BRIEF COMMUNICATIONS

FRACTAL GEOMETRY IS HERITABLE IN TREES

Joseph K. Bailey,[1] Randy K. Bangert, Jennifer A. Schweitzer, R. Talbot Trotter III, Stephen M. Shuster, and
Thomas G. Whitham
Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011
[1]*E-mail: jkb22@dana.ucc.nau.edu*

Abstract.—Understanding the genetic basis to landscape vegetation structure is an important step that will allow us
to examine ecological and evolutionary processes at multiple spatial scales. Here for the first time we show that the
fractal architecture of a dominant plant on the landscape exhibits high broad-sense heritability and thus has a genetic
basis. The fractal architecture of trees is known to influence ecological communities associated with them. In a
unidirectional cottonwood-hybridizing complex (*Populus angustifolia* × *P. fremontii*) pure and hybrid cottonwoods
differed significantly in their fractal architecture, with phenotypic variance among backcross hybrids exceeding that
of F_1 hybrids and of pure narrowleaf cottonwoods by two-fold. This result provides a crucial link between genes and
fractal scaling theory, and places the study of landscape ecology within an evolutionary framework.

Key words.—Architecture, broad-sense heritability, community genetics, *Populus*, scaling.

Habitats occupy space. Depending on how they do this,
variability in the fractal geometry of habitats can have a
strong effect on ecological processes at multiple spatial
scales. For example, complex habitats (e.g., large fractal di-
mension) can support more organisms than less complex hab-
itats (e.g., small fractal dimension; Morse et al. 1985).

Since Mandelbrot demonstrated that complex fractal geo-
metric structures emerge from the repetitive application of
simple rules, ecologists have been interested in the use of
fractals to understand the relationship of spatial scale and
ecological process in complex biological systems (Mandel-
brot 1983; Sugihara and May 1990; Hastings and Sugihara
1993). Although plant architecture is highly variable and
complex, a general rule is that plants grow through the re-
petitive addition of modules. Thus, modular organisms are
model systems to examine the genetic basis of whole tree
fractal architecture.

Studies have shown that individual architectural traits such
as height, branching angle, branch number, and others are
heritable (Bradshaw and Stettler 1995). However, often mul-
tiple architectural traits and even whole tree architecture may
be important factors affecting the distribution and abundance
of associated species. For example, Martinsen and Whitham
(1994) showed that more birds nest in hybrid than in non-
hybrid trees due to architectural differences among them.
Given the potential importance of overall habitat complexity
on community structure (Morse et al. 1985; Milne et al. 1992;
Ritchie and Olff 1999; Haskell et al. 2002), rather than any
single trait, we investigated the hypothesis that whole tree
architecture may be fractal, and that this fractal geometry
may have a genetic basis.

MATERIALS AND METHODS

Using a unidirectional cottonwood hybridizing-complex
(*Populus angustifolia* × *P. fremontii*) as a model system to
examine the genetic basis of whole tree architecture, we used
box-counting methods (Mandelbrot 1983; Morse et al. 1985;
Lovejoy et al. 1987; Bangert and Slobodchikoff 2000) of

standardized digital photographs to calculate the fractal di-
mension of cottonwood trees. Holding focal length constant
at 2 m, we photographed five replicates of 22 genotypes (as
determined by previous restriction-fragment-length poly-
morphism analyses; see Keim et al. 1989; Martinsen et al.
2001) for a total of 110 cottonwood trees (i.e., five genotypes
pure Fremont, five F_1 hybrid, seven backcross hybrid, and
five narrowleaf cottonwood). Fractal dimension of trees
would be $2 < D < 3$, but for practical reasons the branching
pattern is projected onto a two-dimensional surface so that
the resulting measured dimension $1 < D < 2$. We removed
any replicate from the analysis that had a fractal relationship
of R^2 less than 0.9 (Milne et al. 1992). The trees were grown,
in random arrangement, under constant greenhouse condi-
tions and were three-year-old cuttings from common garden
trees that were originally derived from field genotypes.

We considered the fractal geometry of a tree as a quan-
titative trait because it is likely to arise from a suite of genetic
and environmental factors similar to that which produces
other tree phenotypes displaying quantitative inheritance
(Bradshaw and Stettler 1995). Observed estimates of fractal
dimension, measurable for each tree, provide individual trait
values for this quantitative character. When these estimates
are generated according to standard breeding designs (e.g.,
full-sib or half-sib designs, or in this case, among lineages
of clones grown in a common environment), standard quan-
titative genetic methods are appropriate for relating the ob-
servable components of phenotypic variance to the measur-
able components of genetic variance (Becker 1985; Falconer
1989).

