Can the season of burning affect the growth of *Dichrostachys cinerea* populations? A hypothesis of phenology

By Alex Schutz

Abstract

A hypothesis was put forward that summer burning would constrain the population growth of *Dichrostachys cinerea* as at this stage in the plant's phenology carbon reserves are lowest after the initial spring flush and therefore post-burn re-growth would be stunted. Initial slow re-growth would affect the time taken to reach maturity and the size of the plant in the next burn, thus indirectly affecting both fertility and mortality. The hypothesis was tested by collecting data pertaining to the different fertility, growth and persistence levels of *D. cinerea* populations in long term experimental burn plots that have been burnt in different months and at different frequencies. The change in population density of *D. cinerea* in the plots over the last half-century was also investigated to test whether any short term effects of the season of fire on a particular generation have long-term repercussions on the population density of the species. The particular life-history of *D. cinerea* was also investigated and compared against that of *Acacia nigrescens*. It was the average size of plants and their fertility levels are generally lower for plants burnt in mid-summer compared to plants burnt in winter. On all the burn plots investigated *D. cinerea* population numbers have increased n the last half century but averaged across the study areas these increases are most pronounced on winter triennial burns.

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Can the season of burning affect the growth of *Dichrostachys cinerea* populations? A hypothesis of phenology

INTRODUCTION

The primary question that this paper addresses is how the season of burning affects the growth of *D. cinerea* populations. The hypothesis is that *D. cinerea* will be less able to recover from a fire in mid-summer, when stored carbon reserves have been invested in new foliage and root carbon reserves have not yet been replenished. Thus we predict that repeated mid-summer burning will constrain *D. cinerea* population growth compared to burning at other times of the year.

Fieldwork for the project was conducted in and around Satara, in the Kruger National Park, on long term experimental burn plots (EBPs) that were established in 1954 (Enslin *et al..*. 2000, Woods *et al..*. 2002). The fieldwork was carried out over a week starting on the 29 June 2003. The EBPs allowed us to determine what the long term effects, if any, of repeated burning in different seasons and at different frequencies were on *D. cinerea* populations. Persistence, growth and fertility levels were quantified in *D. cinerea* populations on different burn plots, and compared against the change in *D. cinerea* plant density that has occurred in the EBPs since their establishment. Life-history data pertaining to the size at which *D. cinerea* plants become reproductive was also collected, so that the life-history pattern of *D. cinerea* could be compared against other trees with a already described life-history.

The structure for the remainder of the introduction is as follows. The hypotheses underlying the project's main questions will be outlined, the motivation for choosing *D. cinerea* as the study species will be given and finally the main aims and predictions of the project will be stated.

The Phenology hypothesis

The hypothesis is based on the findings of Maze (2001), which showed seasonal fluctuations in the root starch percentages, and differences in re-growth rates, recorded as the sum of stem lengths, after defoliation in different seasons for *D. cinerea* plants. Lowest root starch content was found between November and January and the combined length of resprouting stems was smallest when plants were clipped, which simulated fire damage, between January and March. These results are qualitatively represented in Figure 1, which shows a hypothetical model showing the seasonal fluctuations in plant growth and root carbon reserves. The question of how the season of burning affects *D. cinerea* population growth is considered through a persistence, growth and fertility framework. For a population to grow or decline either the recruitment rate (the equivalent of birth rate in animal populations) or the mortality rate has to change. Within the persistence, growth and fertility framework recruitment rate is directly is positively related to fertility and mortality is negatively related to persistence levels. Growth affects both recruitment and mortality, in that the faster plants grow the sooner they become fertile and reach a stage where they are more likely to survive disturbance events, such as fire, drought or herbivory (Higgins *et al..* 2000). It is predicted (assumed) that because *D. cinerea* root reserves are lower in mid-summer, burning at this time of the year will depress post-burn re-growth rates. Therefore plants burnt at this time will take longer to reach maturity, than plants burnt at other times, and will initially invest in re-growth and the replenishment of lost root reserves rather than reproduction. Secondly shrubs burnt at this time are also less likely to be able to resprout at all if burning occurs at a time when the plants root reserves are completely (or sufficiently) exhausted. It is predicted that *D. cinerea* populations burnt in mid-summer will have lower persistence, growth and fertility levels than a population burnt at another time of the year.

