Contrasting Quantitative Traits and Neutral Genetic Markers for Genetic Resource Assessment of Mesoamerican Cedrela Odorata

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Abstract

We compared within-population variability and degree of population differentiation for neutral genetic markers (RAPDS) and eight quantitative traits in Central American populations of the endangered tree, *Cedrela odorata*. Whilst population genetic diversity for neutral markers (Shannon index) and quantitative traits (heritability, coefficient of additive genetic variation) were uncorrelated, both marker types revealed strong differentiation between populations from the Atlantic coast of Costa Rica and the rest of the species' distribution. The degree of interpopulation differentiation was higher for RAPD markers (F_{ST} = 0.67 for the sampled Mesoamerican range) than for quantitative traits (Q_{ST} = 0.30). Hence, the divergence in quantitative traits was lower than could have been achieved by genetic drift alone, suggesting that balancing selection for similar phenotypes in different populations of this species. Nevertheless, a comparison of pair-wise estimates of population differentiation in neutral genetic markers and quantitative traits revealed a strong positive correlation (r = 0.66) suggesting that, for *C. odorata*, neutral marker divergence could be used as a surrogate for adaptive gene divergence for conservation planning. The utility of this finding and suggested further work are discussed.

Key words: Cedrela odorata, F_{ST}, genetic differentiation, geographic variation, heritability, natural selection, quantitative traits, RAPD, Q_{ST}.

Introduction

Understanding the causes and extent of local adaptation, as well as distribution of genetic variability within and among populations are central themes in evolutionary biology and conservation genetics. Considerable efforts has been devoted to characterising population variability and differentiation for a range of species using neutral genetic markers (e.g. WARD *et al.,* 1992; AVISE, 1994; SMITH and WAYNE, 1996). However, much less work has been undertaken in this respect using quantitative traits and typically, estimates of quantitative genetic variance and heritability are limited to single or few populations of a species. Studies comparing estimates of genetic variation from both neutral and quantitative markers are even less numerous (reviews in: REED and FRANKHAM, 2001; MERILÄ and CRNOKRAK, 2001; MCKAY and LATTA, 2002).

Recently, there has been increased interest in evaluating the usefulness of neutral genetic markers for drawing conclusions about quantitative trait variation (e.g. CHEVERUD *et al.,* 1994; BUTLIN and TREGENZA, 1998; WALDMANN and ANDERSSON, 1998; PFRENDER *et al.,* 2000) and differentiation (reviews in: REED and FRANKHAM, 2001; MERILÄ and CRNOKRAK, 2001; MCKAY and LATTA, 2002). This interest has been motivated by two different, albeit intimately related, desires. First, in conservation genetics, where molecular markers have been utilised at an ever-increasing rate, there is a need to establish whether variability in neutral markers reflects variability at quantitative trait loci involved in local adaptation and selection pressures. Inference based on surveys of variability in molecular markers are now routinely used as a basis for management recommendations under assumptions that maximizing marker variability will provide remnant populations with the greatest evolutionary potential, and at the same time, minimise the negative consequences of inbreeding (e.g. VRIJENHOEK, 1994; AVISE and HAMRICK, 1996; HAIG, 1998; KNAPP and RICE, 1998). Likewise, the degree of differentiation in marker genes has been suggested as a measure for guiding decisions on population conservation (e.g. MORITZ *et al.,* 1995) and sources for translocation or restoration projects (TEMPLETON, 1986; HAIG, 1998; KNAPP and RICE, 1998). Second, from an evolutionary perspective, the utility of neutral genetic markers for evaluating the relative importance of genetic drift and natural selection as causes of population differentiation has been a popular motive fuelling interest in comparative studies of population differentiation (MERILÄ and CRNOKRAK, 2001). This is based on the assumption that variation at neutral genetic markers will be governed primarily by forces of genetic drift and migration (HARTL and CLARK, 1989), whereas quantitative traits will also be affected by natural selection. The difference in the magnitude of standardised genetic differentiation between these two classes of marker is then used to infer the role of selection (WRIGHT, 1951; ROGERS, 1986; SPITZE, 1993; MERILÄ and CRNOKRAK, 2001).

In agreement with theoretical predictions (LANDE and BARROWCLOUGH, 1987; LYNCH, 1996), many empirical studies have found poor correspondence between variation at neutral genetic markers and quantitative traits (CHEVERUD *et al.,* 1994; BUTLIN and TREGENZA, 1998; WALDMANN and ANDERSSON, 1998; PFRENDER *et al.,* 2000; PALO *et al.,* 2003; but see BRISCOE *et al.,* 1992). In addi-

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tion, a review of empirical data by REED and FRANKHAM (2001) failed to find any correlation between levels of differentiation for neutral genetic markers and quantitative traits. In contrast, a recent comparative review (MERILÄ and CRNOKRAK, 2001) of population differentiation for neutral genetic markers (as measured by F_{ST}) and quantitative traits (as measured by Q_{ST}) found that the two measures of differentiation were positively correlated for a range of species (see also: CRNOKRAK and MERILÄ, 2002), and that differentiation for quantitative traits typically exceeded that for neutral markers. However, between population comparisons within a single species are likely to be much more informative about the level of correspondence between marker types than comparisons over species. Still, most intraspecific comparisons of genetic differentiation for marker types have so far focused on average differentiation (cf. mean F_{ST} and Q_{ST}), and not pair-wise estimates among populations. One possible explanation for this is that the number of populations included in each of the case studies is usually small, and hence, the power of such comparisons can be low.

Using data from 30 Mesoamerican populations of the endangered Spanish Cedar (*Cedrela odorata*), we estimated and compared genetic variation and differentiation in quantitative traits and neutral genetic markers to (1) identify possible locally adapted ecotypes and (2) to evaluate whether variability in marker genes is correlated with variability in genes coding quantitative traits. In particular, we evaluated the correspondence between: (1) genetic variability in neutral genetic markers (RAPD) and ecologically important quantitative traits (as reflected in additive genetic variance and heritability) across populations, and (2) degree of population differentiation in neutral genetic markers and quantitative traits, as measured by F_{ST} and Q_{ST} indices, respectively.

