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Stem demography and post-fire recruitment of a resprouting serotinous conifer

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Abstract. The contribution of resprouts and seedling recruitment to post-fire regeneration of the South African fynbos conifer *Widdringtonia nodiflora* was compared eight months after wildfires in 1990. Stems on all trees were killed by fire but resprouting success was > 90 % at all but one site. A demographic study of burned skeletons revealed that prior to these fires, nearly all plants were multi-stemmed (4 - 9 stems/plant) and multi-aged, indicating continuous sprout production between fires. All stems were killed by these 1990 fires and at most sites > 90 % of the stems were burned to ground level. All diameter stems were susceptible to such incineration as, at most sites, there was no difference in average diameter of stems burned to ground level and those left standing. Individual genets usually had all ramets incinerated to ground level or all ramets charred, but intact, suggesting certain micro-sites burned hotter, whereas other sites were somewhat protected. Although not true of the 1990 fires, there was evidence that occasionally *Widdringtonia* stems may survive fire. At one site, four of the 16 plants sampled had a burned stem twice as old as the oldest burned stem on the other 12 plants at the site, suggesting some stems had survived the previous fire (ca. 1970) and this conclusion was supported by fire-scars on these four stems that dated to ca. 1970. Based on the highly significant correlation between stem diameter and cone density left standing after the 1990 fires, we calculated that for most sites > 80 % of the initial cone crop was incinerated by fire. This is important because we observed a strong relationship between size of the canopy cone crop surviving fire and post-fire seedling recruitment. Under these conditions we hypothesize that sprouting confers a selective advantage to genets when fires cause heavy losses of seed. The infrequent occurrence of sprouting in the *Cupressaceae* suggests the hypothesis that resprouting is an apomorphic or derived trait in *Widdringtonia*. Data from this study suggests resprouting provides a selective advantage under severe fynbos fires, which are not only 'stand-replacing fires,' but also are intense enough to incinerate cone-bearing stems.

Keywords: Age structure; *Cupressaceae*; Fynbos; Resprouting; Seedling recruitment; Serotiny; *Widdringtonia*.

Introduction

The life history of conifers with serotinous cones is of particular interest because, despite repeated cone crops, seedling recruitment is largely restricted to a single point in time, making them functionally semelparous. Serotiny is particularly well developed in the *Cupressaceae*, where it is represented in the Northern Hemisphere by ca. 25 *Cupressus* species and one species of *Tetraclinis*, and in the Southern Hemisphere by *Actinostrobus* and *Callitris* species in Australia, and *Widdringtonia* in South Africa (Lamont et al. 1991). In these species cones generally fail to open at maturity and remain closed for years, opening when individual branches die or *en masse* after fire (Fig. 1).

The South African *Widdringtonia nodiflora* (L.) Powrie is noteworthy in that, unlike other serotinous species in the family, it is also a vigorous resprouter after fire (Fig. 2). Thus, it is iteroparous, as resprouting clones may survive and reproduce through countless fire cycles. Indeed, resprouting would seem to be the primary means by which this species tolerates conditions in the fire-prone environments it occupies from fynbos in the Cape Region of South Africa to the northern Transvaal woodlands. Despite its strongly serotinous habit, previous studies in both regions have reported that post-fire seedling recruitment is nil (Scriba 1976; van Wilgen 1981).

The purpose of this study was to compare post-fire regeneration from resprouts and seedlings in Cape fynbos populations. The age structure of pre-fire trunks was sampled in order to make inferences about the role of resprouts between fires. Patterns of post-fire seedling recruitment were compared to pre-fire cone density and the influence of fire severity on cone destruction was investigated.

Species and study sites

Widdringtonia nodiflora is a small tree or shrub that typically occurs in dense populations dispersed in a matrix of fynbos shrubs or woodland elements. Individual patches usually vary in size from 10 - 1000 m^2 in size. Six recently burnt sites in the Cape Region were

Fig. 1. Open serotinous cones of *Widdringtonia nodiflora* six months after fire in the Cape Region of South Africa.

selected for study. All had burned in the autumn of 1990 (February - March) and all sites were sampled in the first growing season (October - November 1990). Sites ranged from the coast to the interior and included various slope aspects and inclines (Table 1). Sites were largely selected by what was available and accessible. The number of plots varied from 1 - 6 per site and was determined by the size of the stand, density of trees and proximity to other sites. As with most fynbos fires, these were 'stand-replacing fires', defined as ones that kill all above-ground biomass.

