

Life-history evolution as an explanation for the absence of the tree life-form in Cape fynbos

J.J Midgley^{a*} and A.G. Rebelo^b

INVASIVE EXOTIC TREES ARE ABLE TO GROW tall (more than 15 m) in the fynbos environment of the southwestern Cape of South Africa, whereas the tallest fynbos plants, generally from the Proteaceae, have much shorter maximum stature (less than 5 m). Analysis of the Protea Atlas Database for the Cape shows a positive correlation between age at maturity and maximum plant size. Monographs of the Proteaceae indicate a shorter period to maturity for resprouters than resprouters. We propose an evolutionary hypothesis for the absence of trees in the fynbos; predictable, frequent fires have favoured early maturity and this has discriminated against any strategies with delays to maturity (such as experienced by resprouters and trees).

There is much current interest in modeling and understanding the determinants of plant biomass and plant traits, especially in relation to the potential impacts of global climate change on vegetation. For this modelling, the most basic and important trait is maximum plant height in a given environment. Models use eco-physiological principles such as plant hydraulics to predict maximum plant height depending on local water supply.¹

^aBotany Department, University of Cape Town, Private Bag, Rondebosch 7701, South Africa.

^bSouth African National Biodiversity Institute, Kirstenbosch, Private Bag X7, Claremont 7735, South Africa.

*Author for correspondence.
E-mail: jeremy.midgley@uct.ac.za

From a life-history perspective, understanding constraints on plant size is also fundamental because plant size correlates with many other plant attributes such as seed, leaf and wood characteristics.² Despite its fundamental importance, however, understanding the determinants of plant height in the fynbos is incomplete.^{3,4}

Mesic fynbos areas (rainfall more than 1000 mm/yr) lack single-stemmed plants more than 5 m tall. Their absence cannot be due to eco-physiological constraints imposed by the environment, because taller trees such as indigenous Cape forest species^{5,6} as well as exotic species such as *Pinus radiata*⁷ and *Pinus pinaster*⁸ can invade these areas of fynbos. There is thus a mismatch between maximum plant size of local plants and resource supply.

The dominant fynbos canopy family, the Proteaceae, has only a few species that can grow taller than 5 m and only the rare *Leucadendron argenteum* reaches 10 m.⁹ There does not seem to be any historical or phylogenetic constraint on the local evolution of the tree growth form because many typical fynbos plant families (Proteaceae, Ericaceae, Asteraceae, Fabaceae, Rutaceae) include tree species. In southern Cape forests, for example, *Faurea macnaughtonii*, a Cape member of the Proteaceae, is a large single-stemmed tree

over 20 m tall, as is *Calodendrum capense* (Rutaceae). It was argued previously^{5,6} that the lack of trees is because fires, especially of anthropomorphic origin,⁵ restrict the distribution, and invasion of, indigenous trees from the forest biome into fynbos. This does not explain why the fire-adapted tree life-form has not evolved within fynbos plant families, as has been the case in other Mediterranean shrublands. Explaining short plant stature and the resulting low biomass in Cape fynbos is thus a significant challenge.¹⁰

We argue that frequent and predictable disturbance by fire has placed a premium on early reproduction. Maximum organism size, in both plants and animals, is linked to other life-history attributes and in particular age to maturity. Among pines, for instance, there is a positive correlation between age at first reproduction and mean longevity and maximum height.¹¹ We argue that fynbos plants do not achieve great height because they are essentially 'fire-weeds' with an early onset of first flowering and the consequent early onset of mortality.

Our aims here are to demonstrate precocious age to maturity of the Proteaceae, to report that there is a correlation between age to maturity and maximum plant size, and therefore that evolutionary constraints may be able to explain the eco-physiological lack of trees in fynbos.

Methods

To obtain age to first flowering from seed, we used the Protea Atlas Database (<http://protea.worldonline.co.za>). It is based on a massive widespread sampling exercise in which at least some populations of all extant Cape Proteaceae species

