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Beyond the Classical Janzen–Connell Hypothesis: The Role of the Area Under the Parent Tree Crown of *Manilkara zapota*

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Abstract: The effect of the parent tree on seedling recruitment has been studied in various research studies. The Janzen–Connell (JC) hypothesis states that the closer the seedlings are to the source tree, the greater the risk of mortality and/or impact from pathogens and herbivores. Despite the extensive existing literature, there are not many studies that evaluate the influence of crown area, as well as the effects on leaf asymmetry, an important measure of biotic and abiotic stress. (1) This study evaluates the effect of distance from the parent tree and the crown's area of influence on mortality, growth, and leaf asymmetry of *Manilkara zapota* seedlings, as well as insect herbivory and damage from leaf pathogens in a Mexican neotropical forest. (2) We selected 10 reproductive adult trees (Diameter at breast height, DBH ~ 10–25 cm) and established four 10 m × 1 m transects around each tree in four directions (north, south, east, and west). Each transect produced 10 quadrants of 1 m^2, and the quadrant where the shadow of the parent tree extended was marked as either under crown or crown-free. All *M. zapota* seedlings were counted in each quadrant. For one seedling in each quadrant, we recorded height, leaf asymmetry (LA), insect herbivory, and damage from leaf pathogens. Herbivory by insects, damage from leaf pathogens, and LA were only measured on the newest leaves. Mortality was determined after 9 months per quadrant, as well as light availability (photosynthetic photon flux density), temperature, and relative humidity. (3) We found that mortality and relative growth rate (RGR_{Height}) increased near and under the parent tree. Furthermore, LA decreased at greater distances from the parent tree and only outside the crown's influence. Additionally, LA had a strong positive influence on damage caused by insect herbivory and leaf pathogens, impacting both more strongly under the crown. A high dependency of leaf pathogens on damage from insect herbivory was also recorded. Finally, the most frequent type of herbivory was that caused by chewing insects. (4) To our knowledge, we present one of the few studies that has addressed the JC hypothesis, considering not only the distance from the parent tree and seedling density but also the influence of the crown on the performance of *M. zapota* seedlings. Studies that consider the influence of the microenvironment are of fundamental importance for a comprehensive understanding of the JC hypothesis.

Keywords: insect herbivory; pathogen leaf damage; RGR_{Height}; seedling density; seedling mortality

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1. Introduction

For decades, ecologists have wondered why some plant species are eaten more than others by herbivores in natural communities [1]. Several hypotheses have been proposed to explain variations in herbivory among different individuals or species within a community. One of them is the Janzen–Connell model [2,3], which emphasizes the role of specialized natural enemies (e.g., seed predators, herbivores, and pathogens). It posits that high species richness is maintained through density-dependent mortality of seeds and seedlings as they are attacked by host-specific predators, pathogens, or herbivores that disperse from the parent tree.

Herbivory is the most common plant–animal interaction in nature [4] and is important in the structuring of plant communities [5], as it impacts the successful recruitment of seedlings or causes their mortality in the early stages (just germinated) [6]. These negative effects can be exacerbated, as the damage inflicted facilitates the entry of leaf pathogens that reduce fitness and increase plant mortality [7,8].

Plants have developed defense strategies against herbivores in a long-term interactive and co-evolutionary process [9]. Certain leaf traits, such as thickness, hardness, leaf area, dry weight, and specific leaf area (SLA), are widely used functional traits as defenses against herbivorous insects [9]. Fluctuating asymmetry is a noteworthy leaf trait, as it can be used to measure patterns of instability in individual development [10]; practically, it represents random variation in bilaterally symmetric traits. For this reason, it has been used to correlate with damage caused by insects [11], suggesting that plants with more asymmetric leaves will experience greater damage than those with symmetric leaves, as a consequence of a combination of nutritional quality and secondary metabolism [12].

The complex set of assumptions, predictions, and hypotheses generated by the JC hypothesis has been extensively examined and supported [13,14] in both tropical forests [15–18] and temperate forests [19,20]. However, in no context has the effect of the synergy of shaded area caused by the parent tree's crown, the distance from the parent tree, and plant density been considered [21].

