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ORIGINAL RESEARCH ARTICLE

Wave effect and shyness phenomenon in homogeneous forests of *Alnus acuminata*

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ABSTRACT

The wave effect and the shyness phenomenon in *Alnus acuminata* (Kunth) are crown parameters rarely studied, but important in the quality of the wood of standing trees, therefore, a morphometric modeling of the crowns of *Alnus acuminata* in homogeneous forests in the Sierra Norte de Puebla was carried out. In 20 rectangular sites of 1,000 m^2, the following were evaluated: total height (TA), normal diameter (ND), crown diameter (CD) and crown cover (CC). The Kruskal Wallis test was applied to data that did not meet the assumption of normality; for those that did, analysis of variance (ANOVA) was used, with Tukey mean comparison tests ($\alpha \leq 0.05$). The forest value index was 14.99, so its two-dimensional structure is normal based on DN, AT and CC. Its average slenderness index was 93.52, which makes the tree not very stable to mechanical damage. The life-space index was 38.92, which is high indicating that trees with low intraspecific competition developed better. At the canopy level, a pattern following an upward, oscillatory and constant wave effect was observed in groups of 10 trees. The shyness phenomenon showed an average crack opening of 27.39 cm between canopies, so this phenomenon is well defined for the species. It is concluded that in the crowns of *Alnus acuminata*, the wave effect is observed as a consequence of inequality in the acquisition of resources, and one way to minimize this inequality is through the phenomenon of botanical shyness.

Keywords: Aile; Homogeneous Forests; Forest Canopy; Slenderness; Living Space; Forest Value

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1. Introduction

It is a pioneer species of fast growth and soft wood that, in the Sierra Norte de Puebla, is mainly used for the manufacture of spoons, handicrafts and musical instruments; but due to its extensive exploitation, the structure and composition of the forests where it is found has changed. The tops of the trees in close proximity form the canopy of a forest. This canopy plays an important role in the amount of photosynthetically active radiation it lets through to the understory[1]; it also influences branch mortality (autopoda), as well as stem size and shape[2].

Canopies, according to their social position within the stand or forest, can be: dominant, co-dominant, intermediate and suppressed[3]; their shape and dimension reflect a tree's vigor and interdimensional relationships (vertical space, competition, stability, vitality and productivity); as well as other little known (ripple effect and shyness phenomenon)[4], and architectural design, which delimits the spatial position of individuals within the neighborhood, to allow or not allow their coexistence within the canopy[5], which is reflected in the allometric relationships between different size attributes[6] and their adaptive significance with respect to their environment[7].

The ripple effect has been observed in some species such as: *Kochia scoparia* (L.) Schrad.[8]; *Pinus taeda* L.[9]; *Fagus sylvatica*, *Fraxinus excelsior*, *Carpinus betulus*, and *Tilia cordata*[10]; *Larix decidua* Mill.[11], because they extend their canopies beyond their assigned growing space; while others, yield part of that space to the dominant species, this effect can be described as a constant period wave[9,12].

Zeide[13], who is studying natural forests in the southern United States of America, observed that around a dominant tree there is usually a ring of suppressed trees; in turn, trees in the next concentric ring behave as dominant, and so on. The overall effect he described as a "density wave" that is damped with distance and propagates in all directions from the dominant trees. The spatial distribution of dominant and suppressed trees is not random, but can show great regularity; this has been demonstrated where the distribution of trees is very regular[14]. Therefore, the occurrence of spatial pattern in individual trees that are evenly spaced, can be analyzed by spectral analysis[15]. But, the development of spatial pattern not only occurs in trees that are evenly spaced, but every time they compete (for water, solar energy, nutrients and physical space), regardless of the planting regime[16,17].

Therefore, the phenomenon of shyness is observed in a certain group of trees (of the same species), which keep their crowns away from each other; to respect a distance that is known as "shyness crack". It is also known as ‘‘*canopyal sensagement*', ‘‘*crown shyness*" or "*shy canopies*". ‘‘Crown shyness was the term given by Australian biologist Maxwell Ralph Jacobs, he studied shyness patterns in eucalyptus and concluded that the shoots were sensitive to branch friction caused by wind, which caused clearings in the canopy[4].

In that sense, tree branches (of the same species) are damaged at the time of friction, so they choose to leave a space between the crowns and thus avoid tissue damage that could limit their growth[10]. In addition, trees have photoreceptors to benefit from a greater amount of available solar energy, thus leaving so-called "shy slots", which can measure between 10 cm and 50 cm, whose objective according to Binkley[16] is to avoid competition for solar energy, a limiting resource in the development and productivity of trees.

Whenever trees compete (inter and intra-specifically), they develop a hierarchy of dominance and suppression[18]. If competition for resources (water, solar energy, and nutrients) limits physical growing space, each individual tree should grow until its weight is proportional to the size of its immediate available space[14]. In the case of botanical shyness, this is only observed where there is intraspecific competition, even with dominance and suppression, since canopy opening acts as a defense and self-protection mechanism[16,19].