To illustrate this among-genotype component of variation
in the fractal architecture of cottonwoods, we calculated the
broad-sense heritability, h_B^2, of cottonwood fractal geometry
(Becker 1985; Falconer 1989) as the among-lineage com-
ponent of variation in fractal phenotype, h_S^2, divided by the
total variance in fractal phenotype for all trees, h_{total}^2, or

$$h_B^2 = h_S^2/h_{total}^2.$$

Calculations of mean squares and methods for partitioning

within-lineage, among-lineage, and total phenotypic variance from ANOVA results are described in detail in Becker (1985; see also Falconer 1989).

RESULTS

We found no significant difference in fractal architecture among replicate clones of individual cottonwood genotypes ($F_{4,79} = 0.22$, $P = 0.92$), demonstrating that cuttings from a clone have similar architecture when planted separately. However, there were significant differences in whole tree fractal architecture among genotypes nested within tree class ($F_{21,62} = 4.45$, $P < 0.05$; Fig. 1A) and at the tree class level ($F_{3,80} = 5.93$, $P < 0.05$; Fig. 1B), indicating that measurable differences in whole tree architecture exist, and that genetic factors may underlie observed differences in tree phenotype.

Overall, we found significant broad-sense heritability of fractal architecture within this cottonwood hybridizing complex ($h_B^2 = 0.56 \pm 0.10$; $\pm$ 95% CI; $n = 21$; Fig. 1C), indicating that phenotypic variance in fractal architecture is highly variable among pure and hybrid cottonwoods and has a genetic basis. When the heritability of whole tree fractal architecture for the pure and hybrid types were calculated separately, the Fremont cottonwood lineage ($n = 4$), h_B^2 was nonsignificant. However, F_1 hybrids and pure narrowleaf trees showed $h_B^2 = 0.36 \pm 0.25$ ($n = 5$) and 0.35 ± 0.25 ($n = 5$) respectively, and in backcross hybrids $h_B^2 = 0.72 \pm 0.07$ ($n = 7$).

DISCUSSION

To our knowledge, these data are the first to indicate that whole tree fractal architecture has a significant genetic basis and is heritable. These results are important and novel for three main reasons: (1) they suggest that the genetic basis to whole tree fractal architecture may be less than the sum of the individual quantitative trait loci that are found for specific architectural traits; (2) they show that hybridization is an important mechanism affecting genetic variation and evolutionary potential; (3) they provide a potential genetic mechanism for ecological patterns and processes related to fractal geometry on the landscape.

Fractal geometric structures, like whole tree architecture, emerge from the repetitive addition of simple rules (Mandelbrot 1983). These data have shown that a group of architectural traits can be measured as a single emergent phenotype. This suggests that the genetic mechanisms controlling this simple rule may be less complex than previously considered. To our knowledge though, no studies have examined whole tree architecture in this way. Typically, quantitative trait loci (QTL) studies measure individual architectural traits and map them onto many locations of the genome of interest (Bradshaw and Stettler 1995). If whole tree fractal architecture is determined by one or relatively few QTL as theory suggests, then depending upon the magnitude of the effect of these loci, it may be easier for offspring to inherit whole tree architecture than a suite of individual traits (Martinsen et al. 2001).