Materials and Methods

Study species

Spanish cedar (*Cedrela odorata* L.; Swietenioideae, Meliaceae) is a deciduous tree native to tropical America. It is economically the second most important species of the Meliaceae in the Neotropics, and also one of the latitudinally most widely distributed tree species on earth, with a range from 26°N in Mexico to 28°S in northern Argentina (STYLES, 1981; NAVARRO, 1999). Although Spanish Cedar is widespread, it is never very common in moist tropical American forests, and its numbers are continuing to be reduced by exploitation without successful regeneration. Individual trees are typically scattered in mixed semi-evergreen or semi-deciduous forests dominated by other trees. Spanish Cedar starts to reproduce at an age of 10–12 years, and the reproductive cycle is strongly influenced by local rainfall patterns, so that flowering occurs at the end of the dry season. Seeds mature during the subsequent dry season and are dispersed by wind (NAVARRO, 1999). The large climatic variation across the range means that flowering time differs among populations by up to five months. Consequently, a climatically driven phenological reproductive barrier is to be expected. In accordance with this, GILLIES *et al.* (1997), using RAPD markers, and CAVERS *et al.* (2003), using AFLP markers, found that populations of the Pacific and Caribbean coasts of Costa Rica were highly differentiated (F_{ST} = 0.452 and 0.83, respectively). Likewise, numerous provenance studies (e.g. BURLEY and LAMB, 1971; NAVARRO and VASQUEZ, 1987) suggest extensive differentiation for

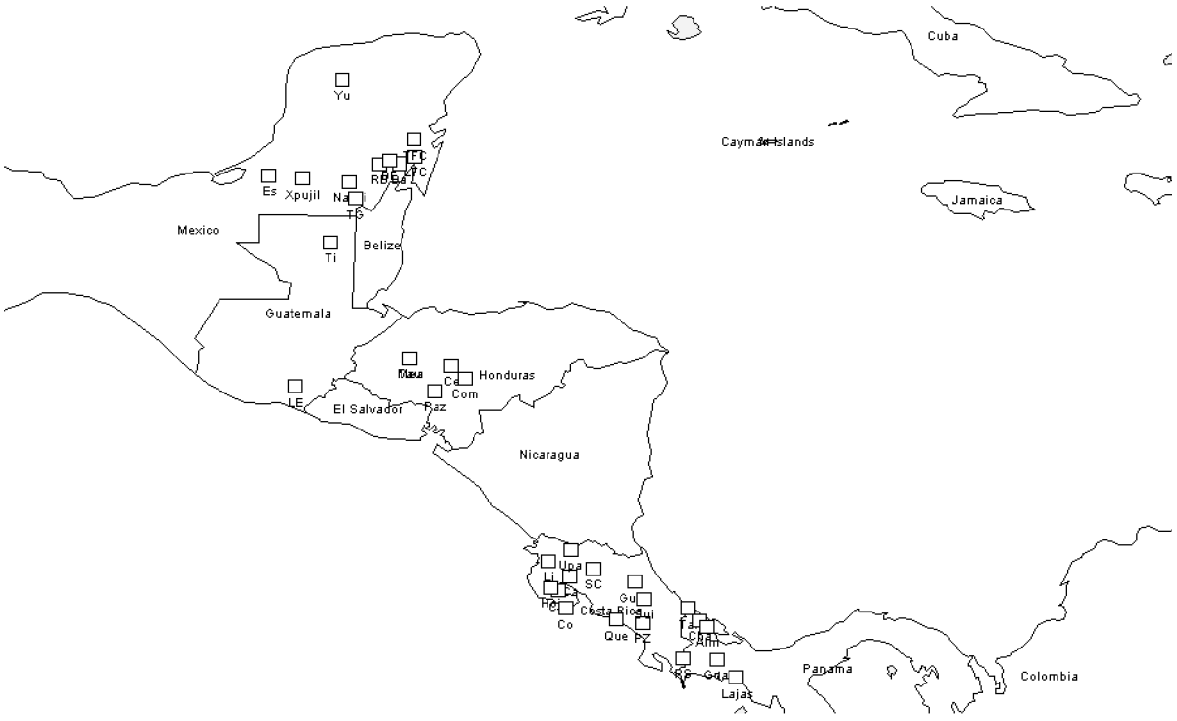

Figure 1. – A map showing the location of the 30 populations of *Cedrela odorata* used in this study.

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Table 1. – The study populations, their coordinates with associated climatic data and seed production. NDM = number of dry months.

Country	Population	Latitude (°N)	Longitude (°W)	Rainfall (mm)	Rain (start-end)	NDM	Seed collection
México	Xpujil	18.54	-90.14	1094*	Jun -Oct	7	March 10th
Mexico	Nachi-Cocoon	18.48	-89.24	1094.0	Jun -Oct	7	March 15
México	Reforma-Bacalar	18.85	-88.67	1094.0	Jun -Oct	7	March 16
México	Tres Garantías	18.12	-89.14	1094.0	Jun -Oct	7	March 17
México	Limones-Felipe	19.01	-88.00	1094.0	Jun -Oct	7	March 20
México	Tulum-FCP	19.35	-88.01	1094.0	Jun -Oct	7	March 22
México	Bacalar	18.85	-88.30	1094.0	Jun -Oct	7	March
México	Escárcega	18.62	-90.78	1094.0	Jun -Oct	7	April 9
México	Blanca Flor	18.92	-88.49	1094.0	Jun -Oct	7	March 15
México	Yucatán	20.59	-89.39	936*	Jun –Sep	8	April 15
Guatemala	Los Esclavos	14.25	-90.28	2834*	May- Oct	6	March 17
Guatemala	Tikal	17.22	-89.61	1366.7**	May –Nov	5	April 5
Honduras	La Paz	14.15	-87.61	1976*	May- Oct	6	March 26
Honduras	Taulabe	14.83	-88.10	2425*	May- Oct	6	March 23
Honduras	Comayagua	14.41	-87.05	912*	May- Oct	6	March 22
Honduras	Cedros	14.66	-87.30	1272*	May- Oct	6	March 3
Honduras	Meambar	14.83	-88.10	2425*	May- Oct	6	March 15
Costa Rica	Cañas	10.32	-85.04	2273.6***	May- Nov	5	15 Feb
Costa Rica	Upala	10.86	-85.02	2558.3***	May- Jan	3	March 10
Costa Rica	San Carlos	10.47	-84.58	4574.1***	Apr- Feb	1	March 20
Costa Rica	Carmona	10.01	-85.25	1779.9***	May -Nov	5	Dec18
Costa Rica	Cóbano	9.65	-85.12	2896.8***	May -Nov	5	Dec
Costa Rica	Talamanca	9.65	-82.79	2812***	Apr -Nov	4	Feb
Costa Rica	Jimenez	10.19	-83.79	4465.8***	May- Apr	0	Jan 9
Costa Rica	Hojancha	10.07	-85.40	2232.3***	May- Nov	5	15 March
Costa Rica	Pacífico Sur	8.62	-82.88	4817.7***	May- Apr	0	Feb 24
Costa Rica	Pérez Zeledón	9.34	-83.65	2934.5***	Apr- Nov	4	Feb 26
Costa Rica	Liberia	10.63	-85.45	1652.7***	May- Nov	5	Feb
Costa Rica	Quepos	9.42	-84.16	3851***	Apr- Dec	3	Feb
Costa Rica	La Suiza	9.85	-83.61	2657.3***	Apr- Feb	1	Feb
Panamá	Charagre	9.40	-82.56	3319*	Apr -Dec	3	Feb 11
Panamá	Almirante	9.28	-82.41	3319.0	Apr -Dec	3	Feb
Panamá	Gualaca	8.59	-82.23	2620*	Apr -Nov	4	March 8
Panamá	Las Lajas	8.22	-81.86	2620*	Apr -Nov	4	March 9

* Data from: FAO 1985. Agroclimatological Data of Latin America and the Caribbean. FAO Plant Production and Protection Series. Roma. 19 p.

