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The tree *Cedrela odorata* (Meliaceae): A morphologically subdivided species in Costa Rica

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Abstract: In Latin America, *Cedrela odorata* is a wide ranging species that occurs in several environments, where it shows significant morphological variation. A common garden experiment was established with seedlings from 63 families of ten populations from two habitat types (mesic and dry), distributed throughout Costa Rica, to examine the relationships between quantitative variation and site of population origin. Seedlings from dry areas tended to be distinct from those from mesic areas, with climatic grouping of provenance explaining a mean of 52% of the total variance and 80% of the genetic variance. Cluster analysis for seedling traits showed two natural groupings of families, which corresponded for the most part with the regional population groupings into mesic (Atlantic and South Pacific) and dry (North Pacific) groups. Cluster analysis based on seed weight and size also separated populations into mesic and dry climatic groups. Seeds from populations in dry areas were 43% heavier, and seedlings were 61% taller, 117% greater in diameter, and with leaflets 39% longer and 81% wider. These differences may be related to fast growth in the dry zone for taking advantage of early life cycle moisture availability. These findings may indicate incipient speciation in *C. odorata* in Costa Rica. Evaluation of reproductive isolating mechanisms between populations from the mesic and dry zones, and of clines at potential zones of hybridization would assist in testing a speciation hypothesis.

Key words: Common garden experiments, geographic variation, *Cedrela odorata*, adaptation, speciation.

Cedrela odorata is one of the best known species of the Meliaceae in Costa Rica and is distributed throughout the country, both in the Pacific and Atlantic watersheds. At present, *C. odorata* is very rare in the natural forests of Costa Rica due to exploitation and, possibly, selective environmental requirements. Herbarium specimens have been collected by the authors in different parts of the country including the north and central Pacific (Cañas, Cobano, Carmona, Hojancha, Liberia), south Pacific (Pérez Zeledón, Coto Brus, Golfito) and Atlantic (Guápiles, San Carlos, Upala) regions. These samples show significant morphological variation that is probably the result of environmental effects, as well as genetic effects. Characterization of environmental and genetic components of variation would improve the understanding of patterns of differentiation and adaptation as well as possibilities for conservation of this wide-ranging species.

Historically, the genetic basis of quantitative variation in plant species has been characterized using common garden experiments (Clausen *et al.* 1940, 1948). Given the time to maturity for trees, traits from early in the life cycle are useful for distinguishing populations. Common garden studies of seedling growth have been useful for relating genetic differences with patterns of environmental variation in the geographic range of a species (Sorenson 1983, Toval and Puerto 1985, Loopstra and Adams 1989, Sorenson *et al.* 1990), including tropical species (Ladiges *et al.*

TABLE 1
Meteorological data of the progenies evaluated

Population	Acronym	Number of families	Climatic station	Annual rainfal (mm)	Number of dry months	Altitude (m)	Life zone[1]	Climatic group[2]
Cañas	CAN	5	Las Juntas	2273	5	140	TMF	d
Hojancha	HOJ	5	Nicoya	2232	5	120	TMF	d
Carmona	CAR	5	Colonia Carmona	1779	5	100	TMF	d
Cobano	COB	3	Cobano	2896	5	160	TMF	d
Cobano	COB	7	Cabuya	2873	4	3	TMF	d
Liberia	LIB	5	Llano Grande, Liberia	1652	5	85	TDF	d
Talamanca	TAL	2	Vesta, Penshur	3981	0	50	TMF	m
Talamanca	TAL	2	Chase, Bri - Bri	2662	0	40	TMF	m
Guapiles	GUA	4	Los Diamantes	4465	0	250	PWF	m
Upala	UPA	4	Upala	2558	3	50	TWF	m
San Carlos	SAN	7	La Fortuna	3608	0	250	PWF	m
San Carlos	SAN	10	Santa Clara	4317	0	160	TWF	m
Zona Sur	ZOS	1	Palmar Sur	3706	3	16	PWF	m
Zona Sur	ZOS	3	Golfito	4817	0	15	TWF	m

1 TDF tropical dry forest, TMF tropical moist forest, PWF premontaine wet forest, TWF tropical wet forest. (After Holdridge 1967).
2 d = dry, m = moist

1981, Navarro and Vásquez 1986, Román Jiménez *et al.* 1996, Kundu and Tigerstedt 1997, Li 1998).

