ALTITUDINAL GENETIC VARIATION AMONG *P. OOCARPA* POPULATIONS ON MICHOACÁN, WESTERN MÉXICO. PRELIMINARY RESULTS FROM A NURSERY TEST[1]

Cuauhtémoc Sáenz-Romero[1,4], Héctor Viveros-Viveros[2] & Ricardo R. Guzmán-Reyna[3]

[1] Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Apdo. Postal 12, Administración La Colina, Morelia Michoacán 58141, México.
[2] División de Ciencias Forestales, Universidad Autónoma Chapingo, Apdo. Postal 37, Chapingo Edo. de México 56230, México.
[3] Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia Michoacán 58041, México.
[4] To whom all correspondence should be addressed.

ABSTRACT

We are investigating if there is genetic differentiation among natural populations of *Pinus oocarpa* along altitudinal gradients. Open pollinated seeds from about eleven individual trees were collected from each of five *Pinus oocarpa* natural populations distributed along an altitudinal gradient from 1100 to 1500 m, near to Uruapan city, Michoacan state, western Mexico. A provenance/progeny test was established in a nursery and evaluated from 1 to 9 months of age. Genetic differentiation among populations was in general weak, significant only for number of cotyledons and nearly significant ($p = 0.076$) for 6-month-old diameter, and not significant for the rest of the examined variables: length of the longest cotyledon, height at 2, 6 and 9 months of age and diameter at 9 months of age. However, variance among half-sib families within populations was significant for all traits and ages. Number of cotyledons shows a clinal pattern, where in general average number of cotyledons is larger in populations from lower altitudes, and smaller in populations from higher altitudes. Diameter at 6 months of age shows an altitudinal variation pattern similar to a normal curve, where populations from the middle of the species altitudinal range show an "optimum" growth -having the largest diameter- and populations at the upper and lower extremes of the altitudinal range show the lowest diameters.

INTRODUCTION

México lives the paradox of being a center of diversity for the genus *Pinus* – about half of the 100 taxa of genus *Pinus* occur in Mexico (PERRY 1991, STYLES 1993) and a germplasm donor for pine species and provenance tests conducted around the world (WORMALD 1975, CAMCORE 2000), and on the other hand, México is depleting its tropical and temperate forest resources with an alarming estimated deforestation rate of 668,000 hectares per year (MASERA *et al.* 1995, MASERA *et al.* 1997).

México needs to know the patterning of adaptative genetic variation among native pine populations in order to delimitate seed production zones for guideline seed and seedling transfer (CAMPBELL 1986, 1991, SORENSEN 1994). This will improve the matching between genotypes and ecological conditions of the planting sites, and increase the success of commercial plantations and ecological restorations. Also we need to know how is partitioned the genetic variation among and within populations in order to decide the number, size and placement of natural protected areas for *in situ* conservation of forest genetic resources (LEDIG 1988, MILLAR & LIBBY 1991, SAGNARD *et al.* 2002) before it is too late.

Pinus oocarpa has the greatest north-south range of all the Mexican and Central American pines (PERRY 1991, DVORAK *et al.* 2000). In Mexico this species is economically important for the production of resin, sawtimber and plywood (ZAMORA-SERRANO 1981) and there are extensive commercial plantations in South Africa and South America (GREAVES 1982, DVORAK *et al.* 2000). *P. oocarpa* has a relatively large distribution within is the state of Michoacán (western México) whitin approximately 1,100 m to 1,600 m of altitude. This species is the most important pine for resin production and Michoacán is nation-wide first state producer of resin in México (COFOM 2001).

However, *P. oocarpa* locally-adapted popula-

---

tions are at risk by deforestation (DVORAK *et al.* 2000) that amounts 30,000 to 40,000 hectares per year of temperate and tropical forest for Michoacán state (COFOM 2001). In particular *P. oocarpa* natural stands are removed to establish avocado orchards, the fruit most economically important for this state (GUERRERO 2002). There are an important Michoacán state reforestation program of 16,000 ha/year (COFOM 2002). Unfortunately, the survivorship is low in average (approximately 35 % or less) (Sheinbaum and Masera 2000), in part due to the lack of information for appropriately matching species and provenances to reforestation sites (SÁENZ-ROMERO & MARTÍNEZ-PALACIOS 2000).

