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THE INFLUENCE OF HEAVY BROWSING ON THE FRACTAL BRANCHING PATTERN OF *ILEX AQUIFOLIUM*

C. Ricotta, L. Canini & G. Avena

Department of Plant Biology, University of Rome "La Sapienza", Piazzale Aldo Moro 5, 00185 Rome, Italy.

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Abstract: This morphometric study describes the relation between branch diameter and branching order in *Ilex aquifolium* using a simple fractal scaling law. The logarithmic plots of mean branch diameter against the logarithm of order were generally linear, suggesting that biological branching structures may be genetically-controlled. However, fractal exponent values varied a function of environmental factors such as heavy grazing, suggesting that while the fractal scaling function is genetically coded, it is also an expression of adaptations to the environment.

Introduction

There exists extensive evidence that different tree species have evolved branching patterns that are governed by genetic rather than environmental factors. Barker et al (1973) related diameters and branch lengths of apple (*Malus* sp.) and birch (*Betula* sp.) trees to branching order. In both tree species, log plots gave linear results. Slopes of the best fitting lines for the length-order relation differed greatly, reflecting differences in the crown form of the species analyzed. In a detailed morphometric study of five tree species (*Quercus rubra, Q. alba, Populus tremuloides, Prunus pennsylvanica*, and *Pinus strobus*), McMahon and Kronauer (1976) concluded that tree structure is self-similar with respect to one branch ratio and one diameter ratio. Crawford and Young (1990) examined the self-similar fractal distribution of branch length as a function of branching order in two oak species (*Quercus petraea* and *Q. robur*). They demonstrated that there is no apparent similarity in the scaling mechanism between the two species. All these studies suggest that different tree branching patterns are genetically-based rather than arising from environmental factors. Conversely, resprouting in response to factors such as environmental stress, fire and herbivores may play an important role in modifying the original branching structure of trees (e.g. Horn 1971; Honda and Fisher 1978). The quantitative description of tree branching pattern may therefore provide some useful information regarding the interaction between plant growth and the environment (Acosta et al. 1996).

The objective of this paper is to use a simple fractal algorithm to describe quantitative variation in the branching pattern of *Ilex aquifolium* induced by herbivory. The study was undertaken in the Natural Park of Monti Lucretili, central Italy.

Materials and Methods

Study Area

The field survey was performed in spring and early summer 1997 in the karst plateaus of Campitello (1028 m above sea level) and Pratone di Monte Gennaro (1024 m above sea level). Both locations occur in the Natural Park of Monti Lucretili in central Italy. The study area belongs to the Mesaxeric climatic region (Tomaselli et al. 1973), which is characterized by an absence of severe summer drought and significant winter cold stress (Blasi 1994). Meteorological data from the Ministero dei Lavori Pubblici station located in Posticciola (540 m above sea level) indicates an average annual air temperature of 12.4 °C. The average annual rainfall is 1054.9 mm, with a principal maximum in the fall and a secondary maximum in winter. The average rainfall from June to August is 156.4 mm. Rainfall in the study area is affected by a strong altitudinal gradient.

Above 900-1000 m the mountainous vegetation is dominated by *Fagus sylvatica*. The numerous karst-plateaus in the area were traditionally used as grazing grounds following the opening of large clearings.

Ilex aquifolium

Ilex aquifolium is an evergreen shrub or low tree (up to 23 m in height) which occurs in north-western, central and southern Europe from Norway to Turkey, west to the Caucasus and western Asia (Peterken and Lloyd 1967). In the Mediterranean region, *Ilex aquifolium* is a widespread and characteristic understory shrub of beechwoods and other mountainous woods. It is also commonly found as large bushes along the margins of open woods (Pavari 1957).