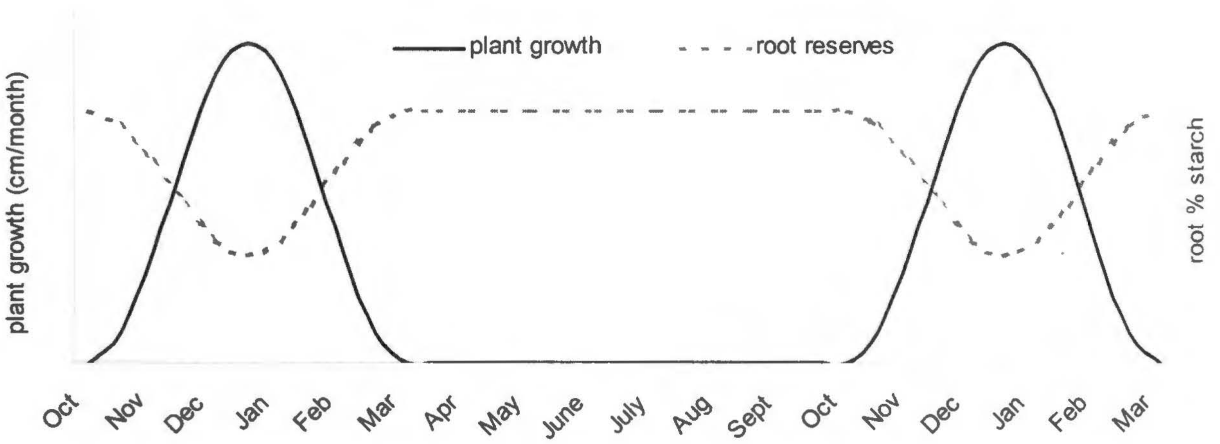

Figure 1: A model of the seasonal fluctuation in plant growth and root starch content based on the findings of Maze (2001). Root carbon reserves are at their lowest in summer, when they have been exhausted on the new season's growth. Burning at this stage will negatively affect the plant's capacity to recover from the fire.

Why Dichrostachys cinerea?

The motivation for choosing for considering *D. cinerea* as a study species are two-fold. Firstly bush encroachment is considered a problem in South African savannas, and *D. cinerea* is one of the prime species associated with this encroachment (Rogues *et al..* 2001, Hoffman *et al..* 1999). Secondly recent models of tree-grass co-existence in savannas have moved away from the root-niche hypothesis (Walker & Noy-Meir 1982), which has dominated the literature on the subject for over tow decades, and have emphasised life history-disturbance interactions (Higgins *et al..* 2000). However the Higgins *et al..*'s (2000) model grapples with the so called Gulliver type life history typical of certain savanna trees (Bond & van Wilgen 1996), e.g. *Acacia nigrescens*, but fails to include trees and shrubs that do not have a Gulliver stage in as part of their life-history, such as *D. cinerea*.

Bush encroachment

It has been estimated that in South Africa 13 million hectares of savanna have been subject to thorn bush encroachment (Trollope *et al..*. 1989 in Roques *et al..*. 2001). *D. cinerea* is included as one of the few indigenous South African species that are perceived as problem elements in bush encroachment (Hoffman *et al..*. 199). In a study conducted by Roques *et al..*. 2001, in the lowveld savanna of north-eastern Swaziland they, using aerial photographs from 1947 to 1990 they found that for the study area as a whole shrub cover increased from 2% in 1947 to 31% in 1990. A ground survey showed that in 1997 *D. cinerea* contributed 81% to total shrub cover in the study area, used by Roques *et al..*. 2001, (Roques *et al..*. 2001). Although bush encroachment was classified as a top priority in 1997 by magisterial districts in the lower half of the Kruger National Park, i.e. below the Olifants River, which is where the fieldwork for this paper's fieldwork was conducted, *D. cinerea* was not considered as one the key bush encroachment species in the area (Hoffman *et al..*. 1999). However Enslin *et al..*. (2000) found that on long-term experimental burn plots in the Knob-thorn/Marula savanna, characteristic of the vegetation in and around Satara, which is in the southern half of the KNP, *D. cinerea* was one of the few woody plants that had increased in density between 1954 and 1998.

Gullivers vs. non-Gullivers.