Coniferous populations differentiate genetically along altitudinal gradients on the Rocky Mountains on traits such as shoot elongation, growth rate and frost resistance, among other traits, apparently in response to differential selection pressures (CAMP-BELL 1979; REHFELDT 1988, 1989, 1991). Although genetic differentiation among *P. oocarpa* prove-nances have been extensively reported, most of the *P. oocarpa* provenances tested were collected from Central America –not from México- and field test were established elsewhere of México (GREAVES 1982, ROBBINS & HUGHES 1983, WRIGHT *et al.* 1988, OTEGBEYE 1991, MUGASHA *et al.* 1996, KARIUKI 1998, MOURA *et al.* 1998, MUGASHA *et al.* 1998, DVORAK *et al.* 2000), with few exceptions of tests made in México (MENDIZÁBAL-HERNÁNDEZ 1999), and in general those studies have not particu-larly addressed the issue of altitudinal genetic variation among natural populations. Thus, altitudinal patterns of genetic variation among *P. oocarpa* populations in Mexican native environ-ments are basically unknown.

We hypothesize than, similarly as conifer popu-lations do at the Rocky Mountains, Mexican pine populations genetically differentiate along altitudin-al gradients on the slopes of the main Mexican mountains systems such as Neovolcanic Axis, Sierra Madre Oriental, Sierra Madre Occidental and Sierra Madre del Sur. One important difference with Rocky Mountains is that Mexican pine species distribute in a narrower altitudinal range. For example, on the Rocky Mountains *Pinus contorta* populations distribute on an altitudinal range of 1,000 m (REHFELDT 1988), whereas for an equiva-lent altitudinal range of 1,000 m, on the southern slopes of the Neovolcanix Axis of Michoacán, México, there are six pine species (*P. oocarpa. P. pringleii, P. leiophylla, P. michoacana, P. pseudostrobus* and *P. montezumae*) growing partially overlapped on an altitudinal sequence of distribu-tion (from lower altitudes at 1,100 m to higher

altitudes at 2,100 m), and within such range *P. oocarpa* for example has an altitudinal range of only 500 m (from 1,100 to 1,600 m) (personal observa-tion). Thus, it remains to be seen if Mexican pine populations differentiate genetically in narrower altitudinal ranges, considering the large gene flow that characterize pine populations (HAMRICK & GODT 1990, HAMRICK *et al.* 1992, LATTA *et al.* 1998, SAVOLAINEN 1998).

We are interested in estimating the genetic differentiation on early-growth quantitative traits among and within *P. oocarpa* natural populations, along altitudinal gradients in the Neovolcanic Axis at Michoacán state, western México.

MATERIAL AND METHODS

Open pollinated cones were collected from approxi-mately eleven randomly selected trees from each of five *P. oocarpa* natural populations distributed along an altitudinal gradient from 1,100 m to 1,500 m on a southern slope of the Neovolcanic Axis in Michoacán state, western México. Populations were sampled on a North-South transect approximately every 100 m of altitudinal difference (1,075 m, 1,220 m, 1,325 m, 1,430 m and 1,505 m). Average geo-graphic distance between contiguous populations was 4 km. Highest sampling site (1,505 m) was located 1 km southern of the most southern edge of Uruapan city, Michoacán (19° 25' N, 102° 04' W, 18.9 °C average annual temperature, 1,608 mm average annual precipitation).

We established a nursery provenance/progeny test on a randomized complete block design with eighteen blocks, five populations and an average of ten half-sib families nested within each populations, making a initial total of 50 half-sib families (the five populations from the lowest altitudinal site to the highest altitudinal site were represented by 10, 8, 10, 13 and 9half-sib families, respectively) and three seedlings per plot.

Seeds were germinated on Petri dishes and then transplanted to 230 cm³ "Cooper-block®" commer-cial containers using a commercial substrate named Creciroot®. Dead seedlings within the first two weeks were replaced and later on in the analysis we used transplanting date as covariate – using one degree of freedom – as a way to substract such effect. Seedlings were raised at a nursery located at the Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia city, Michoacán (19° 42' N, 101° 11' W, 17.5 °C average annual temperature, 776 mm average annual precipitation).

Number of cotyledons and length of the longest cotyledon were evaluated at one month of age. Basal diameter (below the lowest primary leaf or branch) was evaluated at six and nine months of age. Height was evaluated at two, six and nine months of age.

