

ASSESSING THE INVASIVE POTENTIAL OF AUSTRALIAN BANKSIAS:
A COMPARISON OF RECRUITMENT POTENTIAL IN BANKSIA ERICIFOLIA
AND LEUCADENDRON LAUREOLUM.

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ABSTRACT

Several species of *Banksia*, an Australian genus of the Proteaceae, have recently been introduced to the Cape. The invasive potential of *Banksia ericifolia* was investigated by comparing its recruitment potential to an indigenous proteoid, *Leucadendron laureolum*. These are both serotinous, overstorey shrubs which are killed by fire and rely on a canopy-stored seed bank for recruitment. Various aspects of their biology were considered including seed production, rates of seed release after fire, seed dispersal, germination and growth rates.

The seed bank of 8-year old *B. ericifolia* shrubs was almost twice that of 10-year old *L. laureolum* plants (1098 vs 525 viable seeds per m² projected canopy cover). *Leucadendron* released most of its seed in a few days after the cones were burnt, whereas seed release in *Banksia* was spread over 12 weeks. The seeds (samaras) of *B. ericifolia* had lower wingloading and fall rates than *L. laureolum* and were dispersed over greater distances (up to 49m in light wind). The relative seedling growth rates of the two species were very similar (0.03g.g⁻¹.d⁻¹). Below-ground biomass was greater and proteoid roots were more developed in *B. ericifolia* seedlings than in *L. laureolum* after 100 days. 4-year old *Banksia* plants growing in the field had attained over twice the height of indigenous proteoids and accumulated up to ten times the fresh biomass of *L. xanthoconus*, a species which is ecologically similar to *L. laureolum*.

The results of this study show that *Banksia ericifolia* has the potential to be highly invasive in mountain fynbos. Strong serotiny, an enhanced reproductive output in the Cape relative to its native environment, and the absence of ^{natural} seed predators results in the rapid accumulation of a large seed

bank. Slow seed release and germination minimizes the chance of complete recruitment failure due to unfavourable conditions of rainfall. The fact that *B.ericifolia* has well-dispersed seed and similar fire requirements to indigenous Proteaceae further increases the chance of successful invasion.

B.ericifolia is strongly serotinous and hence its recruitment potential will only be realized after fire. It is therefore concluded that the cultivation of banksias does not directly pose a threat to indigenous vegetation, provided they are managed to prevent the accumulation of a seed bank.

INTRODUCTION

Invasives are a major problem in South African fynbos, in particular woody shrubs and trees introduced from other mediterranean-climate regions (MacDonald & Richardson 1986). The success of these invasive species is commonly attributed to the accumulation of a large seedbank (in soil or on the canopy) in the absence of natural predators and disease (Richardson & Van Wilgen 1984; Dean et al. 1986). Other reasons which have been suggested are the increased frequency of man-induced disturbance, especially fire; a superior competitive ability due to high phosphorous reserves in the seed (Mitchell & Allsopp 1984) or high relative growth rates (Witkowski, in press); and the possession of well dispersed seed capable of long-distance dispersal (Van Wilgen & Siegfried 1986).

A study on the history of introductions and the subsequent spread of exotic species in the Cape has shown that most of the major invasive aliens were actively propagated in the past (Shaughnessy 1986). There are exceptions however, such as *Hakea sericea* which, although not widely planted, currently occupies the greatest area of all woody species in the fynbos biome (MacDonald & Jarman 1984). Thus, although the success of invasives is influenced by historical factors and dissemination by man, species differ in their ability to invade mountain fynbos. This ability to invade (viz. invasive potential) is an intrinsic property of the species which can theoretically be quantified.

Research on alien species has focussed primarily on their seed biology and the recommendation of effective control measures. However, in addition to the management and control of current invasions, it is also essential to recognise new potential invaders. Richardson (1989) developed a risk assessment model for determining the invasive potential of serotinous trees and shrubs introduced from mediterranean-

climate regions. Based on theoretical and empirical data from *Pinus* and *Hakea*, he identified a number of life history attributes important for invasion into mountain fynbos. Serotinous species with short juvenile periods, and which produced large numbers of well dispersed seed were identified as high-risk introductions.

Richardson, Cowling and Le Maitre (in press) used the model to investigate the invasive potential of *Banksia*, an Australian genus of the Proteaceae, which has recently been introduced in the Cape. They ran a correspondence analysis of life history data for 69 *Banksia* taxa from which they predicted that tall, serotinous species with many small seeds, short juvenile periods and low fire tolerance would be most likely to invade,

Several species of *Banksia* are grown commercially on wild flower farms in the Cape. As the cultivation of banksias is likely to increase, it is important to know if they have the potential to invade into adjacent fynbos and which species are high risk introductions. Management recommendations and legislation may be required to safeguard indigenous vegetation.

In this study I investigated the invasive potential of *Banksia ericifolia*, by comparing its recruitment potential to an indigenous proteoid, *Leucadendron laureolum*. Various aspects of their biology were compared, including seed bank size, rates of seed release, germination and seedling growth to establish at which stage of its life history *B. ericifolia* has a superior competitive ability.