Some scientists believe that this phenomenon is due to an allelopathy (due to volatile organic compounds) that coordinate certain processes such as growth[20]. Another explanation is that it allows solar energy to better penetrate the forest and provide a selective evolutionary advantage against contagious diseases, as well as the spread of insects, whose larvae feed on leaves[18]. Thus, shy trees will be less likely to be infected by any disease or pest, despite being spatially in a dense distribution[4,21].

2. Objectives

The objective was to carry out a morphometric modeling of *Alnus acuminata* (Kunth) canopies (wave effect and shyness phenomenon) in homogeneous forests in the Sierra Norte de Puebla for which the following hypothesis was proposed: the behavior of *Alnus acuminata* canopies in intraspecific competition will allow a better understanding of the wave effect and shyness phenomenon as growth strategies within the vertical and horizontal gradient of the canopy, in different ecoregions of the Sierra Norte de Puebla.

3. Materials and methods

3.1 Study area

The Sierra Norte of Puebla is a region characterized by mountainous areas, is located northwest of the state, bordering Veracruz to the north, with

Hidalgo and Tlaxcala to the west. It is the second most inhabited region of the state of Puebla, due to the good natural and socio-cultural conditions. Its territorial extension is 5,903.5 km^2 and is made up of 65 municipalities[22].

Climates predominate: warm humid [A(C)f and A(C)m], warm sub-humid [A(C)w_0, A(C)w_1 and A(C)w_2], temperate humid [C(m) and C(f)], temperate sub-humid [C(w_0), C(w_1) and C(w_2)]. The mean annual temperature ranges from 12 °C to 18 °C, that of the coldest month ranges from 3 °C to 18 °C. The precipitation of the driest month is <40 mm; the percentage of winter precipitation, with respect to the annual precipitation, is <5 mm[23]. Frosts almost always occur with a frequency of 20 to 40 days per year; the maximum incidence of frosts is concentrated in the period from December to January.

The landscape is accompanied by fog in the highlands and humidity with rain throughout the year[22]. It is composed of mixed pine forests and pine-oak association, the outstanding species are: *Pinuspatula Schiede* ex Schltdl. Et Cham., *Pinus ayacahuite* Ehren., *Quercus rugosa* Née, *Abies religiosa* (Kunth) Schltd. and Cham., *Alnus acuminata* Kunth, *Cupressus lindleyi* Klotzsch ex Endl., *Taxodium mucronatum* Ten., and *Juniperus deppeana* Steud.[24].

3.2 Sampling sites

The sites were established in different ecoregions of the Sierra Norte de Puebla (**Table 1**). They were rectangular plots of 20 m × 50 m with a cluster sampling design. The criteria for delimiting the sites consisted of meeting the attributes homogeneity, density, purity, total height (AT), normal diameter (DN), crown diameter (DC) and crown cover (CC); in contemporary homogeneous forests without anthropic disturbance. A GPS (SOUTH S750-G2®) was used for positioning and location of the sites. ArcView software® was used to capture the location of the sites (**Figure 1**).

3.3 Tree sampling

The municipalities chosen for sampling cover 2,036 km^2, for this purpose a sampling intensity of 1% of the total municipalities was used[24]. The measurement was carried out in winter (form December 2017 to January and February 2018), because at this time the trees are leafless and their

Table 1. Geographical position of sampling sites in the Sierra Norte de Puebla

Site key	Municipality	Altitude	Latitude coordinates	Geographic longitude
1-Ch1	Chignahuapan 1	2,298	19°48′24″	98°01′47″
2-Ch2	Chignahuapan 2	2,300	19°48′30″	98°01′41″
3-Zt1	Zacatlán	2,071	19°54′38″	97°57′34″
4-Cu1	Cuautempan	1,499	19°54′53″	97°48′55″
5-Zo1	Tetela de Ocampo (Zontecomapan 1)	2,178	19°51′04″	97°43′59″
6-Zo2	Tetela de Ocampo (Zontecomapan 2)	2,164	19°51′05″	97°43′58″
7-Zo3	Tetela de Ocampo (Zontecomapan 3)	2,206	19°51′17″	97°44′12″
8-Zi1	Tetela de Ocampo (Zitlalcuautla 1)	2,287	19°44′18″	97°47′56″
9-Zi2	Tetela de Ocampo (Zitlalcuautla 2)	2,264	19°44′10″	97°47′58″
10-Zi3	Tetela de Ocampo (Zitlalcuautla 3)	2,319	19°44′03″	97°47′55″
11-Ca1	Tetela de Ocampo (Carreragco 1)	1,625	19°52′28″	97°40′46″
12-Ca2	Tetela de Ocampo (Carreragco 2)	1,696	19°52′25″	97°42′04″
13-Xo1	Xochitlán de Vicente Suárez 1	1,564	19°54′54″	97°38′27″
14-Xo2	Xochitlán de Vicente Suárez 2	1,544	19°54′57″	97°38′44″
15-Na1	Nauzontla	1,752	19°56′42″	97°35′26″
16-Zp1	Zacapoaxtla	2,104	19°53′01″	97°33′25″
17-Tq1	Tlatlauquitepec 1	2,069	19°49′30″	97°31′27″
18-Tq2	Tlatlauquitepec 2	2,158	19°49′20″	97°31′54″
19-Tq3	Tlatlauquitepec 3	2,122	19°49′17″	97°32′05″
20-Tq4	Tlatlauquitepec 4	2,111	19°49′05″	97°32′02″