The Gulliver type life history which Higgins *et al..*. 2000 emphasise in the their model of tree-grass co-existence refers to trees that have a distinctive stage in their life history where they are prevented from reaching maturity by recurrent fires which kill their above ground growth, a process referred to as topkill. Once the adolescent trees have experienced topkill they coppice from their base and their subsequent growth rate and the interval between the next fire and the last will determine whether they are tall enough to escape topkill in the next fire. Within this fire-trap where the plants are still susceptible to topkill, which is approximately five meters above the ground, depending on the intensity of the fire (Trollope in Roques *et al..*. 2001 and Archibald & Bond 2003), the plants do not reproductive and reserve the carbon stores produced for growth now or re-growth after the next fire (Bond & Maze, unpublished). Thus population growth of Gulliver type trees is potentially restricted both by a recruitment bottleneck and a release bottleneck (Higgins *et al..*. 2000). Recruitment refers to the establishment of new adolescent trees, or Gullivers, while release refers to the establishment of new adult trees, i.e. once they are released from the fire-trap. *D. cinerea* shrubs are generally no taller than 5m (personal observation) and therefore their whole life cycle must reproduced within the flame-zone. *D. cinerea* shrubs must reach maturity within the flame-zone, as they never escape it. Thus *D. cinerea* population growth is not limited by a release bottle-neck, and as this forms a major component of Higgins *et al..*.*'s* 2000 model, the model cannot be used to explain co-existence of grasses and non-gulliver type trees or shrubs. For a model that explains tree-grass co-existence in savannas based on life history-disturbance interactions to be complete both gulliver-type life histories and non-gulliver-type histories need to be incorporated into the model. The first step in producing such a model is collecting data that quantifies the life-history of both types.

to identify mechanism that relate to persistence, growth and fertility that can explain the predicted population growth under repeated summer burning. Secondly it is predicted that *D. cinerea* will produce pod-clusters within the flamezone while Gulliver type trees will not. Thus the second aim of the project is to identify at what height *D. cinerea* individuals become reproductive and how this compares to the height at which a Gulliver type tree becomes reproductive.

METHODS

Study area

The fieldwork for this project was conducted in the Satara region in the Kruger National Park, Mpumalanga, South Africa (Figure 1). The Satara region is described as Knob-thorn(*Acacia nigrescens*)/ Marula(*Sclerocarya birrea)* savanna (KNP Ecozone Map 2000, Enslin *et al..*. 2000). The main vegetation components of this savanna type are shown in (Figure 2). The data was collected on Experimental Burn Plots (EBP) that were established in the park in 1954 as part of an initiative to study the effects of fire frequency and season on the different veld types of the Park. Within each ecozone of the park there are four strings of EBP's, and each string contains between 12 and 14 different burn treatments that are replicated in the other strings in the same ecozone. Examples of the types of burn treatments used are August triennial burns and December annual burns. The strings in the Satara region are all located near roads, but are separated from the roads by a fire-break, which also acts as an access road to the plots. The same fire-break that separates the plots from the roads stretches around the perimeter of the plots and separates them from the rest of the veld, to prevent unwanted burning of the plots. The plots are rectangular and are approximately 360m x 180m (Enslin *et al..*. 2000) and are separated from each other by fire-breaks. The four strings in the Satara region are the Satara, N'wanetsi, Lindanda and Marheya strings and are shown in Figure 1. The general layout of the plots along a string is shown in Figure 3.