METHODS

Study species

Banksia ericifolia L.f. is a strongly serotinous, shrub or tree growing to 6m which occurs in east and south-eastern Australia (George 1981). It is a prolific, dominant species in fire-prone coastal heathland which is structurally and functionally analogous to fynbos (Specht 1979). *Leucadendron laureolum* (Lam.) Fourcade is a serotinous shrub up to 2m tall which is common in fynbos communities in the south and south-western Cape, South Africa. It has a widespread distribution, often occurring in dense stands, and is the dominant overstorey proteoid in the areas where banksias are currently cultivated. *B.ericifolia* and *L.laureolum* are ecologically similar as they grow vigorously and typically form the dominant overstorey shrub in the communities where they are found.

Seedbank size

The seedbank of *B.ericifolia* was determined in a small plantation on Flora Farms near Cape Agulhas. Shrubs had been planted in rows 5m apart and were closely spaced (3.5m). They had been planted 7 to 8 years previously and were only lightly harvested during this period (less than 1%). The total number of seeds produced per plant was estimated by determining the product of i, ii and iii.

- i. *Mean number of cones per plant* was determined by counting the cones on 10 randomly selected individuals. All fertile cones (i.e. those with closed follicles) occurring on half of the canopy were counted.
- ii. *Mean number of follicles per cone* was determined by counting the number of closed follicles on 30 randomly collected cones.
- iii. *Mean number of seeds per follicle* was obtained from the seed release experiment. Distinction was made between plump (viable) and aborted seed to determine the mean number of viable seeds per follicle.

Measurements of height and mean diameter were used to calculate the canopy volume (m^3) and projected canopy cover (m^2) of each shrub. Canopy volume was calculated as for a cylinder as there were many lateral branches close to the ground. Seedcrop size could therefore be expressed per unit area and per unit volume.

The seed bank size of *L. lauroolum* was estimated in 10 to 12-year old fynbos vegetation on the Cape Peninsula. All closed cones were counted on 10 randomly selected shrubs in each of three populations. Small samples in different populations were used to minimize localised effects of predation and resource availability. Number of viable seeds produced per cone was determined for a random sample of 30 different aged cones.

Projected canopy cover was calculated from the maximum and minimum diameter of each shrub, assuming an oval shape. The canopy volume of *Leucadendron* is best represented as an inverted cone and was calculated accordingly.

Seed release

Ten cones of each species were burnt over an open fire to compare the relative rates of seed release. The burnt cones were immediately bagged and mounted on poles in the field. Seed which had been released was counted and removed weekly for 12 weeks. Rainfall was measured for the duration of the experiment.

Seed dispersal

Seed mass and wing area were measured in 20 seeds from each species to determine the seed wing-loading index. This was calculated as fresh seed mass (mg) / total surface area of seed plus wing (100 mm^2).

The same seeds were used to determine the mean fall rate (m.s^{-1}) of each species. Seeds were dropped in still air from a height of 2 meters and the time taken to reach the ground was determined. Each seed was timed three times and the mean value was used in subsequent calculations.

The relative dispersal ability of *Banksia* and *Leucadendron* was determined by releasing 30 seeds of each species from a height of 2m. The experiment was conducted in an open field in light wind ($2-5 \text{ m.s}^{-1}$). The sites where seeds landed were marked and the distance was measured to obtain an average dispersal distance for each species.

Seed germination

Relative germination rates were determined by incubating 10 replicates of 10 seeds at 15°C for each species. Plump, apparently viable seeds were selected for the experiment. Seeds were checked every two days and were considered to have germinated if the radicle had emerged from the seed coat. The number of germinated seeds was expressed as a proportion of the total which had germinated so that the rates of germination could be compared.

Growth rates

The growth rates of *Banksia* and *Leucadendron* were compared in a controlled growth experiment and a field experiment.

Seeds from each species were planted in early June in acid, Table Mountain sandstone-derived soil collected from a fynbos site on the Cape Peninsula. Pots were kept in a greenhouse and watered twice weekly. Seeds germinated a month later (in July) and were thinned out so that there were 15 seedlings of each species. These were harvested in October, approximately 100 days after germination. Seedling height and the number of lateral branchlets were recorded before they were removed from the pots. Roots were carefully

washed to remove adhering soil. Shoots and roots were separated and dried at 80 C for 48 hours, after which they were weighed. Dry mass of seed embryos was obtained using 10 seeds of each species. Relative growth rates (RGR) were calculated following Hunt (1978):

$$\text{RGR} = (\ln W_2 - \ln W_1) / (t_2 - t_1)$$

where W_2 is total seedling dry mass, W_1 is seed embryo dry mass, and $(t_2 - t_1)$ is 100 days. Root: shoot ratios were calculated to compare biomass allocation in the two species.

The growth rates of 4-year old plants of *Banksia* and *Leucadendron* were compared in a natural experiment at Hagelkraal, near Gansbaai. Indigenous seed which had been accidentally mixed with *Banksia* seed was sown in the field after a fire in May 1986. *B. ericifolia* plants at the site grew among *Protea obtusifolia* and *Leucadendron xanthoconus*, a species ecologically similar to *L. laureolum*. The height, stem diameter and fresh weight were obtained of 10 randomly selected individuals of *B. ericifolia* and *L. xanthoconus*.

Data analysis

The rates of seed release and germination were compared using a Kolmogorov-Smirnov two-sample test (Zar 1984). A Student's t-test was used for the remaining data to test for significant differences between means (provided the assumption of equal variances was met).

