



Stress resistance strategy in an arid land shrub: interactions between developmental instability and fractal dimension

J. Escós*, C. L. Alados*, F. I. Pugnaire†, J. Puigdefábregas† & J. Emlen‡

**Instituto Pirenaico de Ecología, Avenida Montañana 177,
50080 Zaragoza, Spain*

†*Estación Experimental de Zonas Áridas, General Segura 1,
04001 Almería, Spain*

‡*Northwest Biological Science Center (NBS), 6505 NE 65th Str,
Seattle WA 98115.*

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This paper investigates allocation of energy to mechanisms that generate and preserve architectural forms (i.e. developmental stability, complexity of branching patterns) and productivity (growth and reproduction) in response to environmental disturbances (i.e. grazing and resource availability). The statistical error in translational symmetry was used to detect random intra-individual variability during development. This can be thought of as a measure of developmental instability caused by stress. Additionally, we use changes in fractal complexity and shoot distribution of branch structures as an alternate indicator of stress. These methods were applied to *Anthyllis cytisoides* L., a semi-arid environment shrub, to ascertain the effect of grazing and slope exposure on developmental traits in a 2 × 2 factorial design. The results show that *A. cytisoides* maintains developmental stability at the expense of productivity. *Anthyllis cytisoides* was developmentally more stable when grazed and when on south-facing, as opposed to north-facing slopes. On the contrary, shoot length, leaf area, fractal dimension and reproductive-to-vegetative allocation ratio were larger in north- than in south-facing slopes. As a consequence, under extreme xeric conditions, shrub mortality increased in north-facing slopes, especially when not grazed. The removal of transpiring area and the reduction of plant competition favoured developmental stability and survival in grazed plants. Differences between grazed and ungrazed plants were most evident in more mesic (north-facing) areas.

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Introduction

In arid environments, water is the most limiting resource affecting nutrient acquisition and carbon assimilation (Schulze & Hall, 1982). Under water shortage plants

* Address for correspondence: C. L. Alados. E-mail: alados@ipe.csic.es

reduce their metabolic activity and stomatal conductance (Younis *et al.*, 1993), causing a decrease in photosynthesis (Deputt & Caldwell, 1973; Comstock & Ehleringer, 1984). Low carbon fixation may decrease growth rate (Sultan & Bazzaz, 1993; Pugnaire *et al.*, 1993). Low growth rates are found in low-resource environments (Grime, 1977, 1979; Chapin, 1980). Nevertheless, plants growing in infertile environments are adapted to low levels of resources, and show adaptive mechanisms to deal with stress. Therefore, identifying plants living in stressful environments as being stressed may be misleading. In addition, it is important to know whether resistance to one environmental stress will confer resistance to other environmental stresses (Chapin *et al.*, 1993). For example, plants exposed to water stress may show traits similar to plants exposed to low nutrient levels, high temperatures or saline environments (Levitt, 1980). Previous studies have demonstrated that grazing reduces the transpiring leaf area of plants, thereby increasing survivorship during drought periods (Verkaar, 1986; Olson & Richards, 1988; Coughenour *et al.*, 1990; Simoes & Baruch, 1991).

Changes in developmental stability can be used to detect conditions of stress, usually by measuring the increase of intra-individual variability in repeated structures. The measurement of developmental stability has been successfully applied to detect stress caused by human disturbance in natural ecosystems (Soulé, 1967; Zaharov, 1987; Parsons, 1992; Markow, 1994) and has traditionally been measured by fluctuating asymmetry (FA), (Van Valen, 1962; Palmer & Strobeck, 1986). A large number of studies have demonstrated that FA increases under different kinds of stress, including genetic, temperature, food deficit, parasitic and pathogenic, and pesticide stress, among others (Parsons, 1990; Alados *et al.*, 1993; Clarke, 1993; Freeman *et al.*, 1993; Graham *et al.*, 1993; Markow, 1994; Møller & Swaddle, 1997). In addition to bilateral symmetry, statistical noise in allometric relations also can be used to detect random intra-individual variability during development in plants (Freeman *et al.*, 1993; Graham *et al.*, 1993; Sherry & Lord, 1996). Particularly, the statistical noise in the allometric relation between internode length and node order can be used as a measure of developmental instability caused by stress (Alados *et al.*, 1994, 1998*a,b*, 1999*a*; Escós *et al.*, 1995, 1997; Anne *et al.*, 1998).

In addition, fractal complexity in branching structures results in optimal nutritional support of the structure (Sugihara & May, 1990; Eghball *et al.*, 1993; Chen *et al.*, 1994; Shibusawa, 1994). Fractal complexity can be characterized by the fractal dimension. Indeed, previous studies have demonstrated fractal dimension to change under stress situations (Alados *et al.*, 1994, 1995, 1996*a,b*; Escós *et al.*, 1995, 1997).

In this study we have applied measures of translational symmetry and fractal dimension to plants growing in a semi-arid environment to test the effects of grazing and slope exposure on developmental traits. Thus, we investigated how allocation to developmental stability and production (complexity of branching patterns, growth and reproduction) vary in relation to environmental factors. We are interested in knowing how stress resistance mechanisms develop in Mediterranean shrubs living under very xeric conditions and how grazing influences that response.

