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Research article

Aspectos ecológicos, morfológicos y fenológicos de *Canella winterana* (L.) Gaertn. (Canellaceae) en Calakmul, Campeche

Ecological, morphological and phenological aspects of *Canella winterana* (L.) Gaertn. (Canellaceae) in *Calakmul, Campeche*

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Abstract

Wild cinnamon (*Canella winterana*) is a hardwood tree of restricted distribution in the jungles of *Calakmul*, *Campeche*, where it is little known, but with ample timber and non-timber potential. The objective of this study was to characterize and relate the floristic composition associated with the population of *C. winterana* in the forests of *Calakmul*. For this purpose, the composition of the floristic community associated with *C. winterana* was identified; 10 sampling sites similar to those of the National Forest and Soil Inventory (*Infys* by its Spanish acronym) utilized in Mexico were established. Ecological, ordination, and proximity indices between tree communities were calculated based on similarity in their composition by NMDS and UPGMA, using PAST 4.07. In addition to *C. winterana*, 121 tree taxa were identified; most of the individuals of this species were located in medium to low alluvial plain forests and medium sub-evergreen forests, on lithic or mollic leptosols and vertisols. Its distribution pattern was aggregated. The reproductive trees averaged heights of 8.7 m and normal diameters of 15.8 cm. The fruits weighed 0.34±0.06 g, with six seeds on average, which reached an average weight of 0.04±0.001 g. In conclusion, two forest types and three soils associated with *C. winterana* were identified, as were environmental and ecological attributes relevant to its presence in *Calakmul*, and it was determined that it is well integrated into the forest community of the region.

Keywords: Dendrometry, dispersal, forest ecology, phenology, phytoresources, tropical flora.

Resumen

La canela *che* (*Canella winterana*) es un árbol de madera dura y de distribución restringida en las selvas de Calakmul, Campeche, donde es poco conocido, pero con amplio potencial maderable y no maderable. El objetivo del presente trabajo fue caracterizar y relacionar la composición florística asociada a la población de *C. winterana* en las selvas de Calakmul. Para ello, se identificó la composición de la comunidad florística asociada a *C. winterana*; se establecieron 10 sitios de muestreo similares a los del Inventario Nacional Forestal y de Suelos (Infys) usado en México. Se calcularon los índices ecológicos, de ordenación y de proximidad entre comunidades de árboles con base en la similitud de su composición por NMDS y UPGMA, en *PAST* 4.07. Se identificaron 121 taxones de árboles además de *C. winterana*; la mayoría de los individuos de esta especie se ubicaron en bosques de llanura aluvial media a baja y bosques subperennifolios medios; sobre leptosoles líticos o mólicos y vertisoles. Su patrón de distribución fue agregado. Los árboles reproductivos promediaron alturas de 8.7 m y diámetros normales de 15.8 cm. Los frutos pesaron 0.34±0.06 g, con seis semillas en promedio, las cuales alcanzan un peso promedio de 0.04±0.001 g. En conclusión, se identificaron dos tipos de bosques y tres suelos asociados a *C. winterana*, así como atributos ambientales y ecológicos relevantes para su presencia en Calakmul, y se determinó que está bien integrada a la comunidad forestal de la región.

Palabras clave: Dendrometría, dispersión, ecología forestal, fenología, fitorrecursos, flora tropical.

Introduction

The rainforests of Mexico constitute a group of tropical forests of distinctive structure and composition, ranging from low and intermediate to relatively high canopy heights (>20 m); they also contain many endemic or rare species, often poorly known (Dzib-Castillo *et al.*, 2014; Granados-Victorino *et al.*, 2017). In the forests of the state of *Campeche*, one of these species is *Canella winterana* (L.) Gaertn., a tree whose distribution is restricted to a small area of the *Calakmul* Biosphere Reserve, but which nevertheless contributes significantly to carbon storage in the tree biomass (Esparza and Martínez, 2018). Known as wild or white cinnamon, *C. winterana* (Canellaceae family: Canellales) is a tree native to the Antilles and the Caribbean basin (Ochoa-Gaona *et al.*, 2018).

In Southeastern Mexico, it is considered a timber tree, seldom present in inventories; it is rare or scarce due to its restricted distribution, which makes it difficult to obtain in the states of *Campeche* and *Quintana Roo* (Tetetla-Rangel *et* *al.*, 2012). In *Campeche*, the species appears to be moving towards the Gulf of Mexico slope, colonizing areas further away from the Caribbean basin.