Various provenance trials have been conducted in the past for *C. odorata* (Whitmore 1971, 1978, Karani 1973, Rauno 1973, Guevara 1988), but these did not examine the relationship between trait expression and environmental variables. Navarro and Vásquez (1986) evaluated variation in seeds and seedlings of *C. odorata* from a total of six populations from the Pacific and Atlantic regions of Costa Rica and Nicaragua. In this study we examined progenies from ten different areas in the Pacific and Atlantic zones of Costa Rica, and the relative amounts of genetic variation at regional, provenance and progeny levels using seedling growth traits and morphological variation in seeds.

MATERIALS AND METHODS

An extensive collection of *C. odorata* germplasm was made in Mexico and parts of Central America (including Costa Rica) for purposes of germplasm conservation and tree improvement. From this collection, 63 families were selected at random from various provenances on the Atlantic and Pacific slopes of Costa Rica for comparison (Table 1 and Fig. 1). In this paper, we use family to indicate progeny groups from the same parent tree. Populations from the Atlantic and the South Pacific regions experience a shorter dry season than populations in the North Pacific region, and usually have higher rainfall (Table 1). Each population

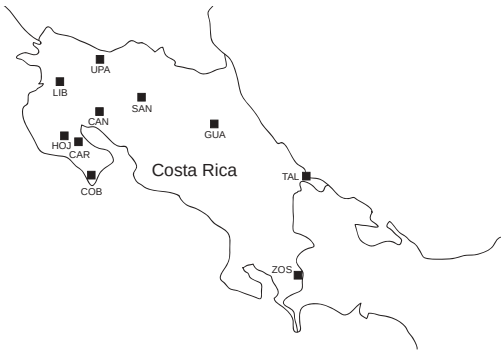

Fig. 1. Distribution of *Cedrela odorata* samples used in this study. Map by Carlos Navarro. Costa Rica 1999.

was assigned accordingly to the mesic (m) or dry (d) climatic group. The dry areas are not necessarily very arid and have a period of at least 1000 mm of precipitation, but the dry period may be of up to six months in length in the North Pacific zone of Costa Rica.

Nursery preparation: The experiment was performed under field conditions in Turrialba. The mean annual conditions for temperature and precipitation were 21ºC and 2479 mm, respectively, relative humidity was 87% and solar radiation was 11.82 $\mu J/m^2$ (F. Jiménez unpublished). Seeds were germinated in a bed filled up to approximately 5 cm with sand previously washed and sterilized with formalin. They were positioned vertically with the embryo closest to the substrate, but were not covered with sand. This position had resulted in superior germination in other trials. Humidity of the seedbed was kept constant to avoid desiccation or fungal growth. Seeds germinated in 7 to 12 days. The time of initiation and termination of germination varied among families.

Seedlings were planted out from the seedbed about a week after germination when they had a hardened stem and two well-developed primary leaves. Plants were removed from the germination bed with care to avoid root damage and the roots were maintained in water during transplanting. Seedlings were replanted in plastic bags 10.2 cm wide by 20.3 cm long, in a soil mix of one part fine sand, three parts compost, and 100 g of a complete fertilizer. Plants were kept under shade cloth for two weeks after removal from the germination bed to permit recovery from transplanting. The identity of the progeny groups was maintained throughout all the steps of this process.

Experimental design and measurements: The experiment was designed as a common garden to minimize environmental variation in order to detect genetic differences among progenies, provenances, and provenance groupings. The 63 progenies were grouped in a randomized complete block design, with one representative per block and three blocks.