This study focuses on the JC hypothesis and the role of the parent tree crown on *Manilkara zapota* seedlings. We selected this species since, being one of the dominant species in the most conserved tropical forests of Calakmul, Mexico, and other Central American forests, it plays a key role as a driver of several ecological processes within the community.

We pose the following questions: (1) Will herbivorous insect and leaf pathogen damage, as well as the growth and density of *M. zapota* seedlings, be affected by the distance from the parent tree and by areas under and outside the influence of the tree crown? (2) Will there be a cause–effect relationship between leaf asymmetry and damage caused by herbivorous insects and leaf pathogens in areas under and outside the influence of the tree crown? (3) Is it possible that damage caused by herbivorous insects increases damage by leaf pathogens, both in areas under and outside the influence of the tree crown? And what type of damage would be most frequent in each area?

To answer these questions, we evaluated the effects of distance from the parent tree and the crown's area of influence on mortality, growth, seedling density, and leaf asymmetry of *M. zapota* seedlings, as well as insect herbivory and damage from leaf pathogens in a Mexican neotropical forest.

We hypothesize that damage and mortality caused by herbivorous insects and leaf pathogens, as well as leaf asymmetry, will increase as *M. zapota* seedlings grow closer to the parent tree and under its crown. Additionally, we expect seedling growth to increase with greater distance from the parent tree and outside the influence of the tree crown, in contrast to seedling density, which we anticipate will be higher closer to the parent tree and under the crown. We also consider a strong cause–effect relationship between leaf asymmetry and damage by herbivorous insects and leaf pathogens. In both cases, this relationship may be stronger under crown. Finally, we hypothesize that damage caused by herbivorous insects will facilitate leaf pathogen infection, and that the predominant type of herbivory damage will be chewing, as it may be more common across various insect species.

2. Results

The availability of light and temperature did not differ among the different areas of the parent tree's crown; only relative humidity was greater under the tree's crown (Table 1).

Table 1. Environmental variables in areas with different crown influence of *Manilkara zapota* trees.

Environmental Variable	Under Crown		Free Crown		BM_{Test}
	(Mean ± Se)	(Min–Max)	(Mean ± Se)	(Min–Max)	
PPFD (µmol m^2 s^{-1})	12.6 ± 0.47	4.46–37.1	11.9 ± 0.38	4.22–40.4	-1.58^{ns}
Temperature (°C)	26.5 ± 0.03	25–27.6	26.6 ± 0.06	25.1–39.1	-0.02^{ns}
Relative humidity (%)	85.2 ± 0.28 a	64.4–90.6 b	84.8 ± 0.22 a	64.9–89.8 b	−2.01

ns = statistically no significant. PPFD: photosynthetic photon flux density. Different letters indicate statistically significant differences within each area of the tree crown's influence.

In general, significant effects of distance from the parent tree and crown area were found. Initially, significant impacts on mortality and insect herbivory were observed, as seedlings closer to the parent tree experienced higher mortality and insect herbivory. Additionally, mortality decreased significantly, more under the crown than outside its influence (Table 2; Figure 1a,b). Insect herbivory was not affected by crown area; meanwhile, leaf asymmetry was significantly affected only by crown area and not by distance from the parent tree. In this regard, it was observed that seedlings under the crown exhibited higher values of asymmetry (Table 2; Figure 1d).

Table 2. Generalized linear models for the variables of mortality, insect herbivory, damage from leaf pathogens, and leaf asymmetry in *Manilkara zapota* seedlings at different distances from the parent tree in areas with varying crown influence.

Model Effects				**Parameter Estimates**			
	Wald χ^2	df	*p*	β	SE	Wald χ^2	*p*
Mortality							
Distance to parent tree	190.2	1	<0.001	−0.206	0.015	−13.1	<0.001
Crown area	4.96	1	0.02	−0.178	0.088	−2.01	0.04
Insect herbivory							
Distance to parent tree	7.66	1	0.006	−0.214	0.087	−2.46	0.01
Crown area	2.44	1	0.11	−0.679	0.498	0.173	0.17
Pathogen damage							
Distance to parent tree	0.57	1	0.44	0.062	0.086	0.722	0.47
Crown area	0.004	1	0.94	−0.032	0.496	−0.656	0.94
Leaf asymmetry							
Distance to parent tree	0.017	1	0.89	2.1^{-4}	0.001	0.132	0.89
Crown area	8.015	1	0.005	−0.026	0.009	−2.831	0.005

Leaf damage from pathogens was similar in seedlings across the distance from the parent tree, regardless of crown area (Table 2; Figure 1c).