It is used as a stimulant, digestive, and for rheumatic conditions and the relief of arthritis (Rodríguez, 2012). Similarly, high levels of phytotoxic sesquiterpenoids or secondary metabolites with potential antifungal and bactericidal compounds with potential application in controlling crop diseases have been reported (Senkoro *et al.*, 2020). In Mexico, however, there are few studies on its propagation and reproduction under natural environmental conditions (*in situ*) and even fewer *ex situ* (Murcia *et al.*, 2016). It is a species that can be considered at risk or in danger of genetic loss due to the reduction of the rainforest ecosystems where it is found; this situation is aggravated by its status as a species of restricted or rare distribution, which is also endemic to the Caribbean basin and the Antilles (Báez-Vargas *et al.*, 2017; Ellis *et al.*, 2017).

The lack of knowledge about the characteristics of this aromatic species makes it interesting to study its morphology and environmental requirements and the forest communities in which it occurs in *Campeche*, as well as aspects of its reproduction and dispersal. Therefore, this study aimed to characterize and relate the floristic composition associated with the population of *C. winterana* in the jungle of *Calakmul*, *Campeche*.

Materials and Methods

Characterization of the vegetation associated with *C. winterana*

Within the narrow strip of distribution of the species in *Calakmul*, after exploration of the species as recommended by Olvera-Vargas *et al.* (2021), a subzone was located in which the presence of the species and the types of primary vegetation in which it usually grows have been recorded (Chiquini-Heredia *et al.*, 2017). The forest landscape units in which *C. winterana* was found consisted of intermediate secondary vegetation or fallow due to agricultural activity for 15 to 30 years (ISV), advanced secondary vegetation or fallow for more than 30 years (ASV); advanced secondary vegetation with forestry management (ASV_FM), low to medium flooded or low flooded forest (MFF), and medium sub-evergreen forest (MSF). Ten plots were used to identify the tree species present as companion species of wild cinnamon.

This scheme allowed for greater representativeness for the studied community, by combining four circular subplots of 11.3 m radius (400 m^2), nested within a larger one of 56.16 m radius (10 000 m^2), which delimits one hectare (Chiquini-Heredia *et al.*, 2017). Each circular subplot was subdivided into eight sections, which always began with a transect with a free north course, from which others were drawn at 45° angles to the previous one, clockwise. This configuration facilitated the inventory and thus, in each section, each tree individual present was counted and identified, with the support of specialized literature on the vegetation of the area (Martínez and Galindo-Leal, 2002; Ochoa-Gaona *et al.*, 2018), and the nomenclature was subsequently updated by consulting a list of flora published by the Center for Scientific Research of *Yucatán* (*Centro de Investigación Científica de Yucatán*, *CICY*) (Fernández-Concha *et al.*, 2010).

The number of individuals per plot was considered an estimator of the abundance of each species and made it possible to establish the list of the arborescent flora community that accompanies the distribution of *C. winterana* in the area. For this taxon, three categories were determined: Seedling (height <1 m), Sapling (1 m>height<3 m), and Pole (height>3 m), modifying the proposal of López-Toledo *et* *al.* (2012). With the field data, we proceeded to estimate ecological and community indices, which included the species richness (Hair, *S*), Shannon-Wiener diversity (*H'*), Simpson's dominance (*D*), and Pielou's evenness (*E*) indices. Ordination analyses were performed using the non-metric dimensional scaling method (NMDS) and unweighted pairwise grouping of means (UPGMA) with the PAST 4.07 software (Hammer *et al.*, 2001); these indices were utilized to determine whether the communities in which the species occurs were distinguishable from each other as distinct landscape units in terms of their floristic composition.

Distribution patterns

The three main distribution patterns were utilized to establish a recognized reference in the scientific literature: uniform, clustered, and random, centered on the parent or reproductive tree (Carrillo-Ángeles *et al.*, 2011; Ledo *et al.*, 2012). In order to determine the type of distribution in *C. winterana*, we counted the number of individuals in the seedling or sapling stage in relation to the parent tree, located towards the center of four sampling plots. The Cox distribution index (Equation 1), which, according to Ledo *et al.* (2012), is usually applied in inventories with sampling units that are not necessarily contiguous, and the Morisita index, which is useful when no data are available on the distance between individuals, were applied. These two indices were used because they provide contrasting information based on the density of individuals detected in the field. Also utilized was the Poisson distribution function (Equation 2), verified with the X^2 test, which includes spatial aspects referred to sampling plots of known limits, and allows estimating a clustering index (*PCI*), which served to validate or reject the previous ones (Hernández *et al.*, 2018).

$$Cox\ distribution = \frac{S^2}{\mu} \qquad (1)$$

Where:

S^2 = Variance

μ = Mean

$$PCI = n\left[\frac{(\sum xi^2 - \sum xi^2)}{(\sum xi)^2 - \sum(xi)}\right] \qquad (2)$$

Where:

n = Sample size

Xi = Number of individuals in quadrant i

Characterization of the habitat of *C. winterana*

Each of the four circular plots was plotted using a model Vertex IV hypsometer and a model T3 transponder (Haglöf® Sweden), starting from the adult *C. winterana* tree in a northerly direction. The ambient humidity and temperature were recorded with a model SR108N Sunroad® digital multifunction altimeter, the soil pH and temperature, with a model HI9813-5 Hanna® portable multiparameter analysis equipment, as well as with a model HI98331 Hanna Groline® and model HI98103 Hanna Checker® portable equipment. The incident illumination on the forest floor was estimated using the model HI97500 Hanna® portable light meter.