Methods

Plots were 20 m × 40 m except at Site 6 where the extremely high density of trees and seedlings required a reduction in plot size to 10 m × 20 m. Within each plot, all *Widdringtonia nodiflora* were reported as either resprouting or dead and the basal diameter and height of all pre-fire stems was recorded. For these skeletal remains, height was a function of pre-fire size and fire intensity. In many cases stems were burned to the ground and height was recorded as zero. Even in these stems that were largely incinerated, the basal diameter was still evident from stem remains at or below-ground. For each standing stem the number of cones was recorded. Occasionally downed-stems had cone remains, which were not recorded as they were extremely charred and it was presumed that no seeds would have survived. Thus our measure of cones reflects the potential post-fire seed rain more than the size of the pre-fire cone crop. Also, within each plot the number of *Widdringtonia* seedlings was recorded and within the borders of each plot, rock cover and plant cover were recorded along 10 evenly spaced 10-m transects.

In each plot a non-random sample of 6 - 16 plants, representing a range of plant sizes, were selected and all stems cut at ground level and a 5 - 10 cm section removed for growth ring analysis. Sections were sanded and polished and rings counted by two persons under 25× magnification. Estimated age was taken as the average of these two independent counts.

One living tree from an unburned stand near Site 5 was sacrificed and a basal stem section was taken for aging and at every stem node where cone clusters occurred another stem sample was taken and the number of cones recorded and a subsample of cones taken. Cones were air-dried and weighed and allowed to dry until dehiscence. Seed number and weight was recorded for each of 10 cones from each cluster and viability was determined by germination tests.

Sites were compared with One-way ANOVA and pairwise comparisons with the Bonferroni test. Relationship of covariates was determined with least-squares regression. Deviation of variance/mean ratios from a random Poisson distribution was calculated according to Cox (1985).

Results

Across the six study sites, pre-fire tree density varied by an order of magnitude and post-fire seedling recruitment varied by two orders of magnitude (Table 1). No stems (ramets) survived the fire but trees (genets) had very high resprouting success, above 95 % at the majority of sites (Table 1).

Pre-fire stem size

Prior to the fire nearly all trees were multi-stemmed, averaging 4 - 9 stems/tree (Table 1), with a range from 1 - 43. Pre-fire stems varied in diameter from a few mm to nearly 400 mm diameter. Many were burned to the ground, a factor likely to affect post-fire recruitment since attached cones were incinerated along with the stems. It was apparent that stems of all diameter classes were vulnerable to such incineration, a factor that undoubtedly contributed to the lack of correlation between diameter and post-fire height of skeletal remains ($r^2 = 0.02$; $P > 0.05$; $n = 1541$ ramets). Percentage of incinerated stems, defined as stems burned to ground-level, was significantly ($P < 0.001$, $n = 225$ genets) lower at Site 2 (56 %) than at all other sites (#1, 4, 5 and 6 had > 90 %). In addition, there were regional patterns, evident in 10 % higher percentage of incinerated stems at the coastal sites (5 and 6) relative to the interior sites ($P < 0.02$, $n = 225$).

Curiously, at all six sites there were two discrete height-vs-diameter distributions, and a surprising lack of overlap between these curves, suggesting stems were either completely incinerated to ground level or left standing (Fig. 3). When incinerated stems were removed from

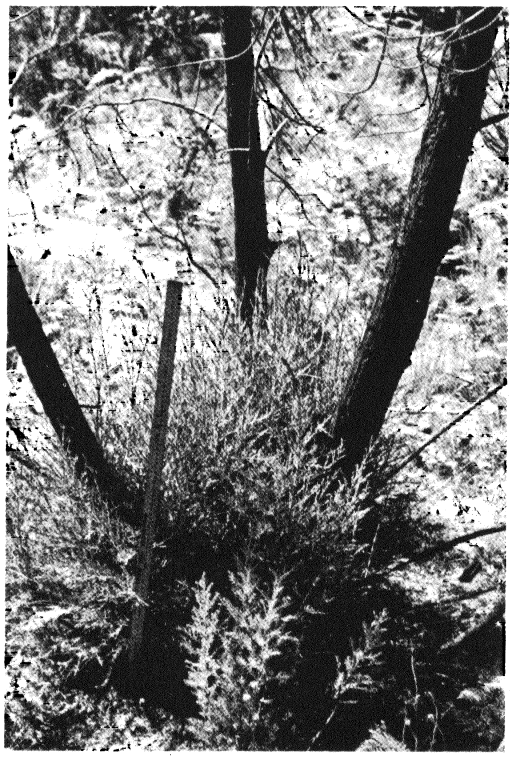

Fig. 2. Burned pre-fire stems and new basal resprouts of *Widdringtonia nodiflora* six months after fire in the Cape Region of South Africa.

