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Article

Variación intraespecífica de rasgos funcionales de *Cedrela odorata* L. en la Península de Nicoya, Costa Rica

Intraspecific variation of functional traits in *Cedrela odorata* L. in the *Nicoya* Peninsula, Costa Rica

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Resumen

El cambio climático modificará el régimen hidrológico global a causa de alteraciones en la magnitud de la precipitación y temperatura, y su interacción con las condiciones físicas y de vegetación de cada lugar; esto representa un gran riesgo para la conservación de las especies, ya que implica variaciones en las condiciones que les son cruciales para su desarrollo. En respuesta a los factores abióticos y bióticos del hábitat, las plantas muestran gran variabilidad intraespecífica de rasgos, esta habilidad les permite sobrevivir, crecer y reproducirse en diversos escenarios. Estudiar la variabilidad intraespecífica de caracteres morfológicos conlleva a entender el potencial de respuesta de las especies a factores de alteración, como el cambio climático. El objetivo del presente estudio fue evaluar la variabilidad intraespecífica del área foliar (mm^2), el área foliar específica (mm^{-2} mg), contenido de materia seca foliar (mg^{-1} g), densidad de madera (g cm^{-3}) y grosor de corteza (cm) de 90 individuos de *Cedrela odorata* en tres bosques naturales con distintos regímenes de precipitación anual. A partir de la hipótesis de que *C. odorata* podría modular la magnitud de expresión de los caracteres morfológicos antes mencionados, de acuerdo con las diferentes condiciones de precipitación. Los resultados demostraron que los valores de los atributos funcionales variaron significativamente entre las poblaciones estudiadas; además, se evidenció que el taxón expresó sus rasgos en un eje de especialización adquisitivo-conservativo en el uso de los recursos. La variabilidad intraespecífica de rasgos en *C. odorata* podría ser un mecanismo de resiliencia ante el cambio climático.

Palabras clave: Ecología funcional, estructura de comunidades, filtro ambiental, plasticidad fenotípica, rasgo funcional, variabilidad intraespecífica.

Abstract

Climate change will modify the global hydrological regime due to changes in the magnitude of precipitation and temperature and their interaction with the physical and vegetation conditions of each place. This entails a great risk for the conservation of species because it involves variations in the conditions that are crucial to their performance in the ecosystem. In response to abiotic and biotic habitat factors, plants can show great intraspecific trait variability; this ability allows them to survive, grow and reproduce in different scenarios. The study of the intraspecific variability of morphological characters allows us to understand the potential response of species to engines of change, such as climate change. The aim of this study was to evaluate the intraspecific variability of leaf area (mm^2), specific leaf area (mm^{-2} mg), leaf dry matter content (mg^{-1} g), wood density (g cm^{-3}) and bark thickness (cm) of 90 individuals of *Cedrela odorata* in three natural forests with different annual rainfall regimes. It was hypothesized that *C. odorata* can modulate the magnitude of expression of the five morphological characters according to different precipitation conditions. Results showed that functional attribute values varied significantly between populations with different rainfall regimes; furthermore, the species was observed to express its traits within an axis of acquisitive-conservative specialization in the use of resources. The intraspecific variability of traits of *C. odorata* may be a mechanism of resilience to climate change.

Key words: Functional ecology, community assembly, habitat filtering, phenotypic plasticity, functional traits, intraspecific variability.

Introduction

Functional traits are all those morpho-physio-phenological characteristics that exert a direct or indirect influence on the biological success of the plant and which are manifest in its growth, reproduction and survival (Lavorel and Garnier, 2002; Violle *et al.,* 2007; Pérez-Harguindeguy *et al*., 2016). Within an ecosystem, the climatic conditions, the availability of resources and the natural and anthropic disturbances act as a natural filter for the species; only those with a given set of attributes overcome the environmental barrier and attain biological success by coexisting with other similar functional characteristics (Keddy, 1992; Zobel, 1997; Díaz *et al.,* 1998; Lortie *et al.,* 2004; Cornwell and Ackerly, 2009).