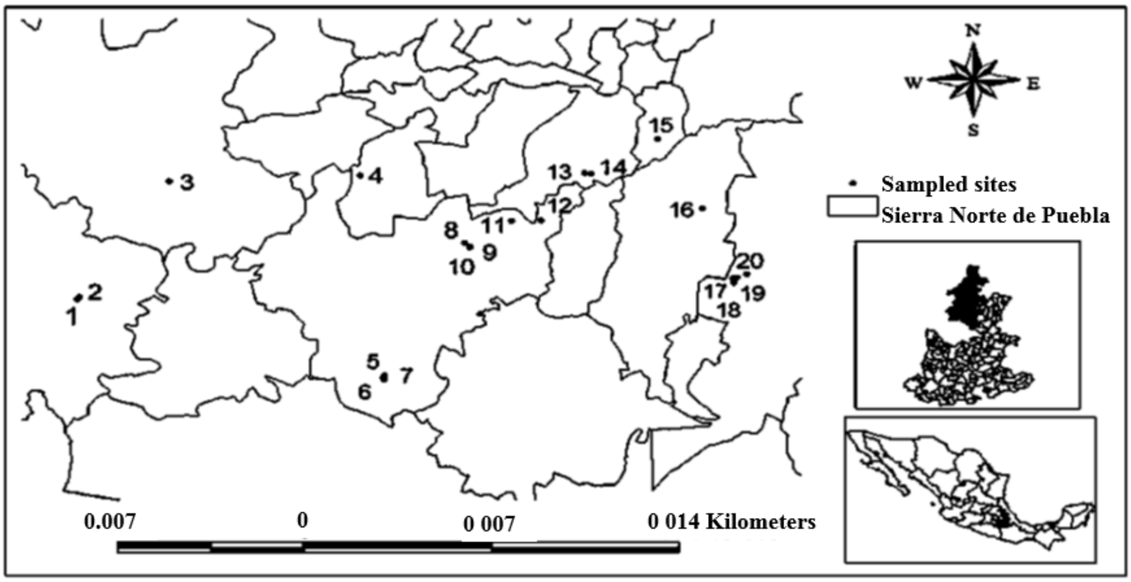


Figure 1. Positioning of sampled sites in the Sierra Norte de Puebla.

branching orders, the wave effect and the shyness phenomenon can be better observed. The classification of the trees, according to their DN was: brinzal (<5 cm); monte bravo (from 6 cm to 12 cm); vardascal (from 13 cm to 30 cm); alto latizal (from 31 cm to 50 cm) and fustal (>50 cm).

3.4 Response variables

Forest Value Index (FVI). It was determined by the sum of relative values of DN, AT and CC[25]. TA were measured with a Nikon Laser Forestry Pro® hypsometer/telemeter, crown measurements with a Stanley® tape measure, DN with a green laser forceps (800 mm Haglof®).

Slenderness index (SI). According to Serrada[17], it expresses the degree of stability of the forest stand, and was estimated with the following formula:

$$IE = \frac{AT}{DN} \times 100$$

In the equation: *AT* = total tree height; *DN* = normal diameter (1.30 m).

Living space index (LSI). It considers two basic indicators of the development or morphology of a tree, a consequence of the thickness in which it lives or has lived[17,27]. It was estimated with the following formula:

$$IEV = \frac{DC}{DN} \times 100$$

In the equation: *DC* = crown diameter; *DN* = normal diameter (1.30 m).

Wave effect (WE). Within each stand, we worked with groups of 10 trees (monopodic, without malformations, without the presence of pests or diseases and without fire or lightning damage). In close proximity, they were observed from above and below (the sampling system was selective and a non-destructive method was applied). Finally, the trend of the pattern that followed the wave effect and its possible changes or similarities with other sites were analyzed using the Multiple Optimization Model on Response Surfaces[27].

Shyness phenomenon (SP). To study the phenomenon of botanical shyness (crack opening), homogeneous stands of *Alnus acuminata* were analyzed, since in heterogeneous stands the species tend to intertwine their branches, making observations difficult due to interspecific competition. The crack opening between canopies was captured using aerial images from the understory with a Nikon B500® digital camera and from the canopy with a DJI Phantom 4 Pro® drone; a graduated rope between canopy and canopy was used as a reference measurement. Aperture sizes were defined as follows: N_0: absent crack opening; N_1: from 0 cm to 10 cm; N_2: from 11 cm to 30 cm; N_3: from 31 cm to 50 cm; N_4: >51 cm opening. To know the aperture sizes, we worked with Image Tool Portable software®, through which we transferred the images taken (which included an aperture with known distance) and proceeded to perform the conversion from pixels to centimeters.