Predicted invasive potential

The risk assessment model developed by Richardson (1989) was originally tested on banksias from south-western Australia. The correspondance analysis was therefore re-run including *B. ericifolia* to predict the invasive potential of this species in mountain fynbos. Life history attributes were obtained from the literature. Juvenile period: 5-10 years (Bradstock & O'Connell 1988); viable seeds per mature 15-year old plant: >500 (Carpenter & Recher 1979); degree of

serotiny: strong; seed area = 18mm^2 ; wing area = 95mm^2 ;
maximum plant height: $>5\text{m}$ (George 1981).

RESULTS

Results of the ordination are given in FIGURE 1. Richardson (1989) predicted that tall, serotinous species with many small (well-dispersed) seeds and short juvenile periods are most likely to invade mountain fynbos (i.e. those taxa at the bottom right hand corner of the diagram). *Banksia ericifolia* occurred among species which were identified as high risk introductions on the ordination. Its invasive potential was similar to that of *B. burdettii*, a non-sprouting, thicket-forming species which produces large seed crops (Lamont & Barker 1988).

Seed production

Banksia shrubs had attained a mean height of 3.95 meters in eight years and accumulated a massive seed bank of approximately 16 500 viable seeds per plant (TABLE 1). *Leucadendron* shrubs are much smaller (mean height 1.25m) and produce fewer seeds per cone and therefore produced relatively fewer seeds per plant (570 viable seeds per plant). *Banksia* produced 1098 ± 263 seeds per m^2 projected canopy cover which was about twice that of *Leucadendron* with 525 ± 225 seeds per m^2 .

Another reason for the large difference observed in seed bank size is that *B. ericifolia* is strongly serotinous whereas *L. laeolium* only exhibits weak serotiny. Less than 1% of the cones on the canopy had open follicles in the former. In contrast, an average of 26.8% of *Leucadendron* cones had opened spontaneously and released their seed. Open cones were not included in calculations as seed released in the interfire period seldom results in seedling establishment.

Seed release

L. laureolum released 63% of its seed within the first few days after the cones were burned, whereas *Banksia* cones released less than 6% during this period and still contained small amounts of seed 12 weeks after they were burned (FIGURE 2). Although *Banksia* released its seed over a longer period of ~~time~~, the rates of seed release were not significantly different between the two species (Kolmogorov-Smirnov two-sample test, $p > 0.05$).

Seed dispersal

Leucadendron and *Banksia* both have wind dispersed seed but differ considerably in their dispersal properties (TABLE 2). Seed of *B. ericifolia* is significantly lighter than that of *L. laureolum* and has almost double the wing area. Samaras of the former rotate and fall relatively slowly due to their shape and low wingloading. Those of *Leucadendron* drop straight to the ground in still air, and had significantly higher fall rates ($p < 0.001$).

Seed dispersal distances were highly variable: *B. ericifolia* seed was transported an average of 7.6 ± 6.0 m compared to 3.0 ± 1.3 m in *L. laureolum*. The maximum dispersal distance was considerably greater in *Banksia* (TABLE 2) due to the spinning motion of the samara which allowed it to be caught by successive gusts of wind.

Seed germination

The two species started germinating within two days of each other (day 15 in *Leucadendron* vs day 17 in *Banksia*). Most of the *Leucadendron* seed germinated within a week and the rate of germination was significantly higher than in *Banksia* (Kolmogorov-Smirnov two sample test, $p < 0.01$, FIGURE 3). Germination success was 100% in *Banksia*, whereas only 88% of apparently viable *Leucadendron* seeds germinated.

Relative growth rates

Relative seedling growth rates were very similar in the two species ($0.03\text{g.g}^{-1}\text{.d}^{-1}$). However *Leucadendron* seedlings were taller than *Banksia* after 100 days and had accumulated significantly more above-ground biomass during this period ($p < 0.01$, TABLE 3). Below ground biomass showed the reverse trend and it was observed that *Banksia* seedlings had several clusters of proteoid roots, which were absent or only just starting to develop in *Leucadendron*. Root dry mass values may be slightly exaggerated in the former due to the difficulty of washing out sand amongst fine proteoid roots. *B.ericifolia* seedlings had several lateral branches and buds whereas *L.laureolum* had a single meristem (TABLE 3).

There were striking differences in the size of 4-year old plants growing in the field (TABLE 4). *Banksia* had accumulated ten times the biomass of *L.xanthoconus* despite the fact that the inflorescences had been removed (to prevent the accumulation of a seed bank). *Banksia* showed considerable size variation however, and biomass ranged from 0.111 to 2.6 kg. Indigenous proteoids were small as the site was poorly drained and unfavourable for the growth of these species. The mean height of *P.obtusifolia* and *L.xanthoconus* was 0.45 and 0.44m respectively whereas *Banksia* had attained a height of over a meter during the same period. Differences in overall size were reflected in stem diameter, which ranged from 5 to 12mm in *Leucadendron*, and from 15 to 47mm in *Banksia*.

DISCUSSION

Seed production

Seed production in *B.ericifolia* is very high, not only relative to *L.laureolum*, but also when compared to other species in the genus. *Banksia leptophylla*, a strongly serotinous species produced an average of 1344 viable seeds per 15-year old plant, which is an order of magnitude less than that produced by *B.ericifolia* (Cowling *et al.* 1987). Species such as *B.attenuata*, *B.menziesii* and *B.burdettii* compare less favourably, with a seed bank ranging from 2 to 832 seeds per plant (Cowling *et al.* 1987; Lamont & Barker 1988).