Climate change will modify the global hydrological regime as a consequence of changes in the magnitude of both the precipitation and the temperature and their interaction with the physical and vegetation conditions of each place (IPCC, 2007; Imbach *et al*., 2010). This entails a great risk for the conservation of the species, as it involves changes in the natural conditions that are crucial to their development within the ecosystem (Sala *et al*., 2000; Nicotra *et al*., 2010).

Based on the climatic variations predicted for Costa Rica, dry and humid ecosystems will be the most exposed and the most sensitive (Locatelli and Imbach, 2010); these are the natural habitats of *Cedrela odorata* L., and therefore the permanence of this species in space and time is at risk.

Cedrela odorata is a tropical tree species of enormous value for the forestry industry; for this reason, its conservation is relevant for Costa Rica and for the world at large (Gillie *et al*., 1997). Its natural distribution stretches from Mexico to northern Argentina; it inhabits a broad range of ecosystems with various environmental conditions (Pennington and Sarukhán, 2005; Rojas-Rodríguez and Torres-Córdoba, 2013). In Costa Rica, it grows in both seasonally dry and very humid environments, exhibiting different phenotypic characteristics in each (Navarro*et al.*, 2002; Cavers *et al.,* 2003).

The taxa adjust the magnitude of the expression of their functional features according to the conditions and restrictions of the habitat, resulting in suitable phenotypes that are able to attain biological success (Bolnick *et al*., 2003; Jung *et al.,* 2010; Bolnick *et al*., 2011). This divergence between individuals of the same species is known as intraspecific variation and is regarded as a microevolutionary process (Masuelli and Marfil, 2011). The intraspecific variability of morphological features/traits may be the source of the resilience of the taxa and, therefore, of the ecosystems in the face of climate modification (Garzón *et al*., 2011; Jung *et al*., 2014; Moran *et al*., 2016).

Studying intraspecific variability makes it possible to understand the response potential of the species to alteration factors, such as climate change (Cianciaruso *et al*., 2009; Salgado, 2016; Des Roches *et al.,* 2018). However, so far there is no clear method to measure it correctly, given that the protocols for its evaluation have focused mainly on the variation between species, *i.e.* interspecific variability, while neglecting intraspecific variation (Albert *et al*., 2010a; Albert *et al*., 2011).

The objective of the present study was to assess the intraspecific variability of the functional traits exhibited by *Cedrela odorata* populations in three types of natural forests with different rainfall regimes in the *Nicoya* Peninsula, in Costa Rica. The selection of the features was based on their acknowledged relationship with vital processes of the plant, such as the acquisition and allotment of resources, adaptation to change factors and survival from disturbances (Cornelissen, 1999; Poorter and Jong, 1999; Poorter and Garnier, 2001; Hacke *et al*., 2001; Mediavilla *et al.,* 2001; Wright and Cannon, 2001; Westoby *et al*., 2002; Wright and Westoby, 2002; King *et al*., 2006; Poorter and Bongers, 2006; Sterkt *et al*., 2006; Álvarez-Clare and Kitajama, 2007; Chao *et al.,* 2008; Curran *et al*., 2008; Wright *et al.,* 2017) (Table 1). *C. odorata* individuals are expected not to exhibit constant values for these features throughout the environmental gradient, as the manner in which an individual expresses its functional attributes is closely related to the specific environmental conditions of the habitat where it pursues biological success (Poorter, 2008; Albert *et al*., 2010b).

Table 1. List of measured functional traits, abbreviation and the units in which they are evaluated.

Functional trait	Abbreviation	Unit
Foliar		
Leaf area	LA	mm^2
Specific leaf area	SLA	mm^{-2} mg
Content of leaf dry matter	CLDM	mg^{-1} g
Stem		
Wood density	WD	g cm^{-3}
Bark thickness	BT	cm

The results contribute to the knowledge of this microevolutionary process and make it possible to glimpse the response potential expressed by vegetal species in the face of environmental variations, as well as its implications for their conservation.

