Seed dispersal and seedling recruitment in *Protea laurifolia*

P.T. Manders
South African Forestry Research Institute, Jonkershoek Forestry Research Centre, Stellenbosch

The pattern of seedling recruitment around a single isolated *Protea laurifolia* Thunb. individual after a fire, was determined using a chi-square goodness of fit test for uniformity and Rayleigh's test for direction. Recruitment occurred largely to the north-west of the parent plant whereas the wind after the fire came largely from the south-east, providing some evidence of the influence of wind on dispersal. The maximum distance of a seedling from the parent plant was 26.3 m, with 95% of recruitment occurring within 15 m of the parent. To speed up the rate of migration in areas where the species has been eradicated the establishment of point seed sources is suggested.

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Die saailingregenerasiepatroon rondom 'n enkele geisoleerde *Protea laurifolia* Thunb. individu na 'n brand is bepaal deur 'n chi-kwadraat-pasgehalte toets vir eenvormigheid en 'n Rayleigh-toets vir rigting. Regenerasie het hoofsaaklik aan die noord-westelike kant van die plant voorgekom, terwyl die wind na die brand hoofsaaklik uit die suid-ooste gewaai het. Dit lever die maksimum afstand wat 'n saailing vanaf die ouer gevind is, was 26.3 m, met 95% van die herwinning binne 15 m vanaf die ouer. Om die tempo van migrasie te versnel na gebiede waar die spesie uitgeroei is, word die vestiging van puntsaadbronne voorgestel.

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**Introduction**

Seed dispersal in members of the genus *Protea* is considered to be limited in space (Jordaan 1972; Bond 1980; Brits 1982; Midgley 1983; Bond *et al.* 1984). There are few direct observations to support this. Bond (1980) noted poor dispersal of serotinous Proteaceae (species with canopy-stored seed) from unburnt vegetation to burnt areas in the Swartberg. Small barriers such as a vehicle track and a thin belt of riverine vegetation were apparently sufficient to stop dispersal. Bond *et al.* (1984) also provide some evidence of the short dispersal distances in serotinous *Protea* species.

Sclerophyllous South African Proteaceae of the fynbos biome (Moll *et al.* 1984) are largely dispersed by either wind or ants (Slingsby & Bond 1982). The wind-dispersed members include all species of the genera *Protea* and *Aulax* which have hairy fruits (Slingsby & Bond 1982), and all the species in the section Alatosperma in the genus *Leucadendron*, in which the species have winged fruits (Williams 1972). The efficiency of dispersal appears to vary considerably between species, with *Protea repens* (L.) L. seeds having the largest diameter of achene plus hairs and the highest dispersal efficiency within the genus *Protea* (Bond *et al.* 1984). A few species in *Leucadendron*, such as *L. argenteum* (L.) R. Br. and *L. rubrum* Burm. f., have distinct parachute-like plumes, although the seeds are relatively heavy (Williams 1972). The remaining genera, and some *Leucadendron* species produce seeds with elaiosomes which are dispersed by ants (Slingsby & Bond 1982). In a third group, comprising a number of species of the genus *Leucadendron*, no dispersal strategy has been identified to date (Slingsby & Bond 1982).

Theoretical relationships exist between the distribution of dispersed seed and the distribution of established seedlings (Janzen 1970; Geritz *et al.* 1984). Serotinous Proteaceae regenerate only after the parent plants have been killed by fire (Bond *et al.* 1984), and regeneration occurs in a biotically uniform environment. It is assumed therefore that the distribution pattern of established seedlings represents the pattern of effectively dispersed viable seeds, and the maximum distance between the parent plant and a seedling indicates the maximum effective seed dispersal distance.

Burrows (1973) defines the aerial path between the position of release of a seed and the position of initial contact with the ground as the primary trajectory. The 'seed' of *Protea laurifolia* Thunb. (a serotinous member of the genus) consists of an achene which is densely covered with trichomes, which project at right angles from the surface. The style is persistent. The seed is therefore apparently suited to wind dispersal, falling into the category of woolly or plumed seeds of Burrows (1975). However, since there is no distinct plume and since
the persistent style decreases the surface area to volume ratio, the seed is probably not specialized in this respect and the primary trajectory may be limited. Bond et al. (1984) and Bond (1985) reported that the structure of Protea seed facilitates rolling over the soil surface in the absence of barriers after a fire. This suggests the existence of a second phase of dispersal after reaching the ground at the end of the primary trajectory. On the other hand, the function of the trichomes and style may be to limit further dispersal after reaching the ground. According to Jordaan (1972), the trichomes of seeds bind together to hold seeds together in clumps, and Brits (1982) observed grains of sand being trapped in the trichomes, apparently helping to weigh down and bury the seed. Major declines in serotinous Protea population densities and even local extinctions can result from both inappropriate intervals between fires (Bond 1980; Van Wilgen 1981) and unfavourable season of burn (Bond 1985; Van Wilgen & Viviers 1985). Therefore the rate at which denuded areas can be re-colonized through migration, which depends on natural dispersal, is important in determining management procedures for conservation areas.