Materials and methods

Study area and species

The experiment was conducted at the Rambla Honda valley, located near Tabernas (Almería, Spain), in Los Filabres range (37°08' N; 2°22' W, 600–900 m a.s.l.). The climate is semi-arid, with average annual precipitation (1965–1991) at Tabernas (9 km to the south, 490 m a.s.l.) at 218 mm and a mean annual temperature of 17.4°C.

(Puigdefábregas *et al.*, 1996). Temperatures and vapour pressure deficits during the summer months can exceed 40°C and 4.5 kPa, respectively (Pugnaire *et al.*, 1996). Rambla Honda is extensively grazed with sheep and goats, with a density of about one animal per ha.

The study was performed on *A. cytisoides*, a summer deciduous leguminous shrub. It is widespread throughout the south-eastern Iberian peninsula and is the preferred food species of domestic ruminants in this area of the Mediterranean basin, where it makes up to 60% of goats' diet (Barroso, 1991).

Experimental design

Two similar plots were chosen for this study. Both were characterized by sparse vegetation dominated by *A. cytisoides*, with a woody plant cover of 30%, and negligible presence of other xerophytic species such as *Artemisia barrelieri*. Both plots exhibited similar geomorphology and soil chemistry, and were separated by only ~200 m. One of these plots, of about 14 ha, had been excluded from grazing since 1 September 1991, while the other one was grazed. In order to determine how the extremely dry conditions of 1995 (rainfall in the spring of 1995 totalled 14.5 mm, i.e. 21% of the last 5-year average; R. Lázaro, pers. comm.) affected shrubs on dry (south-facing slopes) *vs.* more mesic (north-facing slopes) areas and the interaction with livestock grazing, we sampled *A. cytisoides* shrubs in northern and southern exposures, under grazing and non-grazing pressure in a 2 × 2 factorial design with two replicates. Differences between slope exposures are due only to sun radiance and its related effects on water evaporation and enhanced UV-B radiation. North- and south-facing slopes belonged to the same alluvial fan, and two alluvial fans were selected as the two replicates. A total of 160 plants similar in size were sampled during March 1995, 40 per treatment, 20 in each replicate. We selected adult plants of similar size, and cut one 3-year-old well-developed lateral branch from the same specific position. Additionally, we selected a well-developed annual shoot per branch located in second or third position from the previous year's shoot, and measured in the laboratory the internodal distance from base to top. To avoid interference by grazing, only undamaged stems were selected for the analyses. A detailed description of procedures and analyses is elsewhere (Escós *et al.*, 1997).

Data collection and analysis

We determined developmental instability by estimating the error of the arrangement of leaves on the stem. We measured the distance between consecutive nodes with an electronic calipre to the nearest 0.01 mm in one developed shoot per plant, and examined the relation between internodal length (L) and internodal order (N) on vegetative green shoots of *A. cytisoides* using the expression:

$$L = pN^b$$

where p and b are fitted constants. This expression corresponds to the allometric relationship between internode length and node order before the inflorescence development (Escós *et al.*, 1997). Taking logarithms on both sides,

$$\ln L = \ln p + b \ln N.$$

The values p and b can be obtained from regression analysis, and the standard error of the regression ($S_{y,x}$) and one minus the coefficient of determination adjusted to the

degrees of freedom (R^2), are measures of developmental instability, i.e. they measure the extent to which the actual phenotype departs from the hypothetical, undisturbed phenotype, during the developmental process (Alados *et al.*, 1994; Escós *et al.*, 1997).

Fractal dimension

To obtain the box-counting fractal dimension of branch architecture we took slides of 3-year-old branches of *A. cytisoides* in March 1995, when plant canopies were completely developed. Slides were taken at the same distance, focusing on the centre of the branch. Later, slides were digitized with Kodacrome. Images were captured with Adobe Photoshop 4.0 with a resolution of 3072×2048 pixels. Because the thickness of the lines within digitized images can have a large impact on fractal dimension (Berntson, 1994), images were preprocessed similarly, by selecting a window size of 1024×1024 pixels, then filtering, converting to greyscale, and adjusting to the same intensity. A computer program was written to analyse the data. This method was previously calibrated against images of known fractal dimension.

The box-counting capacity dimension (Hausdorff, 1919) consists of calculating the minimum number of n -dimensional cubes of side ε needed to cover the object. It is given by

$$D_c = \lim_{\varepsilon \rightarrow 0} \frac{\ln N_{(\varepsilon)}}{\ln (1/\varepsilon)}$$

where D_c is the fractal dimension of the projection of the plant into a plane. Box counting consists of superimposing a grid on the structure to be described and determining the number of squares that are needed to cover it.

Information dimension is a generalization of the capacity dimension that takes into account the relative probability of the cubes used to cover the set (Farmer *et al.*, 1983). Mathematically it is defined as:

$$D_I = \lim_{\varepsilon \rightarrow 0} \frac{I_{(\varepsilon)}}{\ln (1/\varepsilon)}$$

where $I_{(\varepsilon)} = -\sum_{i=1}^{N_{(\varepsilon)}} p_i \ln p_i$, and $p_i = x_i / \sum x_j$, x_i is the number of occupied pixels for each box of size i . Here we use the same grid as for box-counting, but instead of determining the number of occupied squares we count the number of occupied pixels in each box and calculate $I_{(\varepsilon)}$ for each box size (see Alados *et al.*, 1999b).