** Data from: Aguilar, M. and M. C. Aguilar. 1992. Árboles de la Biosfera Maya Petén. Universidad de San Carlos de Guatemala. 272 p.

*** Data from: Ministerio de Recursos Naturales, Energia y Minas. Instituto Metereológico Nacional. 1988. Catastro de las series de precipitaciones medidas en Costa Rica. San José, Costa Rica. 361 p.

quantitative traits between these two geographic regions.

The study populations

The 30 populations are from Mesoamerica which is defined like the area between Tehuantepec Isthmus in Mexico to the Atrato river in Panama) including the Yucatan Peninsula, a latitudinal distribution from 21°N in Mexico to 8°N in Panama (*Fig. 1*; *Table 1*). The study populations are located throughout an area of ca 41000 km^2 including a wide variety of environmental conditions. For instance, mean annual rainfall among the study populations ranges from 1500 to 3500 mm, and the number of dry months varies from 0 to 5 (*Table 1*). For estimates of quantitative variation, seeds from the 30 populations were raised in a randomised block, common garden glasshouse experiment at the University of Helsinki (Finland). The seedlings were raised in a mix containing sand, 40% vermiculite and 50% peat. Temperature (25°C), humidity (90%) and day-length (12:12

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Table 2. – Summary of mean genetic variability measures for different quantitative traits (h^2 = heritability; C_{VA} = coefficient of additive genetic variance) and RAPD markers (SDI = Shannon diversity estimate) in 14 populations of the Spanish cedar. n_Q = number families/individuals in quantitative genetic analyses. n_M = number of individuals in molecular genetic analyses.

		Mean		Range			
Pop	n_Q	h^2 ± S.E.	CV_A	h^2	CV_A	SDI ± S.E.	n_M
Charagre	15/90	0.488 ± 0.63	14.1	0.196 - 1.109	11.0 - 24.1	0.166 ± 0.292	11
Cóbano	7/40	0.373 ± 0.97	14.2	0.069 - 0.716	3.0 - 26.8	0.337 ± 0.279†	8
Escarcega	22/130	0.742 ± 0.52	25.6	0.315 - 1.499	9.4 - 74.5	0.042 ± 0.115	8
Esclavos	20/110	0.731 ± 0.30	28.7	0.181 - 1.431	7.0 - 59.1	0.027 ± 0.077	19
Hojancha	9/54	0.792 ± 0.67	18.8	0.475 - 1.428	13.4 - 35.7	0.313 ± 0.290†	6
Jimenez	5/25	0.578 ± 0.98	17.1	0.349 - 1.878	11.2 - 58.8	0.240 ± 0.292†	5
La Paz	13/61	0.153 ± 0.22	6.3	0.056 - 0.460	10.8 - 15.3	0.011 ± 0.038	15
Cañas	6/30	1.386 ± 0.81	68.6	0.694 - 1.994	15.7 - 148.6	0.369 ± 0.276†	6
Pacífico Sur.	19/114	0.867 ± 0.14	33.8	0.509 - 1.524	13.1 - 84.4	0.175 ± 0.263	12
San Carlos	15/85	0.507 ± 0.22	19.6	0.060 - 1.299	8.5 - 38.5	0.361 ± 0.281†	14
Talamanca	4/24	0.266 ± 0.72	10.6	0.177 - 0.277	8.8 - 58.0	0.296 ± 0.307†	4
Upala	19/111	1.066 ± 0.36	52.7	0.602 - 1.479	15.8 - 108.9	0.277 ± 0.307†	7
Xpujil	22/132	0.765 ± 0.34	22.4	0.043 - 1.365	2.9 - 60.6	0.071 ± 0.196	13
Yucatan	13/74	0.820 ± 0.59	28.5	0.330 - 1.361	8.3 - 46.8	0.107 ± 0.225	13

† Estimates based on data from GILLIES *et al.,* 1997.

dark/light) were kept constant, and the seedlings were watered daily. For characterisation of molecular genetic variability using RAPD markers, we were constrained to genotype material from only seven of these populations as indicated in *Table 2*. However, data for an additional seven populations (*Table 2*) was obtained from GILLIES *et al.* (1997).

Neutral genetic marker analyses

Estimates of levels of neutral genetic population diversity and differentiation were made using RAPD markers. DNA extraction was performed on seeds germinated from 400 single mother trees using a modified CTAB method (GILLIES *et al.,* 1997). PCR amplification of the DNA was performed in 25 µl volume using 10 pairs of Operon Technologies Ltd primers (OPC1-10) using a MJR thermal cycler. Program conditions were: 45 cycles of 1 minute at 94 °C, 1 minute at 36 °C, and 2 minutes at 72 °C; and a final cycle of 7 minutes at 72 °C. Each PCR reaction included: 1/10 buffer, 2 mM dNTPs, 1 unit of Dynazyme Taq DNA polymerase (Finnzymes), 0.4 µm primers and distilled water to a volume of 25 µl. The products were visualised under UV transillumination (in 0.1%TBE buffer containing a few drops of ethidium bromide) after separation in 1.8% agarose gels (Sigma). Presence/absence of each scorable RAPD fragment was recorded in a binary data matrix and POPGENE v1.2 (YEH, 1997) was used to calculate the frequency of polymorphic bands in each population. On average 13 (range: 8–19) individuals (one per family) were genotyped from each of the populations listed in *Table 2*.