With apical dominance and monopodial branching, Ilex aquifolium develops a single trunk from which branches arise at wide angles to the vertical. Like many other trees, undisturbed individuals do not ordinarily branch beyond five to seven branching orders (Long 1994). The young leaves and twigs are palatable to many ungulate herbivores, and the axillary buds of browsed twigs develop new leading shoots. Furthermore, *Ilex aquifolium* regenerates vigorously from the roots following heavy grazing, producing large multi-stemmed individuals that are characteristic of woodland margins (Peterken and Lloyd 1967). In the study area, mature individuals of *Ilex aquifolium* at the wood-prairie interface are often composed of low, heavily-grazed external stems with a dense, much-branched structure where the original monopodial branching pattern is almost completely lost. More internal stems, which are inaccessible to herbivores, rise to a height of up to 9 m and maintain the original monopodial structure (Fig. 1).

Sampling design

Ten large multi-stemmed individuals of *Ilex aquifolium* showing the above mentioned characteristic growth form were chosen for analysis. For each individual, one internal stem with a well preserved monopodial structure and one external stem showing clear signs of heavy browsing were randomly selected. After the stems were selected, the branching system of each stem was ordered separately by assigning to each branching order an integer label.

The application of quantitative methods to morphometric studies evolved from geomorphic analyses of rivers networks, as developed by Horton (1945). Horton's ordering technique has been successively modified by a number of authors (e.g. Strahler 1957, Weibel 1963) to improve the quantitative description of complex biological branching systems (e.g. Weibel and Gomez 1962, Leopold 1971, Mc-

