

Genetic Consequences of Tropical Second-Growth Forest Regeneration

Uzay U. Sezen,* Robin L. Chazdon, Kent E. Holsinger

Despite a long history of international and local efforts, old-growth tropical forests are still being cleared. Today, second-growth forests cover more area than old-growth forests in many tropical countries (1). Yet we know little about the genetic composition of founding populations in second-growth forests (2). Parentage analysis can reveal patterns of gene flow through pollen and seed dispersal, providing accurate information about the sources of founding populations (3–5). Here, we assess the parentage of founders of the abundant canopy palm *Iriartea deltoidea* in a second-growth forest in Costa Rica.

Iriartea is an abundant canopy palm with a wide geographic distribution in neotropical forests (6). Its monoecious flowers are pollinated by stingless bees (*Trigona* spp. and *Melipona* spp.) and now by honeybees (*Apis* spp.). Seeds are dispersed by a variety of birds and mammals, including toucans, white-faced monkeys, peccaries, tapir, and several species of rodents. This shade-tolerant species shows broad representation of all size classes in mature forests.

We analyzed the entire founder generation of 130 flowering and fruiting trees in a 24-year-old second-growth forest adjacent to old-growth forest at La Selva Biological Field Station in Costa Rica (7). The study area was a 300 m by 1000 m protected area, covering 20 ha of second-growth and 10 ha of adjacent old-growth forest and protected since 1981. *Iriartea* depends on newly dispersed seed to recolonize second-growth forests. In our study area, all potential seed sources reside in old-growth forest. We defined the founder generation as the first generation derived from seeds that colonized abandoned pasture. Monitoring data obtained from a permanent sample plot show that *Iriartea* reached reproductive maturity in as little as 20 years in this second-growth forest. Our parentage analysis with 141 amplified fragment length polymorphism (AFLP) loci revealed high levels of reproductive dominance among parents of the source population (7). Among 66 old-growth forest trees, only two contributed 56% of the genes to the second-growth founder population; 23 contributed the remaining 44%; and 41 had no offspring.

Average seed dispersal distance greatly exceeded that of pollen dispersal. The median

seed dispersal distance was 270 m, whereas the longest (minimum) dispersal distance we detected was more than 875 m (7). Maximum pollen movement was less than 220 m. The median pollination distance was 100 m, and 50% of the pollination events between 80 and 120 m corresponded to pollen movement between the two reproductively dominant trees.

Reproductive dominance of a few old-growth parents had strong genetic consequences in the second-growth forest. Genetic diversity in second-growth founders was significantly low-

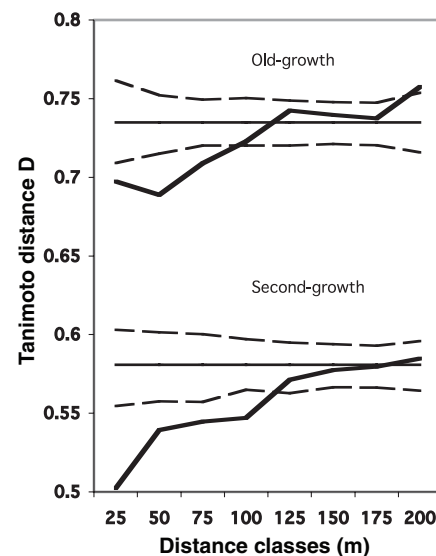


Fig. 1. Spatial autocorrelation distogram of mature trees in both forests using Tanimoto's D (bold lines). Confidence intervals (95%) for no spatial structure are indicated by dashed lines. Overall means of genetic distances for both forests are shown as thin flat lines as a reference for random spatial structure.

er than in adjacent old-growth trees; mean dissimilarity among individuals was 0.58 in second-growth and 0.73 in old-growth forest (Tanimoto's D) (7) (Fig. 1). Patch diameters of similar genotypes were larger in second-growth forest (125 m) than in old-growth forest (96 m).

Reproductive dominance may be especially common in early successional forests. We do not know why two trees in our study show such extreme reproductive dominance. Even

in this best-case scenario of forest regeneration, where numerous and diverse seed sources remain in a protected, adjacent, old-growth forest, where the animal disperser community is intact, and where there are no physical or ecological barriers to dispersal, more than half of the founding *Iriartea* population were full or half-siblings. Dominance patterns may be even more skewed in cases where the pool of parent trees is more restricted in size or genetic diversity.

Similar colonization patterns and genetic consequences may apply to a broad suite of tree and palm species that colonize young second-growth forests and persist as shade-tolerant species in later successional stages. Most studies of gene flow in plants have concentrated on pollen-mediated gene flow and male reproductive success (3, 4). Colonization of second-growth forest depends on seed dispersal; here we demonstrate that dispersal can contribute more to total gene flow than pollen movement during tropical forest succession. We expect dispersal and (to a lesser extent) pollination distances to diminish as local seed production increases during succession.

Reduced genetic diversity of the founder population will likely persist in later generations as closely related founders contribute an increasing fraction of seedlings. Our results on the founders suggest that tree populations in second-growth forests will require continuous gene flow over successive generations to restore genetic diversity to levels currently observed in local old-growth forests.

References and Notes

1. Food and Agricultural Organization of the United Nations (FAO), *FAO For. Pap. 140* (FAO, Rome, 2001).
2. M. Cespedes, V. Gutierrez, N. M. Holbrook, O. J. Rocha, *Mol. Ecol.* **12**, 3201 (2003).
3. J. D. Nason, A. E. Herre, J. L. Hamrick, *Nature* **391**, 685 (1998).
4. M. R. Chase, C. Moller, R. Kesseli, K. S. Bawa, *Nature* **383**, 398 (1996).
5. P. R. Aldrich, J. L. Hamrick, *Science* **281**, 103 (1998).
6. A. Henderson, *Flora Neotrop. Monogr.* **53** (1990).
7. Materials and methods are available as supporting material on Science Online.
8. Supported by the Andrew W. Mellon Foundation.

Supporting Online Material

www.sciencemag.org/cgi/content/full/307/5711/891/DC1

Materials and Methods
References and Notes

9 September 2004; accepted 18 November 2004
10.1126/science.1105034

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269–3043, USA.

*To whom correspondence should be addressed.
E-mail: uzay.sezen@huskymail.uconn.edu