3.5 Statistical analysis

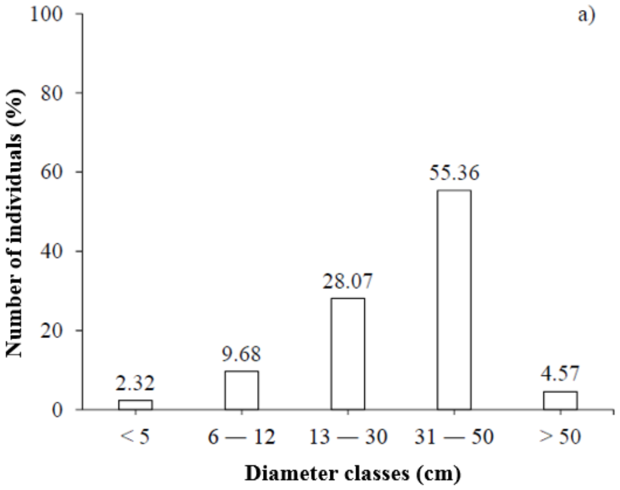
The Kruskal Wallis test[27] was applied to data that did not meet the assumption of normality. For data that met the assumption of normality and homogeneity, analysis of variance (ANOVA) was used, with mean comparison tests by Tukey's method ($\alpha \leq 0.05$), independent for each sampling site. We worked with Minitab® 18 software[28].

4. Results

4.1 Forest value, slenderness and living space

Vertically, the forest structure of *Alnus acuminata* was represented by five developmental stages: brinzal, monte bravo, vardascal, alto latizal and fustal (**Figure 2(a)**). At no site were all five developmental stages observed at the same time; however, 60% of the population diameters had a DN >31 cm (forests with a high commercial value); while seedlings were scarce and only represented 2.32% of the total population (low regeneration per tall forest). Trees with DN >31 cm were found in sites: 2-Ch2, 3-Zt1, 5-Zo1, 11-Ca1 and 14-Xo2; while in the rest of the sites the predominant DN were from 6 cm to 30 cm, which represented 37.75% of the studied population. The DN >50 cm only represented 4.57% of the study population (2,474 trees).

The FVI was higher in site 2-Ch2, an ecoregion with cloud forests characterized by having trees with larger DN, TA and CC than in the other sites (**Table 2**). While the site with the lowest value was: 9-Zi2 (10.49), located in riparian zones, although it did not have the lowest DN, AT and CC in its individuals; but it did have a high natural regeneration (up to 327 trees-ha^{-1}) with a predominance in the sapling stage.



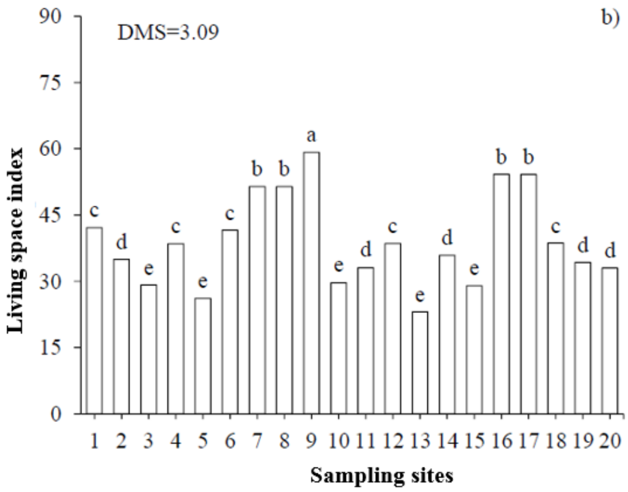


Figure 2. Developmental stages (n = 2,474 trees) (a), and IEV (b), in 20 sites sampled for *Alnus acuminata* in the Sierra Norte de Puebla.

Table 2. Forest value and height of *Alnus acuminata* in the Sierra Norte de Puebla

Site	Relative diameter (%)	Relative height (%)	Relative coverage (%)	Index of forest value	Leanness index
1-Ch1	4.42	4.05	4.26	12.73	81.35
2-Ch2	6.00	6.32	9.74	22.06	90.66
3-Zt1	6.84	5.38	9.15	21.37	72.74
4-Cu1	4.29	4.92	7.57	16.79	105.40
5-Zo1	6.02	5.72	3.60	15.33	82.61
6-Zo2	5.11	5.14	2.43	12.68	87.24
7-Zo3	3.69	5.64	4.34	13.67	141.11
8-Zi1	3.42	5.86	5.03	14.30	153.92
9-Zi2	3.93	3.90	2.66	10.49	86.85
10-Zi3	5.24	4.48	5.36	15.09	79.33
11-Ca1	6.78	5.05	7.71	19.54	63.75

Table 2. (*Continued*)