The reproductive output of *B.ericifolia* shrubs at Cape Agulhas (South Africa) appears to be 'considerably greater than that described for the species in its native environment. Carpenter & Recher (1979) calculated seed production to be 1368 seeds per plant in a 25-year old stand north of Sydney (cf 16 522 seeds/ plant at Cape Agulhas). Morris & Myerscough (1988) recorded the seed yield to be 200-330 seeds.m⁻² in a 9-year old stand (cf 1098 seeds.m⁻²).

There are two factors which may account for the increased size of seed reserves in its new environment: the absence of specialized predators and enhanced resource availability. Pre-dispersal predation by insects and birds may significantly reduce the seed crop of banksias in Australia and many insect predators are host species-specific (Scott 1982; Cowling *et al.* 1987). Seed reserves of introduced *B.ericifolia* are exceptionally high as there are few ^{no} predators which can attack the hard, woody follicles.

B. ericifolia is pollinated by a wide range of pollinators (birds and insects) and the available evidence indicates that seed set is resource limited (Paton & Turner 1985; Copland & Whelan 1989; Stock *et al.* 1989). Fynbos soils are considered to be less nutrient-poor than those of Australian heathland (especially in phosphorous, see Low 1983). Hence reproductive output of *B. ericifolia* may be enhanced by an increase in resource availability. Although the proportion of fertile cones per plant does not differ much, the mean number of viable seeds per cone is significantly higher in introduced shrubs than those growing in Australia (61 cf. 24 seeds per cone quoted by Carpenter & Recher 1979).

Pre-dispersal seed predation by insects may have a considerable impact on the size of canopy stored seed reserves in Cape Proteaceae (Coetzee & Giliomee 1987). Insect-damage causes premature cone-opening in *L. laureolum* and predation significantly reduces the number of viable seeds produced (Honig, unpub. data). Thus although seed production in indigenous proteoids may be high, the size of canopy stored seed reserves is generally a fraction of what is produced.

Seed release

Fire intensity and seasonality affect follicle opening in *B. ericifolia*, causing variation in the rate of seed release (Bradstock & Myerscough 1981). Slow seed release in this species is interpreted as a risk-spreading strategy to reduce the risk of complete recruitment failure (Zammit & Westoby 1987). *Leucadendron* releases all its seed quickly within several days after a fire. These germinate more or less simultaneously after the first rains in autumn or winter, and as a result there is a single cohort of seedlings. Recruitment in *L. laureolum* is strongly related to the amount and distribution of rainfall in the first few months after a fire (Le Maitre 1988), as seedlings are susceptible to drought-induced mortality. This species would

therefore be expected to show poorer recruitment as a result of rainfall variation than *B.ericifolia* which releases its seed slowly and benefits from several germination events.

The requirement for wet-dry cycles in serotinous banksias delays seed release until the onset of cool, moist conditions which are favourable for germination (Cowling & Lamont 1985). Seed release was fairly rapid for *B.ericifolia* in this study as the experiment was conducted during winter and conditions were cool and wet. I would expect seed release to be slower and spread over several months after a summer fire. Bradstock and Myerscough (1981) measured follicle-opening in *B.ericifolia* cones after a fire in Australian heathland and found that it took 95 days for 80% of the seed bank to be released.

Seedling recruitment in serotinous Cape Proteaceae varies enormously according to the season of burn (Bond *et al.* 1984; Van Wilgen & Viviers 1985). This is attributed to differences in the length of time between seed release and germination, which determines the level of post-dispersal predation. Fires in spring or early summer result in poor regeneration due to high seed removal by rodents. Delayed seed release in *B.ericifolia* reduces the time that seed lies exposed on the soil before germination, and will therefore minimize seed loss from post-dispersal predation (Cowling & Lamont 1985).

Seed dispersal

Van Wilgen & Siegfried (1986) suggest that *Pinus pinaster* and *P.radiata* tend to be invasive due to the possession of winged seeds capable of long range dispersal. The wingloading of *B.ericifolia* seed is similar to these species (20-30 mg.100mm²), and as it is released from a height of several meters (shrubs are 3-4m high), seed has the potential to be dispersed over considerable distances.

Leucadendron seed appears to be poorly adapted for long-range dispersal (due to its high fall rate and restricted dispersal range). However I only considered dispersal during free fall from the cones. Seed could be transported large distances over the ground as there are few barriers to obstruct movement in an open post-fire environment.

L. laureolum is considered to be well-dispersed relative to other indigenous proteoids, and its widespread occurrence is attributed to its ability to colonize new habitats after fire (Taylor 1969). Although seed dispersal properties alone do not determine whether a species will become invasive or not, they may play an important role in the rate of spread after establishment.

Seed germination

Gradual seed release and germination in *B. ericifolia* spreads the risk of germination over more than one opportunity for establishment so that the probability of complete recruitment failure is reduced (Zammit & Westoby 1987).