Analysis of variance were conducted to test significance among provenances and among families within provenances for each variable using PROC GLM of SAS (SAS 1988). Results of analysis of variance are presented as intraclass correlation, the ratio of the variance component for the indicated effects to the sum of all components (REHFELDT 1993). Variance components were estimated using PROC VARCOMP of SAS (SAS 1988). The statistical model was:

$$Y_{ijkl} = \mu + b_i + t_j + w_k(t_j) + b_i \times t_j + b_i \times w_k(t_j) + e_{ijkl} \quad [1]$$

where Y_{ijkl} = observation on the lth seedling of the kth family of the jth population in the ith block, μ = overall mean, b_i = effect of the ith block, t_j = effect of jth population, $w_k(t_j)$ effect of the kth family nested in the jth population, $b_i \times t_j$ = interaction of block by population, $b_i \times w_k(t_j)$ = interaction of block by family nested in population, and e_{ijkl} = error term, $i = 1,...b$, $j = 1,...p$, and $k = 1,...t$, and $l = 1,...n$, where b, p, t and n are the number of blocks, populations, families and seedlings-per-plot. We considered blocks, populations and families as random effects because we viewed them as samples of larger populations of possible experimental site conditions, populations and families, respectively, for which we wanted to make inferences.

RESULTS

Number of cotyledons was the only variable significantly different among populations ($p = 0.0004$) (Table 1), which apparently shows a clinal pattern of variation where in general populations from lower altitudes have a larger average number of cotyledons, and populations from higher altitudes have smaller average number of cotyledons, except for the population at the highest sampled altitude (1,505 m), which had an atypical number of cotyledons (Figure 1). Diameter at 6 months of age were nearly significantly different among populations ($p = 0.0760$) (Table 1), with averages by population distributed along the altitudinal gradient in a normal curve shape-like, where the population at intermediate altitude (1,325 m) has the largest diameter, and populations at the extremes of the altitudinal distribution range (1,075 m and 1,505 m) have the smallest diameters (Figure 2). Length of longest cotyle-
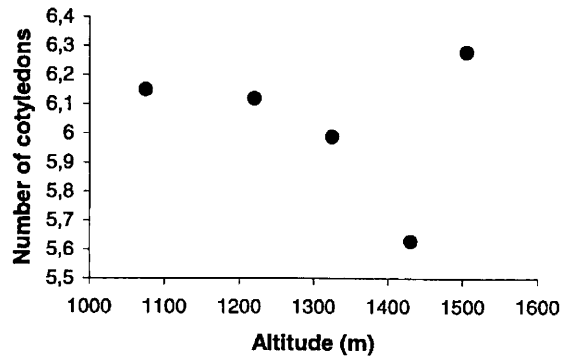

Figure 1. Average number of cotyledons by population altitude on a *P. oocarpa* nursery provenance/progeny test.
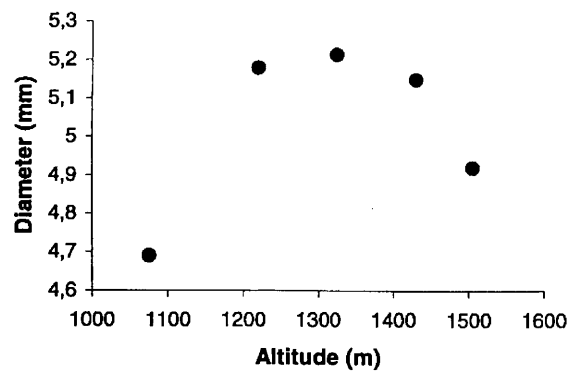

Figure 2. Average basal diameter (mm) by population altitude on a *P. oocarpa* nursery provenance/progeny test.

don, diameter at 9 months (Table 1) and height at 2 months, 6 months and 9 months of age (Table 2) were no significantly different among populations.

Variance among half-sib families within populations was significant for all traits and ages (Tables 1 and 2). Intraclass correlation sizes indicates that contribution of half-sib families variance components to total variance represents roughly twice of the contribution of population variance components to total variance.

Block effect was significant for almost all the traits except for number of cotyledons. Lack of significance of block effect for number of cotyledons is understandable because this trait is preformed on the embryo and consequently it is independent of environmental effects on the experiment. There was no significance for block by population interaction for all the traits (Tables 1 and 2). Block by family interaction was significant for diameter and height at all ages, and it can be interpreted as result of an interaction of the family genotype with the block

Table 1. Analysis of variance results, presented as intraclass correlation (*r*), for number of cotyledons, length of longest cotyledon and diameter (at 6 months and 9 months of age) for a *P. oocarpa* provenance/progeny nursery test.