In order to discriminate between objects that have the same fractal dimension but appear different we measured the heterogeneity of a fractal structure and calculated its lacunarity, i.e. the degree of structural variation within the object. Heterogeneity can be measured by the evenness index:

$$\mathcal{J}_\varepsilon = \frac{\sum_{i=1}^{N_\varepsilon} p_i \ln p_i}{\ln N_\varepsilon}$$

The average of the evenness index for box size ranging between 8 pixels side (16384 boxes grid) to 256 pixels side (16 boxes grid) is a measure of the heterogeneity of the structure similar to the lacunarity measured by Smith *et al.* (1996). In addition, the coefficient of variation of the evenness index is also a measure of the branch structure heterogeneity (Alados *et al.*, 1999b).

Plant allocation to reproductive and vegetative structures was measured as the ratio of the inflorescence length to shoot length in each of the 160 shrubs. We also measured the total length of the shoot. Leaf area was calculated as length \times width of 10 leaves per plant, selected at the same position from 10 different shoots, and assuming an elliptical shape.

Plant survival in each plot was estimated in February 1996. Percentage of living canopy was determined as branch survival in each of 324 *A. cytisoides* shrubs sampled by transects. In *A. cytisoides*, a varying proportion of the canopy dies as a consequence of water stress and remains as standing dead biomass on the plant for several years. When the whole plant was dead, 0% of branch survival was recorded.

Relative water content (*RWC*) was determined by the method of Barrs & Weatherley (1962). Ten 10-cm long terminal segments of branches from each plant were cut, weighed in the field and placed overnight in a dark humid chamber at room temperature. Shoots were weighed after saturation and again after being dried at 70°C for 24 h. *RWC* was determined as $(mf - md)/(ms - md)$, where *m* is mass of shoots when fresh (*mf*), at saturation (*ms*) and when dried (*md*). Plant water deficit was then calculated as $1 - RWC$.

Data were analysed by ANOVA (MGLH routine in SYSTAT, Evanston, Illinois, and GLM in SAS 6.12) using a mixed model factorial design with grazing and slope aspect as fixed factors, and replicate as a random factor. Comparisons of means between grazing treatments for each slope aspect were made using Tukey's multiple comparisons test (Sokal & Rohlf, 1981). Floral-to-vegetative mass ratio was square-root transformed for normality. Shoot length and leaf area were log transformed.

Results

Shoot length varied significantly ($F_{1,155} = 12.83$, $p < 0.001$) with slope exposure (Fig. 1). North-facing plants produced larger shoots (167.33 mm) than south-facing

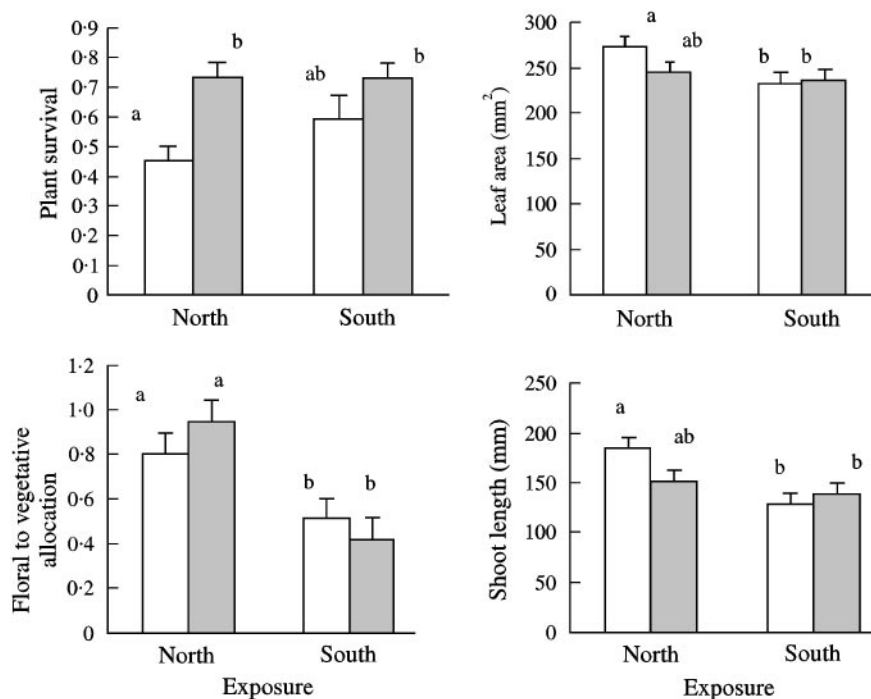


Figure 1. Comparative effects of exposure and grazing pressure on growth (shoot length, leaf area, floral to vegetative allocation) and plant survival of *A. cytisoides*. Means with the same letters show no significant differences at the 0.05 level, Tukey test. (□), ungrazed; (■) grazed.

plants (132.95 mm). This difference is more evident in ungrazed plants ($F_{1,78} = 15.77$, $p < 0.001$) than in grazed plants ($F_{1,77} = 1$, NS). Similar results were observed for the average leaf area. North-facing plants had significantly ($F_{1,155} = 4.45$, $p < 0.05$) larger leaf area (260.0 mm²) than south-facing plants (236.0 mm²), and the difference was also reduced when plants were grazed (Fig. 1). Finally, the allocation of energy to reproductive *vs.* vegetative structures was also significantly larger ($F_{1,155} = 28.01$, $p < 0.001$) in north-facing slopes (0.87) than in south-facing slopes (0.46). No differences between grazing regimes were observed. Plant survival was significantly enhanced ($F_{1,155} = 20.19$, $p < 0.001$) by grazing (Fig. 1), although no significant differences between exposures were observed ($F_{1,155} = 2.04$, NS). Differences between replicants were not significant.