Morphology and reproduction of *C. winterana*

The shape of the *C. winterana* tree was described by means of a field survey of its aboveground components (stem, branches, foliage, fruit); for this purpose, data were obtained on the normal diameter (model 283D Forestry Suppliers® Inc. diameter tape); tree height and height of the clean trunk (model PM-5/360 PC Suunto® clinometer); number of primary, secondary and other minor branches; number of infructescences per terminal branch; and number of fruits per infructescences. Fruit and seed weights were also estimated (model HCB602H Highland® scale), as well as the number of seeds per fruit. Reproductive phenology was described by monthly monitoring of the appearance of flowering and fruiting, largely unknown for this species.

Results

Characterization of the vegetation associated with *C. winterana*

In *Campeche*, wild cinnamon is concentrated in the Northern sector of the *Calakmul* Biosphere Reserve, on irregular terrain and the base slope of the terrain; it occurs in two types of forest formations, widely distributed in the region, the medium sub-evergreen forest (MSF) and the medium and low flooded forest (MFF). It is also possible to find it within the secondary succession coming from agriculture, locally called "*acahuales*", both in old post-agricultural vegetation units (>30 years of fallow or rest, ASV) and intermediate (between 15 and 30 years of abandonment, ISV), as well as in old post-agricultural vegetation (>30 years of fallow or rest with management, ASV_FM), whereby foresters eliminate part of the trees and select those with straight and healthy shafts. It has not been recorded in younger successional vegetation.

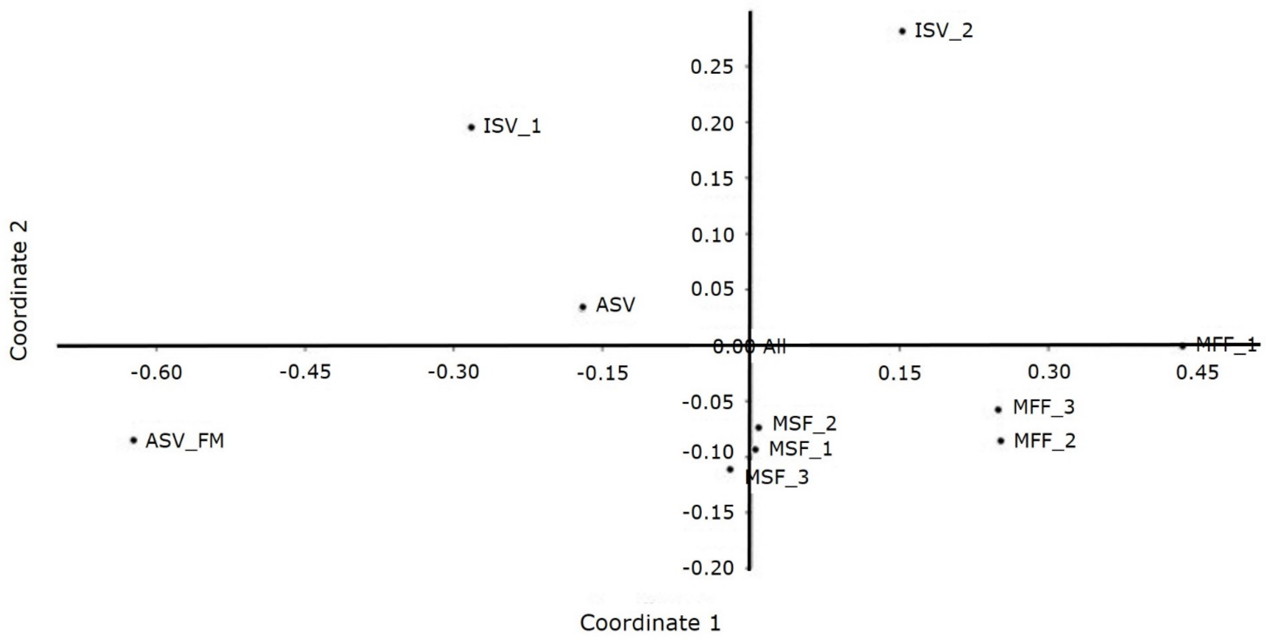
121 tree species associated with *C. winterana* were detected in the area, 12 of which coincided in all landscape units, while 19, 23, 22, and 45 others shared four, three, two, or one of the five different landscape units of the forest ecosystems in *Calakmul* where wild cinnamon is present. Table 1 shows the five taxa that most frequently and abundantly coexisted with *C. winterana* in at least three of the forest environments included in the inventory. Figure 1 shows the arrangement of the landscape units, and Figure 2 shows the grouping of these units based on the similarity of the flora identified as accompanying *C. winterana* in the area.