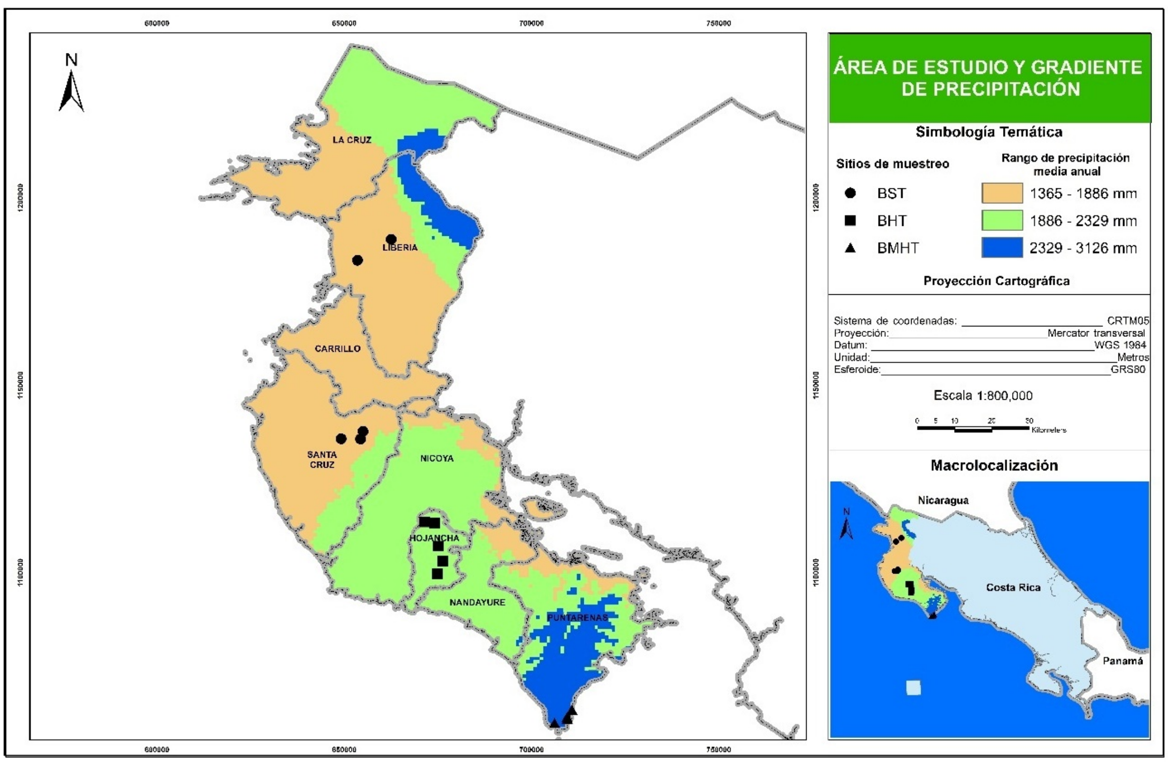
Materials and Methods

The intraspecific variability of five morphological features was assessed: leaf area (mm^2), specific leaf area (mm^{-2} mg), content of leaf dry matter (mg^{-1} g), wood density (g cm^{-3}), and bark thickness (cm) of 90 *C. odorata* individuals in three natural forests under different annual precipitation regimes.

The climate change scenarios suggest that the hydrological regimes will be potentially affected (Arnell, 1999; Arnell 2003); however, the knowledge of how the plants will respond to this situation is scarce. For this reason, the present paper considered only the mean annual precipitation as the environmental filter with an effect on the adjustment process of the values that correspond to the traits cited above.

Study area

The study was carried out in the region of the *Nicoya* Peninsula in Costa Rica (10°51´5´´ - 9°34´10´´ LN; 85° 42´ 27.3´´ - 85° 06´41.6´´ W). The topography is generally flat, with a single elevation at the center reaching 900 masl. According to the climate data of *Worldclim* (http://www.worldclim.org/), the area exhibits a north-south precipitation gradient; the conditions of low precipitation and seasonality of the rains occur toward the northern part of the peninsula, on the border with *Nicaragua*, while toward the south the conditions are more humid (Figure 1).



Área de studio = Study area; *Gradiente de precipitación* = Precipitation gradient; *Sitios de muestreo* = Sampling sites; *Proyección cartográfica* = Cartographic projection; *Sistema de coordenadas* = Coordinates system; *Esferoide* = Spheroid.