the analysis, all sites had a highly significant ($P < 0.001$) correlation between height and diameter (Fig. 3). Comparing stem diameters between incinerated stems and stems with heights > 0 showed that at the majority of sites there was no significant difference ($P > 0.05$). At two sites incinerated stems had slightly smaller diameter stems (Site 4: $P < 0.05$; $n = 237$ and Site 6: $P < 0.01$; $n = 386$).

We hypothesized that this unusual distribution pattern, in which stems were either burned to ground level, or left standing and intact (Fig. 3), was the result of either (1) some stems were dead prior to the fire, making them more subject to incineration, or (2) incinerated stems included both living and dead and the separate distribution patterns seen in Fig. 3 are the result of plants in some micro-sites being subject to incineration, whereas plants in more 'protected' sites were not. Distinguishing between these hypotheses is not a trivial point. If the former hypothesis were true, incineration of stems would likely have minimal impact on the size of the post-fire seed bank, since retention of seeds in closed cones in *Cupressaceae* requires living tissues (Keeley & Zedler 1998). If the second hypothesis were true this could affect local patterns of post-fire recruitment and have potential selective impact. To test this we examined the intra- and inter-plant distribution of incinerated stems. We predicted if (1) were true, incinerated stems would be more evenly distributed across all plants and, since very high post-fire resprouting success indicated most plants were alive at the time of the fire, incinerated stems would not be concentrated within individual plants. Hypothesis (2) would predict the opposite pattern and in fact that was what was observed. Simple inspection of the data revealed that generally, plants had 100 % of their stems burned to the ground or 0 %. Variance/mean ratio for percentage of stems on a genet which were incinerated was 12.3, which deviated significantly from randomness ($P < 0.001$; $n = 225$), and indicated a highly clumped distribution. Apparent 'hotspots' would account for this pattern and this was evident within Site 1 where the percentage of incinerated stems ranged from 3 % in one plot to 100 % in another plot. Observations of living plants support the conclusion that stems burned to the ground were not dead prior to the fire; *Widdringtonia* in stands of these ages are quite vigorous with relatively little dead wood and very rarely are entire plants senescent.

Post-fire resprouting

Very few trees failed to resprout and there was no significant difference in resprouting success between sites (Table 1). The fact that the youngest stands had the lowest resprouting success suggests old age was not a factor in determining resprouting. Resprouting was also not obviously affected by fire severity as there was no significant relationship between average percentage

Table 1. Post-fire *Widdringtonia nodiflora* study sites, estimated pre-fire age, rock cover and total post-fire plant cover, and pre- and post-fire demographic parameters for *W. nodiflora* 7 - 8 months after fire. Mean ± S.E. sites with the same superscript were not significantly different at $P > 0.05$, $n = 19$ (site 3 with one plot was excluded). % gr.s. = % ground surface.

Site/location	Distance from coast (km)	Elevation (m)	Slope aspect (°)	Slope incline (°)	Nr. of plots	Ca. pre-fire age (yr)	Rock cover % gr.s.	Post-fire plant cover % gr.s.	Pre-fire density (genet/ha)	Ramets per genet	Post-fire resprouting (%)	Post-fire recruitment (seedlings/ha)
1 Dutoitskloof	46	350	NE	20	6	17	50[a]	22[a]	204 ± 83[a]	9.2 ± 2.1[a]	94 ± 5[a]	58 ± 30[a]
2 Dutoitskloof	47	300	NE	15	2	17	40[a]	22[a]	388 ± 263[a]	4.2 ± 0.4[a]	80 ± 20[a]	63 ± 38[a]
3 Dutoitskloofpas	51	400	SW	5	1	34	25	22	375	7.8	100	700
4 Bain's kloof	68	600	NW	10	4	20	36[a]	21[a]	313 ± 122[a]	5.9 ± 1.1[a]	96 ± 4[a]	181 ± 56[a]
5 Kogelberg	19	550	E	8	3	20	5[b]	26[a]	281 ± 57[a]	6.6 ± 1.1[a]	100 ± 0[a]	863 ± 236[a]
6 Köelbaii	1	75	W	25	2	22	3[b]	33[a]	2670 ± 1186[a]	8.4 ± 0.1[a]	95 ± 5[a]	8391 ± 2609