Rapid, simultaneous germination of seed in *L. laureolum* confers the competitive advantage of early establishment, but involves a higher risk as it results in a single cohort of seedlings. The probability of total recruitment failure is therefore greater in *Leucadendron*, and as effective recruitment is confined to the immediate post-fire period, it is more vulnerable to local extinction. *In this species killed by fire as obligate serotiny*

Relative growth rates

Leucadendron seedlings were larger than *B. ericifolia* after 100 days, which is not unexpected as it has been shown that seedling size is strongly correlated to seed mass in the Proteaceae (Stock et al. in press). Seedlings rely on cotyledon reserves during early development, but after several months the reserves are depleted and the cotyledons play little role in further growth. Large-seeded indigenous proteoids may therefore have a competitive advantage over

B. ericifolia in the early seedling stage, but it is unlikely that the size advantage will persist for a long time.

The high root:shoot ratio and early development of proteoid roots in *B. ericifolia* seedlings suggests that they may be better adapted to conditions of water stress. Drought is an important cause of seedling mortality in the post-fire fynbos environment and the more extensive root system of *B. ericifolia* may enhance its survival.

Field experiment

Although no differences in growth rate were observed at the early seedling stage, the field experiment clearly showed that the growth rate of *Banksia* far exceeded that of indigenous proteoids in the area. Some of the four-year old plants of *B. ericifolia* at Hagelkraal had already flowered and set seed. Shrubs usually start flowering at 5 years in Australia and seed is therefore first available at 6 years (Bradstock & O'Connell 1988). The increased reproductive output and shorter juvenile periods of *B. ericifolia* in the Cape is not a unique response as a similar phenomenon is observed in introduced species of *Hakea* and *Acacia* (Gill & Naser 1984). Shorter growing seasons and less fertile soils in temperate Australia may restrict growth of these species in their native environment (Lamont *et al.* 1985). Conditions in the Cape are favourable by comparison and prolific growth and reproduction may be due to release from these climatic and edaphic constraints.

A point to consider in this comparative study of *Banksia* and *Leucadendron* is that *L. laurcolum* is fast-growing and has well-dispersed seed relative to other species of the Cape Proteaceae. Taylor (1969) describes it as a "weedy" species, capable of forming dense stands in most of the Inland Fynbos communities of the southern Cape Peninsula. The recruitment potential of myrmecochores and species with long juvenile periods will therefore compare even less favourably

with *B.ericifolia*, and communities with these species will be more vulnerable to invasion.

***Banksia ericifolia* as a potential invasive**

The results of this study show that the seed production and growth rate of *B.ericifolia* far exceed that of South African Proteaceae. The combination of short juvenile period, high reproductive output and strong serotiny results in the rapid accumulation of a large canopy-stored seed reserve. Pre-dispersal predation is negligible and as a result, massive amounts of viable seed will be released after a fire. Delayed seed release minimizes post-dispersal predation and ensures recruitment irrespective of the season of burn. The possession of well-dispersed seed enhances its ability to colonize new areas. The life history attributes of *B.ericifolia* therefore enable it to establish in the fynbos environment and propagate prolifically. Recruitment of *B.ericifolia* in Australia is optimal after late summer, high intensity burns every 10-15 years (Bradstock & O'Connell 1988). This coincides with the fire requirements of indigenous Proteaceae (Van Wilgen & Viviers 1985) and will further enhance its invasive success.

The rapid growth rate of *B.ericifolia* relative to indigenous proteoids is an interesting phenomenon which requires further attention. Differences observed in seedlings suggest that it may be related to the uptake of water and/or nutrients. Measurement of plant xylem water potentials and photosynthetic rate during the first season of establishment and during subsequent summers will elucidate whether *Banksia* has a higher water use efficiency and is less prone to summer drought. *The two are not necessarily related.*

The effect of rapid growth in *B.ericifolia* will not be confined to competitive interactions with indigenous overstorey shrubs: *Banksia* shrubs may attain a height of 4m in eight years and form a dense canopy cover (eg.at Cape Agulhas). Understorey species richness is strongly correlated to overstorey density in fynbos (Cowling & Gxaba 1990), and it has been shown that species richness is significantly reduced under stands of alien trees (Richardson et al.1989). The presence of *Banksia* shrubs in fynbos will therefore not only have a direct effect on indigenous species through shading, but may have an impact on community structure lasting for several generations.

CONCLUSIONS

Banksia ericifolia has the potential to be highly invasive in mountain fynbos primarily due to its ability to accumulate a large viable seed reserve. As it is strongly serotinous its superior recruitment potential will only be realized after a fire. The implications of this result are that the cultivation of *Banksias* does not pose a threat to indigenous vegetation provided the inflorescences are harvested regularly. However, the enhanced reproductive output of *B.ericifolia* in the Cape indicates that species may respond unpredictably to a new environment, and introductions should therefore be tightly controlled for several years before they are widely propagated.

The results of this study confirm the predictions made by Richardson's (1989) risk assessment model and demonstrate its use to screen future introductions of banksias. We have witnessed the rapid spread of *Hakea* and alien acacias into indigenous vegetation and every effort should therefore be made to prevent the introduction of new invasives.