The model for analysis of variance was:

$$Y_{ijkl} = m + B_i + C_l + P_k(C_l) + F_j(P_k*C_l) + e_{ijkl},$$

where Y_{ijkl} is the phenotypic value of an individual tree, m is the population mean, B_i is the block effect, $F_j(P_k*C_l)$ is the progeny effect within population and climate, $P_k(C_l)$ is the effect of the population within climate, C_l is the effect of the climate group to which the population belongs, and e_{ijkl} is the experimental error.

The variables measured of the seedlings included total plant height (ht) in cm, stem diameter at the root collar (dac) in mm, and length (ll) and width (lw) of the largest leaflet in mm. Leaflet width was divided by leaflet length to obtain an index of leaflet shape (lw/ll). The measurements were done at 73 days. A sample of 100 seeds for each of the 63 progenies was weighted in g and the length and width were measured in mm on five seeds per family with a calibrator. The ratio of seed width to seed length was calculated.

Statistical analysis: Least square means were determined for all seedling traits for provenance and regional groupings using the LSMEANS statement of PROC GLM (SAS 6.12, SAS Institute). The Scheffe adjustment for least square mean comparisons was used, as these were *post hoc* comparisons (SAS Institute 1990). The cluster analysis was based on family level means for seedling traits, and on family and provenance level means for seeds. The unweighted group-pair method (UPGMA) for obtaining linkages was used based on unsquared arithmetic means standardized to an overall mean of zero and a standard deviation of one (PROC CLUSTER, SAS 6.12). An analysis of variance (ANOVA) was performed using PROC GLM (SAS 6.12), with the climate grouping a fixed effect and all other effects considered to be random.

In the ANOVA the individual effects may be significant, but contribute only marginally to the explanation of the overall variance. Thus, a variance component analysis was developed to determine the relative contributions of the different effects to the total variance (Fleiss

TABLE 2

Least square means (lsm) and standard errors (se) by provenance for selected seed and seedling traits[1]

Climatic group	Population	Seed weight			Seedling height			Seedling dac			Leaf length			Leaf width			Ratio lw/ll		
		lsm	se	sep[2]	lsm	se	sep[2]	lsm	se	sep[2]	lsm	se	sep[2]	lsm	se	sep[2]	lsm	se	sep[2]
d	Canas	2.31	0.14	1	16.4	0.47	1	6.47	0.22	1	7.61	0.19	1	3.13	0.11	1	0.41	0.02	1
d	Carmona	2.05	0.13	x	14.73	0.47	1	6.07	0.22	1	7.11	0.19	1	2.73	0.11	1	0.39	0.02	x
d	Cobano	2.20	0.09	1	14.67	0.33	1	6.33	0.16	1	7.95	0.14	1	3.05	0.08	1	0.38	0.01	1
d	Hojancha	2.35	0.13	x	14.47	0.47	1	6.13	0.22	1	6.94	0.19	1	2.75	0.11	1	0.4	0.02	1
d	Liberia	2.17	0.11	1	15.67	0.47	1	6.27	0.22	1	7.93	0.19	1	3.04	0.1	1	10.38	0.02	x
m	Guapiles	1.32	0.14	x	11.17	0.52	x	3.58	0.25	2	5.87	0.22	x	1.83	0.12	2	0.31	0.02	x
m	San Carlos	1.25	0.07	2	9.65	0.26	2	2.81	0.12	2	5.44	0.11	2	1.61	0.06	2	0.3	0.01	2
m	Talamanca	1.32	0.14	x	8.58	0.52	2	2.75	0.25	2	6.02	0.22	x	1.65	0.12	2	0.27	0.02	x
m	Upala	1.21	0.13	x	10.4	0.47	2	3.07	0.22	2	5.57	0.19	2	1.63	0.11	2	0.29	0.02	x
m	Zona Sur	1.26	0.14	2	6.67	0.52	2	2.08	0.25	2	4.3	0.22	2	1.45	0.12	2	0.33	0.02	x

1 See Materials and Methods for trait acronyms and units.

2 Also noted for each trait are the provenances which showed differences between the two climatic groups by the Scheffe criteria at the 0.01 significance level from provenances in the opposite climatic group (Sep 1 and 2). X indicates provenances excluded from these comparisons for certain traits because they did not have a minimum 0.01 significant difference for all comparisons with provenances in the opposite climatic group.

