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Scale-invariant structure of size fluctuations in plants

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A wide range of physical and biological systems exhibit complex behaviours characterised by a scale-invariant structure of the fluctuations in their output signals. In the context of plant populations, scaling relationships are typically allometric. In this study, we analysed spatial variation in the size of maize plants (*Zea Mays* L.) grown in agricultural plots at constant densities and found evidence of scaling in the size fluctuations of plants. The findings indicate that the scaling of the probability distribution of spatial size fluctuation exhibits non-Gaussian behaviour compatible with a Lévy stable process. The scaling relationships were observed for spatial scales spanning three orders of magnitude. These findings should provide additional information for the selection and development of empirically accurate models of pattern formation in plant populations.

A wide range of physical and biological systems exhibit spatial and temporal scaling behaviour, from the spatial sequences of DNA nucleotides[1–4] to the dynamics of natural populations[5]. In the context of plant populations, scaling relationships are typically allometric[6–9]. Here, we provide evidence of scale invariance in the size fluctuations of plants in even-aged monospecific stands.

Within plant populations, there is often a large degree of variability in the size of individual plants, which reflects differences in age, genetics, environmental heterogeneity and competition. The study of plant monocultures, which are characterised by a comparatively uniform age, environment and genetic background, typically emphasises competitive effects[10,11]. Nevertheless, size variability also has implications for plant monocultures. For example, size may affect the mortality and fecundity of individual plants as well as the reproductive outcome and survival of suppressed individuals[12,13].

Studies investigating size variability in plant monocultures have generally focused on the skewness of size distribution, but other measures of variability, including the Lorenz curve and the Gini coefficient, have been used to investigate plant population structure[14–20]. In contrast with previous research, the present study emphasises size fluctuations defined as $Z_{\Delta k} = S_{k+\Delta k} - S_k$, where S_k is the size (height) of a given plant at the position k in a linear stand and Δk is a spatial scale (an integer).

Results

Data were collected from well-fertilised maize crops (*Zea Mays* L.) in southern Brazil ($23^\circ 20' S$, $51^\circ 57' W$; approximately 450 m above sea level) with standard plant population densities: the linear density at a given stand was $\simeq 4.7$ plants m^{-1}, and the typical distance between stands was 0.9 m. Successive measures of the heights of surviving plants were recorded along linear stands [see Fig. 1(a)]. The heights of mature plants were measured from the soil surface to the pennant apex. The data sets correspond to the maize hybrids AG 9010, AS 1570, P 30F87 and P 30K75, and the number of data points are 2203, 2111, 1803 and 2109, respectively. The data for the AS 1570 hybrid are shown in Figures 1(b) and 1(c).

The probability density function (PDF) of plant size, $P(S)$, exhibited Gaussian behaviour around the peak and a long left tail, which indicates negative skewness [Fig. 2 (a)]. This finding is consistent with previously reported results for maize crops[21]. In contrast, the PDF of size fluctuation, $P(z_1)$, was nearly symmetric, leptokurtic and non-Gaussian [Fig. 2 (b)]. For comparison, we fitted $P(z_1)$ to a symmetric Lévy distribution, $P_L(z) = (1/\pi)\int_0^\infty \exp(-\gamma q^\alpha)\cos(qz)dq$, with scale factor γ and index α. As shown in Fig. 2 (b), a good agreement with the Lévy distribution was observed.

We also investigated size fluctuations for larger spatial scales. We found that $P(z_{\Delta k})$ exhibits a common functional form for spatial scales in the range $1 < \Delta k < 1000$. When the PDFs at different spatial scales were superimposed, all the data collapsed onto the same curve [e.g., Fig. 2 (c)]. We fitted $P(z_{\Delta k})$, for different values of