Since interpretation of RAPD patterns does not follow segregation rules of standard co-dominant markers, Shannon's Diversity Index (SDI; as calculated by the software package POPGENE v1.31; YEH, 1998) was used as a measure of intra-population genetic diversity. It is well suited to the analysis of RAPD data as it is relatively insensitive to the bias produced by failures to detect heterozygous individuals (DAWSON *et al.,* 1995). Since the indices of variability used for the analysis of RAPD markers (OPC1-17) in the study of GILLIES *et al.* (1997) were different from ours, SDIs were recalculated for their data using the data given in their *Table 2.* Since the primers used in our study and that of GILLIES *et al.* (1997) were not the same, the calculated measures may still not be comparable between the two data sets. In fact, the mean (± S.E.) SDI is significantly higher (0.31 ± 0.17) for the populations genotyped by GILLIES *et al.* (1997) than for populations genotyped in this study (0.09 ± 0.25; MANN-WHITNEY, z = 3.13, P = 0.0017), despite the mean number of individuals genotyped per population being lower in the former study (x = 7.4 and 13, respectively; MANN-WHITNEY, z = 2.43, P = 0.015). Whether the difference in RAPD variability is due to differences in primer specificity, or the geographic range of samples (all populations typed by GILLIES *et al.,* 1997, originate from Costa Rica), cannot be ascertained. However, CAVERS *et al.* (2003) also found low levels of variability for AFLP markers on a similar range of samples

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as those used by GILLIES *et al.* (1997). Hence, to be cautious, we performed separate analyses for the two data sets (henceforth: data-set 1: populations genotyped in this study; data-set 2: populations genotyped by GILLIES *et al.,* 1997), in addition to pooled analyses.

The degree of population differentiation for RAPD markers, corresponding to F_{ST} and its standard error, was obtained from partitioning the variability in the data into within (v_w) and between (v_b) population components of genetic variation (WRIGHT, 1951) using the formula:

$$F_{ST} = \frac{v_b}{v_b + v_w} \quad (1)$$

F_{ST} was calculated separately for the two data sets and on pooled data. Standard errors were obtained using a Bayesian approach (HOLSINGER and LEWIS, 2002; HOLSINGER *et al.,* 2002).

Quantitative genetic analyses

Estimates of population genetic variability and differentiation were obtained for eight quantitative traits. Depending on the population, 4–22 (average = 13.5, see *Table 2*) seeds were sampled from each open pollinated mother tree. One seedling per family was sown in each of the six blocks. Due to mortality (1.2%) during the experiment, on average 5.6 individuals per family (1080 in total) were measured for the traits described below. The wide range of variation in the number of families used per population is due to the scarce and endangered nature of *C. odorata*, and the number of families per population reflects local population size (*Table 2*).

The response variables measured on seedlings at an age of 62 days included: (1) Height (H; in mm), (2) leaflet length (LL; in mm), (3) width of the third leaflet from the tip of the leaf LW), and (4) leaflet shape index as obtained by dividing leaf length by leaflet width (LL/LW). In addition, 252 days after sowing, eight additional measurements were obtained. These were: (5) height (H2 in mm), (6) internodal distance (ID; the length of the stem from the tip to the fourth branch in cm), (7) trunk diameter (D; in cm at 2 cm height from the soil, (8) the number of leaflets per leaf (NL). The mean values (± S.E.) of these traits are given in *Table 3*.

To estimate population specific heritabilities and coefficients of additive genetic variance (CV_A; HOULE, 1992), data for each population and trait was subjected to variance component estimation using the REML algorithm of PROC VARCOMP in SAS. For these analyses, models included the term family (random effect). Because open pollinated trees were used, we assumed that the members of the same family were half-sibs, i.e. that the term family estimates 1/4 V_A. This assumption may lead to overestimation of heritability as the seeds from single trees may also contain full sibs or selfed offspring. Likewise, from the point of view of Q_{ST} estimates (see below), this assumption will render our estimates of interpopulation differentiation conservative.

Narrow sense heritabilities (h^2) were obtained as $h^2 = 4 \times \sigma^2_F/\sigma^2_P$, where σ^2_F is the variance component due to family and σ^2_P is the total phenotypic variance of the trait (i.e. $\sigma^2_F + \sigma^2_E$), where σ^2_E is the residual component of variance. The standard errors for heritability were calculated according to DIETERS *et al.* (1996). CV_As were calculated according to Houle (1992) as $CV_A = 100 \sqrt{V_A}/x$, where V_A is the additive genetic variance, and x is the mean trait value in the sample used to estimate the V_A.

To obtain a standardised estimate of among population differentiation comparable to F_{ST} for molecular markers, we estimated Q_{ST} values as:

$$Q_{ST} = \frac{\sigma^2_{GB}}{2\sigma^2_{GW} + \sigma^2_{GB}} \quad (2)$$

where σ^2_{GB} is the among population component of genetic variance, and σ^2_{Gw} is the within population genetic component of variance (WRIGHT, 1951; MERILÄ and CRNOKRAK, 2001). The among population component of variance for each trait was estimated as the added variance component from a mixed linear model performed using data from all populations (or in the case of pair-

Table 3. – Least square means and standard errors for quantitative traits in *Cedrela odorata* greenhouse study. See methods for trait abbreviations. *n* = number of families/individuals.