1969, Underwood and Petraitis 1993), including models with both fixed and random effects (Vaughan and Corballis 1969, Dodd and Schultz 1973). To determine the components of the variance, the expected mean sums of squares were used for each effect from SAS Proc VARCOMP, according to the formulas provided by Winer *et al.* (1991). Variance components were determined using restricted maximum likelihood (SAS 6.12 PROC VARCOMP). This method is relatively robust both for unbalanced designs (Huber *et al.* 1994) and departures from normality (Westfall 1987).

RESULTS

Seeds and nursery seedlings from the dry areas tended to be distinct from those of the moist areas (Tables 2 and 3). Seeds from the dry areas were 43% heavier, and seedlings from the dry zones were 61% taller and 117% greater in diameter than those from the the mesic regions ($p = 0.0001$ for all traits, Table 3). Leaflets were 39% longer, and 81% wider, and 25% more ovoid on seedlings from the drier regions than those from the mesic areas ($p = 0.0001$ for all traits, Table 3). Provenances from one regional group were usually significantly different from those of the other group in the least square means for these traits (Table 2). Seedlings from Cañas had the greatest dimensions for all the traits and Zona Sur the smallest dimensions (Table 2).

For seed traits, climatic group was always very significant, and explained on average 66% of the total variance (Table 4). For seedling traits, climatic group was also always very significant, and contained the majority of the explained variance (mean of 52% of total variance or 80% of the genetic variance, Table 4). Provenance level effects within climatic regions were never significant, and explained very little of the total variance.

For seedling traits, family level effects within provenances were usually very

TABLE 3
Least square means and standard errors by regional grouping for selected seed and seedling traits[1]

Climatic	Seed weight			Seed length			Seed width		
group	lsm	se	sep[2]	lsm	se	sep[2]	lsm	se	sep[2]
d	2.22	0.05	1	0.98	0.03	1	0.41	0.01	1
m	1.27	0.06	2	0.74	0.03	2	0.34	0.01	2

Climatic	Seedling height			Seedling dac		
group	lsm	se	sep[2]	lsm	se	sep[2]
d	15	0.2	1	6.3	0.09	1
m	9.3	0.21	2	2.9	0.1	2

Climatic	Leaf length			Leaf width			Ratio lw/ll		
group	lsm	se	sep[2]	lsm	se	sep[2]	lsm	se	sep[2]
d	7.5	0.08	1	2.9	0.05	1	0.4	0.01	1
m	5.4	0.09	2	1.6	0.05	2	0.3	0.01	2

1 See Materials and Methods for trait acronyms and units.
2 Also noted for each trait is the regional grouping separation (SEP) by the Scheffe criteria at the 0.0001 significance level.

significant, and explained a mean of 31% of the total variance or 20% of the genetic variation (Table 4).

The cluster analysis for seedling traits (Fig. 2) showed two natural groupings of families which corresponded for the most part with the regional provenance groupings into mesic (Atlantic and South Pacific) and dry (North Pacific) groups. One family of each of the provenances Cobano, Carmona, and Hojancha were classified with the "moist" rather than the "dry" grouping. The cluster analysis based on provenance level seed characteristics also separated provenances, except for Cobano, into corresponding climatic groups (Fig. 3).