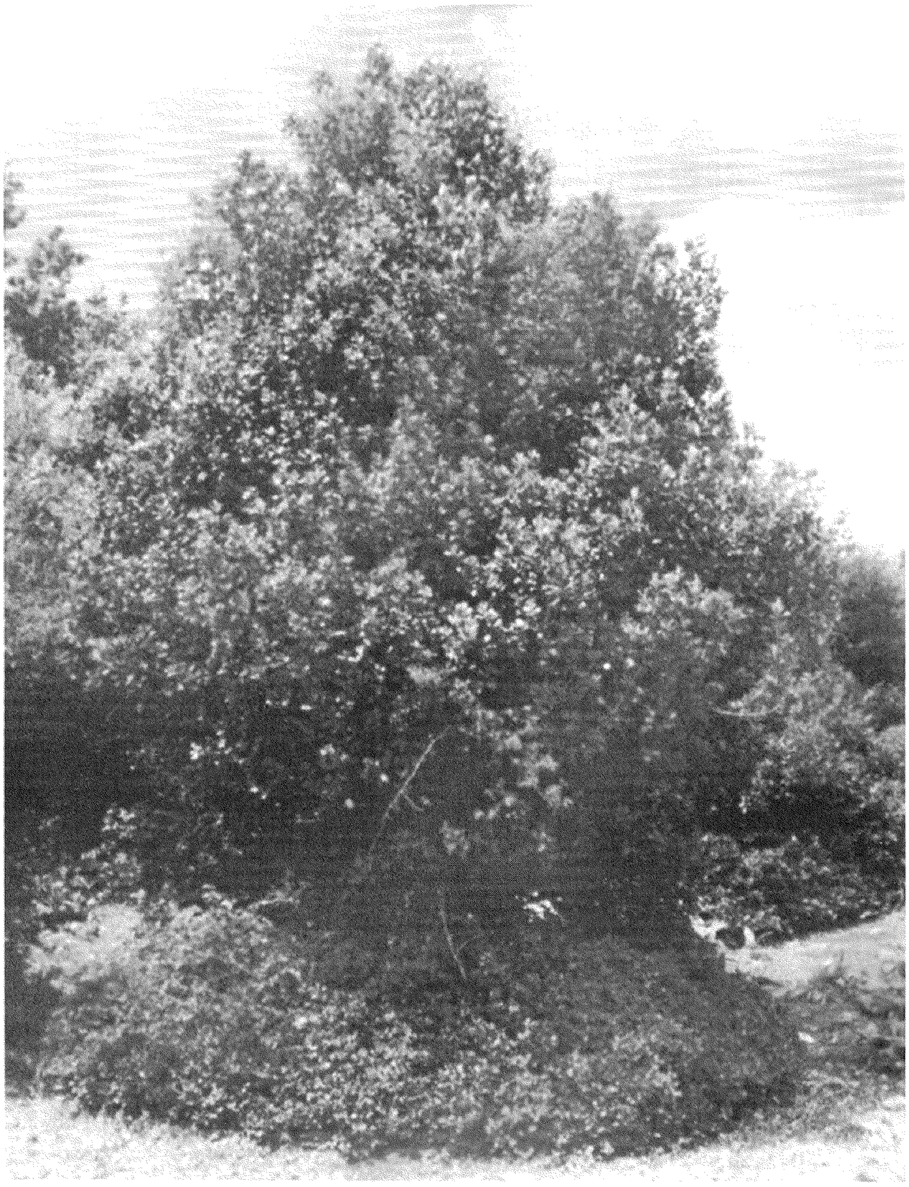

Figure 1. Multistemmed individual of *Ilex aquifolium* in the karst-plateau of Campitello. The low external stems show the classical dense, much-branched structure induced by heavy grazing.

Donald 1983, West and Goldberger 1987, Long 1994). Because of its simplicity, Strahler's method has been widely used for describing both geomorphic and biological branching patterns. Strahler's hierarchy technique assumes that end branches are first order. When two first order branches meet the resulting branch is a second order, when two second order branches meet a third order branch results, and so on up to the main stem. Notice that when two branches of different order meet, the resulting branch takes the same order as the higher of the two joining branches.

Despite its simplicity, Strahler's hierarchy technique has two major disadvantages when applied to ordered plant structures. First, Strahler's technique results in an unnatural branching hierarchy whenever the branching order of the main stem is the result of a process starting at the level of the end branches and not vice-versa. Second, the hierarchical order of different branches can be radically altered by the omission of broken or pruned branch complexes (Crawford and Young 1990). We therefore adopted the ordering scheme proposed by Weibel (1963), in which the branching order of a single branch segment is determined as the number of nodes between the branch and the base of the trunk (Crawford and Young 1990). Note that we assigned an order one to the main stem to avoid branching orders outside the domain of positive numbers (Fig 2).

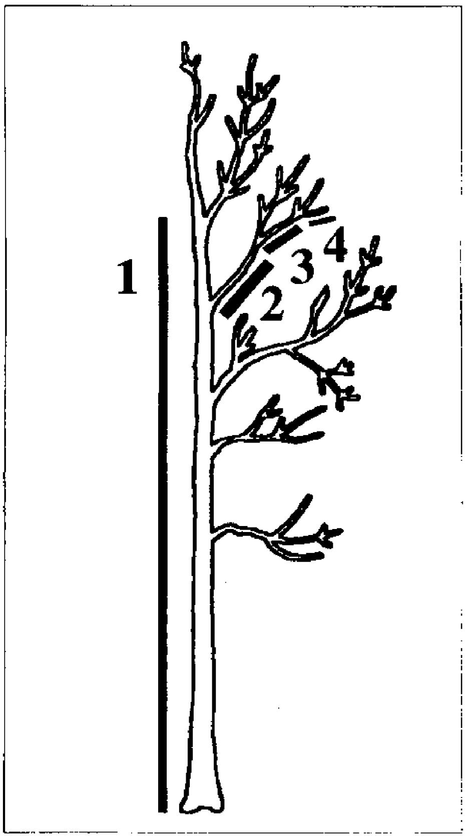

Figure 2. Example of Weibel's ordering scheme for branching structures (from Kenkel and Walker 1996).

Once the branching hierarchy was established, each branch segment was measured with respect to the greatest diameter, usually at the end nearest to the main stem. Diameter was measured with 0.1 mm scale calipers. Following McMahon and Kronauer (1976), only live branches were considered.