This paper reports on the recruitment of seedlings around a single burnt Protea laurifolia plant in the Zachariahoeek experimental catchment near Paarl in the south-western Cape Province (34°49'S and 19°02'E). The presence of this isolated shrub, approximately 24 years old and 2 to 3 m high was noted before a prescribed burn of the catchment on 14 November 1977 (F.J. Kruger pers. comm.). P. laurifolia normally grows in fairly dense stands or at least within a short distance from conspecific individuals. This individual therefore presented an unusual opportunity to determine the recruitment pattern around a point seed source. A further advantage was the presence of a large number of seedlings (215), since mean seedling to adult ratios are generally less than 18:1 (Bond et al. 1984; Van Wilgen & Viviers 1985). This investigation aimed to determine the effective distance of P. laurifolia seed dispersal, and whether dispersal is related to wind speed and direction.

Methods

The site has a slope of approximately 7° with an aspect of 120°. No other large shrub species occur and it was assumed that the site was relatively free of vegetative barriers after the fire. The ground is not stony and there were no other visible barriers to dispersal.

The area of the study site was searched and all seedlings were found to be within an area of 45 m by 25 m around the stump of the parent plant. The positions of all seedlings in this area were recorded in September 1984. From these data the distance and azimuth from true north of each seedling from the parent plant was calculated.

To examine the effects of wind direction on seed dispersal, the mean azimuth of the seedlings was calculated and the uniformity of the seedling distribution around the point of origin was tested by means of a chi-square goodness of fit test. This analysis was performed on the observed circular frequency distribution in eight direction intervals, with the first interval centred on true north. As the sample may have had a non-uniform distribution without a mean direction, the significance of the mean angle was determined with Rayleigh's test (Zar 1974).

Data on wind velocities and direction during the first 31 days after the fire were obtained from the Zachariahoeek weather station situated approximately 1 km from the study site. Wind is recorded at this station by means of a Woelfle type mechanical wind recorder. The data for this period were summarized in velocity and direction categories. The study site is near the top of a ridge and there are no rocky outcrops in the vicinity. Therefore, it was assumed that wind speeds and direction on the site were similar to those measured at the weather station.

Results

The distribution of the seedlings is summarized in Figure 1a in such a manner as to be comparable to the wind rose (Figure 1b) summarizing the wind data.

The mean azimuth of the seedlings from the parent plant is 302°. The total chi-square value for the frequencies in the eight direction categories was 105.8. The null hypothesis, that the observed circular frequency is uniformly distributed around the origin is therefore rejected at \( P < 0.001 \). The value of Rayleigh's R calculated was 95.68, which is significant at \( P < 0.001 \). The mean angle is therefore significant.

The frequency of seedlings with distance from the parent plant (the population recruitment curve) is shown in Figure 2.

Discussion

The marked concentration of seedlings to the north-west of the parent plant's stump (Figure 1a) corresponds with the high frequency and speed of the wind from the south-east (Figure 1b). However, the pattern of seedling distribution is not a perfect inversion of the wind rose. This indicates the need to know the exact time of release of the seeds and the extent to which they move after reaching the ground. Seeds can be fully released from the plant within 24 hours of a fire (D.C. le Maitre pers. comm.). It was assumed here that there would be no significant movement of seeds on the ground after 31 days. Although the site in this study was well exposed, local differences in wind direction relative to those recorded at the weather station may have existed.

Although the results indicate dispersal by wind, dispersal distances in Protea laurifolia were relatively short, with 95% of the recruitment occurring within 15 m of the parent plant. The limited dispersal of protea seed is considered to ensure the establishment of seedlings within a favourable habitat. Midgley (1983) reasoned that as seeds are released after fire, dispersal would be restricted to within the burnt area, which is more favourable for both germination and establishment than the adjacent unburnt vegetation.

Brits (1982) proposed that the limitation of seed dispersal could have adaptive advantage in variable, nutrient poor habitats, such as are found in the fynbos.

Although the data in this study were obtained from one sample only, the site was well exposed to the wind. Therefore the maximum distance here may be regarded as a reasonable estimate of the order of magnitude of dispersal distances. The maximum dispersal distance of 30 m recorded implies that the average size of a homogeneous soil type or a burnt area would have to be less than a few hectares for the limited dispersal of seed to have an adaptive value.

Conclusions

Evidence has been presented to support the hypothesis that Protea laurifolia seed is wind dispersed. Questions regarding the function of the structure of the seed and whether the seed is dispersed during or after the primary trajectory, remain unanswered.

The potential rate of migration into an area which has been denuded of serotinous Proteaceae is in the order of 30 m per generation. Generation intervals are directly related to the
Figure 1. The effect of wind direction and wind speed on the dispersal of Protea laurifolia seeds. (a) The distribution of seedlings around the parent plant. The lengths of the bars show the percentages of the seedlings which occur in a direction class. The bars are subdivided according to the percentages within each distance class from the parent plant. Arcs indicate 10% intervals. (b) Wind rose showing mean percentages of wind of different speeds and directions at Zachariahsoek from 15 November 1977 to 15 December 1977. Arcs indicate 10% intervals. The figure in the centre indicates the percentage of time during which the wind was calm (< 5 km h⁻¹).

Figure 2. The distribution of Protea laurifolia seedling recruitment from the parent plant.

interval between fires. On the basis of a prescribed burn every 15 years it would take roughly 500 years for a population to advance 1 km into a previously occupied area from an upwind source. In areas where serotinous Proteaceae have been exterminated the management option of allowing gradual re-colonization by natural seed dispersal is impractical. The re-establishment of point seed sources through strategic planting could speed up the re-colonization process considerably where nature conservation is a priority. Since seed production is negatively correlated with adult density (Bond et al. 1984), such point plantings should be more effective than establishing large patches of proteas.

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