Figure 1. Study area, precipitation gradient, and location of the sampling sites per stratum.

The Arc Gis software, version 10.2, and the raster layer of the bioclimatic variable "annual precipitation" from the online database of Wordclim were utilized to spatially define the precipitation gradient in the peninsula. The precipitation gradient was divided into three strata (Table 2), each one associated to a Holdridge life zone (Holdridge, 1967).

Table 2. Stratification of the precipitation gradient in the *Nicoya* Peninsula, Costa Rica.

Stratification of the gradient	Mean precipitation interval (mm)	Holdridge life zone
Stratum 1	1 365-1 886	Tropical dry forest (TDF)
Stratum 2	1 886-2 329	Tropical wet forest (TWF)
Stratum 3	2 329-3 126	Tropical very wet forest (TVWF)

Sampling and evaluation of morphological features/traits

The functional traits of 30 *Cedrela odorata* were measured for each stratum of the gradient, using 14 sampling sites (Figure 1) within the patches of secondary forest, according to Finegan's definition (1996). The sampled sites were relatively flat, with a slope of 0 to 15 %, and the minimum separation between individuals was 50 m. Only *C. odorata* trees with a healthy appearance and a normal diameter (ND) of 30 to 100 cm were measured.

Assessed variables

The five attributes mentioned above was measured. The LA, SLA, CLDM and BT were measured and estimated according to the standardized protocol of functional traits of the plants (Pérez-Harguindeguy *et al.* 2013). For the WD, the specific gravity method was used (Williamson and Wieman 2010). The value of this risk per individual corresponded directly to the estimate made with the proposed method. The traits were measured during the sampling period, which coincided with the time when the trees had their full foliage in the year 2017. Only mature leaves of the part exposed to the sunlight and without evidence of herbivory or damage by pathogens were considered.

For the foliar area estimation, a conventional HP Scanjet 300 Flatbed scanner and the Leaf Area Measurement software version 1.3. were used. Also, a H-5851 OHAUS SCOUT analytical balance to weigh the samples, in addition to conventional laboratory equipment such as specimens and Kimax beakers. To measure bark thickness, a Suunto bark caliper was utilized.

The protocol for the record of functional traits indicates that 10 leaves per taxon —or, preferably, 20 leaves from 10 individuals, i.e. two leaves from 10 specimens at random— are required for woody species. However, the procedure is designed for the performance of studies at the interspecific level, which consider only the average value of the traits of the community and disregard the wide variability that may be exhibited by members of the same species.

To the present day, the choice of the best sampling strategy for capturing mean values of morphological traits of a species or population while preserving the information on the variability of the traits and minimizing the sampling size and effort is a topic open for discussion in the ecology of functional traits (Pretuzzelis *et al.*, 2017).

Therefore, in order to include the greatest possible intraspecific variability of morphological features per specimen, in the present study, 20 leaves per tree were collected and measured, without taking into account the petiole of the leaflets, which was withdrawn before processing the samples. Thus, the individual value of the leaf characteristics (LA, SLA, CLDM) was the mean of the values of the 20 leaves considered per tree.

Data analysis

A linear model of mixed effects was executed in order to know the effect of the precipitation gradient on the variation of the values of the functional traits. The attributes were regarded as the response variable of the model; the sampling site, as a random factor, and the life zone of the gradient as the fixed factor. Subsequently, a multiple comparison test was performed using the LSD method (Fisher) with a level of significance of 0.05 (Williams y Abdi, 2010), in order to know what populations differ statistically from one another. Furthermore, a principal component analysis (PCA) of the five assessed traits was carried out in order to obtain the grouping of the 90 assessed specimens according to the magnitude of expression of its morphological traits. All the analyses were performed using the InfoStat statistical platform, version 2008 (Di Rienzo *et al*., 2018).

Results and Discussion

Intraspecific variation of traits between strata

The variability of a set of traits in a given population may be due to local adaptation or to phenotypical plasticity; *i.e.* the range of phenotypes that the same genotype expresses in response to environmental heterogeneity, in space and time (epigenetics, microevolution) (Geber and Griffen, 2003; Richards *et al.,* 2010*;* Violle *et al.,* 2012).

