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Biomechanics of Bark Patterning in Grasstree

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Highlights: Bark patterns are a visually important characteristic of trees, attributed to fractures caused by secondary growth of the trunk and branches. A detailed understanding of bark patterns has been impeded by insufficient information regarding biomechanical properties of bark and the corresponding difficulties in faithfully modeling bark fractures using continuum mechanics. Here we focus on grasstrees, which have an unusual bark-like structure composed of distinct leaf bases connected by sticky resin. Due to its discrete character, this structure is exceptionally well suited for computational studies. We created a dynamic grasstree model, which captures both the phyllotactic patterning of the leaf bases during primary growth and the emergence of fractures due to secondary growth. The model reproduces key features of grasstree bark patterns, including inhomogeneities due to compression of leaf bases at the sites of inflorescences.

Keywords: Bark pattern, fracture mechanics, primary and secondary growth, biomechanical model.

INTRODUCTION

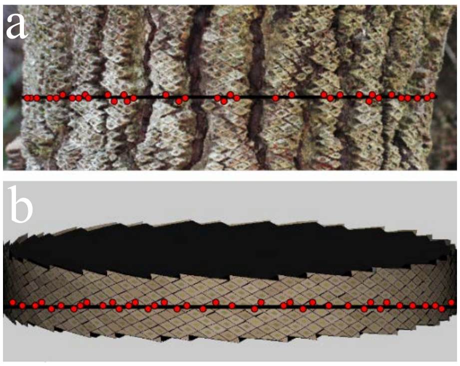
Grasstrees (*Xanthorrhoea*, Fig. 1) are a genus of monocots native to Australia with a morphology adapted to frequent fires. Their stems are pseudomonopodial. The straight course of the stem is disturbed when the terminal apex produces an inflorescence and an auxillary bud takes over further vegetative development (Borsboom 2005). Leaves are arranged into dense spiral phyllotactic patterns (Staff 1968). During fires, leaves are burnt back to their bases, which are cemented together by melting resin to form a type of bark that protects the tree from disease and future fires (Lamont et al. 2004). Over time, this resin fractures, partitioning interconnected leaf bases into separate regions. As a result, grasstree bark gradually progresses from a regular lattice of interconnected leaf bases near the top of the tree to a fractured pattern of patches similar to that observed in other tress near the base. Here we show that this progression, and its disturbances at the sites supporting past inflorescences, can be explained in mechanical terms. To this end, we have constructed a virtual grasstree that combines a descriptive model of primary growth and phyllotaxis with a mechanical model of fractures operating on the discrete lattice of parastichies induced by this phyllotaxis.


Figure 1. Young and older grasstree.

PREVIOUS WORK

Fractures have been simulated using both discrete and continuous models. Skjeltorp and Meakin (1988) introduced a mass-spring model to simulate fractures in an elastic layer under tension. Federl and Prusinkiewicz (1996) adopted this system to model fractures in tree bark. In contrast to the work presented here, they considered the mass-spring as an (imperfect) approxi-mation of bark thought of as a homogeneous material. Improving this approximation, Federl and Prusinkiewicz (2002) modified their previous model by replacing masses and springs with a finite-element method. The resulting model produced several plausible bark patterns, but the question of whether real bark is adequately approximated as a continuous, homogenous sheet was not addressed. The grasstree offers a unique opportunity to create a faithful bark model due to the macroscopic lattice structure induced by the underlying phyllotactic arrangement of leaf bases. This structure justifies the use of a discrete model.

SIMULATIONS



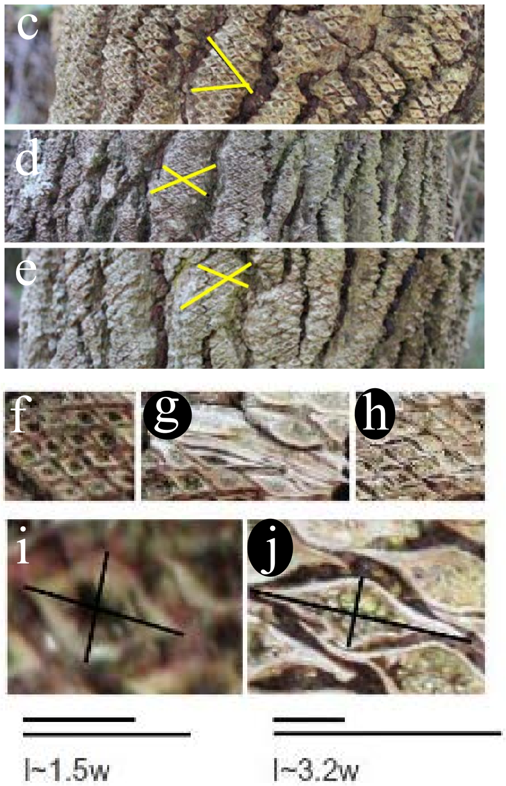


Figure 2. Estimating parameters of the phyllotactic pattern. (a,b) Number of bases that a horizontal line intersects in a real image (~37) and in the model (~40). (c-e) Estimation of the angle between parastichies (~56°). (f-j) The horizontal stretch of bases: (f,i) at the location between inflorescences, (g) at a bend of the stem where leaf bases are severely deformed, and (h,j) at the location of an inflorescence.