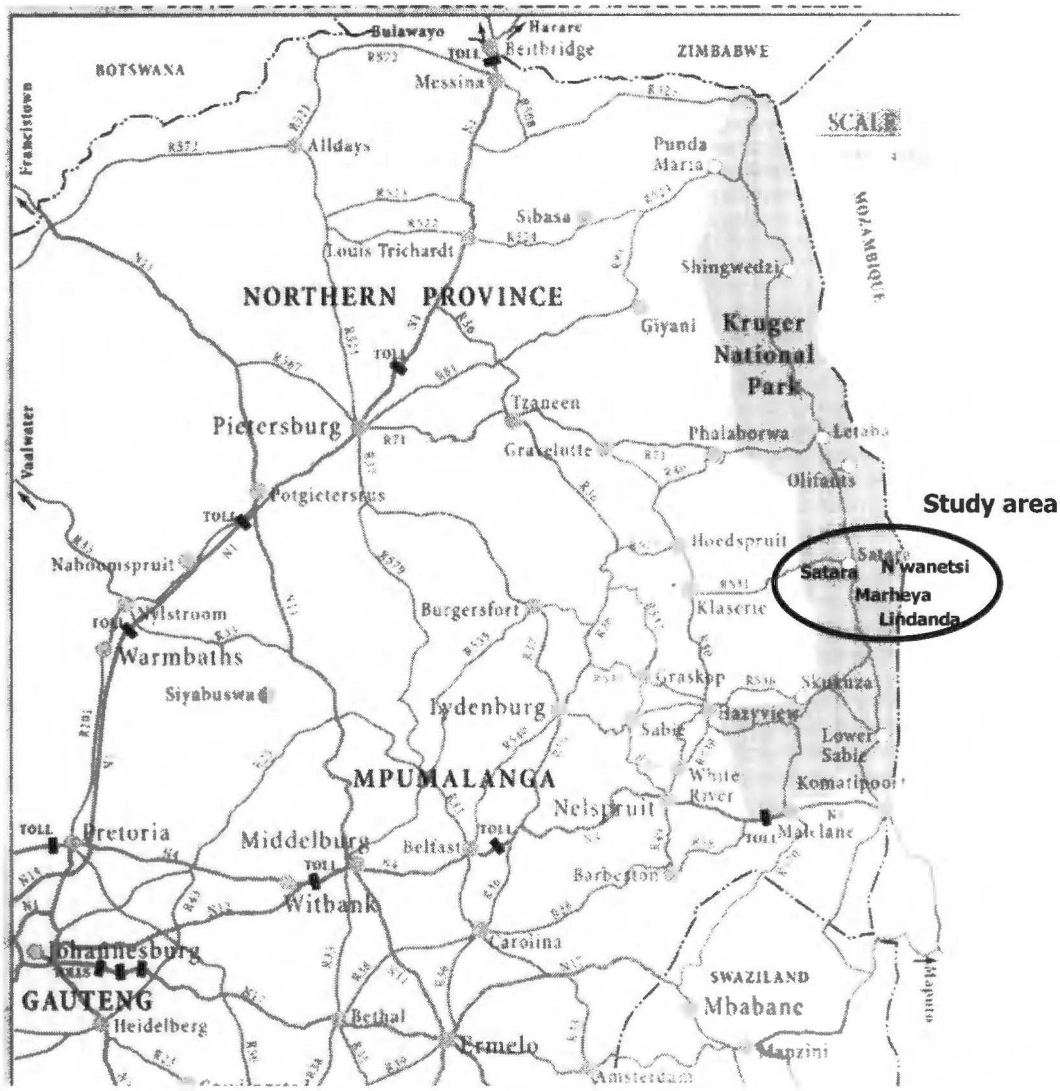

Figure 1: A map of Mpumalanga, South Africa, showing the location of the study area within the Kruger National Park. The location of the four strings of experimental burn plots (EBPs) used in the study are also shown. (KNP visitors' map).

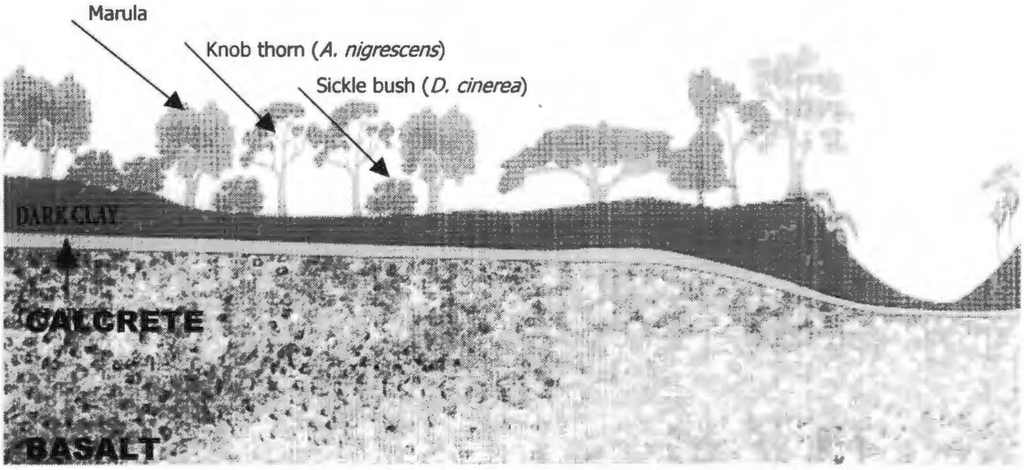

Figure 2: The vegetation structure and geology of Knob thorn/Marula savanna. (KNP Ecozone Map)