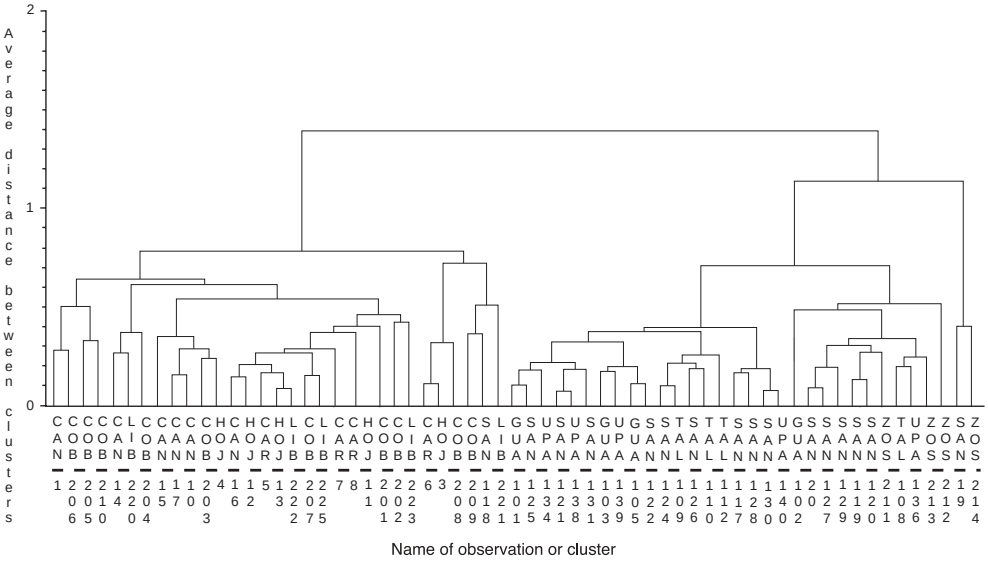

Fig. 2. Phanerogram from cluster analysis on seedling traits with a clear separation between Atlantic and Pacific groups in *Cedrela odorata*. Acronyms for provenance group membership are indicated in Table 1. Can = Cañas, Cob = Cóbano, San = San Carlos, Car = Carmona, Upa = Upala, Tal = Talamanca, Zos = Zona sur, Lib = Liberia, Hoj = Hojancha, Gua = Guápiles.

TABLE 4

Significance of effects (p)[1] from analysis of variance and percentage of total variance explained by each variance component (VC) for seed and seedling trait[2]

	Seed								Seedling						Leaf					
	weight		length		width		Mean[3]		height		dac		length		width		Ratio	Mean[3]
EFFECT	p	VC	p	VC	p	VC	p	VC	p	VC	p	VC	p	VC	p	VC	lw/ll	
Var(BLOCK)								NS	0	**	1	NS	0	NS	0	NS	0	0
Var(CLIM)	****	86	****	62	****	51	66	****	52	***	71	****	44	****	63	****	31	52
Var(POP(CLIM))	NS	0	NS	0	NS	0	0	NS	3	NS	0	NS	4	NS	0	NS	0	1
Var(FAM(CLIM*POP))								****	25	****	11	****	30	****	11	NS	0	15
Var(Error)		14		38		49		34		20		17		22		26	69	31
% of the genetic variance among provenances[4]		ND[5]		ND		ND		ND		68		87		61		85	100	80
% of the genetic variance within provenances[4]		ND		ND		ND		ND		32		13		39		15	0	20

1 NS p > 0.05, **0.001 > p > 0.01, ****0.0001 > p.

2 See Methods for trait acronyms and units.

3 Also calculated are the mean variance components separately for traits measured on seeds and seedlings.

4 For each trait the distribution of total genetic variation is distributed between provenances (CLIM + PROC) and within provenance (FAM) variation.

5 ND = not determined.

Fig. 3. Phanerogram from cluster analysis using seed traits showing the separation of the population in two main groups.