Source of variance	d.f.	Number of cotyledons		Length of cotyledons		Diameter			
						6-months		9-months	
		r	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Block		0.003	0.6440	0.016	0.0051	0.018	0.0088	0.145	0.0001
Population		0.095	0.0004	0.000	0.4068	0.021	0.0760	0.015	0.7868
Family (population)		0.126	0.0001	0.050	0.0001	0.039	0.0001	0.031	0.0001
Block × population		0.014	0.1662	0.000	0.9918	0.000	0.4637	0.000	0.2943
Block × family		0.015	0.2446	0.000	0.9456	0.084	0.0008	0.128	0.0001
(population)		0.747		0.995		0.838		0.681	
Error									

* d.f. for number of cotyledons, length of longest cotyledon, diameter at 6 months and diameter at 9 months of age were 585, 567, 578 and 550, respectively.

** d.f. for number of cotyledons, length of longest cotyledon, diameter at 6 months and diameter at 9 months of age were 1064, 959, 1224 and 1002, respectively.

Table 2. Analysis of variance results, presented as intraclass correlation (*r*), for height (at 2, 6 and 9 months of age) for a *P. oocarpa* provenance/progeny nursery test.

Source of variance	d.f.	Height					
		2-months		6-months		9-months	
		r	*p*	*r*	*p*	*r*	*p*
Block	17	0.110	0.0001	0.046	0.0001	0.067	0.0001
Population	4	0.000	0.3948	0.022	0.1074	0.007	0.5143
Family (population)	45	0.086	0.0001	0.065	0.0001	0.080	0.0001
Block × population	68	0.011	0.0680	0.000	0.8265	0.000	0.9957
Block × family (population)	*	0.060	0.0091	0.156	0.0001	0.175	0.0001
Error	**	0.742		0.729		0.700	

* d.f. for height at 2, 6 and 9 months of age were 584, 577, and 549, respectively.

** d.f. for height at 2, 6 and 9 months of age were 1044, 1224, and 1007, respectively.

microenvironmental conditions. Covariate day of transplanting of germinated seed from Petri dishes to containers was significant for diameter at 6 months and 9 months of age ($p = 0.0031$ and $p = 0.0123$, respectively) and for height at 2 months of age ($p = 0.0001$) (F test not shown in tables). Thus, the use of that covariate was useful to substract the effect of day of transplanting.

DISCUSSION

Genetic differentiation among populations along altitudinal gradients at the early age examined is in general weak, significant only for number of cotyledons and nearly significant for 6-month-old diameter, and not significant for the rest of the examined

variables and ages. The lack of a clear altitudinal cline might be due to: (i) the altitudinal range examined (400 m) is too small to be a selective force strong enough to create genetic differentiation among populations, or (ii) populations are genetically differentiated but we did not detected such differences due to the early age of the seedlings examined (9 months), or (iii) the species has achieved adaptedness to the differential environmental conditions along the mountain slopes by phenotypic plasticity, rather than by genetic differentiation among populations (VIA & LANDE 1987, REHFELDT 1994), like *P. monticola*, which occurs on a broad range of environments but genetic differentiation among population has not been demonstrated (REHFELDT *et al.* 1984).

Number of cotyledons (the only significant variable among populations) shows a clinal pattern, where average number of cotyledons decreases as altitude increases (except for one atypical population). SAENZ-ROMERO and GURIES (2002) found on *Pinus banksiana* a clinal pattern of variation for average number of cotyledons following a soil-moisture spatial pattern, where number of cotyledons decreases as site humidity increases (*Pinus banksiana* seedlings originated from trees growing on sandy and dry sites have an average larger number of cotyledons than seedlings originated from trees growing on mesic sandy-loamy sites). We speculate that the clinal pattern that we found on *P. oocarpa* also parallels a moisture cline, because in our studied area humidity decreases as elevation decreases: Uruapan city (close of the upper altitude sites) have a larger precipitation (annual average 1,608 mm) and lower temperature (annual average 18.9 °C), whereas El Cobano (the closest climatic station downhill to the lowest altitude site) has significantly less precipitation (annual average 895 mm) and a higher temperature (annual average 26.4 °C). Regarding the unexpected large average cotyledon number of the population at the highest altitude, it has been reported atypical average cotyledon number on populations located at the extremes of the species natural distributions: *Sequoiadendron giganteum* (giant sequoia) shows an atypically large average cotyledon number on a northern population, in comparison with lower average cotyledon numbers of the central and southern populations (FINS & LIBBY 1982).