Site	Relative diameter (%)	Relative height (%)	Relative coverage (%)	Index of forest value	Leanness index
12-Ca2	3.30	3.83	5.82	12.95	100.09
13-Xo1	5.82	5.53	4.62	15.97	84.72
14-Xo2	6.59	5.65	2.71	14.96	78.30
15-Na1	5.73	5.17	3.81	14.70	83.05
16-Zp1	3.16	4.80	3.93	11.88	135.50
17-Tq1	4.42	5.28	4.11	13.80	107.91
18-Tq2	4.65	4.81	4.12	13.57	88.62
19-Tq3	5.53	4.23	3.26	13.02	70.70
20-Tq4	5.08	4.25	5.76	15.09	76.55
	100	100	100	300	$\mu = 93.52$

The majority of the sites had a tree stand that was not very stable to mechanical damage, the presence of strong winds or hurricane, since the mean EI between populations are statistically different ($\alpha \leq 0.05$); only sites 3-Zt1, 10-Zi3, 11-Ca1, 14-Xo2, 19-Tq3 and 20-Tq4, had normal EI (from 63.75 to 79.33).

The average EI for natural forests of *Alnus acuminata* in the Sierra Norte de Puebla was 93.52 (off-normal and close to critical); for each cm of tree diameter increase, there was an average increase of 93.52 cm in TA. The DN ranged from 11.65 cm to 25.23 cm on average for all sites, while the TA ranged from 12.43 m to 20.14 m (**Figure 3**).

It was at site 9-Zi2 (Tetela de Ocampo locality Zitlalcuautla) where *Alnus acuminata* trees developed with little competition (IEV = 59.17); while sites 3, 5, 10, 13 and 15 were those with the lowest IEV, that is, the sites with the highest inter- and intraspecific competition; to have an average of 38.92 in the Sierra Norte de Puebla (**Figure 2(b)**).

4.2 Wave effect and shyness phenomenon

The wave effect followed an oscillatory trend where one was dominant, four co-dominant, three intermediate and two suppressed, which is a generality for homogeneous *Alnus acuminata* forests in the Sierra Norte de Puebla (**Figure 4**).

Of 2,474 trees sampled, 247 were dominant, their large crowns were above the general level of the forest canopy, they received full vertical and partially lateral solar energy; 990 were codominant, their medium crowns were part of the general level of the canopy, they received full vertical and little lateral solar energy; 742 were intermediate, their small canopies extended below the canopy formed by the co-dominants, absorbed little solar energy vertically and none laterally; 495 were suppressed, their small canopies were located completely below the general canopy level, receiving no solar energy.

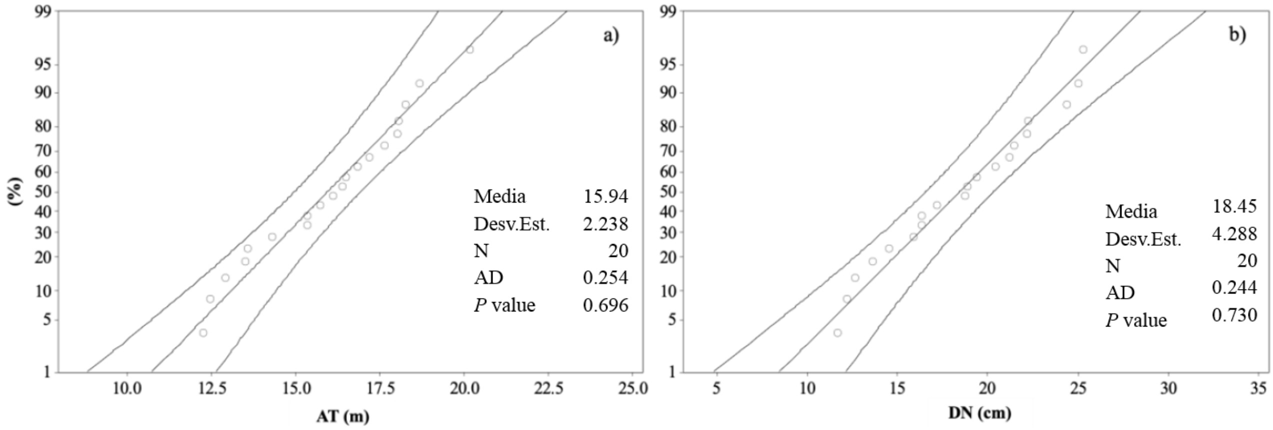


Figure 3. Normal probability with a 95% confidence index, for AT (a) and for DN (b), in trees of *Alnus acuminata* in the Sierra Norte de Puebla.