The relation between branch order number and mean branch diameter within a given order was examined separately for each selected stem following a simple fractal relation proposed by West and Goldberger (1987) for the analysis of bronchial structures. The defining fractal relation is:

$$R(z) = k/z^D \qquad (1)$$

where $R(z)$ is the mean branch diameter for the zth order, k is a constant, and D is the fractal dimension. This fractal model predicts that decreases in mean branch diameter with each branch order follow a power-law relationship (Kenkel and Walker 1996).

Results and Discussion

The fractal dimension D of the scaling relation between the mean branch diameter and the branching order was calculated (following Equation 1) from the slope of the best fitting line of the log-log plot of $R(z)$ vs. z (Fig. 3). For all stems of *Ilex aquifolium* analyzed, the mean branch diameter showed a strong linear dependence to branching order. Thus the relationship between mean branch diameter and branching order is scale-invariant over a wide range of orders. The fractal dimension D ranged from 1.231 to 1.963 for internal, unbrowsed stems (Table 1). Conversely, external browsed stems were significantly different in their branching pattern, with fractal dimension values ranging from $D = 0.481$ to 1.149.

The implication of this kind of fractal scaling law is that a very small amount of coded information is needed to fully determine the pattern of natural branching systems over several branching orders (Crawford and Young 1990). Furthermore, since the fractal dimension D dictates the rate at which $R(z)$ decreases as a function of z, the variation of D following heavy grazing directly influences the overall appearance of stems. Thus, if D assumes a low value, the branching pattern is rather compact. By contrast, high fractal dimensions give rise to more slender branch forms. The significance of the difference among the fractal dimensions of the internal, rather undisturbed stems and the external, heavily grazed stems was assessed separately for each individual of *Ilex aquifolium* using a two-tailed Student's t-test to compare slopes of the best fitting lines of the log-log plots (Figure 3). In all cases, pairwise comparisons revealed that individuals of *Ilex aquifolium* significantly alter their branching pattern in response to heavy grazing (Table 1). This demonstrates the high plasticity of response to specific limiting conditions for plant growth and development.

In our opinion, the overall fractal power-law governing the branching pattern of *Ilex aquifolium* is evidence that branch scaling is genetically controlled. Previous studies