DISCUSSION

The clear segregation of the progenies into two distinct groups in the present study is remarkable (Figs. 2 and 3). Other studies using seedlings had demonstrated a relationship between characteristics of the seedlings and environmental parameters but have not shown such clear phenotypic segregation in few groups (Ladiges *et al.* 1981, Sorenson 1983, Toval and Puerto 1985. Loopstra and Adams 1989, Sorenson *et al.* 1990, Kundu and Tigerstedt 1997).

Navarro and Vásquez (1986) also found strong differentiation in *C. odorata* between populations of dry and wet zones based on seed and seedling characteristics of progenies from the Pacific and Atlantic of Costa Rica and Nicaragua with annual rainfall ranging from 1500 mm to 4240 mm. Significant differences occurred between Pacific and Atlantic provenances in length, width, and surface area of the seeds, and in the height, dac, and root length of seedlings. Alvarez (1999) compared seeds and fruits of *C. odorata* trees from Las Juntas (Pacific) and Jimenez (Atlantic). The trees from Jimenez had smaller fruits and more seeds per fruit than the trees from Las Juntas.

Other studies have also noted a larger seed weight in tree populations from dry areas than wet areas (Sorenson 1983, Toval and Puerto 1985, Loopstra and Adams 1989, Sorenson *et al.* 1990, Wright *et al.* 1992). Early seedling

growth in populations from dry areas may (Toval and Puerto 1985, Sorenson *et al.* 1990, Wright *et al*. 1992) or may not (Sorenson 1983, Loopstra and Adams 1989, Román Jiménez 1996, Li 1998) be greater in populations from dry areas. In the *Abies procera/A. magnifica* species complex, Sorenson *et al*. (1990) found that seedlings from southern, drier areas were larger in the first year, but that their growth rate slowed down considerably in subsequent growing seasons, and related initial faster growth to larger seed size and a longer growing season. Wright *et al.* (1992) also found that faster early seedling growth was mostly attributable to larger seed size in populations of *Pinus banksiana* from dry areas than from adjacent wet areas and that the differences in seedling growth decreased by 35 days.

In our study, the differences in growth rates in the nursery between the dry and wet provenances may be in part attributable to adaptation for survival in the natural environment. The lower availability of moisture and the extensiveness of the dry season in the North Pacific part of Costa Rica may select for rapid growth at the seedling stage. Larger leaves allow for more photosynthesis, and potentially faster root and stem growth during a short wet period would facilitate plant survival during the dry season. However, these patterns may change at a later phase of the life cycle. In *Cedrela* provenance/species trials in St. Croix (USVI), Puerto Rico, Uganda, and Tanzania, from the nursery stage up to 14 months, the provenance from Guanacaste, Costa Rica (dry zone) was usually superior in growth to other sources (Whitmore 1971, Karani 1973, Rauno 1973). After two years, other sources passed up the Guanacaste provenance in height (Karani 1973, Rauno 1973, Whitmore 1978).

Although the nature of the variation is different, the distribution of genetic variation between (80%) and within populations (20%) in this study parallels earlier findings using RAPDs molecular markers for these same populations (Gillies *et al.* 1997). RAPDs are neutral markers resulting from dominant alleles, quantitative traits are multigenic and more influenced by selection. With RAPDs markers, 35% of the genetic variance occurred between the wet and dry zones, none among populations within zones, and 65% within populations. By the Shannon diversity index, 55% of the variation occurred among populations (including among the two zones) and 45% of the genetic variation occurred within populations. The current study and the molecular marker work are in contrast with the general observation that the vast majority of the genetic variation is within populations (80-90%) in woody and perennial outbreeding species (Hamrick and Godt 1990). *Cedrela odorata* is a wide-ranging species and the overall genetic variability is high compared with species with narrower geographic or ecological distributions (Hamrick and Godt 1990).