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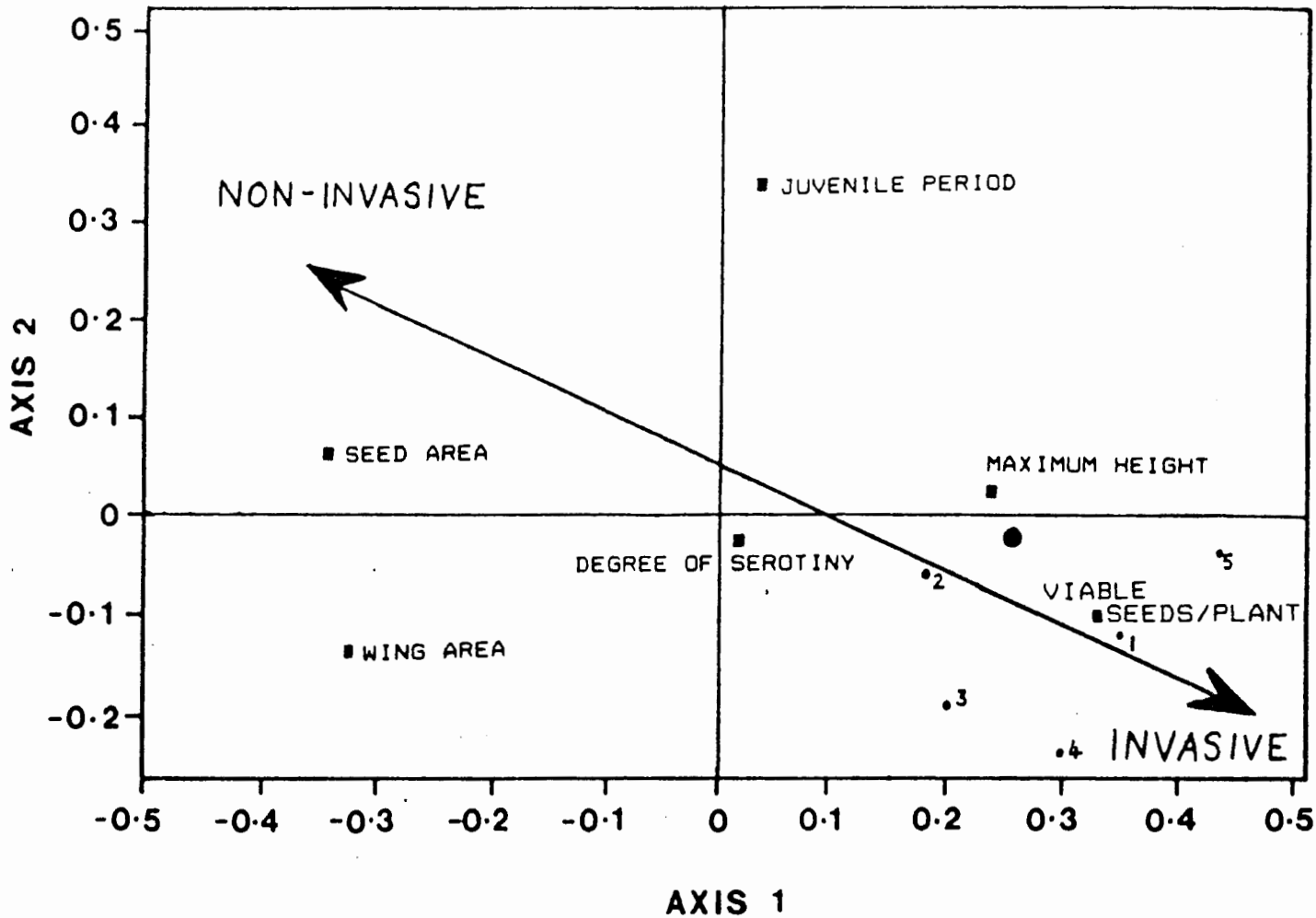


FIGURE 1: Plot of the first two axes from a correspondance analysis of life history attributes of 70 *Banksia* taxa. Life history attributes (blocks) are marked on the ordination diagram. The arrow reflects a likely gradient of increasing invasive potential in mountain fynbos. *B.ericifolia* (●) occurs at the invasive end of the gradient and is predicted to be a high risk introduction. Other species which are identified as potential invasives are: 1. *B. quercifolia*, 2. *B. burdettii*, 3. *B. meisnerii*, 4. *B. leptophylla*, 5. *B. cuneata*. [Co-ordinates supplied by D. Richardson and diagram adapted from Richardson (1989)]