Table 1. Main species of flora accompanying *Canella winterana* (L.) Gaertn. in the forest landscape of the *Calakmul* Biosphere Reserve region, *Campeche*, Mexico.

Species	Family	Ecosystems	Density (ind. ha^{-1})
Gymnanthes lucida Sw.	Euphorbiaceae	ISV, MFF, MSF	32
Pouteria reticulata (Engl.) Eyma	Sapotaceae	ISV, ASV, MFF, MSF	21
Piscidia piscipula (L.) Sarg.	Fabaceae	ISV, ASV, ASV_FM, MFF, MSF	17
Bursera simaruba (L.) Sarg.	Burseraceae	ISV, ASV, ASV_FM, MFF, MSF	15

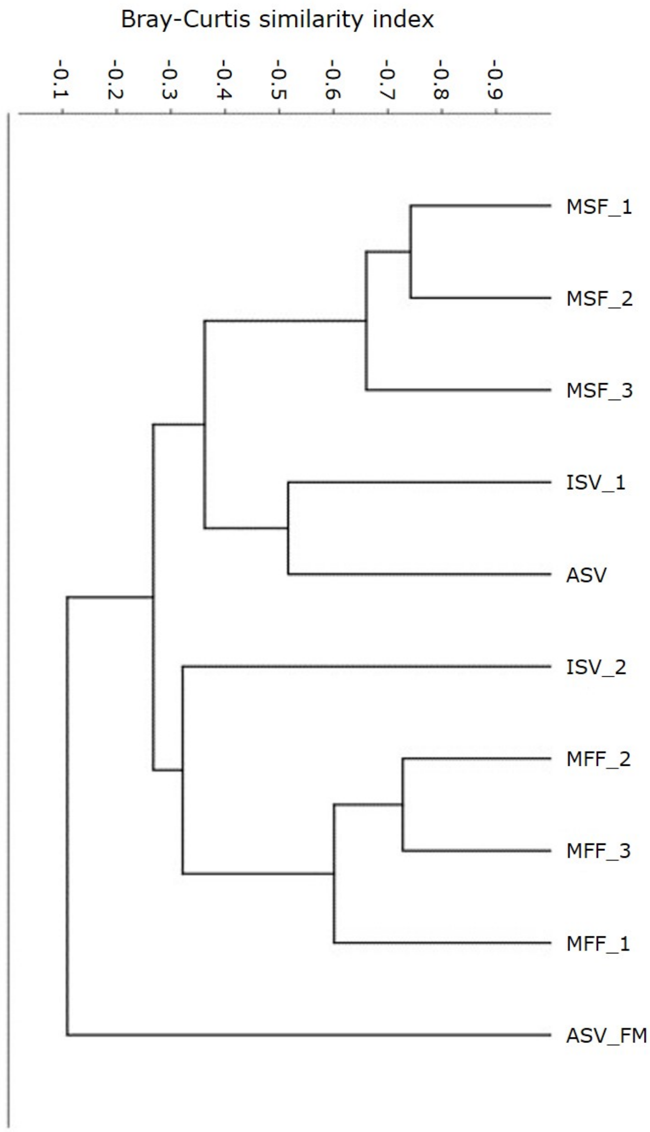
Manilkara zapota (L.) P. Royen	Sapotaceae	ISV, ASV, ASV_FM, MFF, MSF	13

Ecosystems: Shared forest landscape units with *Canella winterana* (L.) Gaertn. in *Calakmul*, *Campeche*, Mexico. ISV = Intermediate secondary vegetation (15 to 30 years of agricultural fallow); ASV = Advanced secondary vegetation (fallow land older than 30 years); ASV_FM = Advanced secondary vegetation with forestry management; MFF = Low to medium flooded rainforest (low flooded); MSF = Medium sub-evergreen rainforest.



MSF = Medium sub-evergreen forest; MFF = Medium to low flooded forest; ASV = Old secondary vegetation (>30 years of post-agricultural fallow) of MSF; ASV_FM = ASV with management whereby foresters remove part of the trees and select those with straight and healthy stems; ISV = Intermediate secondary vegetation (15 to 30 years fallow). NMDS Stress = 0.03744; R^2 axis 1 = 0.7218; R^2 axis 2 = 0.05282; Bray-Curtis distance index.

Figure 1. Management of landscape units in the *Calakmul* Biosphere Reserve in *Campeche*, Mexico, where *Canella winterana* (L.) Gaertn., a timber and aromatic tree associated with the Caribbean-Antilles basin in tropical America, is distributed.