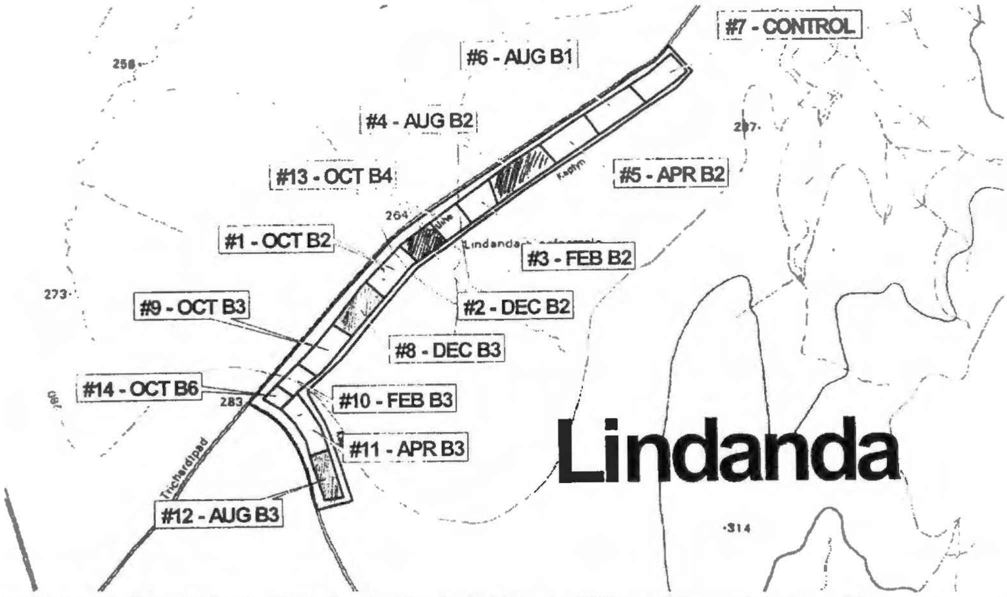

Figure 3: A map of the Lindanda string showing the typical layout of EBPs and the combinations of treatments used.

Fieldwork

The project aimed to identify if the season of burning has an affect on the density of *D. cinerea* through its affect on the fertility, persistence or growth levels of individual plants. Thus it was necessary to measure features or record data that pertained to fertility, persistence or growth.

Fertility and Size

The number of pods or seeds on an individual is an obvious and relatively easily recorded index fertility levels of plants, however as there was the possibility that seed production in the more recently burnt plots was not at its optimum (as the plants were still recovering from the last burn) an index of the populations' potential for seed production needed to be determined. Three possible options were considered, namely the size structure of the populations, the current productivity of the shrubs, in terms of photosynthetic activity, in the different plots and the number of new recruits in the various plots. To look at the relationship between plant size and reproduction, the heights, widths and number of pod-clusters of plants were recorded in the Octb6 plots. The Octb6 plots were last burnt in 1997 and it was assumed that the plants in these plots had had sufficient time to recover from the last burn and that carbon stores would no longer be preferably allocated to post-burn recovery. Foliage density was recorded on a qualitative scale that consisted initially of four categories but eventually of five, ranging from very sparse foliage to dense foliage. To consider the number of new recruits in a population it was noted whether a plant showed any evidence of surviving a previous fire, namely a skeleton of dead burnt wood. If the plant did not have a skeleton it was considered to have germinated after the last fire and labelled as a new recruit.

Growth and re-growth

Growth or re-growth rates were calculated by dividing the height or width of the plants by the time since the last fire, and were thus cumulative growth rates rather than instantaneous growth rates. One would expect that the size of a plant before a fire will affect post-burn re-growth rates plants in that bigger plants will have more established root systems that can access more water and nutrients and hold more carbon reserves than smaller plants. Assuming that above ground size is positively correlated with below ground size the height of the plants' *skeletons* was recorded as an indicator of plant size before the fire. The skeleton of a plant was defined as dead burnt wood that was still attached to the plant. This wood was normally the remains of the main stem or stems that were burnt in the last fire.

Persistence and Mortality

Persistence and mortality rates were quantified at the same time as recruitment rates were measured. If a plant was not classified as a new recruit then it was either labelled as dead, if it had no live stems, or as having persisted (survived), through the last burn, if it did have live stems and a skeleton.

In summary to consider the effect of fire season on *D. cinerea*, the number of pod-clusters, the height, width, number of stems, foliage density and the skeleton height of plants were recorded (Figure 4). Heights and widths were measured using a five-meter pole that was marked at half metre intervals. Foliage density was classified as into one of four categories (A-D), where A was sparse and D was dense. (A was further divided into A1 and A2, where A1 indicated that there was almost no foliage on the tree). Pod clusters were counted and recorded as one of the following: A 1-4; B 5-9; C 10-14; D15-19; e 20+ and f >30. If there were more than 30 pod clusters on the shrub then the number of pod clusters to the closest 10 was recorded. These features were measured for ~ 25 randomly chosen plants in the same five EBPs at the four strings. The EBPs used were August and December triennial and biennial burns and an October biennial burn (Table 1). These treatments were used as they enabled a comparison of the effect of winter (August) and spring (October) burns on *D. cinerea* plants against the effect of mid-summer burns on *D. cinerea* individuals. I predicted that in mid-summer, when the plants have not yet replenished the reserves exhausted on new growth, they will be most vulnerable to fire. The plants were chosen randomly using the *wandering quarter* method. The first plant was chosen by walking into the plot for a few metres away from the edge and the choosing the closest *D. cinerea* individual (shrub hereafter). The next shrub was chosen by facing towards the opposite side of the plot that we entered upon and then walking towards the shrub that was closest to us but within 45 degrees to the left or right of the fixed transect direction. To cover as much of the plot as possible, the fixed transect directions where varied where necessary. If a thicket of shrubs was encountered then only between five and four of the plants in the thicket would be sampled.