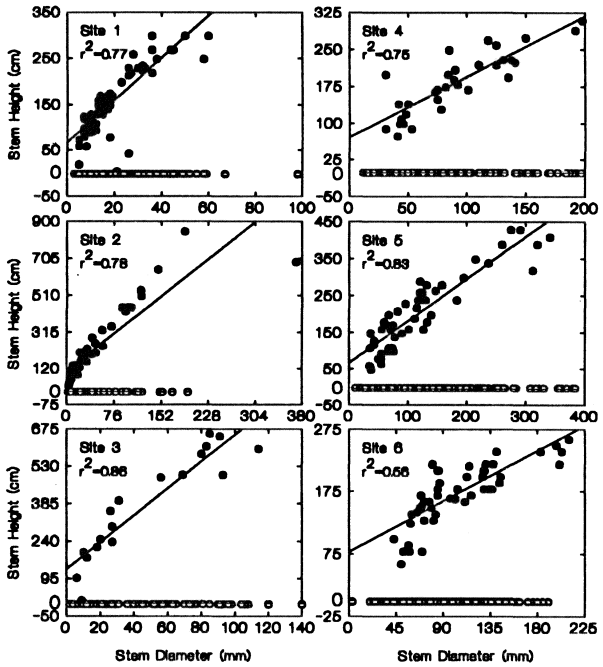

Fig. 3. Diameter vs height relationships for burned stems of *Widdringtonia nodiflora* after the 1990 wildfires at the six study sites. r^2-values calculated for standing-stems (filled circles) only; open circles are stems burned to ground level.

resprouting per plot and percentage of stems burned to ground level ($P > 0.05$, $n = 19$ plots). Plant size also had no apparent effect on whether or not a plant resprouted as indicated by no significant difference between resprouting vs. non-resprouting (dead) plants in number of stems per plant or pre-fire stem diameter ($P > 0.05$, $n = 225$). Number of cones, however, was significantly less on plants failing to resprout ($P < 0.05$, $n = 225$). As mentioned above, resprouting was not determined by fire severity, therefore lower number of cones likely indicates that these plants were either dead for some time prior to fire or were less vigorous at the time of fire.

Cone density

Post-fire cone density is a function of cone production and survivorship. Number of cones varied from 0 to 522 per stem and was significantly correlated with stem diameter (Fig. 4). Ignoring stems that were incinerated (where the cone crop was destroyed), the average number of cones per standing-stem, varied from 5 to 36 across sites, but was not significantly different between sites ($P > 0.05$, $n = 261$ stems). Cone density within a plot was determined by tree density (Fig. 5), thus, it is not surprising that Site 6, with the highest tree density (Table 1), had the highest cone density ($P < 0.001$, $n = 19$ plots).

An estimate of the cone crop destroyed by fire was made as follows. For Sites 1, 2, 3, and 5, where there was no significant difference in stem diameter for incinerated and standing stems, we multiplied the number of incinerated stems by the average number of cones per standing-stem. This calculation is justified by the correlation between cone density and stem diameter (Fig. 4). For Sites 4 and 6, we used the average number of cones per standing-stem estimated from a subset of standing-stems with a comparable mean diameter as observed for incinerated stems. Based on this analysis we estimate that across the six sites, 65 - 85 % of the cone crop at a site was destroyed during fire, and the majority of sites had > 80 % loss.