On the other hand, it was found that growth in RGR_{Height} (Relative Growth Rate in height) decreased significantly with greater distance from the parent tree and was higher in seedlings free from crown influence (Table 3; Figure 2a). Seedling density showed significant differences only along the distance from the parent tree but not between crown areas. It was observed that seedling density increased as the distance from the parent tree became greater (Table 3; Figure 2b).

Leaf asymmetry significantly affected damage from pathogens and insect herbivory, with differential effects across the areas of influence. In both cases, a high degree of dependence was observed in more asymmetrical leaves, although this was more pronounced in seedlings under the crown (Table 3; Figure 3a,b).

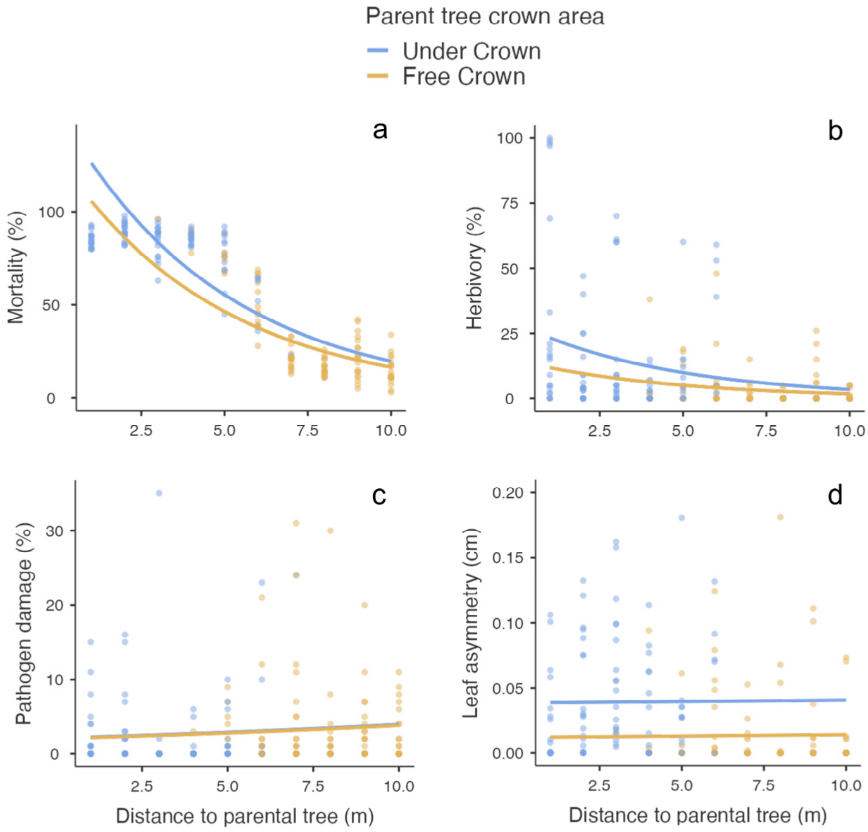

Figure 1. Effect of distance from the parent tree on seedling mortality (**a**), insect herbivory (**b**), leaf pathogens (**c**), and leaf asymmetry (**d**) in areas with varying crown influence.

Table 3. Generalized linear model of the effects of herbivory, pathogen damage, and the influence of herbivory on pathogen damage.