The plants exhibit a great intraspecific variability of traits in response to the abiotic or biotic restriction of the ecosystem (Violle *et al.,* 2007; Violle *et al.,* 2012). This ability allows them to survive, grow and reproduce under new environmental conditions (Joshi *et al.*, 2001). Many vegetal populations have been proven, even in relatively small areas, to exhibit a great phenotypical variation in a set of features that include characteristics of life forms, resistance to pathogens and herbivory, as well as the differentiation of strategies of acquisition and distribution of nutrients (Wellstein *et al*., 2013).

In this study, *C. odorata* exhibited intraspecific variation in all the assessed functional traits. The interval of variation of the morphological traits was the following: WD: 0.27-0.48 g cm^{-3}, BT: 0.7-4.34 cm, CLDM: 115-372 mg^{-1} g, LA: 22 048–68 566 mm^2, and SLA: 15.4-53.6 mm^{-2} mg. The bark thickness and the specific leaf area were the functional attributes with the largest variation along the gradient of precipitation (Table 3). The analysis of the linear model of mixed effects and their mean comparison test proved the existence of a significant effect of the stratum on the variation in the values of the functional features of each assessed individual (Table 4).

Table 3. Descriptive statistics of the functional attributes assessed in *Cedrela odorata* L. in the *Nicoya* Peninsula, Costa Rica.

Trait	Unit	n	Mean	S.E	C.V	Min.	Max.
LA	mm^2	90	40 287	872	20.53	22 048	685 666
SLA	mm^{-2} mg	90	26.2	1	36.25	15.4	53.6
CLDM	mg^{-1} g	90	242.2	6.04	23.65	115	372.2
WD	g cm^{-3}	90	0.4	0	11.748	0.27	0.48
BT	cm	90	2.2	0.08	34.37	0.74	4.34

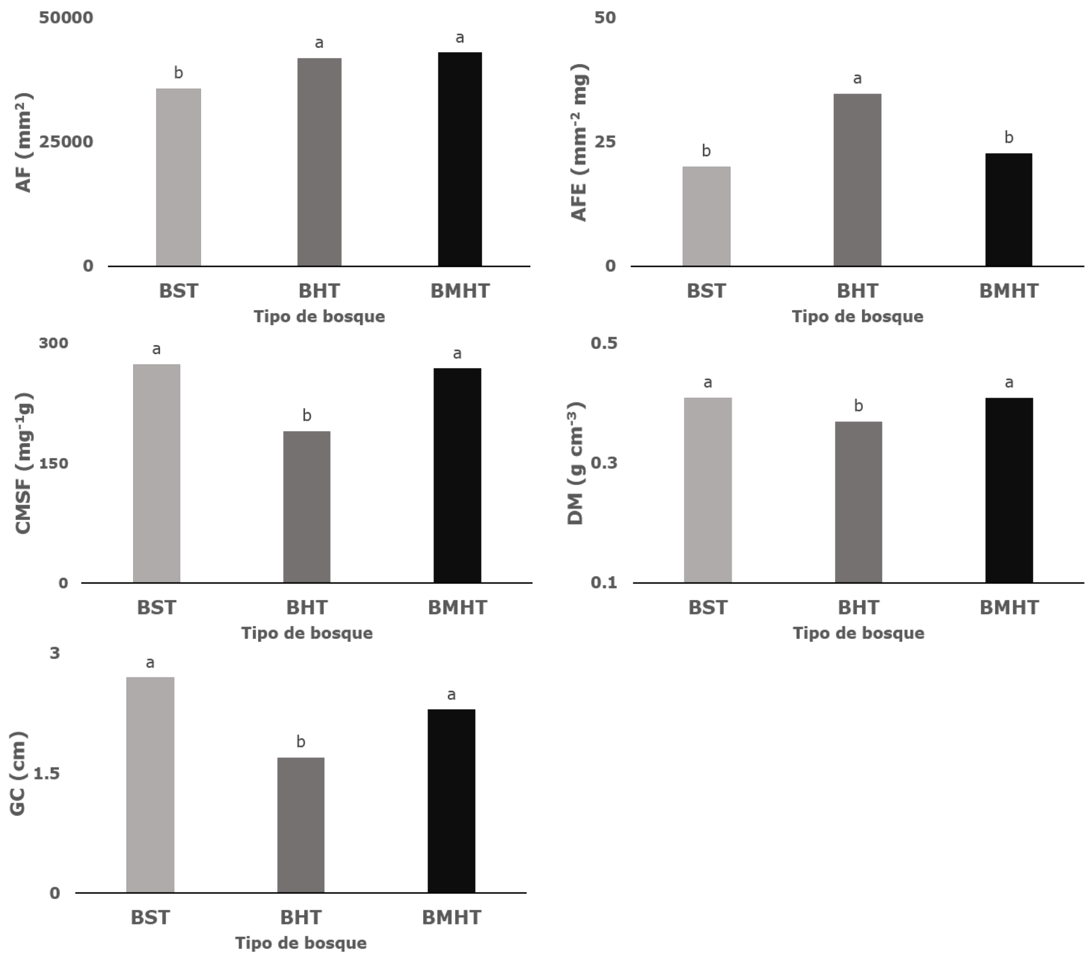
LAF = Leaf area; SLA = Specific leaf area; CLDM = Content of leaf dry matter; WD = Wood density; BT = Bark thickness; S.E = Standard error; CV = Coefficient of variation.