MSF = Medium sub-evergreen forest; MFF = Medium to low flooded forest; ASV = Old secondary vegetation (>30 years of post-agricultural fallow) of MSF; ASV_FM = ASV with management whereby foresters remove part of the trees and select those with straight and healthy stems; ISV = Intermediate secondary vegetation (15 to 30 years fallow).

Figure 2. Management of landscape units in the *Calakmul* Biosphere Reserve in *Campeche*, Mexico, where *Canella winterana* (L.) Gaertn., a timber and aromatic tree associated with the Caribbean-Antilles basin in tropical America, is distributed.

The difference between forest communities was greater when all were compared with ASV-FM, because forestry management practices applied in this type of environment are based on the suppression or elimination of species considered not useful by foresters; this, in turn, may modify the densities of certain taxa, as preferred taxa are favored. Table 2 describes the ecological indices for the various environmental conditions where *C. winterana* has been observed.

Table 2. Ecological indices recorded in circular plots established in the forest landscape of *Calakmul*, *Campeche*, Mexico, where *Canella winterana* (L.) Gaertn. trees were located.

Ecosystem	Richness	Individuals	Diversity	Dominance	Evenness	*Chao1*
ISV	53±3	358±13	3.0±0.2	0.1±0.01	1±0.03	62
ASV_FM	30±2	391±41	2.0±0.3	0.2±0.01	1±0.08	33
ASV	60±6	373±64	4.0±0.4	0.05±0.01	1±0.02	74
MFF	56±13	408±32	3.0±0.2	0.06±0.01	1±0.02	73
MSF	47±2	371±23	3.0±0.1	0.09±0.02	1±0.04	63

ISV = Intermediate secondary vegetation (15 to 30 years); ASV_FM = Old secondary vegetation with forestry management (>30 years); ASV = Old secondary vegetation (>30 years); MFF = Medium to low flooded forest; MSF = Medium sub-evergreen forest. Hair Richness = Number of species; Individuals = Average number of individuals (trees) counted in a community (ind. ha^{-1});

Diversity = Shannon-Wiener Index base 10; Dominance = Simpson's Index; Evenness = Pielou's Index; *Chao1* = Estimator of sampling intensity efficiency associated to each unit by *Chao* Index, based on the total number of species detected in the landscape.

The soil characteristics in which *C. winterana* grows range, according to the World Reference Base (WRB), from Vertisol or Gleysol (*Aak 'al che'* in the Mayan soil classification) and histic Vertisol (*Ya 'ax hom* in the Mayan classification) to the lithic or mollic Leptosol (*Box lu´um* in the Mayan classification), which in the area correspond, according to Bautista and Zinck (2010), to those areas in which floodable forests are distributed in the first case and medium sub-evergreen forests in the second (Table 2).

Distribution patterns

Wild cinnamon presented a distribution pattern that moved away from the parent, so it would be associated with a random pattern concerning its most likely parent, since in the field the seedlings and other recruits of the species were located at a distance of over 6 m, both from the central reproductive tree of each plot and concerning their nearest neighbor (Table 3). However, both the Morisita Index (I_{mor}=7.2; if I_{mor}>0, the distribution is aggregated) and the Cox Index (*Cox*=1.5; if *Cox*>1, the distribution is uniform) showed that the species tends to be distributed in an aggregated or uniform manner, respectively.

Table 3. Distribution pattern of *Canella winterana* (L.) Gaertn. individuals, based on data on the distance of individuals from the reproductive tree centered in circular plots in the forest landscape of *Calakmul*, *Campeche*, Mexico.

Category	**Distance to central *C. winterana* (L.) Gaertn. tree (m)**	**Distance to nearest neighbor *C. winterana* (L.) Gaertn. tree (m)**	**Detected distribution pattern**
Pole	6.7±4.8	6.1±4.6	Random based on the distance >5 m from the central tree or nearest neighbors. Uniform aggregation based on the Cox (*Cox*=1.5), Morisita (I_{mor}=7.2), and Poisson distribution function aggregation indices (*PCI*=15.69, X^2=11.502, p<0.001).
Seedling	6.5±3.3	3.6±4.3	
Sapling	11.7±1.2	8.6±5.6	

The discrepancy described above may explain why the conventional Cox and Morisita indices do not take into account the locations and distances of individuals from each other. To resolve this, the most appropriate estimator has been the Poisson Clustering Index (Hernández *et al.*, 2018), which showed that the distribution is not random, confirming that the pattern of *C. winterana* as a clustered type (*PCI*=15.69, X^2=11.502, p<0.001).