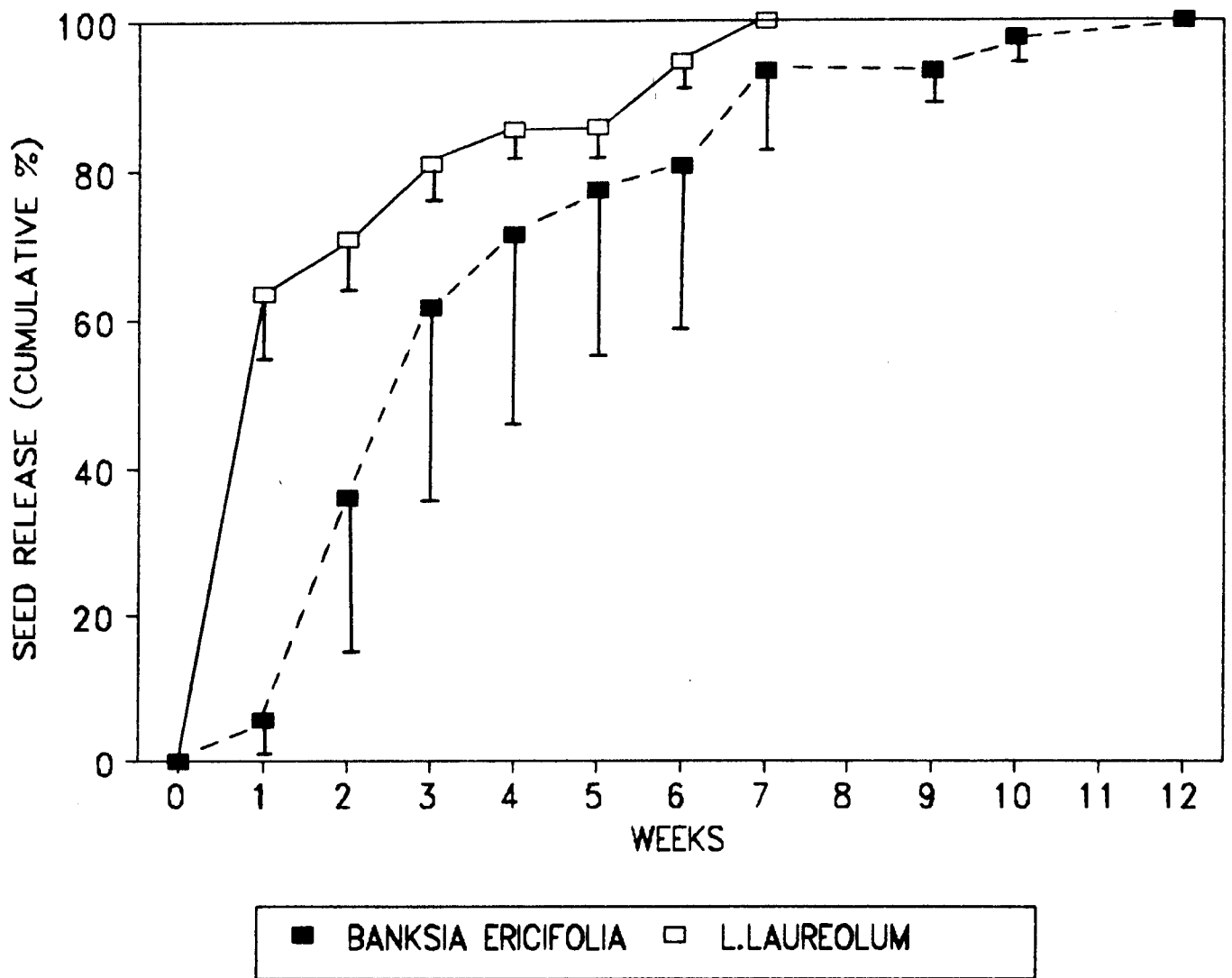


FIGURE 2: Rate of seed release from burnt cones of B.ericifolia and L.laureolum. Number of seeds released per week expressed as a percentage of the total number of seed in each cone. S.E. bars shown below the means.