	Model Effects			**Parameter Estimates**			
	Wald χ^2	**df**	***p***	**β**	**SE**	**Wald χ^2**	***p***
RGR_{Height}							
Distance to parent tree	11.05	1	<0.001	−0.003	0.0009	−3.32	<0.001
Crown area	7.92	1	0.005	0.015	0.005	2.81	0.005
Seedlings density							
Distance to parent tree	8.86	1	0.003	0.083	0.028	2.93	0.003
Crown area	2.06	1	0.151	−0.220	0.167	−1.32	0.188
Herbivory							
Leaf asymmetry	21.6	1	<0.001	9.53	2.053	4.64	<0.001
Crown area	28.8	1	<0.001	−1.07	0.205	−5.19	<0.001
Pathogen damage							
Leaf asymmetry	24.5	1	<0.001	9.996	1.923	5.20	<0.001
Crown area	24.7	1	<0.001	−0.947	0.196	−4.83	<0.001
Influence of herbivory on pathogen damage							
Herbivory	172.8	1	<0.001	0.069	0.005	13.154	<0.001
Crown area	11.8	1	<0.001	−0.554	−0.168	−3.298	<0.001

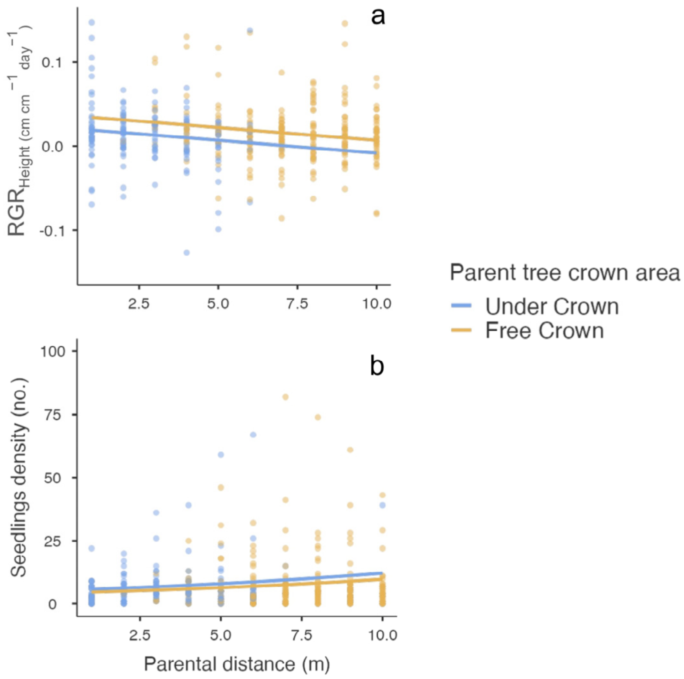

Figure 2. RGR_{Height} (**a**) and seedling density (**b**) of *Manilkara zapota* at different distances from the parent tree in areas with varying crown influence.

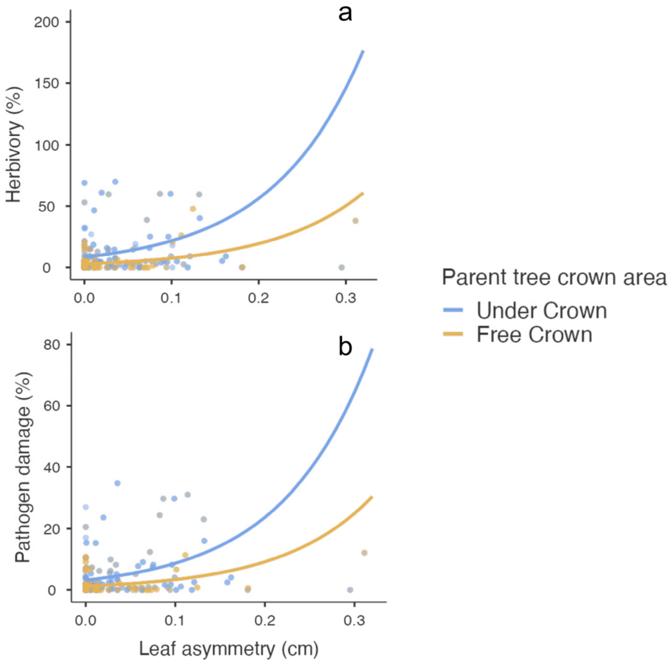

Figure 3. Effect of leaf asymmetry on insect herbivory (**a**) and pathogen damage (**b**) in *Manilkara zapota* seedlings in areas with varying crown influence.