All cones present on burned skeletons were open and observations on unburned trees suggests very few were likely to have been open before the fire. For example, in an unburned stand outside our study site 5, one living tree was cut down and the cone production examined in detail. This tree was 21 yr old and had produced seven cone crops beginning at age 15 and continuing more or less annually. Very few cones were open and only cones ≥ 5 yr old. This tree had produced 25 - 75 cones per crop and cone cohorts showed no significant change with age in number of seeds per cone, seed weight or viability, with the exception that the last two crops were not yet mature. Average number of seeds was 16 ± 1

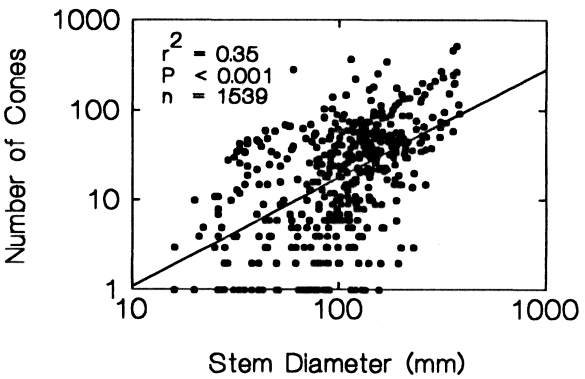

Fig. 4. Relationship between number of cones and stem diameter for all stems at all six study sites combined.

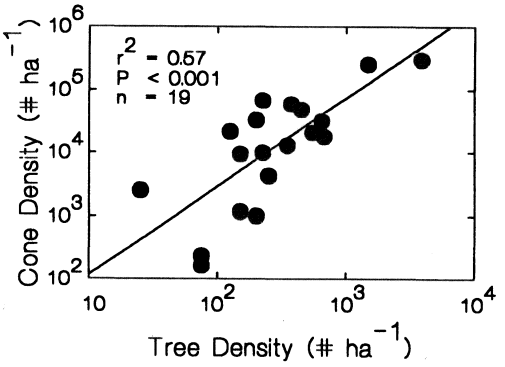

Fig. 5. Average tree density in a plot vs cone density for all six sites combined.

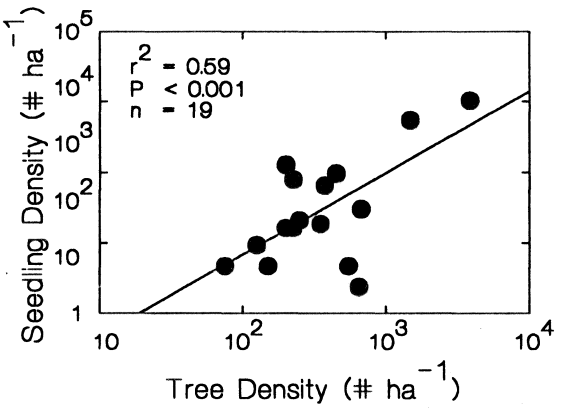

Fig. 6. Average density of pre-fire trees vs. post-fire seedlings in all plots from the six sites.

(mean ± S.E., $n = 56$) with an average mass of 116 ± 16 mg. Seeds comprised a small percentage of the mass as 96 % of the fresh cone mass was protective cone tissue.

Seedling recruitment and cone density

At some sites, seedling recruitment was extremely poor, e.g., fewer than 1/100 m^2, at other sites, recruitment was better with ca. 1/10 m^2, and at a single site there was nearly 1/m^2 (Table 1). There was a highly significant correlation between pre-fire tree density and post-fire seedling recruitment (Fig. 6), and in terms of recruitment 'success' (measured by offspring/parent ratio), there was a slightly significant correlation ($r^2 = 0.23$, $P < 0.05$, $n = 19$) between pre-fire tree density and this ratio.

Seedling recruitment is potentially limited by the canopy seed bank and at our sites cone density was significantly correlated with the offspring/parent ratio (Fig. 7). Using an average of 16 seeds per cone we estimate that for half the sites the ratio of dispersed seeds/seedling was 500 - 900 but ranged upward to 6900 for a single site. Site factors may account for some of this difference. For example, seedling recruitment was negatively correlated with rock cover (Fig. 8) and the two sites with the highest rock cover also had the highest seed/seedling ratios.

Age determination

Widdringtonia nodiflora produced clearly visible growth rings but often there were faint rings between darker more densely packed rings, the latter of which were interpreted as 'annual' rings and the others ignored as 'false' inter-annular rings. Other features used to recognize false rings were lack of continuity of the ring around the circumference of the stem and fuzzy borders. Precise ages for stems requires the use of cross-dating (Stokes & Smiley 1968). Cross-dating of this material was not feasible due to the irregular pattern of ring width on different sides of many trees and the lack of congruence in ring widths between trees on the same site, likely due to variable competitive effects. Consequently, precise ages were not possible, however, there is evidence that age determinations were approximately good estimators of age. This conclusion is based on the similarity between ring counts and known stand age at one site (#5). Our ring counts gave a pre-fire age of 20 - 21 yr and fire records for that site indicated it had last burned 19 yr prior to the fires of 1990. Other circumstantial evidence is the highly significant correlation between stem diameter and estimated age (Fig. 9).