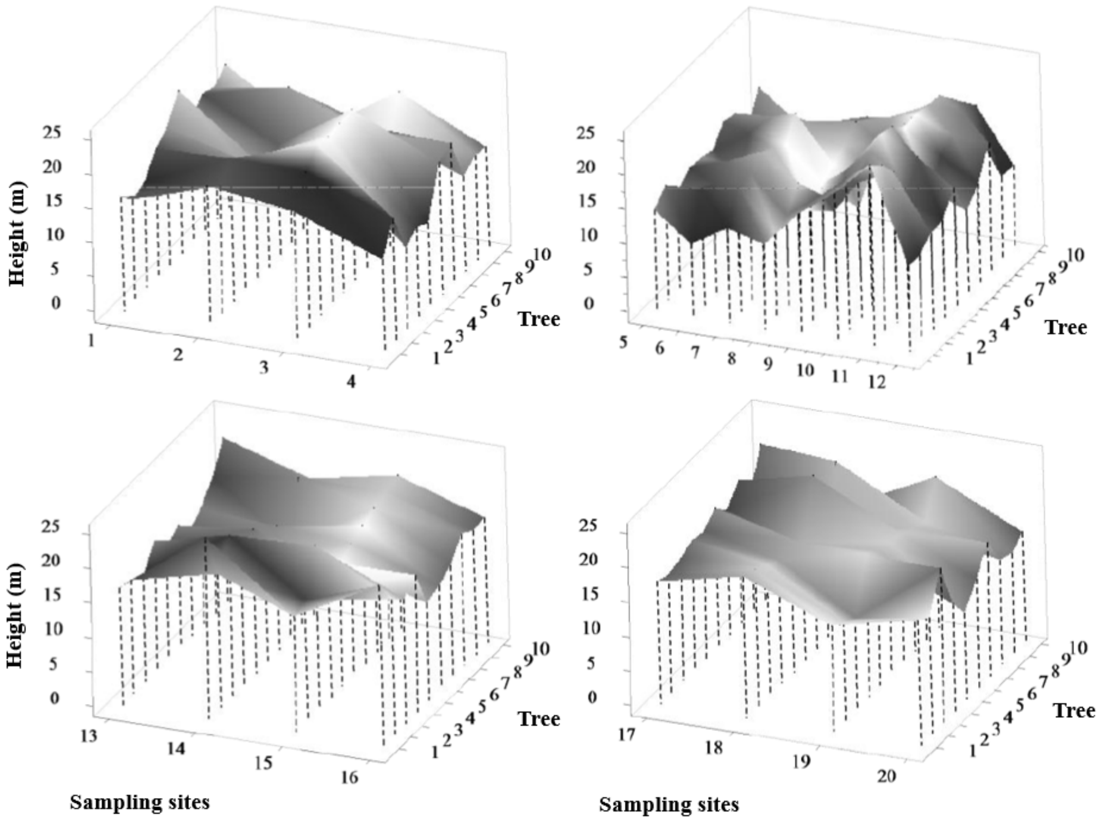


Figure 4. Response surface wave effect expressed for *Alnus acuminata* at sampling sites in the Sierra Norte de Puebla. From 1 to 4: Chignahuapan, Zacatlán and Cuautempan; from 5 to 12: Tetela de Ocampo; from 13 to 16: Xochitlán de Vicente Suárez, Nauzontla and Zacapoaxtla; from 17 to 20: Tlatlauquitepec.

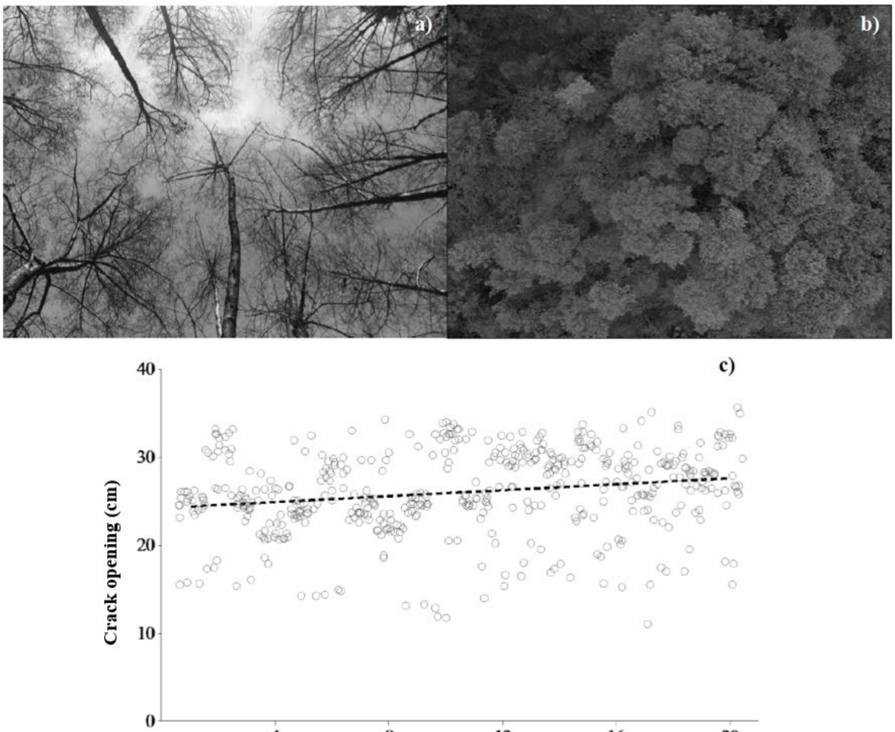


Figure 5. Crack opening (shyness phenomenon) in *Alnus acuminata* canopies in the Sierra Norte de Puebla; (**a**): canopies without autumn-winter foliage; (**b**): canopies with spring-summer foliage; (**c**): dispersion of opening sizes in canopies (n = 2,474).