Diameter at 6 months of age shows an altitudinal variation pattern (only nearly significant) similar to a normal curve, where populations from the middle of the species altitudinal range show an "optimum" growth – having the largest diameter – and populations at the upper and lower extremes of the altitudinal range show the lowest diameters. A similar patterning of variation was found for *Pinus brutia*, where provenances from the middle elevation zone (400 m to 900 m) had greater growth than provenances from the peripheral distribution of the species (ISIK *et al.* 2000). We hypothetize that populations from middle altitudes perhaps might express their full growth potential, whereas populations from altitudinal range extremes have a more conservative growth strategy: populations at the lower altitudinal extreme might be conditioned to growth less to avoid drought stress, and populations at the upper altitudinal extreme might be conditioned to growth less to avoid potential frost damage (REHFELDT 1988). However, we need to take with caution our findings since evaluation were made at a early seedling age and differences among populations for diameter was only nearly significant ($p = 0.076$). We need to wait for field results for further conclusions.

If altitudinal genetic differences among populations showed to be significant at later ages, delimitation of altitudinal bands for seed transfer zoning should be suggested to improve the matching between genotypes and environmental conditions of reforestation sites for *P. oocarpa* in México.

Genetic control at family level was significant for all traits and at all ages. Significant variation among half-sib families seems to be common for early growth seedling traits. It has been documented for number of cotyledons for other conifer species (CAMPBELL 1979, KAYA & TEMERIT 1994), for diameter and height for *P. oocarpa* at one year of age (MENDIZÁBAL-HERNÁNDEZ *et al* 1999), for *P. greggii* at two years of age (ALBA-LANDA *et al.* 1998) in field tests in México, and for other pine species in nursery tests (KAYA & TEMERIT 1994, RAMÍREZ-GARCÍA *et al.* 2001).

Significant genetic differences among families suggests that if field results showed significant age-age correlations, it would be possible take advantage of such genetic control at early ages doing early selection of the best families and (probably) of the best provenances for converting field tests to seed orchards.

ACKNOWLEDGMENTS

REFERENCES

ALBA-LANDA, J., MENDIZÁBAL-HERNÁNDEZ, L. & APARICIO-RENTERÍA, A. 1998: Respuesta de un ensayo d eproce-dencias/progenie de *Pinus greggii* Engelm. en Coatepec, Veracruz, México. *Foresta Veracruzana* 1(1): 25–28

CAMCORE (Central America and Mexico Coniferous

Resource Cooperative) (ed.). 2000: Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative. College of Natural Resources, North Carolina State University, Raleigh, N.C., USA, 233 p.

CAMPBELL, R.K. 1979: Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology* **60**(5): 1036–1050.

CAMPBELL, R.K. 1986: Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. *Silvae Genet.* **35**(2–3): 85–96.

CAMPBELL, R.K. 1991: Soil, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in Southwestern Oregon. *For. Sci.* **37**(4): 973–986.

COFOM (Comisión Forestal del Estado de Michoacán). 2001: Atlas Forestal del Estado de Michoacán. México, COFOM, 97 p.

COFOM (Comisión Forestal del Estado de Michoacán). 2002: Anexo Técnico del Programa Nacional de Reforestación para el Estado de Michoacán. Internal report. Morelia, Michoacán, México, Comisión Forestal del Estado de Michoacán. 14 p.

DVORAK, W.S., GUTIÉRREZ, E.A., OSORIO, L.F., HODGE, G.R. & BRAWNER, J.T. 2000: *Pinus oocarpa. In:* Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative (ed. CAMCORE Cooperative). pp. 129–147. College of Natural Resources, North Carolina State University, Raleigh, North Carolina, USA.

FINS, L. & LIBBY, W.J. 1982: Population variation in *Sequoiadendron*: seed and seedling studies, vegetative propagation, and isozyme variation. *Silvae Genet.* **31**(4): 102–109.