A high degree of dependence of pathogen damage on insect herbivory was also observed, with a significantly greater increase in seedlings under the crown (Table 3; Figure 4a). Additionally, it was found that the most common type of insect herbivory was caused by chewing insects [n = 245 leaves, p(BF10) = 0.006] (Figure 4b), both in seedlings under the crown (43.7%) and those free from crown influence (33.1%), while other recorded types did not reach even 10% frequency.

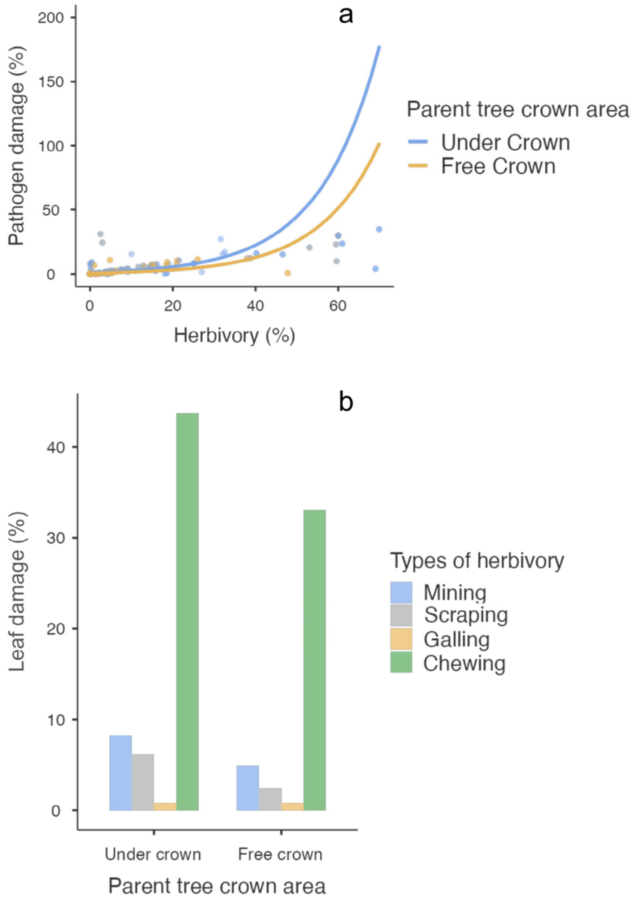

Figure 4. Dependence of leaf pathogens on insect herbivory (**a**) and the types of herbivory (**b**) associated with *Manilkara zapota* seedlings in areas with varying crown influence.

3. Discussion

The Janzen–Connell (JC) model has been extensively studied in various species of tropical plants belonging to different ecosystems [21–23]. Our study reveals that, in addition to distance from the parent tree, the area of influence of the tree's crown can have significant effects on the seedling population of the species. Furthermore, it not only negatively impacts the survival and growth of seedlings and positively facilitates diseases and insect herbivory (mainly by chewing insects), but it also affects leaf asymmetry, which is related to nutritional stability and secondary metabolism [24].

Initially, it was found that the closer the seedlings are to their parent tree, the more susceptible they are to insect herbivory [25]. Similar results have been recorded in other tropical species and even in temperate forests [21,23,26]. However, there are also records that present differential patterns with tropical species such as *Quercus costarricensis* [27]. These differential patterns suggest a high dependence on various aspects, such as forest types [22], ontogenetic state, and even processes related to the phylogeny of the species [23]. Additionally, we observed that seedling mortality and $\mathrm{RGR}_{\mathrm{Height}}$ were higher in proximity to the parent tree, regardless of whether they were under the crown or outside its influence [28]. Other studies, although not with the same species but from the same functional group (non-pioneers), have reported partially similar results, as they record higher seedling mortality near the parent tree, but also in areas farther away [27], as has been reported for the Sapotaceae family [23]. In this regard, these studies suggest that the growth of conspecific seedlings near the parent tree would be lower due to strong attacks from leaf diseases [28,29] and herbivorous insects [29,30], which could even lead to their death [25,29]. Conversely, we believe that the reduction in growth at a greater distance from the parent tree was largely dependent on negative conspecific density-dependent

(CNDDD) effects as a consequence of competition for resources among seedlings of the same species [31], as a high density of seedlings was recorded at greater distances from the parent tree. It is also quite probable that the high mortality near the parent tree was indeed due to damage caused by herbivorous insects and leaf pathogens [25,29], rather than competition among seedlings, as suggested by the higher percentages of insect herbivory and the strong dependence of leaf pathogens on herbivory [32], as well as the lower density of conspecific seedlings near the parent tree.