	Trait mean ± S.E								
Population	H	LW	LL	LL/LW	H2	D	ID	NL	*n*
Charagre	99.7 ± 1.5	11.2 ± 0.2	32.0 ± 0.3	2.93 ± 0.05	8.3 ± 0.5	0.30 ± 0.01	5.7 ± 1.9	4.3 ± 1.7	15/90
Cobano	99.2 ± 3.3	12.8 ± 0.6	31.8 ± 1.3	2.56 ± 0.09	60.9 ± 5.3	0.92 ± 0.08	36.1 ± 1.7	15.6 ± 0.7	7/40
Escarcega	133.8 ± 1.7	15.2 ± 0.2	36.6 ± 0.4	2.46 ± 0.03	64.3 ± 3.9	0.80 ± 0.04	37.7 ± 1.8	17.1 ± 0.7	22/130
Esclavos	126.8 ± 2.7	15.3 ± 0.3	37.2 ± 0.6	2.48 ± 0.04	65.9 ± 3.3	0.80 ± 0.03	36.9 ± 1.5	17.0 ± 0.6	20/110
Hojancha	123.0 ± 2.3	16.6 ± 0.3	43.0 ± 0.7	2.63 ± 0.05	64.1 ± 2.7	0.89 ± 0.03	42.5 ± 1.5	18.2 ± 1.1	9/54
Jiménez	86.5 ± 5.0	9.4 ± 0.4	27.8 ± 1.1	3.04± 0.13	10.1 ± 1.0	0.31 ± 0.02	8.1 ± 2.6	5.1 ± 2.0	5/25
Cañas	97.5 ± 2.9	12.7 ± 0.4	32.4 ± 1.1	2.63 ± 0.13	50.9 ± 0.8	0.68 ± 0.02	24.4 ± 1.7	14.5 ± 1.2	6/30
La Paz	120.4 ± 2.9	14.5 ± 0.4	38.4 ± 0.8	2.71 ± 0.07	70.3 ± 7.3	0.89 ± 0.08	38.1 ± 2.9	16.2 ± 0.8	13/61
Pacífico Sur	116.6 ± 2.6	11.7 ± 0.2	32.2 ± 0.3	2.82 ± 0.03	12.9 ± 0.7	0.32 ± 0.02	8.1 ± 2.2	3.2 ± 1.4	19/114
San Carlos	77.0 ± 1.5	7.6 ± 0.2	24.2 ± 0.4	3.25 ± 0.07	9.0 ± 0.9	0.23 ± 0.01	8.9 ± 5.9	7.1 ± 1.9	15/85
Talamanca	58.8 ± 3.3	8.7 ± 0.5	28.1 ± 1.5	3.41 ± 0.13	8.4 ± 0.5	0.25 ± 0.02	7.3 ± 5.5	7.3 ± 2.8	4/24
Upala	111.8 ± 1.9	11.6 ± 0.2	34.2 ± 0.4	3.11 ± 0.07	17.8 ± 13	0.40 ± 0.02	14.6 ± 1.7	9.4 ± 4.6	19/111
Xpujil	119.0 ± 1.7	14.7 ± 0.2	36.9 ± 0.4	2.55 ± 0.03	73.7 ± 4.1	1.04 ± 0.06	39.9 ± 2.1	19.3 ± 1.0	22/132
Yucatán	124.4 ± 1.9	14.6 ± 0.2	34.0 ± 0.5	2.36 ± 0.03	52.7 ± 5.4	0.80 ± 0.04	35.0 ± 2.8	15.8 ± 0.6	13/74

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wise estimates, for the two populations in question). The within population component was obtained as explained above. To evaluate the implications of assuming members of a given family were half- rather than full-sibs (or a mixture), we also estimated Q_{ST} values under assumptions that all the offspring in a given family were full-sibs.

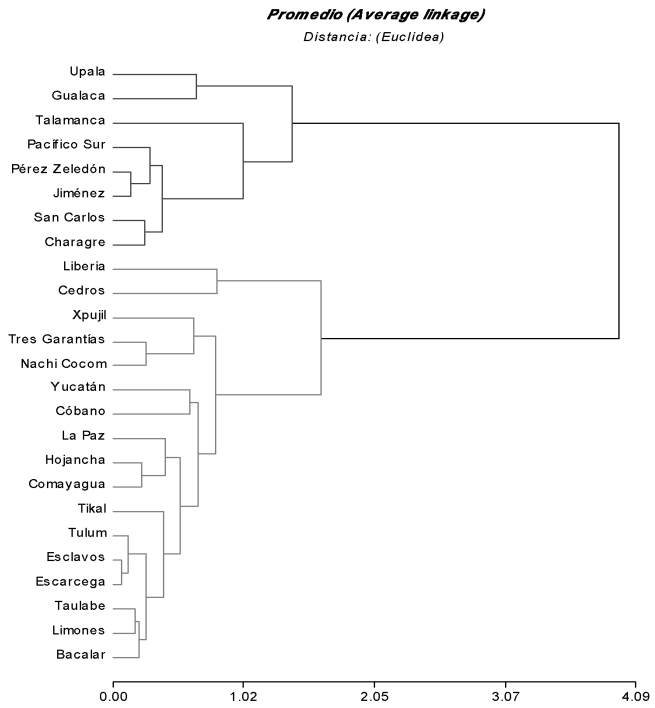

Figure 2. – Cluster analyses of quantitative traits in a greenhouse in Finland. Note that the clusters correspond to mesic (Almirante to Upala) and dry (Bacalar to Yucatan) environment populations. The morphological distances are based on Euclidean distances and the genetic distances on Nei's (1987) genetic distances.

Cluster analyses were used to examine similarities between populations for all quantitative characters using Euclidean distances and the software (Infostat, 2005).

Comparison of neutral and quantitative genetic variability

To investigate correspondence between neutral and quantitative genetic variability across the populations, we calculated pair-wise Spearman product moment correlations between Shannon's Diversity Index for RAPD markers and heritability estimates for (1) each of the quantitative traits separately, and (2) for the mean heritability estimates for different traits. Since the different traits vary greatly both in terms of size and dimensionality, we also performed analyses using standardised measures of additive genetic variance using coefficients of additive genetic variability (CV_A; HOULE, 1992). Because the genetic variability measures based on RAPD markers may not be comparable between the two RAPD data sets, we performed tests for data involving (i) only populations scored for this study, (ii) only populations scored by GILLIES *et al.* (1997), and (iii) on combined data.

To investigate correspondence between levels of neutral and quantitative genetic differentiation, we first compared the overall estimates of F_{ST} and Q_{ST} for the two data sets using two-sample *t*-tests. For these tests, each locus and trait were considered as independent observations. To see whether pairwise population estimates of F_{ST} and Q_{ST} are correlated, we performed a