The shyness phenomenon can be best observed at the time of the year when the trees are leafless (being a deciduous species) (**Figure 5(a)**); although the crack could be observed even with well-developed foliage and independently of the canopy level, when including dominant, co-dominant, intermediate and suppressed trees (**Figure 5(b)**).

In 25% of the sites there was a crack opening >30 cm (the widest observed), in the sites: 2-Ch2, 10-Zi3, 13-Xo1, 15-Na1 and 20-Tq4. The other 75% of the sites had an opening between 20 cm and 30 cm, in the sites: 1- Ch1, 3-Zt1, 4-Cu1, 5-Zo1, 6-Zo2, 7-Zo3, 8-Zi1, 9-Zi2, 11- Ca1, 12-Ca2, 14-Xo2, 16-Zp1, 17-Tq1, 18-Tq2 and 19-Tq3. Throughout the Sierra Norte de Puebla, there was no broad distinction between sites for greater or lesser crack opening in *Alnus acuminata* canopies; having an average of 27.39 cm of observable opening between one canopy and another (**Figure 5(c)**).

5. Discussion

5.1 Forest value, slenderness and living space

The highest forest value for *Alnus acuminata* was presented in those sites of the Sierra Norte de Puebla, where there are cloud forests or mountain mesophyll forest, characterized by having a high concentration of fog especially at the canopy level. Although in all sites, a two- and three-dimensional spatial pattern was shown as a result of intraspecific competition, patterns that are repeated at the canopy level occur[8,9].

At the understory level, out of a sample of 2,474 trees, there were 495 suppressed trees, suggesting that young plants can adapt to a shaded environment; however, this species grows best in full sun[24]. The crown growth of *Alnus acuminata* is narrow, irregular and open, in individuals with less competition for physical space and solar energy (e.g. those located at the edges), although it can develop from the base; however, in homogeneous forests the trees reach a higher TA, with a proportion of stem free of branches and knots due to natural pruning[29].

Growth in DN and AT can increase only with an opening of the canopy, due to a higher photosynthetic rate[16]. Although this species can establish in gallery forests (along riverbanks), it is not a hydrophytic species, but rather a fast-growing, heliophilous, soft-wooded species that needs a lot of water for its development[29]. In the gallery forests of the Xaltatempa River, it can be found associated with *Ligustrum japonicum* Thunb., *Parathesis serrulata* (Sw.) Mez., *P. Patula*, *Platanus mexicana* Moric. and *Q. Rugpsa*, and have a high forest value, only inferior to *P. Mexicana*[30].

The vertical structure of *Alnus acuminata* is of great importance for its development in the homogeneous forests of the Sierra Norte de Puebla, where tall trees with relatively thin trunks develop (IE = 93.52); however, this IE places them outside the normal and close to the critical, since normal values are close to 70 and critical values are higher than 100[17]. In a comparative study with *Eucalyptus urophylla* S.T. Blake, in the warm-humid climate of Huimanguillo, Mexico, IE of 114 $cm \cdot cm^{-1}$, 118 $cm \cdot cm^{-1}$ and 122 $cm \cdot cm^{-1}$ were obtained[31]; similar results were obtained with *Eucalyptus nitens* H. Deane & Maiden, with an IE = 124[32]; with *Hieronyma alchorneoides* L., with an IE= 111 and with *Terminalia amazonia* (J.F. Gmel.) Exell, with an IE = 106[27].

Thus, by having a high slenderness value, the trees are not very stable to mechanical damage[33], it is assumed that they are thin and that care should be taken when applying strong thinning intensities[27,32]. Despite this, the average height (AT = 15.94 m) and average diameter (DN = 18.44 cm), suggest a low ratio (0.86), which is associated with conical trees, i.e., more slender[31]; which may be more resistant to strong winds, snow and hurricanes[34]. The presence of basal reiterations especially in suppressed trees is a direct consequence of a high population density (1,237 $trees \cdot ha^{-1}$) due to competition for solar energy and nutrients; since a deficit of solar energy over the canopy can produce a decrease in its yield[10].

The IEV expresses how many times the DC was greater than the DN, in relation to the occupation that the latter needs to develop without competition[12], this index grew as the tree thickens in diameter[27,33]. In homogeneous forests with *Alnus acuminata* in the Sierra Norte de Puebla, intraspecific competition was common, as variants in growth with dense-dependent effects were observed at the sites, subject to greater space for individual development[35].

The absolute size of *Alnus acuminata* was a measure of its productive and reproductive potential, but this potential only manifests itself if it can prevent other adjacent trees from overlapping and shading it, which is why, for each group of 10 trees, only one was dominant. Minor AT, DC and CC in adjacent trees, can be more evident with time, and probably decisive in the final result of dominance and suppression[16]; even if the trees have almost the same height or with a difference of a few millimeters, this is decisive because when one leaf overlaps another, it photosynthesizes more[36]; which confers competitive advantages, since species with individuals taller than their neighbors can intercept more light[5].