GREAVES, A. 1982: *Pinus oocarpa. For. Abstr.* **43**(9): 503–532.

GUERRERO, M.J. 2002: Exportan fruta. *Provincia* (Michoacan newspaper). Wednesday 8 May 2002, Section B, p. 6.

HAMRICK, J.L. & GODT, M.J.W. 1990: Allozyme diversity in plant species. *In:* Brown, A.D.H., M.T. Clegg, A.L Kahler and B.S. Weir (Eds.) Plant Population Genetics, Breeding and Genetic Resources. Sunderland, Sinauer, pp 43–63.

HAMRICK, J.L., GODT, M.J.W. & SHERMAN-BROYLES, S.L. 1992: Factors influencing levels of genetic diversity in woody plant species. *In:* Adams, W.T., S.H. Strauss, D.L. Copes, A.R. Griffin (Eds.) Population Genetics of Forest Trees. Boston, Kluwer, pp 95–124.

ISIK, F., KESKIN, S. & MCKEAND, S.E. 2000: Provenance variation and provenance-site interaction in *Pinus brutia* Ten.: Consequences of defining breeding zones. *Silvae Genet.* **49**(4–5): 213–223.

KARIUKI, J.G. 1998: Provenance and family-whitin-provenance variation in *Pinus patula, Pinus patula* subspecies *tecunumanii* and *Pinus oocarpa* planted at Turbo, Kenya. *For. Ecol. Manage.* **107**(1–3): 127–133.

KAYA, Z. & TEMERIT, A. 1994: Genetic-structure of marginally located *Pinus nigra* var *pallasiana* populations in central Turkey. *Silvae Genet.* **43**(5–6): 272

–277.

LATTA, R.G., LINHART, Y.B., FLECK, D. & ELLIOT, M. 1998: Direct and indirect estimates of seed versus pollen movement within a population of *ponderosa pine. Evolution* **52**: 61–67.

LEDIG, F. T. 1988. The conservation of diversity in forest trees. *Bioscience* **38**(7): 471–478.

MASERA, O. R., BELLON, M. R. & SEGURA, G. 1995: Forest management options for sequestering carbon in México. *Biomass and Energy* **8**(5): 367–367.

MASERA, O. R., ORDÓÑEZ, M. J., & DIRZO, R. 1997: Carbon emissions from Mexican forests: Current situation and long-term scenarios. *Climat. Change* **35**: 265–295.

MENDIZÁBAL-HERNÁNDEZ, L., ALBA-LANDA, J. & REBOLLEDO-CAMACHO, V. 1999: Pruebas de proceden-cia/progenie de *Pinus oocarpa* Schiede en el estado de Veracruz, México. *Foresta Veracruzana* **1**(2): 9–12.

MILLAR C.I. & LIBBY, W.J. 1991. Strategies for conserving clinal, ecotypic and disjunct population diversity in widespread species. *In:* Genetics and Conservation of Rare Plants. (eds. D.A. Falk & K.E. Holsinger). pp 149–170. Oxford Univ. Press, New York.

MOURA, V.P.G., DVORAK, W.S. & HODGE, G.R. 1998: Provenance and family variation of *Pinus oocarpa* grown in the Brazilian Cerrado. *For. Ecol. Manage.* **109**(1–3): 315–322.

MUGASHA, A.G., CHAMSHAMA, S.A.O., IDDI, S., & NSHUBEMUKI, L. 1996: Survival, growth, and wood density of *Pinus oocarpa* provenances at Kihanga Arboretum, Sao Hill, Tanzania. *For. Ecol. Manage.* **87**(1–3): 1–11.

MUGASHA, A.G., MGALLA, H.A., IDDI, S., NSHUBEMUKI, L., CHAMSHAMA, S.A.O., & MALIMBWI, R.E. 1998: Survival, growth, yield, stem form and wood basic density of *Pinus oocarpa* provenances at Buhindi, Mwanza, Tanzania. *Silvae Genet.* **47**(2–3): 102–107.

OTEGBEYE G.O. 1991: Variation among *Pinus oocarpa* provenances tested in the Savanna region of Nigeria. *For. Ecol. Manage.* **43**: 61–68.

PERRY, P.J. 1991: The Pines of Mexico and Central America. Timber Press, Portland, Oregon, 231 p.