All burned stems on at least five trees at each site were aged and showed the following patterns. At all sites, stems (ramets) on the same individual (genet) were multi-aged, ranging from 1 to > 16 yr. The maximum stem age on an individual was generally consistent (within a year or two) across all individuals that were aged at a site and this maximum age was taken to be the pre-fire stand age (Table 1). A typical tree would have one to several burned stems that dated back to the last fire prior to the 1990 fire, as well as many younger burned stems, indicating recruitment was more-or-less

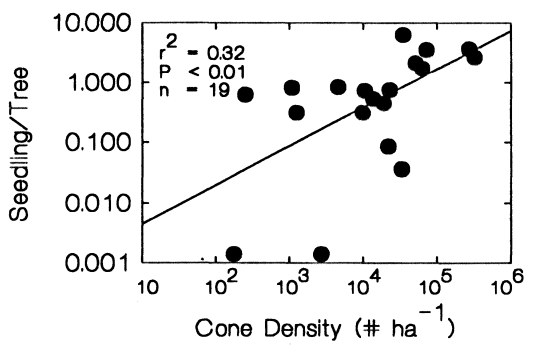

Fig. 7. Average cone density vs offspring/parent ratio for all plots from the six sites.

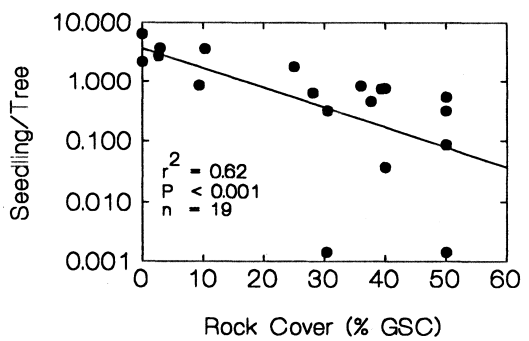

Fig. 8. Relationship of average rock cover (% ground surface covered) vs offspring/parent ratio for all plots at the six sites.

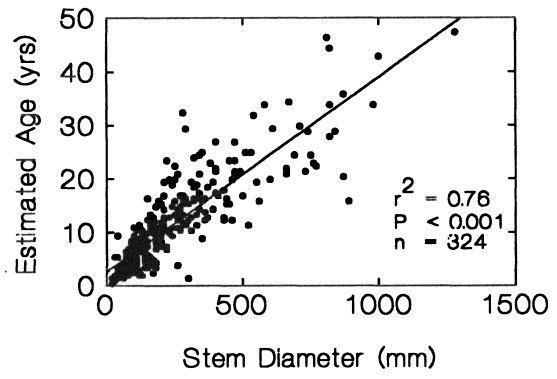

Fig. 9. Regression of estimated age vs. stem diameter for all stems aged at the six sites.

continuous between fires. This pattern is evident in the age distributions constructed with all pre-fire stems that were aged from a site (Fig. 10). Since all plants (genets) studied had at least one stem (ramet) that dated back to the last fire prior to 1990, it is apparent that the continuous age distribution of stems (Fig. 10) is not the result of recruitment of seedlings between fires, but rather of vegetative sprouts. Also, nearly all trees examined had relatively massive rootstocks which indicated repeated resprouting following many fires.

One seeming anomaly in the age distributions (Fig. 10) was the gap in ages of burned stems observed at Site 2.