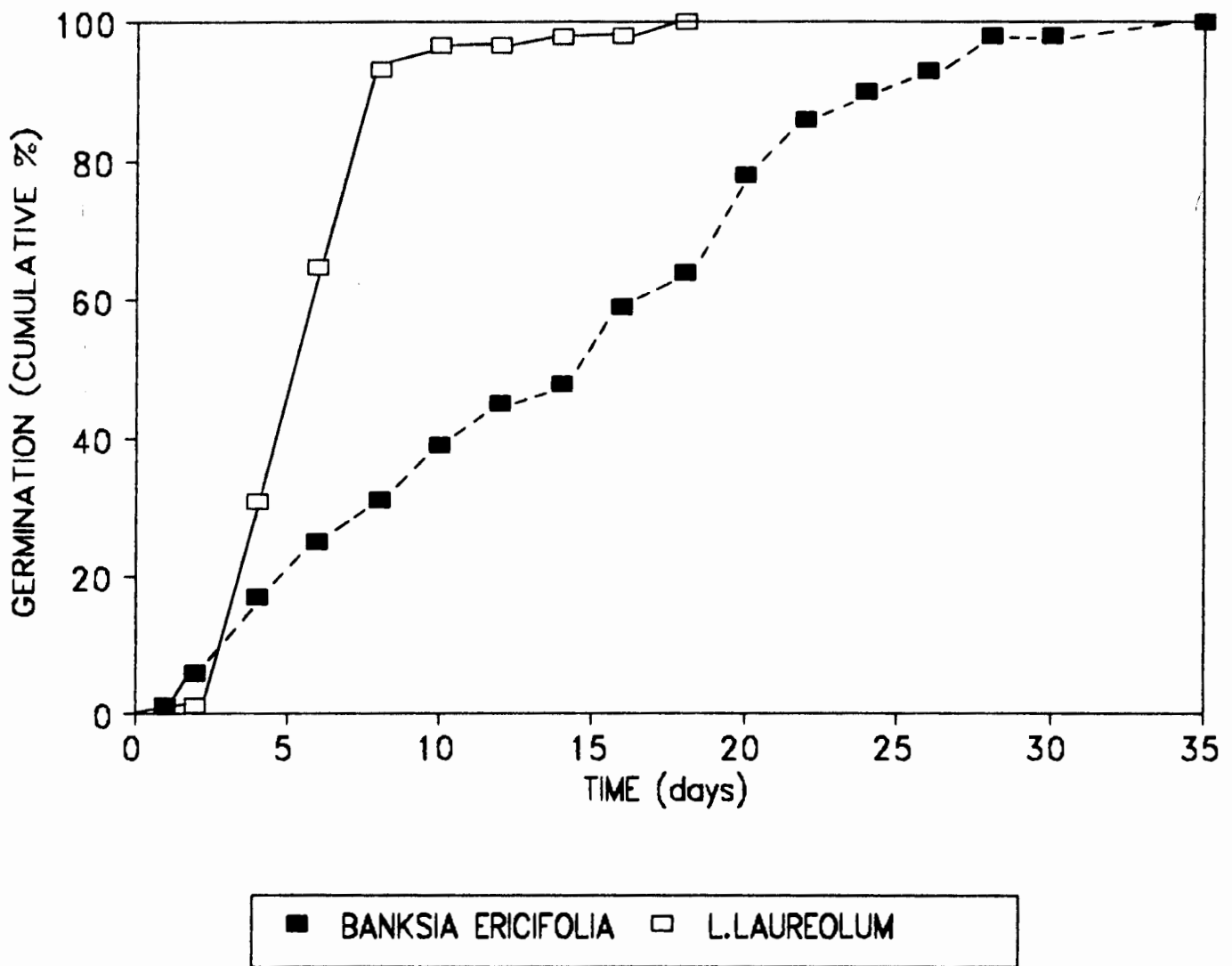


FIGURE 3: Germination rates of B.ericifolia and L.laureolum.
 Number of germinated seeds expressed as a % of the
 total number which germinated for each species.

*Back to plot absolute
 germination (cumulative %)*

TABLE 1: Canopy stored seed reserve of *B.ericifolia* (in an 8-year old plantation) and *L.laureolum* (in 10-year old populations on the Cape Peninsula). Values are given for the mean \pm S.D.

	<i>Banksia ericifolia</i>	<i>Leucadendron laureolum</i>
Plant height (m)	4.0 \pm 0.5	1.3 \pm 0.2
Canopy volume (m ³)	61.5 \pm 5.9	0.5 \pm 0.3
Projected canopy cover (m ²)	15.3 \pm 3.1	1.0 \pm 0.4
No. of cones/ plant	269.2 \pm 73.7.	24.8 \pm 20.1
No. of follicles/ cone	75.4 \pm 23.3	-
No. of viable seeds/ follicle	0.81 \pm 0.25	-
No. of viable seeds/ cone	61.4	23.01 \pm 4.70
Total no of seeds/ plant ¹	16 522	570
Seeds per m ³ canopy volume	286 \pm 97	1266 \pm 576
Seeds per m ² PCC ²	1098 \pm 263	525 \pm 225
% cones with open follicles or cone scales	< 1%	26.8% \pm 14.1

1. Calculated as (# cones/plant) x (# follicles/cone) x (# seeds/follicle)
2. PCC = projected canopy cover

TABLE 2: Differences in seed dispersal properties of *B. ericifolia* and *L. laureolum*. Dispersal distances were measured in light, gusty wind (2-5 m.s⁻¹). Values are given for the mean \pm S.D. P denotes the level of significance for the difference between means (t-test).

	B.ericifolia	L. laureolum	p
Seed mass (mg)	25.59 \pm 2.82	31.92 \pm 6.27	< 0.001
Wing area (mm ²)	92.2 \pm 12.1	51.7 \pm 7.0	< 0.001
Wing loading (mg.100 mm ²)	28.2 \pm 4.4	62.2 \pm 11.2	< 0.001
Fall rate (m.s ⁻¹)	1.52 \pm 0.64	2.49 \pm 0.43	< 0.001
Dispersal distance (m)	7.59 \pm 6.02	3.03 \pm 1.26	NS?
Dispersal range	1.2 - 48.0 m	1.3 - 6.4 m	

TABLE 3: Differences in relative growth rate and biomass allocation in 100-day old seedlings of *B. ericifolia* and *L. laureolum*. Values are given for the mean \pm S.D. P denotes the level of significance for the difference between means (t-test).

	B.ericifolia	L. laureolum	p
Seedling height (cm)	8.99 \pm 1.06	10.34 \pm 0.89	< 0.001
No. of lateral branches	1 - 5	0	
Shoot dry mass (mg)	280 \pm 65	362 \pm 71	< 0.01
Root dry mass (mg)	307 \pm 99	169 \pm 99	< 0.001
Root:shoot ratio	1.179 \pm 0.527	0.505 \pm 0.339	< 0.001
RGR (g dry mass.g ⁻¹ .d ⁻¹)	0.035 \pm 0.001	0.033 \pm 0.02	NS

TABLE 4: Differences in height, stem diameter and fresh weight in 4-year old plants of *B.ericifolia* and *L.xanthoconus* sampled at Hagelkraal, South Africa. Values are given for the mean \pm S.D. P denotes the level of significance for the difference between means (t-test).

	<i>B.ericifolia</i>	<i>L.xanthoconus</i>	p
Plant height (m)	1.12 \pm 0.2	0.44 \pm 0.07	< 0.001
Stem diameter (mm)	26 \pm 9.9	7.6 \pm 2.5	< 0.001
Fresh weight (g)	651 \pm 732	68.3 \pm 50.2	< 0.05