Variation in whole tree fractal architecture can have a strong effect on ecological processes across the measured scales (Morse et al. 1985). We observed variability in D at
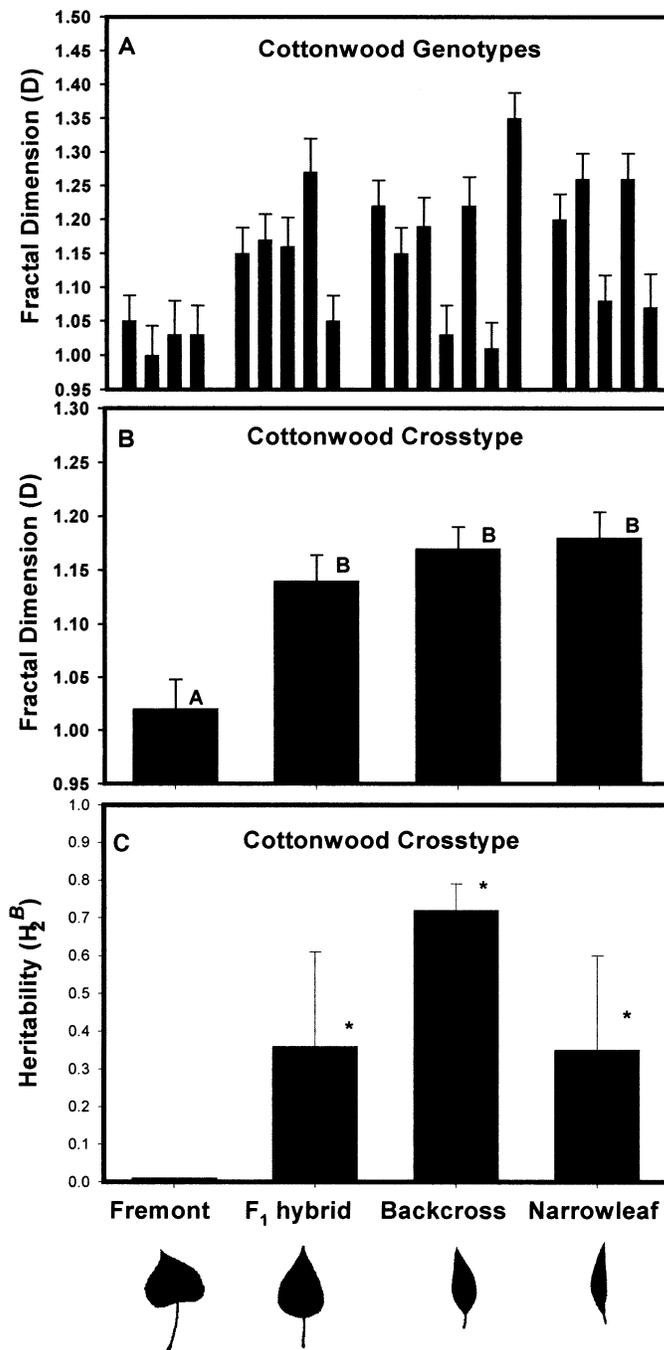

FIG. 1. Pure and hybrid cottonwoods differ in their fractal architecture at the genotype and cross-type level. (A) Bars represent the fractal architecture of pure and hybrid cottonwood genotypes. The fractal dimension of pure and hybrid cottonwood genotypes range from $D = 1.0$–1.35 representing >22-fold difference in how genotypes fill space. (B) These genetically based differences in fractal architecture can be generalized at the cross-type level where Fremont cottonwood fills the least space, F_1 hybrids are intermediate, and backcross and narrowleaf cottonwoods have the largest fractal dimension (letters represent significant differences; means $\pm$ 1 SE are shown). (C) Cottonwood cross types have different heritability of this trait. Backcross hybrids, which have the greatest genetic variation, also have the greatest heritability (error bars represent 95% confidence intervals and asterisks represent significant heritability).

the genotype level between 1.00 and 1.35. This range represents a 220% difference in how these cottonwood genotypes fill space. Even at the tree class level, there was greater than a 100% difference in how these trees fill space. This magnitude of difference in the scaling exponent (D) of fractal habitats can affect patterns of arthropod abundance (Morse et al. 1985), mammalian herbivory, home ranges for many arthropods (Wiens and Milne 1989; Bangert and Slobodchikoff 2004), mammals, and birds (Haskell et al. 2002) and may provide a unifying theory for biodiversity (Ritchie and Olff 1999). Furthermore, because genotype was nested within tree type and there were significant genotype differences, these data indicate that the observed patterns of whole tree architecture and heritability were driven by both inter- and intraspecific genetic variation.

We found significant broad-sense heritability of fractal architecture within this cottonwood hybridizing complex (h_B^2 = 0.56 ± 0.10; ± 95%). There are probably many selective forces that could have influenced this trait. Whole tree architecture can affect precipitation interception, soil litter dynamics (Chapman et al. 2003), susceptibility to herbivores (Larson and Whitham 1998), and water use (Koch et al. 2004), all of which may feed back to influence plant fitness. Interestingly, the heritability of fractal architecture was not equal among all cross types. Fremont cottonwood had very little variability (h_B^2 was nonsignificant) and backcross hybrids had very high variability in architecture (h_B^2 = 0.72 ± 0.07). High variability in the backcross hybrids is not surprising as Martinsen et al. (2001) showed genetic variation to be greatest in that tree class.