Table 4. List of analyzed functional traits, mean values, and effect of the gradient for each stratum.

Trait	Unit	TDF	TWF	TVWF	F	P
LA	mm^2	35 869±1 712.5 b	41 936±1 681.1 a	43 059±17 36.7 a	4.95	0.029*
SLA	mm^{-2} mg	20.1 ± 2.8 b	35 ± 2.82 a	23 ± 3.13 b	7.59	0.009**
CLDM	mg^{-1} g	274 ±16.87 a	190 ±16.8 b	269 ± 18.6 a	7.63	0.008**
WD	g cm^{-3}	0.41 ±0.1 a	0.4 ± 0.1 b	0.41 ±0.1 a	4	0.05*
BT	cm	2.7 ± 0.14 a	1.7 ± 0.14 b	2.3 ± 0.15 a	13.7	0.001**

LA = Leaf area; SLA = Specific leaf area; CLDM = Content of leaf dry matter; WD = Wood density; BT = Bark thickness; TDF = Tropical dry forest; TWF = Tropical wet forest; TVWF = Tropical very wet forest; Mean values with different letters represent statistically significant differences. The level of significance is expressed as: *P<0.05, **P <0.01.

The TDF and the TWF exhibited significant differences in all the assessed functional traits ($p \leq 0.05$); i.e. the populations of both ecosystems are significantly different, since each expressed the five considered traits to a different extent. The population of the TDF had a thinner foliar lamina, a smaller specific leaf area, a larger content of dry matter per leaflet and of specific wood density and a greater bark thickness, in relation to the TWF (Figure 2).



Different letters represent statistically significant differences ($p \leq 0.05$).

Figure 2. Intraspecific variability of functional traits of *Cedrela odorata* L. between forest types.

The TDF and the TVWF registered no significant differences ($p \leq 0.05$) with regard to the WD, BT, CLDM, and SLA, but the LA did. For this trait, the TWF and the TVWF were significantly different from the TDF, which exhibited smallest the foliar lamina of all three forests (Figure 2).

The variation of the LA was gradual, according to the conditions of humidity of the precipitation gradient (Figure 2). The mean value was higher in the TWF and the TVWF, with 41 936 ± 1 681.1 mm^2 and 43 059 ± 1 736.7 mm^2, respectively; these ecosystems exhibited the highest precipitation within the study area, while in the TDF the LA was 35 869 mm^2, with a significant difference ($p \leq 0.05$).

The reduction in the size of the foliar lamina is generally interpreted as an adaptation to drought and to the high degree of radiation (Givnish, 1987; Cornelissen *et al.,* 2003). This trait has been observed to have a positive relationship with the precipitation (Hamann, 1979; Mencuccini and Grace, 1995; Yates *et al*., 2010; Wright *et al.,* 2017). Xu *et al*. (2009) argue that the variation in the size of the leaf sheet along a climate gradient may be due to the various demands of evapotranspiration.