Preferred habitat conditions of *C. winterana*

Most of the individuals of *C. winterana* were located in landscape units of medium to low flooded forest and predominantly in the medium sub-evergreen forest, as well as in secondary post-agricultural succession of the latter, in irregular terrain and on the base slope of the terrain, which is characterized by a range of black to gray lithic or mollic Leptosols to Vertisols —soil types that are often saturated with moisture for more than two months (Table 4).

Table 4. Edaphic and environmental characteristics of the landscape units where *Canella winterana* (L.) Gaertn. reproductive trees are found in the *Calakmul* Biosphere Reserve, *Campeche*, Mexico.

	Characteristics of ecological conditions							
Environment	**Soil**	**S**	**Exp.**	**Surf. St.**	**Int. St.**	**Disturb.**	**Text.**	**Str.**
MSF/MFF 18°31'59.268" N, 89°12'0.828" O	Grayish black Vertisol (*Aak ´al che´*), abundant fine roots in the first 10 cm and coarse at greater depths	2	South-North	Null	Null	High	Clayey	Blocky
MSF 18°31'58.836" N, 89°12'0.576" O	Dark gray lithic Leptosol (*Box lu'um*), with little sand and abundant fine roots in the first 20 cm	25	North-South	High	Intermediate to high	Low	Loamy-clayey	Granular
MSF 18°31'55.956" N, 89°11'42.000" O	Dark gray mollic Leptosol (*Box lu´um*), with little sand and abundant fine roots in the first 20 cm	5	North-South	High	Intermediate to high	Low	Sandy-loamy	Granular to massive
MSF/MFF 18°32'7.548" N, 89°11'34.224" O	Dark gray histic Vertisol (*Yaxhoom*), with little sand and abundant fine roots in the first 20 cm	20	West-East	Null	Null	High	Loamy	Crumbly granular

	Characteristics of ecological conditions							
Environment	RM	Tem.	pH	Lux	Alt.	LLT	Mineral depth	Act. Mac.
MSF/MFF	56	28.7	7.7	14 000	177	3	50	None
MSF	88	32.2	7.5	21 000	178	6	40	Scarce and not very

								mobile
MSF	82	31.2	7.6	12 000	199	6.5	40	Abundant and activa
MSF/MFF	21.6	26.9	7.4	8 000	181	4.4	18	Abundant and active

MSF = Medium sub-evergreen forest; MFF = Medium to low flooded rainforest; Soil = Soil type; S = Slope as percentage; Exp.= Slope exposure; Surf. St. = Surface stoniness; Int. St. = Internal stoniness; Disturb. = Level of anthropic disturbance observed; Text. = Soil texture class; Str. = Soil structure; RM = Relative moisture as a percentage; Tem. = Temperature °C; pH = Hydrogen concentration or soil reaction; Lux = Illuminance in Lux; Alt. = Altitude above sea level; LLT = Leaf litter thickness (cm); Mineral depth = Depth of friable mineral soil (cm); Act.Mac = Observed activity of soil macrofauna.

Morphology and reproduction of *C. winterana*

The trees had an average height of 8.7 m and a normal diameter of 15.8 cm in the crown, 1.9 m in height and 3.7 cm in diameter in the sapling, and 0.4 m in height and 0.7 cm in average diameter in the seedling (Table 5). All sites were dominated by seedlings over poles and saplings (Figure 3). Branching goes up to the eighth order, from which the inflorescences will form into thyrsus-like cymes and infructescences, varying from one to more than 60. On terminal branches, the relatively small, globose fruits or indehiscent berries, weigh an average of 0.34±0.06 g, and contain one to six seeds (Figure 4) immersed in an aromatic resin.

Table 5. Morphological aspects of the stem of *Canella winterana* (L.) Gaertn. individuals recorded in forest plots in the *Calakmul* Biosphere Reserve, *Campeche*, Mexico.

Category	Height	*BD*	*ND/DM*	Branches 1	Branches 2	Leaves	Fruits/branch (amplitude)
Seedling	0.4±0.2	1.8±2.4	0.7±0.6	2±1	2±2	36 379±9 904	
Sapling	1.9±1.0	6.4±7.2	3.7±4.4	3±3	6±3	60±2	
Pole	8.7±2.1	16.1±8.4	15.8±13.8	4±4	15±7	20±8	15±3 (1 a 135)

Height = Plant height (m); *BD* = Basal stem diameter at 10 cm from the ground (cm); *ND/DM* = Normal diameter at 1.3 m stem height for plants taller than 1.5 m or diameter in the middle zone of the stem for plants less than 1.5 m tall (cm); Branches 1 = Number of primary branches; Branches 2 = Number of secondary branches; Leaves = Number of leaves on the plant; Fruits/branch (amplitude) = Number of fruits per branch with terminal infructescences (amplitude of the number of fruits counted) on reproductive trees.