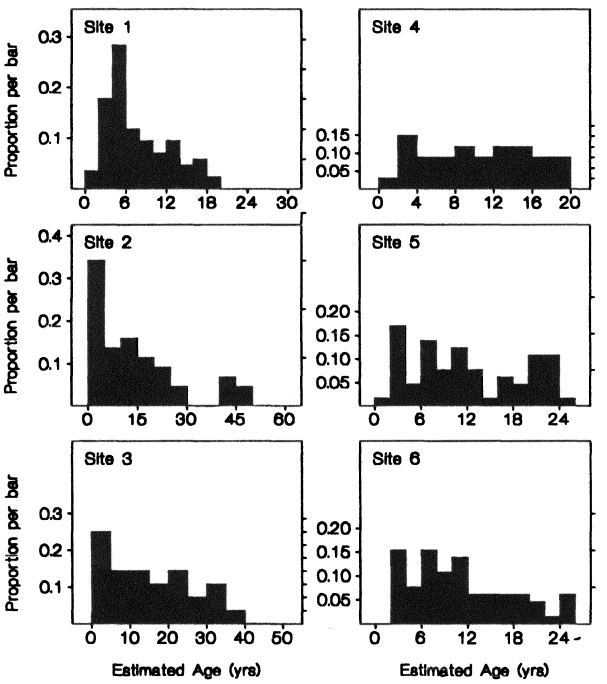

Fig. 10. Age distribution for all stems on 5 - 16 plants from each site.

Four of the 16 individuals that were aged at this site had a single stem with a maximum age that was nearly double the maximum age of 20 - 22 yr observed for the other 12 trees. These four stems all had a distinct fire scar that was produced about 20 - 22 yr earlier, indicating that, unlike the 1990 fire, these four stems had survived the previous fire in about 1970. Although this 1970 fire killed all stems on the majority of *Widdringtonia* at the site, it apparently burned some patches with unusually low intensity. The fact that any stems could survive a fire is surprising since mature stems (100 - 200 mm diameter) typically have thin bark (2-3 mm). Age distributions for all burned stems showed that at several sites the majority were initiated within the last 5 yr, whereas other sites exhibited an even distribution of sprout production over time (Fig. 10).

Discussion

Resprout demography

Widdringtonia nodiflora is a vigorous resprouting tree or shrub resilient to relatively intense wildfires. Although we found few trees killed by fire this may be peculiar to the Cape Region and not universal throughout its range. Scriba (1976) reported mortalities of 28, 41 and 85 % for high elevation subtropical populations in the northern Transvaal. It is unknown what factors account for these differences, although the Transvaal summer-rain climate, which stands in stark contrast to the winter-rain Cape climate, may be involved.

Fire severity may account for differences in resprouting success. Stands of *Widdringtonia* produce relatively high intensity fires (van Wilgen & van Hensbergen 1992), although, depending upon burning conditions, intensity can vary dramatically (Trollope 1984). In Scriba's study the highest resprouting success (82 %) was in a stand where 7 % of the stems survived the fire, whereas sites with lower resprouting success had only 0 - 1 % stem survival, suggesting that intensity may have been a factor in resprouting success. In contrast, our study showed all stems were killed by fire at all sites, yet resprouting was high (Table 1). Other evidence suggesting that intensity is not the determining factor in resprouting success is the very high proportion of stems that were incinerated at all of our sites and the lack of correlation between this surrogate measure of fire intensity and resprouting success.

Internal physiological rhythms such as carbohydrate storage patterns vary seasonally and may account for differences in resprouting success between our study and Scriba (1976). Such seasonal effects may be involved as the fires studied here burned in autumn and those studied by Scriba (1976) burned in spring. In other species,

resprouting has been strongly correlated with seasonal changes in root or lignotuber storage carbohydrates (Rundel et al. 1987) and this may be a factor with *Widdringtonia* as well.

Recruitment of vegetative shoots is not restricted to post-fire conditions and appears to occur continuously throughout the interval between fires (Fig. 10). The estimated age-distribution for stems indicates that at some sites a significant proportion of plants are still initiating new shoots whereas at other sites this has tapered off considerably.

Seedling demography

Complete lack of post-fire seedling recruitment has previously been reported for Cape populations (van Wilgen 1981) and those in other regions (Scriba 1976). The extremely low seedling recruitment observed at two of our interior sites (Table 2) is consistent with these earlier reports, but other sites in our study illustrate that significant seedling recruitment can occur after fire. Population variation in degree of serotiny may contribute to differences in post-fire recruitment, although we know of no evidence of this. Abiotic factors such as amount of rock cover are correlated with poor recruitment (Fig. 8), but whether or not there is a causal relationship is unknown. Pre-fire tree density is strongly correlated with post-fire seedling recruitment (Fig. 6) and this likely reflects the greater canopy seed bank in denser populations (Fig. 5). However, tree density is also weakly correlated with recruitment success (offspring/parent ratio), suggesting factors other than just larger cone crops are involved.