The variation seen in the populations sampled for this study is ecotypic rather than clinal. This indicates limited gene flow between the two groups of populations that have become differentiated (Ridley 1990). There are several potential explanations for the observed patterns of variation. Differentiation may have occurred when the cordilleras Volcanica Central and Guanacaste raised a barrier within the range of the species in Costa Rica, reduced gene flow, and the populations in two zones began to evolve independently. Alternatively, these two groups could have spread from different refugia after the Pleistocene glaciations where they had started to diverge.

The Cobano population is similar in seedling traits to other dry Pacific provenances, but is located at the tip of the Nicoya Peninsula in an area of higher rainfall. The area may have been colonized by or maintained in common gene pool with trees from the dry Pacific provenances, because seed movement or gene flow from other mesic areas was prevented by the central mountains (Volcanica Central and Guanacaste). The Upala population is similar to the mesic Atlantic populations but is in an area intermediate in rainfall between the Pacific and the east Atlantic. It may have been colonized by or formed a common gene pool with Atlantic populations if movement from the Pacific was blocked by the cordillera. Although it is on the

south Pacific coast of Costa Rica, the Zona Sur population has affinities with the Atlantic mesic populations. A RAPDs study of *C. odorata* indicated similarity between Zona Sur and a population from northern Panama (C. Navarro unpublished). Central Panama may serve as a pathway for gene flow between the Atlantic and southern Pacific populations, or have been a refugium for these populations during glacial periods (Colinvaux 1996, p. 397).

The differentiation could also be the result of adaptations to the contrasting moisture regimes encountered by the two sets of populations. These climatic differences could have resulted in separation in flowering time that would reduce gene flow between climatic regions. In that case, the RAPDs markers identified by Gillies must be either linked to loci subjected to selection, or be under selection themselves, rather than neutral markers.

The amount of differentiation among populations within a species can range from almost none to distinctness usually attributed to different species (Mayr 1963 cited by Ridley 1990). The differentiation seen in these populations in RAPDs markers is greater than that seen in some closely related species (Gillies *et al.* 1997), and suggests that *C. odorata* may be in the process of forming new species in Costa Rica. The distinction between these two groups of populations investigated should be maintained by a pre- or post-reproductive isolating mechanism (Ridley 1990), which should be further investigated. The potential cline between the Upala and Liberia populations should also be investigated as evidence for incipient speciation.

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RESUMEN

En latinoamérica, *Cedrela odorata* es una especie ampliamente distribuida que está presente en varios ambientes, donde muestra una variación morfológica significante. Se estableció un experimento común de jardín con plántulas de 63 familias de 10 poblaciones de dos tipos de hábitat (mésico y seco), distribuidas por toda Costa Rica, para examinar las relaciones entre la variación cuantitativa y el sitio de origen de la población. Las plántulas de áreas secas eran distintas de las de áreas mésicas, con el agrupamiento climático del sitio de origen explicando un promedio de 52% de la varianza total y 80% de la varianza genética. El análisis de conglomerados para los rasgos de las plántulas mostró dos grupos naturales de familias, que correspondieron en su mayor parte con los grupos de las poblaciones regionales en grupos mésico (Atlántico y Pacífico Sur) y seco (Pacífico Norte). El análisis de conglomerados basado en el peso y el tamaño de las semillas también separó las poblaciones en los grupos climáticos mésico y seco. Las semillas de poblaciones en áreas secas fueron 43% más pesadas y las plántulas fueron 61% más altas y 117% mayores en diámetro, y con las hojuelas 39% más largas y 81% más anchas. Estas diferencias pueden estar relacionadas a un crecimiento rápido en la zona seca para tomar ventaja de la disponibilidad de humedad en el ciclo de vida temprano. Estos resultados pueden indicar una especiación incipiente en *C. odorata* en Costa Rica. La evaluación de los mecanismos de aislamiento reproductivo entre poblaciones de las zonas mésica y seca y de las clinas en las zonas potenciales de hibridización ayudaría a probar una hipótesis de especiación.

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