Leaf arrangement in the stem fitted the equation $L = 2.43 N^{0.93}$, averaged for the 160 samples. The scaling parameter b increased significantly with grazing ($F_{1,155} = 7.00$, $p < 0.01$) equally in northern and southern exposed sites. This parameter measured how the distance among leaves scaled as we moved up the stem. The higher the parameter the larger the increase in internodal distance. There were no significant differences between slope exposure ($F_{1,155} = 1.64$, NS).

The adjusted coefficient of determination, R^2 , and the standard error of the regression, S_{yxx} , were significantly affected by slope exposure ($F_{1,155} = 11.09$, $p < 0.001$; $F_{1,155} = 9.14$, $p < 0.01$, respectively), and showed that *A. cytisoides* was developmentally more stable on south-facing than on north-facing slopes (Fig. 2). Similarly, grazing favoured stability ($F_{1,155} = 9.28$, $p < 0.01$ for R^2). This effect was more evident in plants located on north-facing slopes than on south-facing slopes.

The capacity fractal dimension (D_c) of branch structure in plants under different slope aspects and grazing regimes showed that north-facing plants had a significantly ($F_{1,154} = 69.99$, $p < 0.001$) larger fractal dimension (1.682) than south-facing plants (1.531), and that grazing reduced fractal dimension on both slopes ($F_{1,154} = 17.39$, $p < 0.001$). Similar results were observed for the information fractal dimension, D_T ($F_{1,154} = 83.69$, $p < 0.001$, for slope aspect; $F_{1,154} = 33.30$, $p < 0.001$, for grazing pressure). As expected information fractal dimensions present larger values, making the differences between treatment more pronounced (Fig. 2). The heterogeneity of branch distribution was measured by the averaged evenness index (\mathcal{J}_e) and the coefficient of variation of evenness index (\mathcal{J}_{cv}). As \mathcal{J}_e increases, the more homogeneously distributed the branches. Thus, \mathcal{J}_e is larger in north-exposed plants ($F_{1,154} = 14.63$, $p < 0.001$), especially when ungrazed ($F_{1,154} = 59.07$, $p < 0.001$). In the same way, as \mathcal{J}_{cv} increases, the heterogeneity of branch distribution into the canopy also increases. Thus, south-exposed plants presented more pronounced gaps in the crown, that is larger lacunarity (\mathcal{J}_{cv}), than north-exposed plants ($F_{1,154} = 23.18$, $p < 0.001$, Fig. 2).

Water deficit was significantly ($F_{1,44} = 7.78$, $p < 0.01$) higher in ungrazed (0.62 ± 0.02 , $n = 24$) than in grazed plants (0.56 ± 0.02 , $n = 24$), while exposure did not significantly affect water deficit ($F_{1,44} = 0.2$, NS).

Discussion

The concept of environmental stress has unknown implications for organism functioning and population persistence. The most common definition of stress is 'an environmental factor that causes a reduction in fitness' (Koenh & Bayne, 1989; Hoffman & Parsons, 1991; Lenski & Bennett, 1993). But the relation between stress and fitness is not expected to be linear. Lenski & Bennett (1993) observed that high temperature stress (42°C) leads to greater fitness in organisms such as *Escherichia coli* before mortality occurs at 43°C. In this study, *A. cytisoides* shrubs increased mechanisms preserving plant architecture (measured with developmental