In light of the very strong relationship between cone crop and seedling recruitment (Fig. 7), our estimates of the proportion of the canopy seed bank destroyed by fire is potentially of profound significance. At the majority of sites > 80 % of the cone crop was estimated to have been incinerated, although it is unknown how widespread this phenomenon is since other authors have not reported these statistics. This observation has important ecological and evolutionary implications.

Assuming that cones (and stems) stand a greater chance of being incinerated under high intensity fires, then managing sites for lower intensity burns may contribute to higher post-fire seedling recruitment.

The observation that stem (and cone) incineration is concentrated in particular individuals in the population raises the specter of potential selective effects. More often than not, plants either survived fire with most stems left standing or all stems were incinerated (Fig. 3 and Results). Thus, a genet's entire cone crop was either destroyed or left largely untouched, indicating some plants were more vulnerable than others. Although energy content (J/g) is an important fuel property and quite high in *Widdringtonia* (van Wilgen & van Hensbergen 1992), it is unknown how much intra-specific variation there is in this parameter. Very likely the differences in degree of incineration are related to micro-site differences as suggested by the fact that at one site the percentage of incinerated stems varied from 3 - 100 % between plots. While abiotic site factors may account for these differences, it is intriguing to consider the possibility that nearest neighbor differences in flammability may be responsible (Bond & Midgley 1995).

Evolutionary origin of sprouting in Widdringtonia nodiflora

Serotiny is widespread in the *Cupressaceae*, being reported from five genera and 40 species (Lamont et al. 1991). The sole representatives of the family in South Africa are three species of *Widdringtonia,* all of which are serotinous (Lamont et al. 1991), although not all are strongly serotinous (Manders 1987). The sister genus to *Widdringtonia* is apparently the Australian *Callitris* and these genera are both closely related to *Tetraclinis*, a monotypic genus in the Mediterranean Basin (van Gelderen & van Hoey Smith 1996). These three genera are all serotinous (Lamont et al. 1991), suggesting that serotinous cones are homologous structures, and the fact that these taxa are distributed in arid fire-prone environments supports an adaptive argument for the origin and persistence of serotiny.

Resprouting on the other hand is not widespread in the Cupressaceae, apparently present in only a few species, including a couple of Mediterranean Basin *Juniperus* spp. (Keeley 1994) as well as *Widdringtonia nodiflora.* Other *Widdringtonia* spp., *Callitris* spp. and *Actinostrobus* spp. are apparently unable to resprout and lack the basal swelling typical of *Widdringtonia* (Kruger 1984; Gill 1981; Bond pers. observ.; weak sprouting has been observed in one species of *Actinostrobus,* Byron Lamont, pers. comm.). Thus, resprouting in *Widdringtonia* is apparently a derived or apomorphic character. Conditions that gave rise to its derivation are worth exploring as resprouting is a rare condition in conifers (Keeley 1981) and not commonly associated with serotiny (Lamont et al. 1991).

We hypothesize that a combination of high fire intensity and high fire frequency have played significant roles in the evolution of resprouting in *Widdringtonia.* In this study we estimated that at most sites only 15 - 20 % of the canopy seed bank survived fire; the majority of cones and stems being incinerated by high intensity fire. The result was nearly complete failure in seedling recruitment at some sites. Such poor recruitment in *Widdringtonia* appears to be widespread and represents significant selective pressure for resprouting ability. It is unknown what factors might account for particularly high fire intensity

in stands of this species, relative to those of other arid-land *Cupressaceae*.

High fire frequency could also play a significant role in the evolution of resprouting ability. Seedlings require 20 yr to reach reproductive maturity (Kruger 1984), which means that at all but one site in our study, few if any mature cones would have been present if trees had recruited from seed. Resprouts on the other hand reach maturity in 6 yr (Kruger 1984) suggesting an additional advantage for resprouting in *Widdringtonia,* which is distributed in environments where fires typically occur at < 20 yr intervals (Kruger & Bigalke 1984; Tainton & Mentis 1984).

It is interesting that despite this double insurance against fire, *Widdringtonia* is apparently quite sensitive to frequent fires and readily eliminated from many sites (Palmer & Pitman 1972; Tainton & Mentis 1984). In this regard, it is like other *Cupressaceae*, such as the obligate-seeding species of *Cupressus* in North America which are decimated by frequent fires (Zedler 1977; Kuhlman 1986).

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