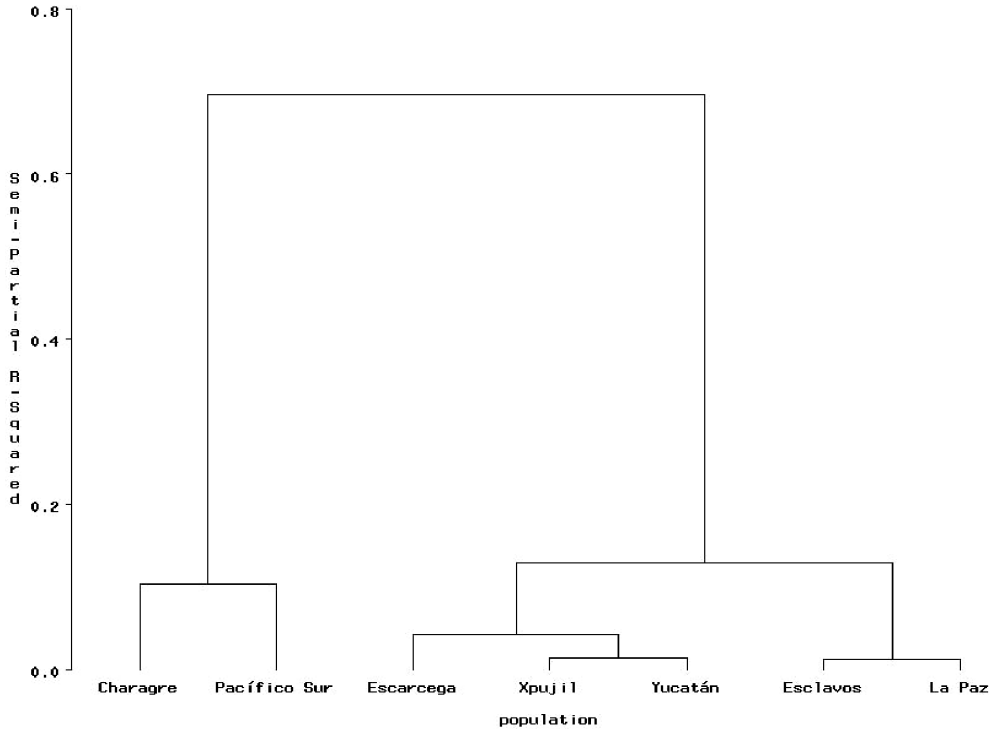

Figure 3. – Cluster analyses of RAPD data for the seven *C. odorata* populations in the sub-set 1 (see methods).

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Table 4. – Nested analyses of variance of quantitative traits and RAPD markers, together with associated Q_{ST} and F_{ST} estimates for different subdivisions of data. Q_{ST} estimates are given under assumption of half-sib (HS) and full-sib (FS) structure of the data. POP = population, FAM = family (nested within population), ERR = error variance components, respectively.

Trait	POP	FAM	ERR	$Q_{ST(HS)}$ ± SE	$Q_{ST(FS)}$ ± SE
All populations					
H62	410.24**	130.06***	429.63	0.283 ± 0.014	0.441 ± 0.034
LW62	7.182**	1.95***	5.88	0.315 ± 0.017	0.479 ± 0.039
LL62	22.549**	5.56***	26.37	0.336 ± 0.019	0.503 ± 0.043
LL/WL62	0.090**	0.05***	0.23	0.172 ± 0.006	0.293 ± 0.017
HC252	711.66**	205.29***	319.62	0.302 ± 0.015	0.464 ± 0.037
D252	0.08**	0.02***	0.05	0.324 ± 0.014	0.489 ± 0.033
ID252	246.14**	26.47**	115.13	0.538 ± 0.048	0.699 ± 0.081
NL252	44.46**	6.48**	32.55	0.462 ± 0.037	0.632 ± 0.069
Mean Q_{ST}				0.341 ± 0.021	0.500 ± 0.044
Subset 1					
H62	100.06*	119.40***	485.50	0.230 ± 0.004	0.173 ± 0.012
LW62	2.71*	1.83***	5.962	0.260 ± 0.009	0.270 ± 0.027
LL62	5.78*	5.39***	24.75	0.260 ± 0.006	0.211 ± 0.018
LL/WL62	0.04*	0.02***	0.158	0.150 ± 0.000	0.282 ± 0.001
HC252	737.04*	219.01***	463.720	0.230 ± 0.013	0.457 ± 0.045
D252	0.07*	0.02**	0.060	0.270 ± 0.008	0.490 ± 0.030
ID252	226.69*	15.25	141.230	0.430 ± 0.014	0.788 ± 0.053
NL252	43.24*	1.27	33.837	0.460 ± 0.009	0.895 ± 0.035
Mean Q_{ST}				0.286 ± 0.008	0.446 ± 0.028
F_{ST}				0.667 ± 0.064	
Subset 2					
H62	422.09*	152.33***	321.080	0.257 ± 0.026	0.409 ± 0.065
LW62	9.34*	2.18***	5.729	0.348 ± 0.044	0.517 ± 0.097
LL62	36.37*	5.89**	29.521	0.436 ± 0.063	0.607 ± 0.123
LL/WL62	0.08*	0.12***	0.376	0.083 ± 0.004	0.153 ± 0.013
HC252	635.71*	162.38***	88.442	0.329 ± 0.039	0.495 ± 0.089
D252	0.08*	0.02***	0.024	0.320 ± 0.035	0.485 ± 0.080
ID252	252.55*	43.95**	72.621	0.418 ± 0.063	0.590 ± 0.126
NL252	43.99	15.60**	30.453	0.261 ± 0.028	0.413 ± 0.069
Mean Q_{ST}				0.306 ± 0.038	0.459 ± 0.083
F_{ST}				0.325 ± 0.093	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Mantel's test (5000 permutations; Excel add-in 'PopTools' ver. 2.3; www.cse.csiro.au/CDG/poptools). Note that only 42 out of 66 possible pair-wise comparisons among 14 populations were possible because of the different marker systems used for the two RAPD data sets. Pair-wise comparisons were again performed separately for the two data sets (21 pair-wise comparisons for each subset).

Results

Descriptive patterns differentiation

Cluster analyses of quantitative traits revealed a strong differentiation between Atlantic populations of Costa Rica/Panama and Mexico/Honduras (*Fig. 2*). This same pattern was also evident in RAPD data (*Fig. 3*), showing that differentiation between populations from the Atlantic coast of Costa Rica and the rest of the species' distribution can be seen both in marker and quantitative trait data. Approximately 68% of the variation in quantitative traits was partitioned among populations, with populations from northern Central America and Mexico being larger in all traits than populations from the Atlantic coast of Costa Rica (*Table 4*).

Comparison of genetic variability

Mean heritabilities and CV_As, as well as their ranges are given in *Table 2*. Fifty-eight out of the 112 heritability estimates were significant, and average per population estimates of trait heritability ranged from 0.15 to 1.38, with CV_As between 6 and 81 (*Table 2*). The average Shannon's diversity index for the RAPD data ranged from 0.01 to 0.17 (*Table 2*). There was no correlation between levels of genetic variability for neutral genetic markers and average heritability in combined ($r_s = 0.03$, $n = 14$, $P = 0.50$), or in the separate datasets (Data-set 1: $r_s = 0.14$, $n = 7$, $P = 0.41$; Data-set 2: $r_s = 0.04$, $n = 7$, $P = 0.65$). The same was true for CVAs (Combined data: $r_s = 0.07$ $n = 14$, $P = 0.35$; Data-set 1: $r_s = 0.08$, $n = 7$, $P = 0.54$; Data-set 2: r_s 0.08, $n = 7$, $P = 0.53$). When tested on a per trait basis for different groupings of data, none of the 24 (i.e. 8 traits x 3 groupings) possible corre-

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lations were significant for heritability or CVA based analyses, respectively.