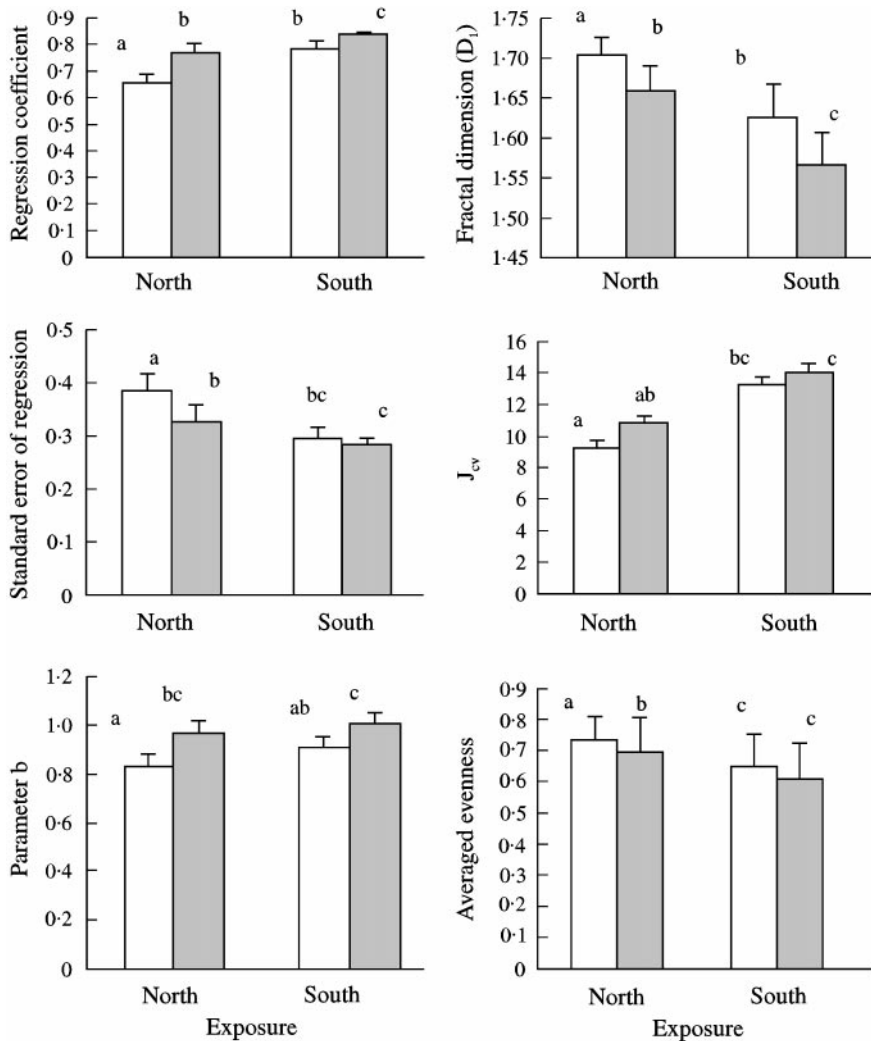


Figure 2. Comparative effects of exposure and grazing pressure on developmental stability (adjusted coefficient of determination R^2 and standard error of the regression, $S_{y,x}$), slope parameter b , and branch complexity (information dimension, D_1 , averaged evenness index, \mathcal{J}_e , and variation coefficient of the evenness index, \mathcal{J}_{cv}). Means with the same letters show no significant differences at the 0.05 level, Tukey test. (□), ungrazed; (■) grazed.

stability) at the expense of productivity (growth and reproduction), leading to an increase stress tolerance. Consequently, defining stress exclusively in terms of production decline may be misleading. Here we define stress as any environmental factor that causes a reduction in the efficient use of energy, causing a reduction in developmental homeostasis, and finally reducing long-term, total inclusive fitness.

In response to stress, organisms increase their metabolic rate (Parsons, 1993), and hence oxygen consumption and free radical production. This oxidative stress reaction is common in all living beings, and has been reported for organisms ranging from plants (Herouart *et al.*, 1993) to rodents (Atkinson *et al.*, 1993; Toraason *et al.*, 1993) to

humans (Kakkar *et al.*, 1993; Yoshida *et al.*, 1994). During development, organisms divert energy to a series of processes that buffer the disruptive effects of developmental noise during growth, which are called developmental stability or developmental homeostasis processes (Palmer, 1996). When a perturbation appears, there is less energy available and organisms have to choose between reduced maintenance (i.e. reduced developmental stability or developmental homeostasis) or reduced complexity, that is relative plant production independent of scale (fractal dimension) and reproduction (lower allocation to reproductive structures). One way to resist stress is by conserving energy normally available to plant production in order to allocate more energy to developmental homeostasis. Our data show evidence for this plant allocation strategy. *Anthyllis cytisoides* shrubs growing on south-facing slopes were developmentally more stable during the extreme 1994–1995 drought than individuals inhabiting more mesic, north-facing areas. This could be explained as a consequence of the greater growth experienced by individuals inhabiting more benign areas (with larger leaves and longer shoots), which cannot be supported when water resources are scarce. As a consequence, north-facing plants show reduced branch survival, especially when they were not grazed.

Plants are fractal structures, and as a consequence plant biomass is not linearly related to plant size. An indirect but non-destructive standardized measurement of relative biomass production independent of scale is the fractal dimension of branch structures, which is independent of branch size. The fractal dimension measures the complexity with which plants fill space. A higher complexity in branch structure increases the efficiency of gas exchange at the whole-plant level. Previous studies have demonstrated a reduction in the fractal structure and in physiological processes under stress situations (Alados *et al.*, 1994, 1995, 1996a; Escós *et al.*, 1995). In this study, we observed that plants with larger fractal dimension, as north-exposed plants, presented larger developmental instability. The response of an organism to a potential stress could result in a cascade of time-scaled responses where impaired growth and complexity may compensate for further levels of stress in a predictable environment. Our results suggest that under the extreme xeric conditions of 1995, shrubs with low complexity of fractal structures are developmentally more stable than plants with larger biomass production. By reducing growth, a plant reduces its dependency on the environment for the acquisition of new resources (Chapin, 1991). However, by doing so the plant also reduces its photosynthetic efficiency and thereby water deficit. Thus, a reduction in transpired water by reducing the photosynthetic area in our south-facing shrubs may counteract the loss of water in the more xeric (south-facing) slopes, as shown in the similar water deficit of north- vs. south-facing slope plants. Allocation to reproductive structures was also reduced in south-facing plants.