RAMÍREZ-GARCÍA, E.O., ALBA-LANDA, J. & MENDIZÁBAL-HERNÁNDEZ L.C. 2001: Evaluación en vivero de un ensayo de procedencias/progenies de *Pinus teocote* Schl. & Cham. *Foresta Veracruzana* **3**(1): 27–34.

REHFELDT, G.E., HOFF., R.J., & STEINHOFF, R.J. 1984: Geographic patterns of genetic variation in *Pinus monticola. Bot. Gaz.* **145**: 229–239.

REHFELDT, G.E. 1988: Ecological genetics of Pinus contorta from the Rocky Mountains (USA): a synthesis. *Silvae Genet.* **37**(3–4): 131–135.

REHFELDT, G.E. 1989: Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. *For. Ecol. Manage.* **28**: 203–215.

REHFELDT, G.E. 1991: A model of genetic variation for Pinus ponderosa in the Inland Northwest (USA): applications in gene resource management. *Can. J. For. Res.* **21**: 1491–1500.

REHFELDT, G.E. 1993: Genetic variation in the Ponderosae of the southwest. *Am. J. Bot.* **80**(3): 330–343.

REHFELDT, G.E. 1994: Adaptation of *Picea engelmannii* populations to the heterogeneous environments of the Intermountain West. *Can. J. Bot.* **72**: 1197–1208.

ROBBINS A.M.J. & HUGHES, C.E. 1983. Provenance Regions for *Pinus caribeae* and *Pinus oocarpa* within the Republic of Honduras. *Tropical Forestry Papers* **18**. Department of Forestry, Commonwealth Forestry Institute, University of Oxford, Oxford, 29 p.

SAENZ-ROMERO, C. & GURIES, R.P.. 2002: Landscape genetic structure of *Pinus banksiana*: seedling traits. *Silvae Genet.* **51**(1): 26–35.

SAENZ-ROMERO, C. & MARTÍNEZ-PALACIOS, A. 2000: Varia-ción genética altitudinal de pinos. *Nuestro Bosque* **1**(2): 10–11.

SAGNARD, F., BARBEROT, C. & FADY, B. 2002: Structure of genetic diversity in *Abies alba* Mill. from southwestern Alps: multivariate analysis of adaptive and non-adaptive traits for conservation in France. *For. Ecol. Manage.* **157**(1–3): 175–189.

SAVOLAINEN, O. 1998: Gene flow and local adaptation in Scots pine. *In*: Proceedings from a Workshop on Gene Flow in Fragmented, Managed and Continuous Populations. Research Paper No. 3. (eds. V.L. Sork, R.D. Campbell, J. Fernandez, J. Nason, R. Petit, P. Smouse, & E. Steinberg). National Center for Ecological Analysis and Synthesis, Santa Barbara, California. Available at "http: /www.nceas.ucsb.edu/nceas-web/projects/ 2057/ nceas-paper3".

SHEINBAUM, C. & MASERA, O. 2000: Mitigating carbon emissions while advancing national development priorities: the case of Mexico. *Climat. Change* **47**: 259–282.

SORENSEN, F.C. 1994: Genetic variation and seed transfer guidelines for ponderosa pine in central Oregon. Research Paper PNW-RP-472. Portland, OR, Department of Agriculture, Forest Service, Pacific Northwest Research Station, 24 p.

STYLES, B.T. 1993: The genus *Pinus*: a México purview. *In*: Biological diversity of Mexico: origins and distribution. (eds. T.P. Ramamoorthy, R. Bye, A. Lot, & J. Fa). pp 397–420. Oxford Univ. Press, New York.

VIA, S. & LANDE, R. 1987: Genotype – environment interaction and the evolution of plasticity. *Evolution* **39**: 505–522.

WORMALD, T.J. 1975: *Pinus patula. Tropical Forestry Papers* **7**. Department of Forestry, Commonwealth Forestry Institute, University of Oxford, Oxford, 172 p.

WRIGHT, J.A., GIBSON, G.L. & BARNES, R.D. 1988: Provenance variation in stem volume and wood density of *Pinus caribea, P. oocarpa* and *P. patula* spp. *tecunumanii* in Puerto Rico. *Turrialba* **38**(2): 123–126.

ZAMORA-SERRANO, C. 1981: Algunos aspectos sobre *Pinus oocarpa* Schiede en el estado de Chiapas. *Ciencia Forest.* **32**: 25–53.