Fluctuating asymmetry has been considered a variable that expresses plant stress [33], caused by abiotic factors such as industrial pollution [34] and climatic factors [35], as well as biotic factors like herbivory and leaf diseases [36]. In our study, we found that leaf asymmetry decreased as seedlings moved away from the parent tree, and this was only true for seedlings free from the influence of the crown. Additionally, leaf asymmetry was strongly and positively associated with insect herbivory and leaf pathogens, with this pattern intensifying under the crown. Our results support the idea that fluctuating asymmetry is a good indicator of stress levels, as high values of asymmetry were observed under conditions of greater stress, such as near the parent tree and under the crown. This may relate to the plant stress hypothesis [37], which posits that environmental stress negatively affects plants' resistance to herbivory by altering foliar biochemical and chemical properties, producing leaves that are more attractive and palatable to herbivores [38]. Furthermore, areas under the crown may have greater insect abundance [39] and diversity of chewing insects [40], which was the most frequent type of herbivory recorded in our study. Additionally, along with microclimatic conditions such as high humidity and lower light availability [41], these factors can create various niches for pathogenic organisms and facilitate opportunistic infections through wounds created by herbivorous insects [42,43].

An important contribution of our study was the analysis of four different types of herbivory simultaneously at the seedling level. However, while we found chewing to be the most frequent type of insect herbivory, ref. [32] recorded that mining was the most frequent type of herbivory in woody species in the Calakmul rainforest, followed by chewing, galling, and scraping. Conversely, another study by [44] conducted in a tropical dry forest found similar results, as they observed that the only damage recorded was caused by chewing insects, specifically by the ant *Acromyrmex octospinosus*.

To our understanding, we present one of the few studies that have addressed the Janzen–Connell hypothesis (JC), considering not only the distance from the parent tree and seedling density but also the influence of the crown on the performance of *M. zapota* seedlings. In conclusion, we found that mortality and $\mathrm{RGR}_{\mathrm{Height}}$ increased in proximity to and under the crown of the parent tree. Furthermore, leaf asymmetry decreased at greater distances from the parent tree and only outside the influence of the crown. Additionally, leaf asymmetry strongly and positively influenced damage caused by insect herbivory and leaf pathogens, with both cases having a greater impact under the crown. There was also a high dependence of leaf pathogens on damage from insect herbivory. Finally, the most frequent type of herbivory was that caused by chewing insects.

4. Materials and Methods

4.1. Study Site

The study was conducted in a semideciduous tropical humid forest at Calakmul Biosphere Reserve (17°50′33.7″ N, 89°17′11.4″ W), located in the southeastern part of the state of Campeche, in the ejido of Arrollo Negro. Estimates of total plant richness in Calakmul range from 1569 to 1600 species in the 723,185 ha reserve [45,46]. Dominant trees are 15–25 m tall, sometimes up to 30 m. Some of the main tree species are *Manilkara zapota* (L.) P. Royen, *Brosimum alicastrum* Sw. subsp. *alicastrum* C.C. Berg, *Bursera simarouba* (L.) Sarg., *Vitex gaumeri* Greenm., and *Cecropia obstusifolia* Bertol. [47]. Annual average precipitation is around 1400 mm and is characterized by two main seasons: a dry season between November and April, followed by a wet season from May to October [48], with a mid-summer drought locally called canícula between the end of July and August. In addition, winter frontal systems originating in Canada, called Nortes, bring rain, wind, and cold air masses to the Gulf of Mexico [49]. The average annual temperature is 24–26 °C [50]. The predominant soils are karstic, with abundant calcium outcrops and less acidity than other tropical rainforests [51]. *Manilkara zapota* was used as the study model because this species is characterized by being one of the dominant species in the crown of several tropical forests in Mexico and Central America [52].