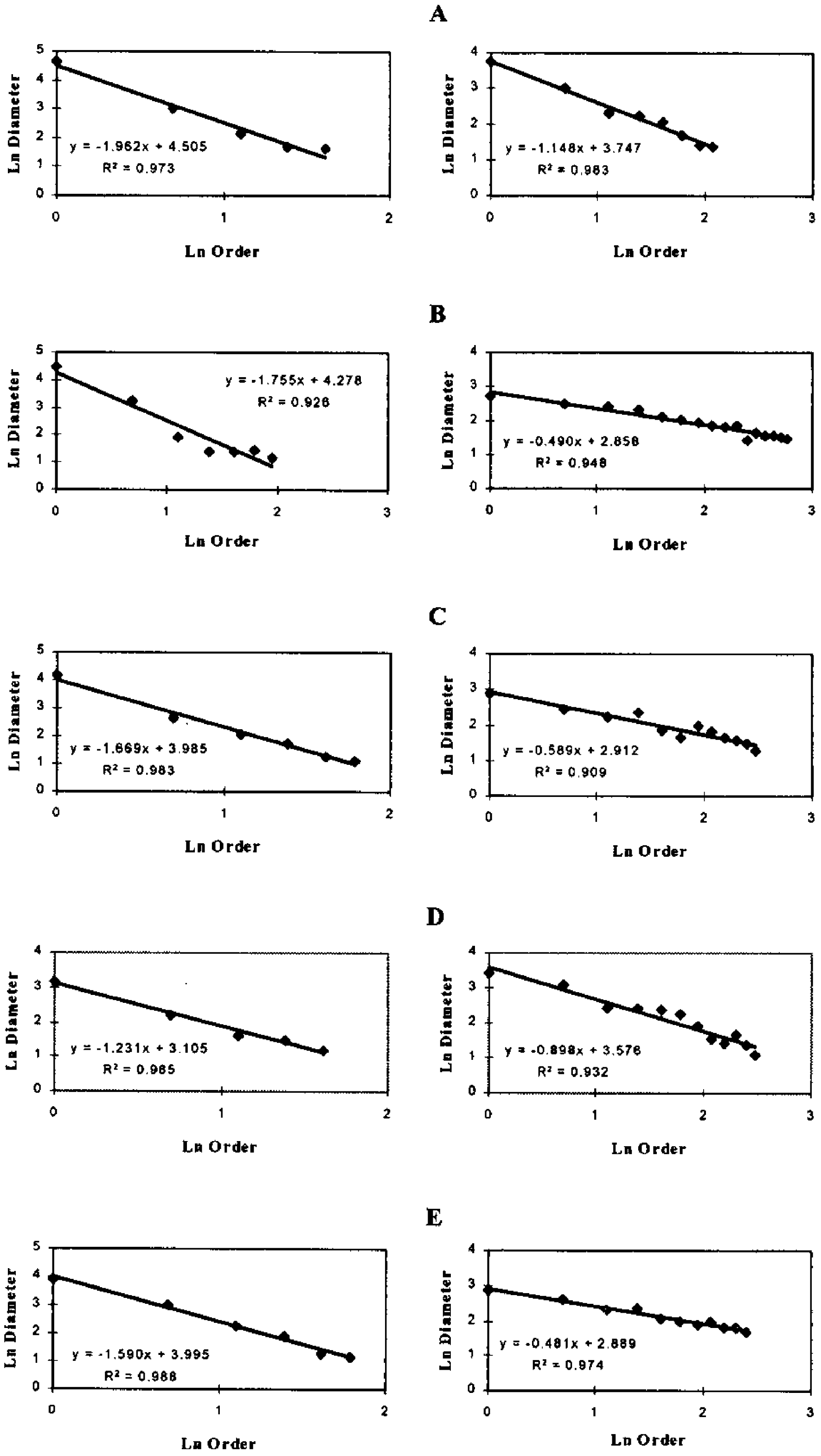

Figure 3. Mean branch diameter vs. branch order relationships for each individual of *Ilex aquifolium* analyzed. The best fitting line of the log-log plots is used to estimate *D*. A-J sample code of each individual. Internal stems on the left, external stems on the right.