The effects of grazing have already been documented on *A. cytisoides* (Alados *et al.*, 1996b, 1997; Escós *et al.*, 1996, 1997), showing a higher incidence of environmental disturbance under both heavy grazing pressure and lack of grazing. Grazing increased both survival and fecundity, and developmental stability measurements provided useful, early indicators of this impact (Escós *et al.*, 1997). These results are partially due to the lower water deficit of grazed plants, because of the removal of transpiring material, and partially due to reduced plant competition (P. Haase, pers. comm.). When we compared the effect of grazing in shrubs of north- and south-facing slopes, we observed that the effect of grazing was more evident in more mesic (north-facing slopes) areas than in plants inhabiting more extreme conditions (south-facing slopes). This result supports Parson's (1994) hypothesis that in extreme environmental conditions the potential for evolutionary change is low because of the high costs of accommodation to environmental stress, and its reverse formulation, i.e. plants from high resource environments have a broader reaction norm (Sterans, 1989).

Thus, developmental stability was higher in grazed than in ungrazed *A. cytisoides* shrubs, which had a higher branch survival, resulting in a smaller transpiring area and lower water deficit in grazed shrubs.

Considering fitness only in terms of reproductive success we should conclude that, after an extreme drought period, shrubs inhabiting more benign conditions (north-facing slopes) may have higher fitness than plants inhabiting more xeric areas (south-facing). But assessing fitness requires the consideration of not only reproduction but also survival. The allocation of energy to stress tolerance mechanisms increases survival, but reduces energy for reproduction. Thus, in long-living species, survival is more important than reproduction from a final, global fitness point of view (Emlen & Pickett, 1989; Escós *et al.*, 1997).

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References

- Alados, C.L., Escós, J.M. & Emlen, J.M. (1993). Developmental instability as an indicator of environmental stress in the Pacific hake (*Merluccius productus*). *Fisheries Bulletin*, **91**: 587–593.
- Alados, C.L., Escós, J. & Emlen, J.M. (1994). Scale asymmetry: a tool to detect developmental instability under the fractal geometry scope. In: Novak, M.M. (Ed.), *Fractals in the Natural and Applied Sciences*, pp 25–36. North-Holland: Elsevier Science B.V. 451 pp.
- Alados, C.L., Escós, J. & Emlen, J.M. (1995). Fluctuating asymmetry and fractal dimension of the saggital suture as inbreeding depression indicators in Dama and Dorcas gazelle. *Canadian Journal of Zoology*, **73**: 1967–1974.
- Alados, C.L., Escós, J. & Emlen, J.M. (1996a). Fractal structure of time distribution activities: an indicator of stress. *Animal Behaviour*, **51**: 437–443.
- Alados, C.L., Barroso, F.G., Aguirre, A. & Escós, J.M. (1996b). Effects of early season defoliation on further herbivore of a Mediterranean brows species. *Journal of Arid Environments*, **34**: 455–463.
- Alados, C.L., Barroso, F.G. & García, L. (1997). Effects of early season defoliation on above-ground growth of *Anthyllis cytisoides*, a Mediterranean browse species. *Journal of Arid Environments*, **37**: 269–283.
- Alados, C.L., Navarro, T., Cabezudo, B., Emlen, J.M. & Freeman, D.C. (1998a). Developmental instability in gynodioecious *Teucrium lusitanicum*. *Evolutionary Ecology*, **12**: 21–34.
- Alados, C.L., Emlen, J.M., Wachocki, B. & Freeman, D.C. (1998b). Instability of development and fractal architecture in dryland plants as an index of grazing pressure. *Journal of Arid Environments*, **38**: 63–76.
- Alados, C.L., Navarro, T. & Cabezudo, B. (1999a). Tolerance assessment of *Cistus ladanifer* to serpentine soils by developmental stability analysis. *Plant Ecology*, **143**: 51–66.
- Alados, C.L., Escós, J.M., Emlen, J.M. & Freeman, D.C. (1999b). Characterization of branching patterns by fractal analyses to detect plant adaptive strategies. *International Journal of Plant Science, Suppl.*, **160**: S147–S155.
- Anne, P., Mawri, F., Gladstone, S. & Freeman, D.C. (1998). Is fluctuating asymmetry a reliable biomonitor of stress? A test using life history parameters in soybean. *International Journal of Plant Science*, **159**: 559–565.
- Atkinson, A., Meeks, R.G. & Roy, D. (1993). Increased oxidative stress in the liver of mice treated with trichlorethylene. *Biochemical and Molecular Biology International*, **31**: 297–304.
- Barroso, F. (1991). Estudio sobre el comportamiento alimentario y social de la cabra doméstica en el sureste árido español. Tesis Doctoral. Granada. 312 pp.