4.2. Experimental Sampling

Ten dioecious parent trees of *Manilkara zapota* with similar diameters at breast height (DBH) and heights between 15 and 25 m were selected. Around each tree, four lines of 10 m in length were marked in the north, south, east, and west directions. Each line was divided into 1 m^2 sections, and within each section, a seedling was marked that met the following criteria: production cohort of 3 to 4 months, determined by marking the seeds from the previous fruiting; height between 15 and 20 cm; and a range of 5 to 10 fully expanded leaves. Plant growth was estimated through the relative growth rate in height [53].

Additionally, the mortality of all seedlings in each of the 10 m^2 sections was recorded. Sampling was conducted over a period of nine months. In the newest leaf of each sampling, insect herbivory (chewing, mining, galls, and scraping), pathogen damage, and leaf asymmetry were estimated (n = 400 leaves).

Within each 1 m^2 quadrant, at a height of 30 cm above the ground, environmental measurements of light were recorded based on the photosynthetic photon flux density (PPFD) using a quantum sensor (Li-400 Data Logger, Li-Cor, Lincoln, NE, USA), as well as temperature and relative humidity with a thermo-hygrometer (THWD-3, Amprobe, Eindhoven, The Netherlands). All measurements were taken from 08:00 to 13:00 and from 14:00 to 16:00.

4.3. Leaf Asymmetry

To estimate fluctuating asymmetry (FA), absolute leaf asymmetry (LA) was used instead of fluctuating asymmetry due to the low number of leaves per sampling. For this, the left width (LW) was subtracted from the right width (RW), and the absolute value of the result was taken. Leaf asymmetry was chosen due to the low number of leaves present in the seedlings. However, other studies have shown that leaf asymmetry provides similar results to fluctuating asymmetry [54].

Measurements of left and right symmetry were taken from the central vein toward each side of the leaf, usually at the middle, which is the widest part of the leaf. The measurements were performed on photographs taken in the field for herbivory analysis using the morphometric software Tps Dig 2.05 [55]. Each LA measurement was taken from one leaf per seedling (n = 400).

4.4. Insect Herbivory and Pathogen Damage

To estimate herbivory and damage caused by leaf pathogens, we used the same leaves as for LA (n = 400). The leaves were placed on a blue panel with a 2 × 2 mm grid (as a size reference) and photographed with a 4-megapixel digital camera. The photographs were processed with the image analysis software ASSESS 2.0 [56] to quantify the leaf damage (percentage of leaf area removed or affected by insects and/or infected by pathogens). Four types of herbivory were identified: chewing, galling, mining, and scraping [32]. Additionally, potential diseases caused by viruses, fungi, and bacteria were identified, following the symptom descriptions produced by leaf pathogens [43,57].

4.5. Data Analysis

To examine the variation in light availability, temperature, and relative humidity among crown influence areas, Brunner–Munzel analyses were performed. Additionally, to evaluate the effect of distance to the parent tree and the crown influence area on mortality, insect herbivory, pathogen damage, leaf asymmetry, RGR_{Height}, and seedling density, generalized linear models were used. In the case of mortality, insect herbivory, pathogen damage, and seedling density, a negative binomial distribution with a log link function was employed. For leaf asymmetry and RGR_{Height}, a normal distribution with an identity link function was used.

Furthermore, to examine the influence of leaf asymmetry and the crown influence area on pathogen damage and herbivory, generalized linear models were applied in both cases, using a negative binomial distribution with a log link function. To analyze the facilitation of herbivory on pathogen damage in both crown influence areas, a generalized linear model was conducted, applying a negative binomial distribution with a log link function. Finally, to assess the variation in the types of herbivory in the crown influence areas, a Bayesian contingency table was employed for independent multinomial sampling, as the types of influence were fixed but not the recorded types of herbivory. All analyses were conducted using jamovi 2.6 [58].

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