retarded by the intense competition with the *Cistus* shrubs (Lahav 1988; Ne'eman 1997). Competitive advantage of the pines over the other plants is

achieved only at a later stage when they grow above the shrubs and interfere with their light interception (Moravec 1990; Kazanis & Arianoutsou 1996).

The establishment of sparse seedling stands that are dominated by pines insures their rapid development without interference by other plants. Two of the factors analyzed in this article, seedbank variability and high soil pH, are responsible for this spatial distribution pattern. The few pine seedlings that develop in these stands are most likely to form the tree layer of the regenerating woodland. The location of these seedlings in the mother sites that were occupied by pines before the fire increases their chance to establish symbioses with mycorrhizae, which will also enhance their development during the early years of the post-fire succession. Chances are that this maintenance of mother sites by a seeder tree species helps preserve the spatial distribution of plants in the area and the genetic makeup of the population through fire cycles. This makes the final outcome of the effect of fire on the population dynamics of the seeders similar to that of the resprouter species that regenerate from underground plant parts.

Moreover, the inhibition of annuals growth in the open area among the old burned trees by the dense stand of seedlings of the seeder tree species plays an important role in that stage of the succession. It prevents crowding of the sparse stands around the burned trunks by annuals. If annual growth in the whole area would not have been suppressed, they were likely to invade these sparsely populated locations by seed dispersal within two or three years and overshadow the slow growing tree seedlings. In this ecosystem it takes at least five years until the young pine seedlings are tall enough to avoid being outcompeted for light by the shrubs and annuals. The massive germination and the resulting dense stands of the *Cistus* shrubs in the open area among the trees help the pines in this suppression of the annuals population growth. Even though these shrubs begin producing seeds at the third year after the fire (Katz 1993) they will not germinate until exposed to the intense heating of the next one, so they are not likely to interfere with the development of the tree seedlings.

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