Table 1: The Experimental Burn Plots (EBP) used in the investigation of the effect of season on burning on *D. cinerea* populations in the Satara region. (* The Lindanda AugB3 plot was accidentally burnt in 2001.)

Code	Season of burn	Month of burn	Frequency of burn	Last burnt	Moths Since last burn
Augb3 or 8b3	Mid-winter	August	Triennial	2000*	34
Decb3 or 12b3	Mid-summer	December	Triennial	2000	30
Augb2 or 8b2	Mid-winter	August	Biennial	2002	10
Octb2 or 10b2	Spring	October	Biennial	2002	8
Decb2 or 12b2	Mid-summer	December	Biennial	2002	6

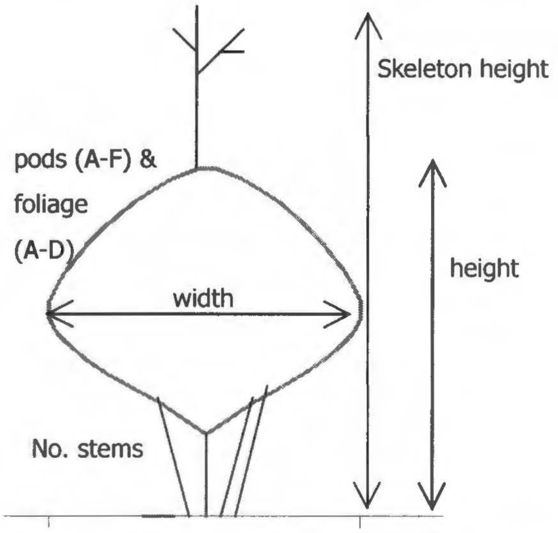

Figure 4: The features of *D. cinerea* measured in the plots burnt in the biennial and triennial plots.

Demographic effects of burn treatments

To test the prediction that mid-summer burns would impede the growth of *D. cinerea* populations, when compared to winter burns, the increase in *D. cinerea* population densities various burn treatments was compared. As mentioned earlier the EBP were first established in 1954 and in this year before the first burns two criss-crossing 2m diagonal transects were traversed across each newly marked plot and among other things the number of different plant species and the number of plants per species in the diagonal were recorded (Enslin *et al..*. 2000). In 1998 these original diagonals were re-visited and species counts and plant numbers were recorded. Using this data the increase in *D. cinerea* density (plants/hectare) between 1954 and 1998 in the different Satara streams was calculated for the triennial and biennial burn treatments. (KNP Scientific Services)

Tree vs. Shrub architecture and life history patterns

To compare the architecture and life-history of *D. cinerea* against the architecture and life-history of a Gulliver type plant, features of *D. cinerea* and *Acacia nigrescens* were recorded in the October sexennial burn plots (Octb6) at the four strings. (The data from these plants was also used to determine the relationship between the size of a shrub and its potential seed output.) These plots were first burnt in 1979, and the plots had been burnt four times up to the time of the fieldwork. The Octb6 plots were used because they were last burnt in 1997 and were therefore likely to have fully recovered from the last burn. **The purpose of considering the *D. cinerea* populations in these plots was to determine at what height the shrub starts producing seeds and how this compares to Gulliver type trees which only produce seeds once they have escaped the fire-trap (Maze 2001, Bond & van Wilgen 1996). *Acacia nigrescens* was used as an example of a tree with a Gulliver type life-history. For each tree the same features that were recorded in the younger plots were recorded here, except for the foliage density and the skeleton height. For the *A. nigrescens* individuals if there were too many pods to count individually, i.e. > ~200, then the number of pods on one branch unit was counted and the number of branch units in the canopy was estimated to give the total number of pods (Archibald & Bond, 2003). For the *D. cinerea* individuals the number of pod clusters was counted and put in categories as described earlier. Pods were counted for *A. nigrescens* and pod-clusters for *D. cinerea* because in the case of *D. cinerea* there are a number of seed pods clumped together per attachment (petiole) while in *A. nigrescens* there is only one seed-pod per attachment to the supporting branch. The number of pods or pods-clusters was later converted into a number of seeds, based on a median of seeds in pods or pod clusters for *A. nigrescens* and *D. cinerea*, respectively, that were collected in the field. The features that were recorded per plant are shown in . To collect a sample that included a complete range of plants in terms of height, 6 plants were recorded in each size-class. For *D. cinerea* the size class intervals 0m – 1m, 1.0m - 1.5m, 1.5m – 2.0m, 2.0m – 2.5m, 2.5m – 3.0m and >3.0m; for *A. nigrescens* 1m size class intervals were used up to a height of seven metres after which plants were recorded as taller than seven metres. To sample the plants within one size class randomly we adopted a modified wandering quarter method where some plants were ignored if we had almost filled the quota for the particular size class interval.