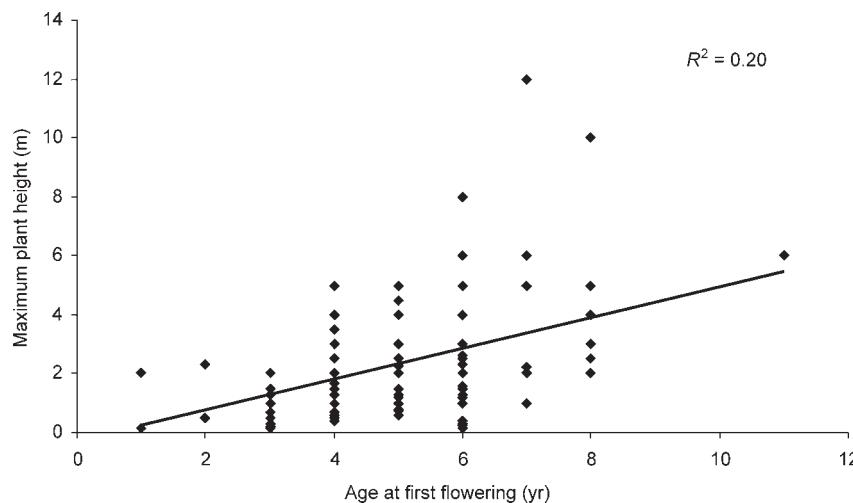


Fig. 1. Correlation between mean age to maturity and maximum plant height per species for reseeding Cape Proteaceae ($n = 122$). Age to maturity was the post-fire age for a species, when more than 50% of populations had more than 50% of individuals that had flowered.

were sampled across their distribution range. Among other measurements, populations were aged since the last fire and percentage flowering was estimated in three classes (some flowering, 50% flowering, and more than 50% flowering). From these data (more than 1000 observations from across the biome) we determined the mean post-fire age per species, as the mean of all sample populations, that had some individuals flowering, as well as for more than 50% of individuals per population that were flowering. We ignored resprouting species as they rarely produce seedlings; the data on the post-fire period to flowering for resprouters derived from the atlas is therefore from fire survivors. Resprouter survivors typically mature rapidly after fire whereas seedlings of resprouters have a longer period to first flowering (see below). Rebello⁹ was used to determine plant height for the species for which there were data in the atlas. We referred to monographs to obtain age to first flowering from seed, for *Protea*¹² and *Banksia*,¹³ an Australian equivalent proteoid. These times to maturity are for plants grown in horticulture and are therefore somewhat standardized for growing conditions to maturity of seedlings of both seeders and sprouters. Species from both strategies are likely to reach maturity earlier in the benign conditions of cultivation compared with wild-grown individuals.

Results

Mean time for the 111 reseeder species, which had at least some populations that had some individuals that were flowering, was 2.8 years according to the protea atlas. The mean age to more than 50% flowering was 5.0 years ($n = 122$ species). There is a significant correlation between

age at first maturity (with 50% of individuals in more than 50% populations per species) and maximum size (Fig. 1, $P < 0.01$). Quantile regression of the top 10% values was also strongly significant ($P < 0.003$). Mean age to maturity from seed for *Protea* seeders was 4.5 years ($n = 40$), whereas for *Protea* sprouters it was 6.6 years ($n = 18$). For *Banksia*, seeders took 4.0 years ($n = 31$) to first maturity, whereas resprouters took 7.0 years ($n = 26$).

Discussion

Given the woody nature of the Cape Proteaceae and the relative nutrient poverty and summer water stress of the Cape environment,¹⁰ it is striking that in most species some individuals have flowered in the wild from seed within 2–3 years after fire. This implies an evolutionary fire regime with a relatively short but predictable return period of intense fires, which favoured precocious seeders. Delayed reproduction would have been strongly selected against and this would restrict the evolution of resprouters and trees within the Proteaceae.

We suspect that the explanatory power of the regression in Fig. 1 is rather low because the influence of site factors and growth on age to maturity was not taken into account. The unexpectedly prolonged time to maturity of a short proteoid, for example, may be because of local environmental constraints on growth rates (such as their being from a cold mountain top or from arid fynbos).

The exotic trees which most often invade the mountain fynbos landscape are *Pinus pinaster* and *Pinus radiata*. There are no data on age to maturity for these species within the fynbos environment; age to maturity was mostly derived from monographs of these species in their country of

origin.¹⁴ Kruger⁸ cites personal communications for a period of nine years to 50% maturity in a *P. pinaster* plantation, and a similar age to reproductive maturity has been proposed for *P. radiata*.⁷ Both of these data were from mesic sites and we consider that this represents a far greater age to maturity than for proteoids from mesic areas.

Why should early maturity lead to small maximum plant size and early senescence? In the Cape Proteaceae maximum size correlates negatively with the degree of branching.¹⁵ Early flowering implies early branching and therefore possibly early mortality. Our argument is that the life-forms of the Proteaceae represent the optimized demographic solution for the Cape environment, especially the fire regime.

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