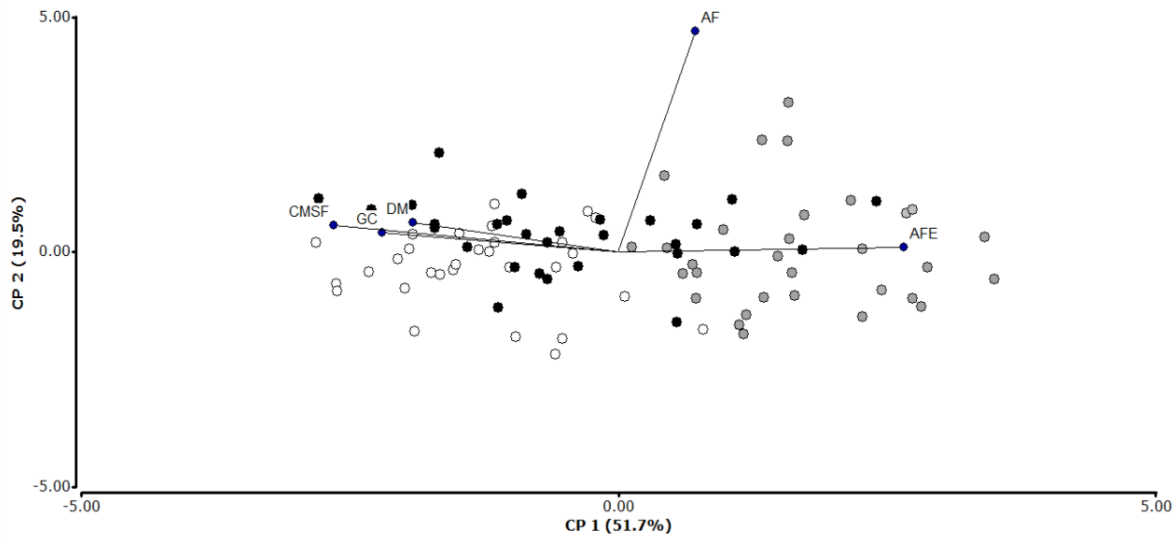
It is barely appropriate to interpret the variation of each trait separately, as the organs of the plants perform more than one function, as in the case of the bark thickness, which not only has protective functions against biotic and abiotic factors, but is also related to the allotment and distribution of the nutrients and the water within the plant, and to the respiration and photosynthesis at the level of the stem (Roth, 1981; Pfanz *et al*., 2002; Paine *et al.,* 2010, Cernusak and Hutley, 2011; Lawes *et al*., 2011; Poorter *et al*., 2014; Pausas, 2015; Rosell *et al*., 2015; Rosell, 2016). The compensation may be in the entire plant, not just in a particular organ. The adjustment of the values of the functional traits may be the result of the coordinated compensation within each individual (Rosell, 2014).

Functional strategies in the use of the resources

In response to the heterogeneous availability of resources in the environment and for purposes of their efficient exploitation, functional ecology suggests that the vegetal species may migrate within a range of functional variation along specific specialization axes (Wright *et al*., 2004; Freschet *et al*., 2010; Freschet *et al.,* 2012; Reich, 2014), and alternate between conservative strategies in environments where the natural conditions accentuate the environmental barrier (conservative species) and acquisitive strategies, in which a rapid acquisition and renewal of resources (acquisitive species) is pursued. This compensation is based on the investment of resources in the various organs and tissues of the plant to enhance its durability and degree of tolerance to different types of environmental conditions.

The conservative species are characterized by investing in more dense, lasting and protective tissues, while acquisitive species choose soft, rapid-growing tissues (Díaz *et al.,* 2004; Chave *et al*., 2009; Baraloto *et al.,* 2010; de la Riva *et al*., 2014; Díaz *et al*., 2016).

The principal component analysis (Figure 3) shows a main axis that explains the largest part of the variability (51.7 %), in which the functional traits and the individuals are distributed along this first specialization axis of acquisitive and conservative strategies in regard to the use of resources. Thus, the individuals associated with conservative strategies (high contents of leaf dry matter, higher wood density and greater bark thickness) were located at the negative extreme, while the individuals associated with more acquisitive strategies (with high values for specific areas of their leaves) were placed at the opposite end.