Comparison of genetic differentiation

F_{ST} estimates of RAPD markers revealed a high degree of population subdivision for both data sets (Data-set 1: F_{ST} = 0.670 ± 0.060; $P < 0.001$; Data-set 2: F_{ST} = 0.329 ± 0.002; $P < 0.001$). The results were also similar when NEI's (NEI, 1987) G_{ST} estimator of F_{ST} is used (Data-set 1: G_{ST} = 0.60; Data-set 2: G_{ST} = 0.36). The lower degree of differentiation for Data-set 2 compared to 1 is not surprising given the more restricted geographic coverage of the former (average [± S.E.] geographic distance between populations: Data-set 1 = 818.3 ± 107.4 km, Data-set 2 = 142.2 ± 17.34 km; Mann-Whitney, $z = 4.67$, $n = 42$, $P < 0.001$).

In contrast, the degree of quantitative trait differentiation, albeit substantial, was much lower than that observed for RAPD markers, under the assumption of half-sib family structure (*Table 4*). Average Q_{ST} across all populations was 0.30 (S.E. = 0.02), ranging from 0.17 to 0.53 for individual traits (*Table 4*). Q_{ST} values for Data-set 1 was 0.29 (S.E. = 0.01) and for Data-set 2 was 0.31 (S.E. = 0.04): these are significantly lower than (Data-set 1) or similar to (Data-set 2) the corresponding F_{ST} estimates for neutral genetic markers (*t*-tests; Data-set 1: t_{21} = 19.34, P < 0.001; Data-set 2: t_{16} = 0.63, $P = 0.53$). If full-sib family structure is assumed (*Table 4*), Q_{ST} estimates are lower than F_{ST} estimates for Data-set 1 (t_{21} = 6.66, $P < 0.0001$), but statistically indistinguishable for Data set 2 (t_{16} = 1.61, $P = 0.15$).

Although the degree of among population differentiation was much higher (or approximately equal if full-sib family structure is assumed) for RAPD markers compared to quantitative traits, pair-wise Q_{ST} estimates were strongly positively correlated with F_{ST} estimates, for both data sets (Mantel's tests; Data-set 1: $r = 0.69$, $P < 0.001$; Data-set 2: $r = 0.55$, $P = 0.020$; *Fig. 4a* and *b*). This is also true also for the pooled data sets (Mantel's test: $r = 0.93$, $P < 0.001$; *Fig. 4c*).

Discussion

The most salient findings of this study were that while the degree of differentiation for quantitative traits was lower than (or at best, similar to) that observed for neutral genetic markers, these two measures were strongly positively correlated in pairwise population comparisons. However, the levels of intra-population diversity for neutral genetic markers and quantitative traits were uncorrelated across populations. In what follows, we will discuss each of these findings, as well as their general implications, in turn. We end up with discussing the specific implications of the results for management and conservation of *C. odorata* populations.

Selection, drift or stabilising selection?

A common pattern in studies which have compared F_{ST} and Q_{ST} values for neutral genetic markers and quantitative traits, respectively, is that the degree of differentiation for the latter typically exceeds the former,

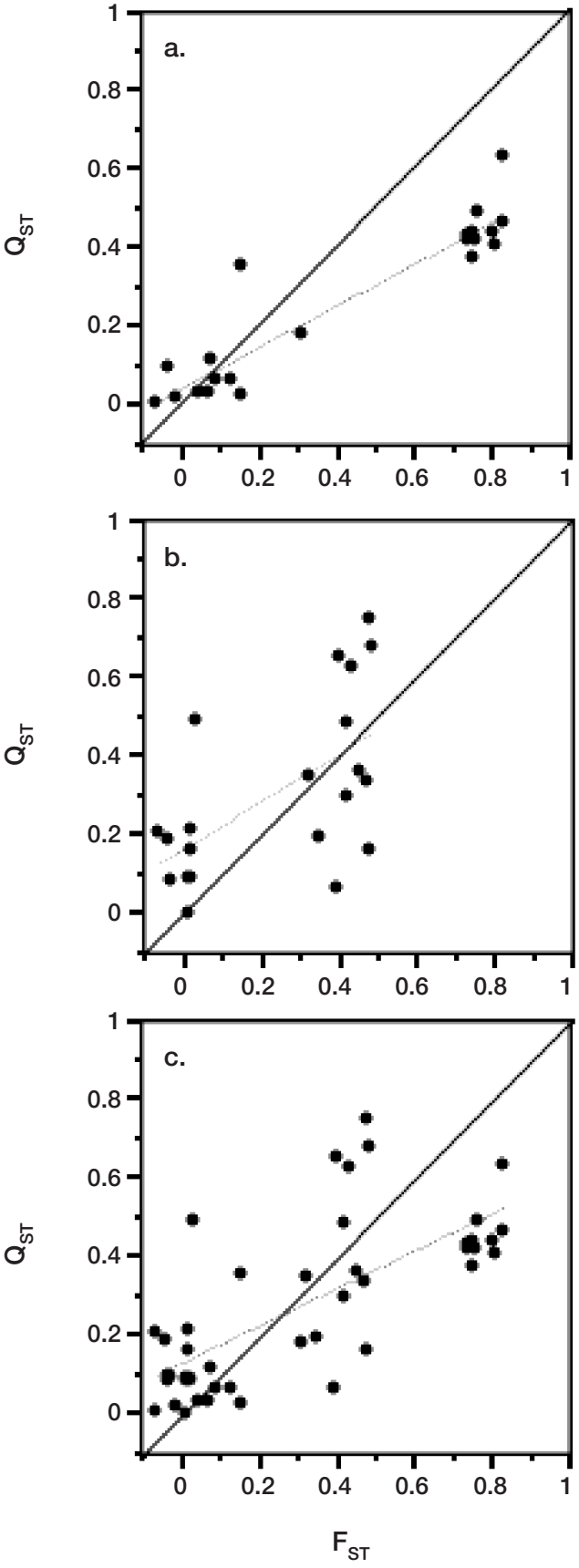

Figure 4. – Comparison of pair-wise Q_{ST} and F_{ST} estimates across the study populations for (a) Sub-set 1, (b) sub-set 2 and (c) and combined data. The solid line marks a 1:1 relationship for the correspondence between Q_{ST} and F_{ST} estimates, and the dotted lines are least square regression lines given for the ease of interpretation. See text for statistical tests.