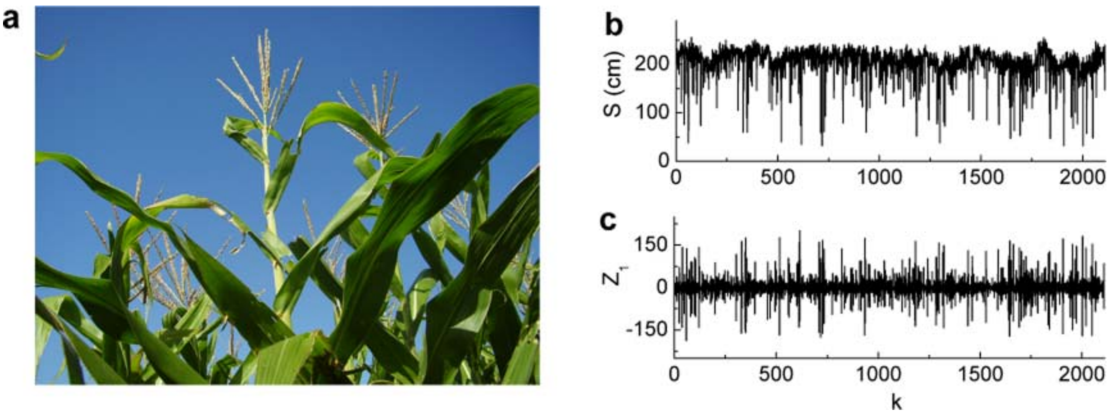

Figure 1 | Definition of size fluctuation. (a) Typical plants from a crop of maize (*Zea Mays* L.) grown in southern Brazil. (b) Successive plant size, S (height in centimetres), measured in a linear stand for the AS 1570 hybrid. (c) Successive size increments, $Z_1 = S_{k+1} - S_k$, obtained from the series shown in (b).

Δk, to the symmetric Lévy distribution $P_L(z)$. In spite of local fluctuations, the index α stayed approximately constant in the range $1 < \Delta k < 1000$ [Fig. 2 (d)].

Discussion

According to the analysis described above, the scaling of the probability distribution of size differences in maize crops exhibits non-Gaussian behaviour that is compatible with a Lévy stable process. The heavy-tailed character of the distribution of size differences, which is consistent across different spatial scales, indicates that rare but relatively large size differences—compared to Gaussian processes—can occur along the stand. As a result, clusters of small fluctuations are connected by these rare and large fluctuations. The analysis of size differences may therefore provide an alternative method for quantifying size inequality in plant populations.