Because the *D. cinerea* plants in the Octb6 plots were not sampled randomly it was necessary to create a sub-sample of randomly selected individuals before any comparison that was affected by size-class structure could be made between these plants and the plants in the younger plots. This was done in a spreadsheet using a random function and an algorithm that ensured that the ratios of plants in different size-classes in the Augb3 samples and the Octb3 samples were similar (Microsoft® Excel 2000).

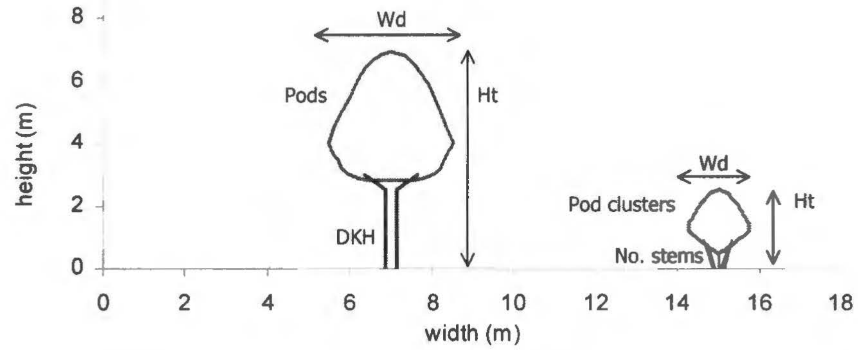

Figure 5: The features of *A. nigrescens* (on the left) and *D. cinerea* (on the right), that were measured in the October sexennial (Octb6) plots.

Data Analysis

Fertility and Size

To test whether there was a relationship between size and seed output the seed production in the Octb6 plots was plotted against size (height). A student's t-test was used to test whether there was a significant different between the average heights and widths of shrubs in the Augb3 and Decb3 plots. The average sizes of the shrubs in the Augb2, Octb2 and Decb2 were not tested for significant differences as these plots had been burnt i.e. between eight to ten months before the fieldwork (Table 1). The assumptions of normality and homoscedasticity for a t-test of were tested graphically using normal probability plots and Levene's test for homogenous variances (Zar 1999; StatSoft, Inc. (2002)). Significant differences are reported at $p < 0.05$.

I wished to compare the effects of different season of burning on fertility. However season effects may be confounded by differences in post-burn recovery. For example the Augb3 plots had been burnt 34 months before the fieldwork while the Decb3 plots had been burnt 30 months before the fieldwork (Table 1). Could four months difference in recovery time account for size differences between August and December burns rather the hypothesized effect of burning at different phonological stages? In place of actual growth rates, which were unknown, potential growth rates were extrapolated based on the average sizes of the shrubs in the different plots and the time since the plots were last burnt. The time elapsed since the last burn was assumed to indicate the age of the above ground growth. It was assumed that the plants would grow rapidly soon after the fire but that the growth rate would asymptote as plants approached their maximum size. A linear regression was fitted to the data points, with the height data log transformed, and the regression equation provided an estimate of the growth rate of the average shrub in the different burn treatments. The equation was used to predict whether the populations from December burn plots would increase in size over four months to a size similar to that of the average for the August burn plots. The biennial burn plots were not considered in this part of the analysis. The relative difference in the time since the plots were last burnt was much greater than it was for the triennial treatments (Table 1), therefore any differences in the average sizes of plants in the biennial burnt plots were more easily explained by the period since the last burn than by a seasonal effect.

Pre-burn height and re-growth rates

To compare post fire re-growth rates of the shrubs in the August and December burn treatments linear regressions were performed between the pre-burn heights (skeleton height) and the post-fire re-growth rates. Re-growth rates were calculated by dividing the size of the shrub at the time of the fieldwork by the number of months since the particular plot was burnt. As we had data for the biennial and the triennial plots the regression lines were used to predict the change in the re-growth rate over time of a 1.5m shrub burnt in August and a 1.5m shrub burnt in December.