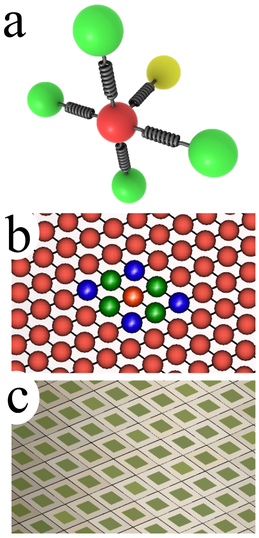


Figure 3. (a,b) Mesh of masses and springs. Yellow mass belongs to the inner layer that cau-ses growth in diameter. Blue masses complete leaf bases. (c) Resulting pattern of leaf bases.

The shoot apical meristem produces leaves sequentially in a phyllotactic pattern. Parameters of this pattern were inferred from photographs of real grasstrees (Fig. 2). In the model, we represented leaf bases as masses and their resin connections as (Hookean) springs, connecting each base to its four nearest neighbors (Fig. 3). The bark layer increased in radius, and thus in circumference, due to secondary growth. This was simulated by gradually pushing each mass outwards with springs that connected leaf bases to the inner core of the tree. Consequently, the spring forces between masses increased until a critical threshold value was reached and some springs broke (the threshold value was subject to small random variations, needed to break the symmetry of the system). The bark pattern was defined by the resulting fractures, which separated patches of bases connected by the remaining springs.

To simulate the influence of inflorescence sites, we have periodically shifted the growth axis and/or the radius of the bark layer. We used measurements of a real grasstree (Lamont et al. 1979) to calibrate proportions of this system. We also observed that leaf bases near the flowering sites have different aspect ratios, compared to the stem segments between flowering sites (Fig. 2c), and we incorporated these changes into the model by modifying parameters of the phyllotactic pattern.

RESULTS AND DISCUSSION

We have created a model of grasstree development (Fig. 4) as a basis for studying the emergence of grasstree bark patterns. These patterns are different near the sites of inflorescences and between these sites (Fig. 5). The areas near flowering sites are characterize by a network of diagonal fractures that run along the parastichies. Areas between flowering sites have long fractures running approximately parallel to the stem axis. Our biomechanical model emergently captures these differences. Although the generality of this result is qualified by the unusual structure of grasstree bark, it supports the hypothesis that bark pattern formation is primarily a biomechanical phenomenon. From a broader perspective, this result increases the spectrum of morphogenetic phenomena in which biomechanics and properties of space, rather than detailed genetic patterning, play a key role (Prusinkiewicz and de Reuille, 2010).

Figure 4. Simulation of grasstree development

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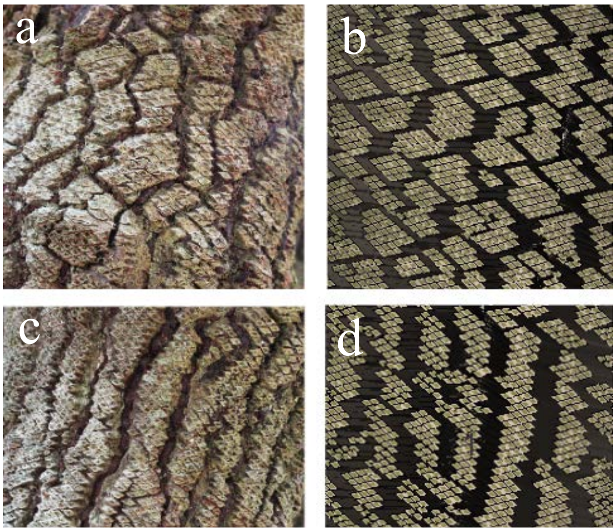

Figure 5. Fracture patterns in a real grasstree stem (a,c) and simulation (b,d). Areas near inflorescence sites have compressed bases with more diagonal fractures (a,b), regions without flowering have primarily vertical fractures (c,d).

LITERATURE CITED

Borsboom AC. 2005. *Xanthorrhoea:* A review of current knowledge with a focus on *X. johnsonii* and *X. latifolia,* two Queensland protected plants-in-trade. Environmental Protection Agency, Queensland, 87 pp.

Federl P, Prusinkiewicz P. 1996. A texture model for cracked surfaces. In *Proceedings of the Seventh Western Computer Graphics Symposium*, pp. 23-29.

Federl P, Prusinkiewicz P. 2002. Finite element model of fracture formation on growing surfaces. In *Proceedings of ICCS 2004,* Part II, *LNCS 3037*, pp. 138-145.

Lamont BB, Downes S. 1979. The longevity, flowering and fire history of the grasstrees *Xanthorrhoea preissii* and *Kingia Australis*. *Journal of Applied Ecology* **16**:893-899.

Lamont BB, Wittkuhn R, Korczynskyj D. 2004. Ecology and ecophysiology of grasstrees. *Australian Journal of Botany* **52**:561-582.

Prusinkiewicz, P, Barbier de Reuille, P. 2010. Constraints of space in plant development. *Journal of Experimental Botany* **61**:2117-2129.

Skjeltorp AT, Meakin P. 1988. Fracture in microsphere monolayers studied by experiment and computer simulation. *Nature* **335**:424-426.

Staff IA. 1968. A study of the apex and growth patterns in the shoot of *Xanthorrhoea media* R. Br. *Phytomorphology* **18**:153-165.