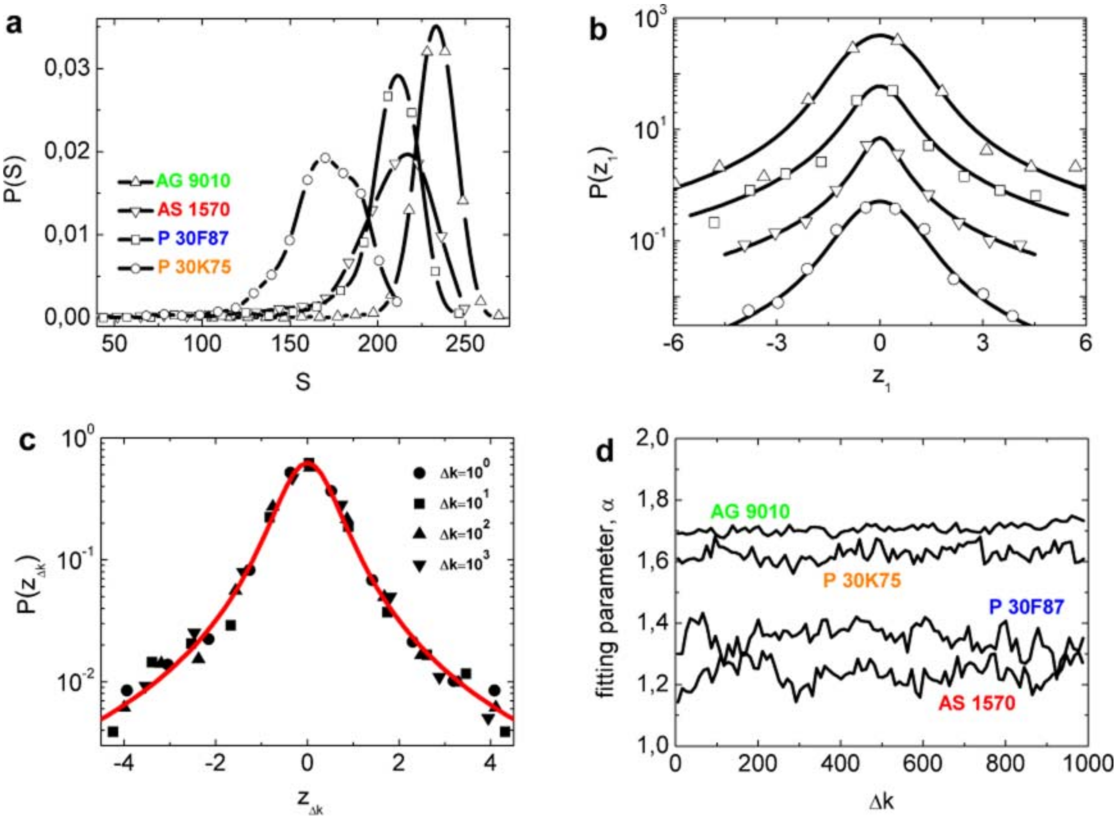

Figure 2 | Scaling structure of size fluctuations. (a) Probability density of plant size, $P(S)$, for all records. (b) Probability density of size fluctuation, $P(z_1)$, for all records; $z_{\Delta k} = Z_{\Delta k}/\sigma$, where σ is the standard deviation. Empty symbols are according to the legend in (a). The solid lines are symmetrical Lévy distributions, $P_L(z)$, with a scale factor of 0.4 and the following index values: $\alpha = 1.68$ (AG 9010); $\alpha = 1.28$ (P 30F87); $\alpha = 1.10$ (AS 1570); and $\alpha = 1.57$ (P 30K75). α was obtained by minimum squares fitting. Some curves are vertically shifted for better visualisation. (c) Superposition of $P(z_{\Delta k})$ at distinct spatial scales, Δk, for the AS 1570 hybrid. The solid line is given by the Lévy distribution, $P_L(z)$, with a scale factor of 0.4 and an index of 1.23. (d) Index α of $P_L(z)$ obtained from fits to $P(z_{\Delta k})$ for $1 < \Delta k < 1000$. The average values of α, $\bar{\alpha}$, were 1.71 (AG 9010), 1.62 (P 30K75), 1.35 (P 30F87) and 1.23 (AS 1570).

Our findings suggest that the complexity of crowded plant populations may be characterised by scaling properties of size fluctuations. The underlying mechanisms responsible for this pattern may be better understood by considering examples of heavy-tailed distributions in human dynamics. The burst nature of individual activities has been linked to a decision-making process in which individuals execute tasks based on a perceived priority. These priority-based mechanisms can be used to explain a wide range of collective human activity patterns[22,23]. Analogously, bursts and heavy tails in plant populations may reflect some fundamental and potentially generic features of individual plants. These collective patterns may be related to individual ecological strategies, such as competition for resources and plant physiology, and naturally, the effects of different strategies must be considered in tandem. For example, taller plants more readily access light and therefore possess a competitive advantage at any moment during the growth process. However, height incurs numerous costs including past investment, the maintenance of stems and support structures and disadvantages associated with the transport of water to increased heights[24].

Size inequality in plant populations has been previously shown to be related to competition, but the underlying mechanisms are still debated. A favoured hypothesis is size-asymmetric competition: larger individuals obtain a disproportionate resource advantage (for their relative size) over smaller individuals, as in the example of competition for light[17,25,26]. Another hypothesis is related to variations in local crowding: the ability of individuals to obtain resources is affected by the size, proximity and number of neighbours[27–29]. Other proposed mechanisms consider functional interactions among plants that trigger morphological and physiological changes in response to the proximity of other plants. The role of informational photoreceptors in these responses suggests that light-dependent mechanisms contribute to changes in the size structure of plant populations[30–33].

With the goal of identifying and quantifying the mechanisms responsible for size inequality, several approaches, such as reaction-diffusion models, patchy-environment models and neighbourhood models, have been applied to assess the spatiotemporal behaviour of plant populations[34,35]. However, the distribution of size fluctuation was not addressed in these studies. Our approach should provide additional information for the selection and development of empirically accurate models of pattern formation in plant populations. A natural extension of the present work would be to investigate the robustness of the results with respect to plant development from germination to maturity. Future studies should also include a parallel analysis in other natural plant populations along with a two-dimensional analysis in crop fields.

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Author contributions

R. S. M. & S. P. J. collected data and designed research; S. P. J., R. S. M., E. K. L. & L. C. M. performed research and wrote the manuscript; S. P. J. performed the statistical analysis.

Additional information

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