The role of structural and life-history tradeoffs in plant architecture: a model study of *Protea lepidocarpodendron* (Proteaceae)

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Summary: We present research in progress, aimed at explaining the tradeoffs between vegetative and reproductive structures in the architecture of Protea. The species of interest, *Protea lepido-carpodendron*, reproduces only after a fire that kills it. We aim at using a biomechanical developmental functional-structural model to demonstrate that *Protea lepidocarpodendron* is adapted to the statistical distribution of fires over time.

The bodies of most plants are comprised primarily of vegetative structures, with reproductive organs being comparatively ephemeral and involving relatively little investment. The greater investment in vegetative structures reflects their fundamental roles in resource capture and distribution, and in maintaining a plant's structural integrity. Nevertheless, from an evolutionary perspective, vegetative structures exist ultimately to support and nourish reproductive organs, which directly determine a plant's genetic contributions to subsequent generations. Thus, natural selection should favor plant architectures and mechanical characteristics that promote reproductive output within a specific environment. Conflicting demands for vegetative and reproductive functions may lead to vegetative characteristics that do not maximize photosynthetic capacity, resource deployment, and/or mechanical stability.

Many upright, shrubby *Protea* species of the Western Cape in South Africa (Midgley and Kruger 2000; see also Bond and Maze 1999) illustrate this conflict. These species produce orthotropic modules, which form sympodia with no distinct main stem (Fig. 1). Each module bears a terminal capitulum surrounded by showy involucral bracts. After flowering, a capitulum matures into a woody cone, which persists for several years, as long as the subtending stem maintains its evergreen, sclerophyllous leaves.

Figure 1. *Protea lepidocarpodendron*. Left, form of ~14-year old plant. Center, changes in branch width at a branching point. Right, a plant after fire reveals sympodial architecture and the distribution of cones.

In general, the species of interest occupy relatively open habitats that burn with an average frequency of 10–20 years. Seed dispersal occurs only when the heat of a fire opens the serotinous cones in a living canopy, releasing the seeds that can establish seedlings only in mineral soil exposed by fire. *Protea lepidocarpodendron* and similar species die during fire, so each individual reproduces once, when it dies, and its effective seed production depends on the number of cones in a shrub's canopy when it is burned. If fire does not occur for a long period, plants can become so large that they collapse during intense winds (Midgley and Kruger 2000). Such plants die without reproducing. We thus hypothesize that the vegetative structure of *Protea* is adapted to probability density distribution of inter-fire intervals: the plant does not invest in the creation of a long-lasting vegetative structure, but is built to maximize the number of reproductive structures at the time of its death by fire.

To test this hypothesis, we developed a biomechanical model of *Protea* trees (Fig. 2). The sympodial architecture of the trees is generated using an L-system implementation (Prusinkiewicz and Remphrey 2000) of a variant of Leeuwenberg's architectural model (Hallé et al. 1978). In Leeuwenberg's model, the growth of branches ends with the formation of terminal inflorescences; the thrust of the development then transfers to the lateral branches. In our model, a terminal bud may also initiate another annual growth increment or abort. According to observations of *Protea* in nature, continuation of a branch is a likely event in young trees, whereas production of an inflorescence is the usual event in older trees. The fate of buds (initiation or continuation of a branch, production of a terminal capitulum, or abortion) depends on the amount of photosynthate produced by the standing crop of leaves, which are allocated to specific buds using a stochastic process (Gillespie's [1976] algorithm). The distribution of shoot lengths is modeled stochastically according to measured data. The cost of growing a shoot includes its primary growth and the secondary growth of subtending branches, as needed to develop vasculature (pipe model, Shinozaki et al. 1964). On this basis, branch shape is modeled as the combined effect of gravity, reorientation of branch directions due to the production of reaction wood, average wind directions, and tropisms, using the biomechanical model of branch shape proposed by Fournier et al (1994) and adapted to L-systems by Jirasek et al. (2000) and Taylor-Hell (2005). A new element of the model is the combination of turtle geometry, which makes it possible to conveniently specify branching architecture of the tree (Prusinkiewicz and Lindenmayer 1990), and affine geometry, which is convenient in biomechanical simulations (Prusinkiewicz et al. 2007a).

Another novel element is the simulation of branch breaking, which occurs when bending moments exceed a threshold value. As an approximation, we assume that this threshold depends on the allocation of resources available to the tree: greater allocation to individual branches increases their resistance to breaking. This process creates a competitive situation, whereby a given pool of resources can be used to create either a more durable structure or one that ramifies more frequently. Competition is intertwined with developmental decisions: the plant may produce more capitula and cones at the expense of vegetative development, or invest in more extensive vegetative development with the prospect of supporting more capitula and cones in the future.

To our knowledge, the perspective that plant form represents an evolutionary compromise between vegetative and reproductive function has not been studied previously using simulation models. Early plant (tree) models addressing the question of the optimality of plant form focused on the influence of branching patterns on a plant's total leaf area (e.g., Horn 1971, Honda and Fisher 1978). Subsequent analyses accounted for the reduced energy-gathering efficiency that occurs when a plant's leaves shade each other (reviewed by Fisher 1992, see also Pearcy et al. 2005). In addition, more recent models have incorporated two mechanical properties of branched structures that impose functional limits on their size and form (e.g., Niklas 1986, Farnsworth and Niklas 1995). First, branches must be able to support themselves and the organs that they produce, with dissimilar branching patterns having different implications for structural integrity (King and Loucks 1978, Brüchert et al. 2003). Second, branching constricts the vessels that distribute water, nutrients, and products of photosynthesis and metabolism, thus

highly branched plants distribute these chemicals less efficiently (Zimmermann 1978). In contrast to this historical emphasis on vegetative function, our model aims at the exploration of tradeoffs associated with reproduction. The described model provides the foundation for this exploration, which is currently in progress.

Figure 2. A biomechanical model of a 5-year-old protea. Top: trees generated using (left to right) low, medium and high photosynthate allocation to secondary growth. The low-allocation structure exhibits highest branching and the most fruit, but is also subject to gravitational stress at the base of lower branches (shown in red in color figures), and so is more susceptible to breakage than the high-allocation structure. Bottom: the same trees, with the branches with the highest gravitational stress broken off. The low-allocation structure has suffered the most extensive damage, the high-allocation structure has experienced none, but the tree with medium allocation retains the most fruit and so would have highest fitness if fire now killed the trees and produced suitable conditions for seed germination.

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