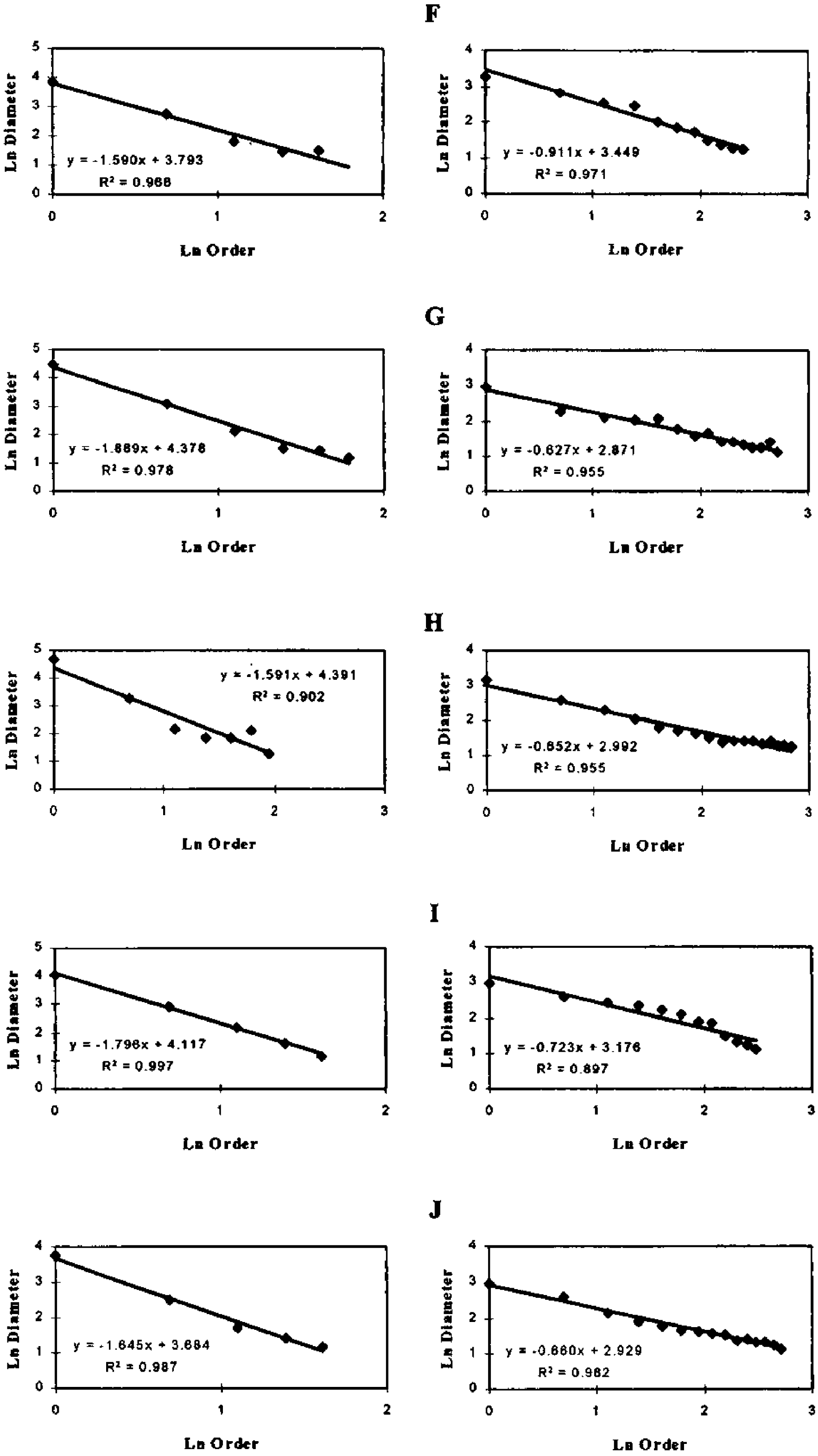

Figure 3 (continued).

Table 1. Pairwise comparison between the internal and the external stem of each of ten individuals of *Ilex aquifolium* analyzed using a two-tailed Student's t-test to compare slopes of the best fitting lines of the log-log plots. * $p > 0.05$

Sample code	Fractal Dim. (Internal stem)	Fractal Dim. (External stem)	d.f.	t	crit. t ($p > 0.01$)
A	1.962	1.148	13	5.174	3.012
B	1.755	0.490	19	9.028	2.861
C	1.669	0.589	14	9.078	2.977
D	1.231	0.898	13	2.934	2.160*
E	1.590	0.481	13	15.966	3.012
F	1.590	0.911	12	5.082	3.055
G	1.889	0.627	17	11.993	2.898
H	1.591	0.652	20	6.313	2.845
I	1.796	0.723	13	7.049	3.012
J	1.645	0.660	16	13.323	2.921

(e.g. Barker et al. 1973, Crawford and Young 1990) found evidence of genetic control in branch scaling, but their analyses were based on very small sample sizes. In this study, the range of D-values in *Ilex aquifolium* is too large to hypothesize a genetic mechanism where both the fractal scaling law and the fractal exponent(s) are rigidly coded. Instead, it appears that the fractal dimension of branching patterns can assume a large range (bounded perhaps by upper and lower limits) in response to environmental factors such as incident light intensity (Peterken and Lloyd 1967).

It should also be recognized that the overall appearance of trees is influenced by several independent characters (e.g., Barker et al. 1973, McMahon and Kronauer 1976, Orshan 1986, Crawford and Young 1990, Montalvo et al. 1991, Acosta et al. 1996), which may or may not be modeled using fractal power-law relationships. The decrease in the mean branch diameter as a function of the branching order should therefore be viewed as one component in a complex design, where each element is controlled to varying degrees by both genetic and environmental factors.

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