We suggest that the spatial distribution of plant genotypes on the landscape that vary significantly in their whole tree fractal architecture represents a genetic landscape to which associated community members may respond. Recent studies suggest that community and ecosystem traits like arthropod community composition or leaf litter decomposition are heritable components of biological systems (Whitham et al. 2003). If so, then selective processes that determine which plant genotypes persist and where they occur, such as beaver herbivory (Bailey et al. 2004), may have extended effects on the spatial distribution of biodiversity and influence the variability of community compositions (heritable plant traits) that persist at local and landscape levels. This largely depends upon the relative strength of links between heritable traits, such as whole tree fractal architecture, and community composition.

LITERATURE CITED

Bailey, J. K., J. A. Schweitzer, B. J. Rehill, R. L. Lindroth, G. D. Martinsen, and T. G. Whitham. 2004. Beavers as molecular geneticists: a genetic basis to the foraging of an ecosystem engineer. Ecology 85:603–608.

Bangert, R. K., and C. N. Slobodchikoff. 2000. The Gunnison's prairie dog structures a high desert grassland landscape as a keystone engineer. J. Arid. Environ. 46:357–369.

———. 2004. Prairie dog engineering indirectly affects beetle movement behavior. J. Arid. Environ. 56:83–94.

Becker, W. A. 1985. Manual of quantitative genetics. 4th ed. Academic Enterprises, Washington, DC.

Bradshaw, H. D., Jr.,and R. F. Stettler. 1995. Molecular genetics of growth and development in *Populus*. IV. Mapping QTLs with large effects on growth, form, and phenology traits in a forest tree. Genetics 139:963–973.

Chapman, S., G. Koch, S. Hart, N. S. Cobb, and T. G. Whitham. 2003. Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. Ecology 84:2867–2876.

Falconer, D. S. 1989. Introduction to quantitative genetics. 3rd ed. Longman, New York.

Haskell, J. P., M. E. Ritchie, and H. Olff. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418:528–530.

Hastings, H. M., and G. Sugihara. 1993. Fractals: a user's guide for the natural sciences. Oxford Univ. Press, New York.

Keim, P., K. N. Paige, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. Genetics 123:557–565.

Koch, G. W., S. C. Sillett, G. M. Jennings, and S. D. Davis. 2004. The limits to tree height. Nature 428:851–854.

Larson, K. C., and T. G. Whitham. 1998. Competition between gall-aphids and natural plant sinks: plant architecture affects resistance to galling. Oecologia 115:161–166.

Lovejoy, S., D. Schertzer, and A. A. Tsonis. 1987. Functional box-counting and multiple elliptical dimensions in rain. Science 235:1036–1038.

Mandelbrot, B. B. 1983. The fractal geometry of nature. Freeman, New York.

Martinsen, G. D., and T. G. Whitam. 1994. More birds nest in hybrid cottonwoods. Wilson Bull. 106:474–481.

Martinsen, G. D., T. G. Whitham, R. J. Turek, and P. Keim. 2001. Hybrid populations selectively filter gene introgression between species. Evolution 55:1325–1335.

Milne, B. T., M. G. Turner, J. A. Wiens, and A. R. Johnson. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theo. Popul. Ecol. 41:337–353.

Morse, D. R., J. H. Lawton, M. M. Dodson, and M. H. Williamson. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature 314:731–733.

Ritchie, M. E., and H. Olff. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400:557–560.

Sugihara, G., and R. M. May. 1990. Application of fractals in ecology. Trends Ecol. Evol. 5:79–87.

Whitham, T. G., W. P. Young, G. D. Martinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, G. M. Wimp, D. G. Fischer, J. K. Bailey, R. L. Lindroth, S. Woolbright, and C. R. Kuske. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. Ecology 84:559–573.

Wiens, J. A., and B. T. Milne. 1989. Scaling of ''landscapes'' in landscape ecology, or landscape ecology from a beetle's perspective. Lands. Ecol. 3:87–96.

Corresponding Editor: C. Goodnight