White circles = TDF individuals; Gray circles = TWF individuals; Black circles = TVWF individuals (see abbreviations in Tables 1 and 2).

Figure 3. Principal component analysis for the 5 functional traits and the 90 *Cedrela odorata* L. individuals considered in this study.

The trees of the TDF and 66 % of the population of the TVWF have been observed to grow in the conservative region of the axis. Based on the values of the SLA, CLDM, WD and BT, we infer that this population of *C. odorata* has a low photosynthesis rate and a low relative growth, as it invests its resources in leaf tissues and has a denser, stronger stem, which affords it greater resistance to pathogenic agents, to herbivority, and to physical damage due to abiotic factors; therefore, these individuals have a higher life expectancy. All specimens of the THG and the rest of the population of the TVWF are at the opposite extreme. According to the values of the traits of this population, these trees have a higher photosynthesis rate than the conservative population, and therefore, they have a greater relative growth. However, the tissues of their leaves and stem are less resistant to biotic and abiotic factors, so they have a lower life expectancy.

The LA had no relationship with these traits because its variance is associated to axis two (19.5 %) and is independent from other features; the variation of this morphological feature may be associated to a different specialization axis.

The functional attributes of the populations of the extremes of the gradient (TDF and TVWF) showed similar values, which suggests that precipitation is not the filter with the greatest effect on the process of adjustment of these attributes. There may be another factor or a synergy of various factors that influence the intraspecific variation in *C. odorata* in the study area (Bergholz *et al.*, 2017). Lohbeck *et al.* (2013) suggest that, when the effect of the availability of water diminishes, other environmental elements, like the availability of light due to inter- and intraspecific competition, acquire greater strength and therefore the individuals focus their functional strategies on tolerating the low availability of light due to the presence of a tighter canopy.

Based on various climate change scenarios for the study area, Fung *et al.* (2017) estimate that, by the year 2060, the dry forest of the *Nicoya* Peninsula will displace the wet forest. Apparently, this change will be rapid, as the flat terrain that is characteristic of this area will favor the process. In this sense, the results of this research suggest that the populations of *C. odorata* existing in the *Nicoya* Peninsula have the potential to modulate the expression of their functional traits and adapt to the new environmental conditions that climate change will bring about in this area of the planet. However, the rapidity with which the species may adjust its traits and, therefore, whether these adjustments will allow the survival of the species, is unknown.

The results indicate that the plants have a great variability between phenotypes and highlight the importance of considering the intraspecific variability of traits when seeking to understand the adaptive responses of the species to environmental alterations. The study of the variation of the functional traits is necessary to know how the living organisms may respond to global changes (McGill *et al.* 2006). These responses will depend on the type of character and its inheritability (Lloyd-Smith *et al.*, 2005).

Conclusions

The study of the variation of functional risks of *Cedrela odorata* proves that there is a degree of divergence between phenotypes along a precipitation gradient in the *Nicoya* Peninsula, in *Costa Rica*. Furthermore, the leaf area was observed to be larger in individuals belonging to humid ecosystems.

In his geographical area, *Cedrela odorata* has been shown to exhibit its morphological traits within an acquisitive-conservative specialization axis of resource use. In this regard, the results suggest that this species has the potential to adapt to the new environmental conditions that are predicted for the *Nicoya* area; however, climate change is a complex scenario where the response of the species can be strongly conditioned by the geography of the study area, the time-space scale considered, the nature and width of the sampled environmental gradient, or even the genotype of the individuals. Therefore, further research on the intraspecific variability of the morphological traits is required in order to determine how climate change will affect the performance and distribution of the taxa.

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Conflict of interests

The authors of this paper declare that they have no conflict of interests.

Contribution by author

Luis Alan Galindo Segura: planning and execution of the project, and revision and editing of the manuscript; Bryan Finegan, Diego Delgado and Francisco Mesén Sequeira: counseling in the development and execution of the Project, and drafting and editing of the manuscript.

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