- Barrs, H.D. & Weatherley, P.E. (1962). A reexamination of the relative turgidity technique for estimating water deficits in leaves. *Australian Journal of Biological Sciences*, **15**: 413–428.
- Berntson, G.M. (1994). Root systems and fractals: how reliable are calculations of fractal dimension? *Annals of Botany*, **73**: 281–284.
- Chapin, F.S. III (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematic*, **11**: 233–260.
- Chapin, F.S. (1991). Integrated responses of plants to stress. *BioScience*, **41**: 29–36.
- Chapin, F.S., Autumn, K. & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *American Naturalist*, **142**: S78–S92.
- Chen, S.G., Ceulemans, R. & Impens, I. (1994). A fractal-based *Populus* canopy structure model for the calculation of light interception. *Forestry Ecological Management*, **69**: 97–110.
- Clarke, G.M. (1993). Fluctuating asymmetry of invertebrate populations as a biological indicator of environmental quality. *Environmental Pollution*, **82**: 207–211.
- Comstock, J. & Ehleringer, J. (1984). Photosynthetic responses to slowly decreasing leaf water potentials in *Encelia frutescens*. *Oecologia*, **61**: 241–248.
- Coughenour, M.B., Detling, J.K., Bamberg, I.E. & Mugamb, M.M. (1990). Production and nitrogen responses of the African dwarf shrub *Indigofera spinosa* to defoliation and water limitation. *Oecologia*, **83**: 546–552.
- Deput, E.J. & Caldwell, M.M. (1973). Seasonal patterns of net photosynthesis of *Artemisia tridentata*. *American Journal of Botany*, **60**: 426–435.
- Eghball, B., Settimi, J.R., Maranville, J.W. & Parkhurst, A.M. (1993). Fractal analysis for morphological description of corn roots under nitrogen stress. *Agronomic Journal*, **85**: 287–289.
- Emlen, J.M. & Pikitch, E.K. (1989). Animal population dynamics: identification of critical components. *Ecological Modelling*, **44**: 253–273.
- Escós, J., Alados, C.L. & Emlen, J.M. (1995). Fractal structures and fractal functions as disease indicators. *Oikos*, **74**: 310–314.
- Escós, J., Barroso, F.G., Alados, C.L. & García, L. (1996). Effects of simulated herbivory on reproduction of a Mediterranean semi-arid shrub (*Anthyllis cytisoides*). *Acta Oecologica*, **17**: 139–149.
- Escós, J.M., Alados, C.L. & Emlen, J.M. (1997). Grazing impact on plant fractal architecture and fitness of a Mediterranean shrub (*Anthyllis cytisoides*). *Functional Ecology*, **11**: 66–78.
- Farmer, D., Ott, E., Yorke, J.A. (1983). The dimension of chaotic attractors. *Physica*, **7D**: 153–180.
- Freeman, D.C., Graham, J.H. & Emlen, J.M. (1993). Developmental stability in plants: symmetries, stress and epigenesis. *Genetica*, **89**: 97–119.
- Graham, J.H., Freeman, D.C. & Emlen, J.M. (1993). Developmental stability: A sensitive indicator of population under stress. In: Landis, W.G., Hughes, J.S. & Lewis, M.A. (Eds), *Environmental Toxicology and Risk Assessment. ASTM STP 1179*, pp 136–158. Philadelphia: American Society for Testing and Materials.
- Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**: 1169–1194.
- Grime, J.P. (1979). *Plant Strategies and Vegetation Processes*. Chichester: John Wiley. 222 pp.
- Harvey, A. (1984). Aggradation and dissection sequences of Spanish alluvial fans: influence on morphological development. *Catena*, **11**: 289–304.
- Hausdorff, F. (1919). Dimension and Äußeres Maß. *Mathematisches Annalen*, **79**: 157–179.
- Herouart, D., Bowler, C., Willekens, H., Van-Camp, W., Slooten, L., Van-Montagu, M. & Inze, D. (1993). Genetic engineering of oxidative stress resistance in higher plants. *Philosophical Transactions of the Royal Society of London, Series B*, **342**: 235–240.
- Hoffmann, A.A. & Parsons, P.A. (1991). *Evolutionary Genetics and Environmental Stress*. New York: Oxford University Press. 283 pp.
- Kakkar, P., Jaffery, F.N. & Viswanathan, P.N. (1993). Unity and diversity of responses to xenobiotics in organisms. *Biomedical and Environmental Sciences*, **6**: 352–366.
- Koehn, R.K. & Bayne, B.L. (1989). Towards a physiological and genetical understanding of the energetics of the stress response. *Biological Journal of Linnaean Society*, **37**: 157–171.
- Lenski, R.E. & Bennett, A.F. (1993). Evolutionary response of *Escherichia coli* to thermal stress. *American Naturalist*, **142** (Suppl.), S47–S64.
- Levitt, J. (1980). *Responses of Plants to Environmental Stresses*. New York: Academic Press. 697 pp.