Figure 3. Relative frequency of the number of individuals of three growth categories in the tree species *Canella winterana* (L.) Gaertn. in *Calakmul*, *Campeche*, Mexico.

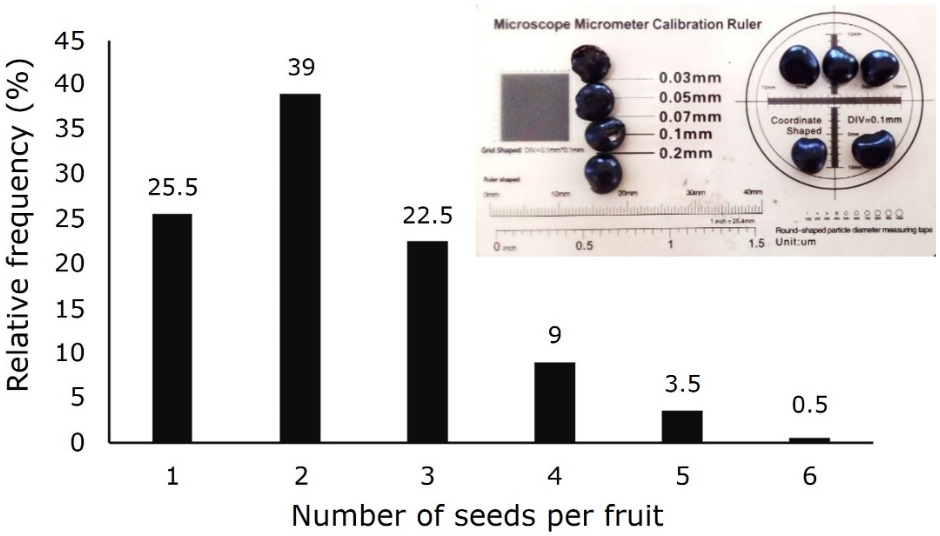


Figure 4. Relative frequency of the number of seeds per fruit in reproductive trees of *Canella winterana* (L.) Gaertn. in *Calakmul*, *Campeche*, Mexico.

Flowering was detected from May to June, while fruit formation began in July and lasted until January and February as production peaks, to decrease towards March, when they ripen turning reddish and can be used in sexual seed propagation of the species. Seeds 4 to 5 mm wide, flattened, circular, and shiny jet black in color, reached weights of 0.04±0.001 g.

Discussion

The types of soils where *C. winterana* frequently grows are characterized by poor internal drainage and are associated with seasonal flooding or moisture saturation for several months during the rainy season. This situation seems to influence the distribution of the species, but fails to explain its restricted occurrence in *Calakmul*, given that the same soil conditions are found in other areas where the species does not occur.

The type of forest association seems to follow the classification of *chicozapote* forest (*Manilkara zapota* (L.) P. Royen) proposed by Martínez and Galindo-Leal (2002) in the study region, which includes wild cinnamon and other species that are tolerant to water saturation in soils. This is consistent with the notion that the greatest floristic affinities are due to ecological similarities rather than other factors (Stevenson *et al.*, 1999). When comparing the three vegetative stages in which wild cinnamon occurs in the analyzed forest landscape units, it is interesting to note that the highest proportion of plants corresponds to the seedling stage (juvenile recruits) and that the proportion decreases in the sapling stage (larger juveniles), reflecting a high mortality rate in the species before it reaches canopy size (pole). This characteristic may influence the distribution pattern detected by the indices, because even with a higher rate of early young recruits, which favors the aggregate distribution, the high relative mortality tends to reduce the detection of this population aggregation for the species, and thus hinders the efficient use of the measures included in the study.

The predominant soils in the medium rainforests, widely preferred for *milpa* agriculture, are the edaphic type mostly associated with secondary vegetation in *Calakmul* (Díaz *et al.*, 2001). However, *C. winterana* is a slow-growing species, which limits its ability to tolerate higher levels of disturbance or damage from habitat modifications, such as the removal of the forest cover for agricultural land use. This may be the reason for their absence from units of early forest succession (<10 years fallow) in other inventories (Esparza and Martínez, 2018; Gómez *et al.*, 2020). Notably, in the environments with forestry management in *Calakmul*, known as ASV_FM, the species appears to be intentionally suppressed from the canopy.

In Tropical America, mammachory, chiropterochory, and ornithochory are the most frequent means of seed dispersal in plants for indehiscent fruits similar to those of *C. winterana* (Contreras and Varela, 2016). Seemingly, surface water flows may also be necessary for the transfer of fruits and seeds in the field (hydrochory), which would partly explain the presence of resins in these reproductive structures.

Both clustered and uniform distribution are dispersal strategies in tropical tree species that are widely related to high rates of fruit and seed predation, as well as to the use of dispersal mechanisms or, rather, vectors of the frugivorous type. Clustered dispersal is frequent in trees with fruit offered as a reward to the disperser (Sánchez-Gutiérrez *et al.*, 2019).