These small differences in TA favored the formation of patterns in spaced gradients, which allowed the transmission of competition effects (inequality in resource acquisition) to occur as trees along the gradient began to interfere with their neighbors at different times. According to Ibáñez-Moreno *et al*.[12] from the competition among trees, a negative correlation can be predicted in the growth of neighboring trees, and an increase in the size of that tree with increasing physical space available.

5.2 Wave effect and shyness phenomenon

To determine the pattern of the wave effect in *Alnus acuminata*, it was useful to classify the canopy, which also served as a parameter to judge the vigor and maturity of the tree or the site, which may serve in the future to prescribe some cuts of different types (release, thinning, regeneration, etc.). The pattern that followed the wave effect in this species had an upward, oscillatory and constant movement in its canopy, which was presented in groups of 10 trees where only one was dominant; similar to the study of Liu *et al*.[11], who also stated that the diameter and propagation distance of the wave, can influence the propagation patterns.

This wave manifests a competition effect in which the degree of interference experienced by each individual depends on the degree of interference experienced by its neighbors[12]. Because trees cannot escape the interference effects of their neighbors by changing their position, the movement is restricted to the plasticity of the growth of the population of meristems present in different parts of the tree[8].

Another theory, advanced by Hallé[37], suggests that this phenomenon has genetic origins and that the configuration of the tree crowns is not random, but the product of a specific development program controlled by genes. The sites studied were incoetaneous due to the selective use of *Alnus acuminata* by local inhabitants for fuel and for making spoons and handicrafts, which gives rise to a regeneration of coppice by stands with different ages (between 10 years and 40 years). Natural (sexual) regeneration was very low (<5%), however, reiterations have maintained the vitality of the forest by producing asymmetric competition, which occurs whenever a branch or tree dies and leaves a physical space in the canopy that existing neighbors or newly recruited plants can invade, or whenever an individual acquires an advantage (dominance) over its neighbors[16].

However, the formation of hierarchies and spatial patterns in natural populations is uneven, because trees located at the edges, on the borders or without adjacent competition in any of the four cardinal points, have more space to develop and behave as dominant over their immediate neighbors, since this dominance frees neighbors from competition, which produces a periodic distribution of dominant and suppressed trees[36].

The phenomenon of shyness in *Alnus acuminata* was observed in all the sites sampled in the Sierra Norte de Puebla (with an average crack opening of 27.39 cm between crowns), which may be due to controlled endogenous development (in mature trees) to prevent the crowns from joining. With respect to this behavior, observable only in some tree species, several authors have expressed their opinion: Rudnicki *et al*.[19] demonstrated that this phenomenon in *Pinus contorta* Douglas was the result of crown abrasion caused by winds, since the crowns can collide hundreds of times per hour.

Smith and Long[38], studying age-related decline in forests, speculated that botanical shyness is due to wind-induced canopy collisions that limit leaf area. Delagrange *et al*.[2], affirmed that, in temperate forests, the empty space around tree crowns (botanical shyness) is due to a disconnection of the crown due to internal factors; although there are other factors such as IE, site quality or spatial distribution of trees, which can also influence the presence of the phenomenon[10,17].

Shyness tends to increase in the best sites, because canopy size is related to site fertility[39,40]; which was observable in temperate forests with *Alnus acuminata*. The approach of Cabrelli *et al*.[1], through hemispheric photographs of the canopy, provides important functional relationships between wave effect and crack opening size; also, tree crowns subjected to wind influence and the resulting collisions can lead to branch breakage and foliage abrasion[19].

However, Smith and Long[38] concluded that the abrasion only represents a certain amount of foliage, proportional to that which begins to decline with crown closure. According to Hajek *et al*.[10] this phenomenon has also been observed (with variable crack openings) in *F. Sylvatica*, *F. Excelsior*, *C. Betulus* and *T. Cordata*; which has important implications for modeling forest dynamics and management.

6. Conclusions

In the homogeneous forests of the Sierra Norte de Puebla, *Alnus acuminata* is found at a high population density, with 1,237 tree·ha^{-1}, vertically represented by five developmental stages. Its average forest value was 14.99 and this was higher in ecoregions with cloud forests. The average slenderness index was 93.52, which makes the trees not very stable to mechanical damage by winds, hurricanes or snow; although their marked conicity protects them. The life space index was 38.92, which means that the trees develop better with little competition, but can sustain a high-density occupancy. In the canopy, an upward, oscillatory and constant wave effect pattern was observed, where for every 10 trees there can be one dominant, four co-dominant, three intermediate and two suppressed. The phenomenon of shyness could be observed, especially when the trees have no foliage, and was manifested with a crack of 27.39 cm on average, which prevents the crowns from joining each other and function as a growth strategy.

Conflict of interest

The authors declare that they have no conflict of interest.

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