- Markow, T.A. (1994). *Contemporary Issues in Genetics and Evolution. Developmental Instability: Its Origins and Evolutionary Implications*. Dordrecht: Kluwer Academic Publishers. 335 pp.
- Møller, A.P. & Swaddle, J.P. (1997). *Asymmetry, developmental stability and evolution*. Oxford University Press. 291 pp.
- Olson, B.E. & Richards, J.H. (1988). Annual replacement of the tiller of *Agropyron desertorum* following grazing. *Oecologia*, **76**: 1–6.
- Palmer, A.R. (1996). Waltzing with asymmetry. Is fluctuating asymmetry a powerful new tool for biologists or just a alluring new dance step? *BioScience*, **46**: 518–532.
- Parsons, P.A. (1990). Fluctuating asymmetry: an epigenetic measure of stress. *Biological Reviews*, **65**: 131–145.
- Parsons, P.A. (1992). Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity*, **68**: 361–364.
- Parsons, P.A. (1993). The importance and consequences of stress in living and fossil populations: From life-history variation to evolutionary change. *American Naturalist*, **142**: S5–S20.
- Parsons, P.A. (1994). Developmental variability and the limits of adaptation: interaction with stress. In: Markow, T. (Ed.), *Developmental Instability: Its Origins and Evolutionary Implications*, pp. 247–256. Dordrecht: Kluwer Academic Publishers. 335 pp.
- Pugnaire, F.I., Haase, P., Incoll, L.D. & Clark, S.C. (1996). Responses to watering of the perennial tussock grass *Stipa tenacissima* L. *Functional Ecology*, **10**: 265–274.
- Pugnaire, F.I., Serrano L. & Pardos, J.A. (1993). Constraints by water stress on plant growth. In: Pessarakli, M. (Ed.), *Handbook of Plant and Crop Stress*, pp. 247–259. New York: Marcel Dekker. 697 pp.
- Puigdefàbregas, J., Alonso, J.M., Brenner, J.A., Clark, S.C., Domingo, F., Cueto, M., Gutiérrez, L., Incoll, L.D., Lázaro, R., Nicolau, J.M., Sánchez, G., Solé, A., Torrentó, J.R. & Vidal, S. (1996). Interactions of soil and vegetation along a catena in semiarid Spain. In: Thornes, J. & Brandt, J. (Eds), *Mediterranean Desertification and Land Use*, pp 137–168. New York: John Wiley. 554 pp.
- Schulze, E.D. & Hall, A.E. (1982). Stomatal responses, water loss, and CO₂ assimilation rates of plants in contrasting environments. In: Lange, O.L., Nobel, P.S., Osmond, C.B. & Ziegler, H. (Eds), *Encyclopedia of Plant Physiology. New Series*, Vol. 12B, pp. 181–230. Berlin: Springer-Verlag.
- Sherry, R.A. & Lord, E.M. (1996a). Developmental stability in leaves of *Clarkia tembloriensis* (Onagraceae) as related to population outcrossing rates and heterozygosity. *Evolution*, **50**: 80–91.
- Shibusawa, S. (1994). Modelling the branching growth fractal pattern of the maize root system. *Plant and Soil*, **165**: 339–347.
- Simoes, M. & Baruch, Z. (1991). Responses to simulated herbivory and water stress in two tropical C4 grasses. *Oecologia*, **88**: 173–180.
- Smith, T.G., Lange, G.D. & Marks, W.B. (1996). Fractal methods and results in cellular morphology — dimensions, lacunarity and multifractals. *Journal of Neuroscience Methods*, **69**: 123–136.
- Sokal, R.R. & Rohlf, F.J. (1981). *Biometry*. New York: Freeman and Company. 859 pp.
- Soulé, M. E. (1967). Phenetics of natural populations, II. Asymmetry and evolution in a lizard. *American Naturalist*, **101**: 141–160.
- Sterans, S.C. (1989). The evolutionary significance of phenotypic plasticity. *BioScience*, **39**: 436–445.
- Sugihara, G. & May, R.M. (1990). Applications of fractals in ecology. *Trends in Ecology and Evolution*, **5**: 79–86.
- Sultan, S.E. & Bazzaz, F.A. (1993). Phenotypic plasticity in *Polygonum persicaria* II. Norms of reaction to soil moisture and the maintenance of genetic diversity. *Evolution*, **47**: 1032–1049.
- Toraason, M., Heinroth-Hoffmann, I., Richards, D., Woolery, M. & Hoffmann, P. (1994). H₂O₂ induced oxidative injury in rat cardiac myocytes is not potentiated by 1,1,1-trichloroethane, carbon tetrachloride, or halothane. *Journal of Toxicology and Environmental Health*, **41**: 489–507.
- Van Valen, L. (1962). A study of fluctuating asymmetry. *Evolution*, **16**: 125–142.
- Verkaar, H.J. (1986). When does grazing benefit plants? *Trends in Ecology and Evolution*, **1**: 168–169.

- Yoshida, S.H., German, J.B., Fletcher, M.P. & Gershwin, M.E. (1994). The toxic oil syndrome: a perspective on immunotoxicological mechanisms. *Regulatory Toxicology and Pharmacology*, **19**: 60–79.
- Younis, M.E., El Shahaby, O.A., Hasaneen, M.N.A. & Gaber, A.M. (1993). Plant growth, metabolism and adaptation in relation to stress conditions: XVII. Influence of different water treatments on stomatal apparatus, pigments and photosynthetic capacity in *Vicia faba*. *Journal of Arid Environments*, **25**: 221–232.
- Zakharov, V. (1987). *Animal Asymmetry: Populations Phenogenetic Approach*. Moscow: Nauka.