Local informants have reported that the fruits (reddish berries) of *C. winterana* show high predation by birds and terrestrial and flying mammals, which is why this species is rare in the forest landscapes of the area, as reported by Ibarra-Manríquez and Cornejo-Tenorio (2010), who have observed that the small fruits, black to red drupes or berries, are associated with zoochoric distribution, particularly by birds.

The proposition proffered in that paper that the greater distance between trees than the inner radius of plots centered on the parent tree is unreliable for estimating the spatial distribution of the species is discarded herein. An analysis of the distribution pattern based on dispersal strategies and their life table may result in a better strategy for this type of tree with a low frequency of occurrence in tropical rainforest stands.

C. winterana individuals are within the average heights and canopy dimensions of the forests where it is distributed in *Calakmul* (Martínez and Galindo-Leal, 2002); their phenology corresponds to a species that does not require immediate rainfall for its seeds to start germination, as its fruits and seeds ripen in the dry season (January to March), after a long period of formation. This reproductive phenology and the abundant production of fruits that occur simultaneously on the tree, together with the characteristics of these fruits and their probable dispersal syndromes mediated by consumers, which correspond to the high predation mentioned by the local informants, may imply that *C. winterana* colonizes spaces in the area through dispersers that feed on fruits during the season of greatest food scarcity in the forests. This species' dispersal strategy, based mainly on zoochory, but also occurring by hydrochory, may favor an increase in the surface area it occupies and on which it will establish itself in the future. Therefore, it may be considered a species of the Caribbean-Antillean basin that advances as a colonizer towards the Gulf of Mexico basin in the *Yucatan* Peninsula.

Its presence in soils prone to flooding may also be associated with the presence of animals that seek food where residual moisture occurs at the stage when the tree ripens its fruits/rewards, rendering it a keystone species for the survival of many organisms during the critical dry season in *Calakmul*, which should be used to improve the management of this natural protected area. In this regard, García-García and Santos-Moreno (2014) state that this type of species with fruiting in the dry season is scarcer in tropical forest ecosystems, but its high fruit production strategy is due to several successful evolutionary axes, such as niche partitioning and the use of dispersal vectors with a greater range, which is an adaptive advantage and justifies the sacrifice of energy and resources in the production of highly depreciated but better-dispersed fruits.

The autecological attributes described above enhance the ecological value of wild cinnamon and its role in wildlife conservation. *C. winterana* fruit culling is due to a strategy of predator saturation, which may facilitate, on the one hand, the survival of some seeds and seedlings close to the parent tree (favoring the clustered pattern), but also the dispersal away from the parent tree by highly mobile agents such as birds, bats, and terrestrial mammals, encouraging the non-clustered, more random pattern of distribution (van Schaik *et al.*, 1993; Muscarella and Fleming, 2007). This may imply that *C. winterana* colonizes spaces in the area through dispersers that feed on its fruits during the season of greatest food scarcity in the forests, allowing this tree species to profit from this period of high need in the fauna through the dispersion of its seeds. In this regard, it should be noted that the fruits and seeds of wild cinnamon are embedded in a resin or resinous aril, on top of a hard and impermeable pericarp that protects the embryos during their passage through the animals' digestive systems. This, however, should be the subject of more detailed investigations in the future.

Conclusions

Two forest types and three soil types associated with *C. winterana* were identified, as were environmental and ecological attributes relevant to its presence in *Calakmul*. The species flowers from May to June and fructifies abundantly between June and January, extending the ripening stage until March, when the fruits are dispersed by the fauna, so it has a clustered distribution. Although the spatial distribution pattern tends to be clustered, this attribute is not conclusive based on the two indices included in the study, Cox and Morisita, as well as on the Poisson distribution function. New models or approaches may be needed to obtain better explanations for the distribution of *C. winterana*, particularly those that include elements associated with the species' dispersal strategies and biogeographical elements, given that *C. winterana*, as a species native to the Caribbean-Antillean basin, appears to be moving towards the Gulf of Mexico basin, gradually crossing the *Yucatan* Peninsula. Further studies are required to illustrate this phenomenon.

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Conflict of interest

The authors state that they have no link with the institutions sponsoring the research that supports the contributions; therefore, the published data do not confer any professional, labor, or economic advantages.

Contribution by author

Noel Antonio González-Valdivia: sampling design and drafting of the manuscript; Jorge Luis García-Lanz: coordination of sampling logistics; Enrique Arcocha-Gómez: field data collection; Brígido Manuel Lee Borges: data capturing and organization; Patricia Sandoval Pech: literature search; Edith González Lazo: field sampling; Benito Bernardo Dzib-Castillo: drafting of the article.

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