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i.e. $Q_{ST} > F_{ST}$ (reviewed in: MERILÄ and CRNOKRAK, 2001; MCKAY and LATTA, 2002). This suggests that quantitative traits are typically under directional selection, and different populations exhibit different mean trait values, because under an assumption of neutrality, F_{ST} and Q_{ST} values are expected to be approximately equal (e.g. WHITLOCK, 1999). On the other hand, if $Q_{ST} < F_{ST}$, this suggests that quantitative trait divergence among populations is less than that expected due to a balance between genetic drift and migration. This is what we observed in the case of Spanish Cedar, suggesting that quantitative traits across populations are under some form of stabilising selection favouring similar phenotypes in different areas. This notwithstanding that the populations were shown to be strongly differentiated for mean values of all traits, and that the magnitude of differentiation in quantitative traits (mean $Q_{ST} = 0.34$) was comparable to that observed in other studies (mean Q_{ST} of 18 published studies = 0.37; MERILÄ and CRNOKRAK, 2001). Isolation in small populations is a likely explanation for high degree of differentiation at neutral loci, but in the case of quantitative traits, differentiation can be counteracted by selection. Another explanation for the observation that $Q_{ST} < F_{ST}$ is that we underestimated the degree of differentiation in quantitative traits. There are two reasons why this could be so. First, our estimates of additive genetic variance are likely to include maternal and dominance effects, which will lead to downward biased estimates of Q_{ST} (see Equation 2). Secondly, since we used open pollinated mother trees, it is not entirely certain whether the offspring were full- or half-sibs or even selfed. In the absence of more detailed information, it is perhaps safest to assume that the offspring in a given family were half- rather than full-sibs (SQUILLACE, 1974). Nevertheless, even if we assume a full sib family relationship, the mean Q_{ST} is 0.44 and 0.45 for the two data sets. Hence, even if the degree of differentiation might actually be in the range explained by genetic drift alone, it is fairly clear that the quantitative trait differentiation does not exceed that expected due to drift. Similar results have been recently obtained from few other studies (e.g. PETIT *et al.,* 2001; EDMANS and HARRISON, 2002; LEE and FROST, 2002).

Marker vs. quantitative trait divergence across different populations

In a review of earlier studies, MERILÄ and CRNOKRAK (2001) showed that the degree of differentiation among populations for quantitative traits was predictable from knowledge of the degree of differentiation at neutral genetic markers. Although MERILÄ and CRNOKRAK (2001) indicated that neutral genetic markers can be used as surrogate estimates for adaptive differentiation among populations, this may be a premature conclusion as the data on which this result is based comprised studies where both F_{ST} and Q_{ST} values ranged from zero to unity. Such variation is seldom observed in intraspecific studies, and in fact, only few studies to date has attempted to test for this relationship with intraspecific data (LONG and SINGH, 1995; MORGAN *et al.,* 2001; STEIGER *et al.,* 2002; GONZALES-MARTINEZ *et al.,* 2002; PALO *et al.,* 2003). In our study, we found a strong positive correlation between pair-wise F_{ST} and Q_{ST} estimates, corroborating the interspecific-level comparisons of LYNCH *et al.* (1999) and MERILÄ and CRNOKRAK (2001). This is noteworthy, as it suggests that knowledge of the degree of population differentiation for neutral genetic markers is informative about the degree of genetic differentiation for ecologically important traits in *C. odorata.* Similar positive correlation has been earlier observed also in some other intraspecific studies (e.g. MORGAN *et al.,* 2001; STEIGER *et al.,* 2002), but found to be trait and environment dependent in others (e.g. GONZALES-MARTINEZ *et al.,* 2002; PALO *et al.,* 2003).

For neutral genetic markers, differentiation among populations typically, but not always, increases with geographic distance, as is the case for our data (correlation between geographic distance and F_{ST} for Data-set 1: $r = 0.64$, $P < 0.001$). In quantitative traits, patterns of differentiation are governed mainly by local selection pressures. Thus, one would expect a similar distance relationship if the heterogeneity in selection pressures is also a function of geographic distance. While this remains currently an untested hypothesis, it seems plausible that the correlation between F_{ST} and Q_{ST} estimates could be driven by different processes which bear a similar relationship to geographic distance separating pairs of populations.

Marker vs. quantitative genetic diversity

We found that the levels of intrapopulation genetic variability in neutral markers was unrelated to intrapopulation variability in quantitative traits, as measured by heritability and coefficient of additive genetic variance. This is in accordance with the few similar tests conducted so far (e.g. CHEVERUD *et al.,* 1994; WALDMANN and ANDERSSON, 1998; LYNCH *et al.,* 1999; HURME *et al.,* 2000; PFRENDER *et al.,* 2000; but see: BRISCOE *et al.,* 1992; ZHAN *et al.,* 2005). This results is perhaps not surprising, given the multitude of factors that might influence levels of variability in quantitative traits (reviewed in PFRENDER *et al.,* 2000). Furthermore, despite *C. odorata* having a very small genome (WILSON *et al.,* 2001), the relatively few RAPD loci included in this study may not give a representative picture of genome-wide genetic variability. Hence, together with the limited number of populations surveyed, the results of our comparison may be viewed as conservative. However, given that our sample sizes were not smaller than those used in a typical conservation genetic study of wild populations, our results are in line with the conjecture that neutral genetic markers may not be very useful for purposes of inferring levels of variability in quantitative traits (LYNCH, 1996; PEARMAN, 2000; PFRENDER *et al.,* 2000).

Implications for management of endangered Spanish cedar populations

Our analyses of neutral genetic markers and quantitative traits revealed strong differentiation among the Mesoamerican populations of *C. odorata.* For quantitative traits, these results are concordant with earlier reports of high differentiation within and among Costa Rican and Nicaraguan C. odorata populations (NAVARRO

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and VASQUEZ, 1987; NAVARRO *et al.,* 2002). However, the much wider geographical range covered by the current study shows that these earlier studies capture only a limited proportion of the diversity exhibited by this wide-spread species. In particular, there appears to be clear ecotypic differentiation to two forms corresponding to populations inhabiting dry and mesic environments (*Fig. 2* and *3*). Hence, for quantitative traits, there exist at least two well-differentiated forms or ecotypes of *C. odorata*, each of which may be locally adapted to contrasting environmental conditions (see also GRAHAM, 1999). The practical implication of these results is that there is a need to maintain *in-situ* conservation areas, as well as *ex-situ* and *circa-situ* gene banks and plantations, for not only one, but at least for two forms of the endangered *C. odorata.* Naturally, the priority should be given to the areas where the species is most endangered.

Likewise, our analyses of RAPD differentiation concurred with results of GILLIES *et al.* (1997) and CAVERS *et al.* (2003), but covered a much wider geographic range. Given the socio-economic importance and endangered status of *C. odorata*, our results highlight the need for future studies encompassing the species' whole natural distribution including as yet unstudied populations in South America.

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