RESULTS

Fertility and size

Figure 6 shows two important results. Firstly pod production is low in the year after a fire (on average less than one pod cluster per plant). Secondly the Augb3 plots (on average 4.8 pod clusters/plants) are much closer to their optimal pod production than their DecB3 counter-parts (on average 1.7 pod-clusters/plant) even though they were only 4 months older. The Octb6 plants, last burnt almost 6 years ago, produced on average 7.9 pod clusters per plant. These values might seem quite low but the values were calculated using a random selection of plants, many of which would not have reached maturity.

Figure 7 shows the relationship between the size of *D. cinerea* individuals in the Octb6 plots and seed output. The graphs show that below a certain size, approximately 1m high or wide, plants do not produce any pods. Above this size if there is a positive and near linear relationship between size and seed production. The relationship is quite strong for both height and width, with R^2 values of 0.7 (N=7) and 0.9 (N=7) respectively, although width or crown diameter is the stronger of the two.

Using the relationship between size and seed production I was able to compare the average size of the plants in the August burns against the December burns and infer similar discrepancies between the potential for seed production in the different treatments. Figure 8 and Figure 9 show the differences in average heights and widths of the *D. cinerea* individuals in the Augb3 and Decb3 within each string. Plants were on average larger in the Augb3 (winter triennial) plots than the Decb3 (summer triennial) plots. T-tests for independent sample means showed that within each string the mean heights of Augb3 and Decb3 plants were significantly different (Table 2). The differences between the mean heights and widths of the plants in the Augb3 and Decb3 plots are shown in Table 3.

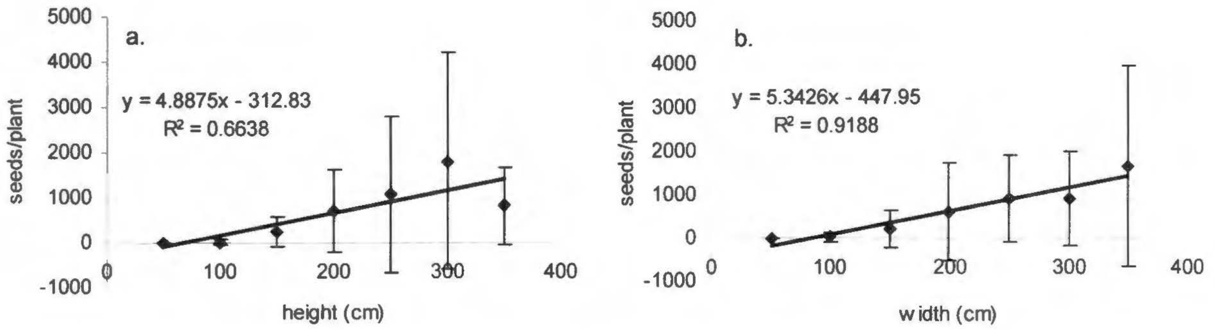

Figure 7: The relationship between the time since a *D. cinerea* population was last burnt and the average number of pod-clusters per plant. The value between the AugB2 and the DecB3 values is taken from the Lindanda AugB3 plot which was accidentally burnt in 2001. The error bars indicate the standard deviation of the means from each string.

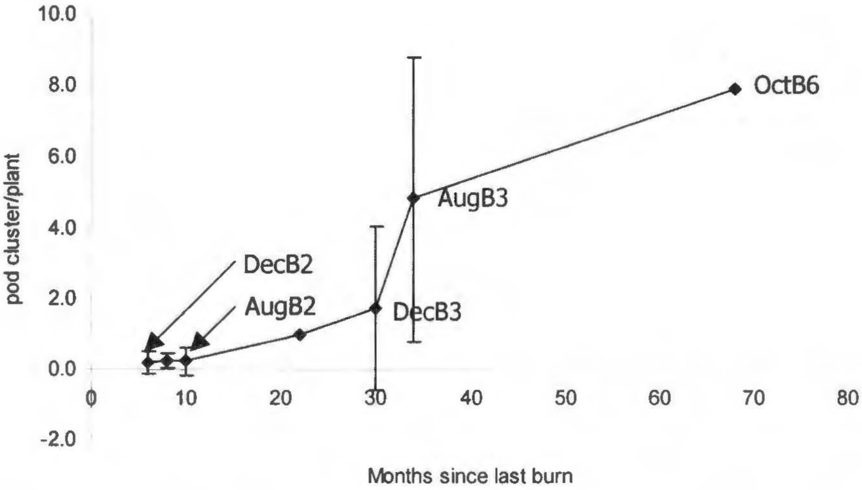

Figure 6 The relationship between a.) height and b.) width and the average number of seeds per plant in the OctB6 plots. The error bars show the standard deviation expressed between the different strings. The error bars show the standard deviation of the means in each size class.

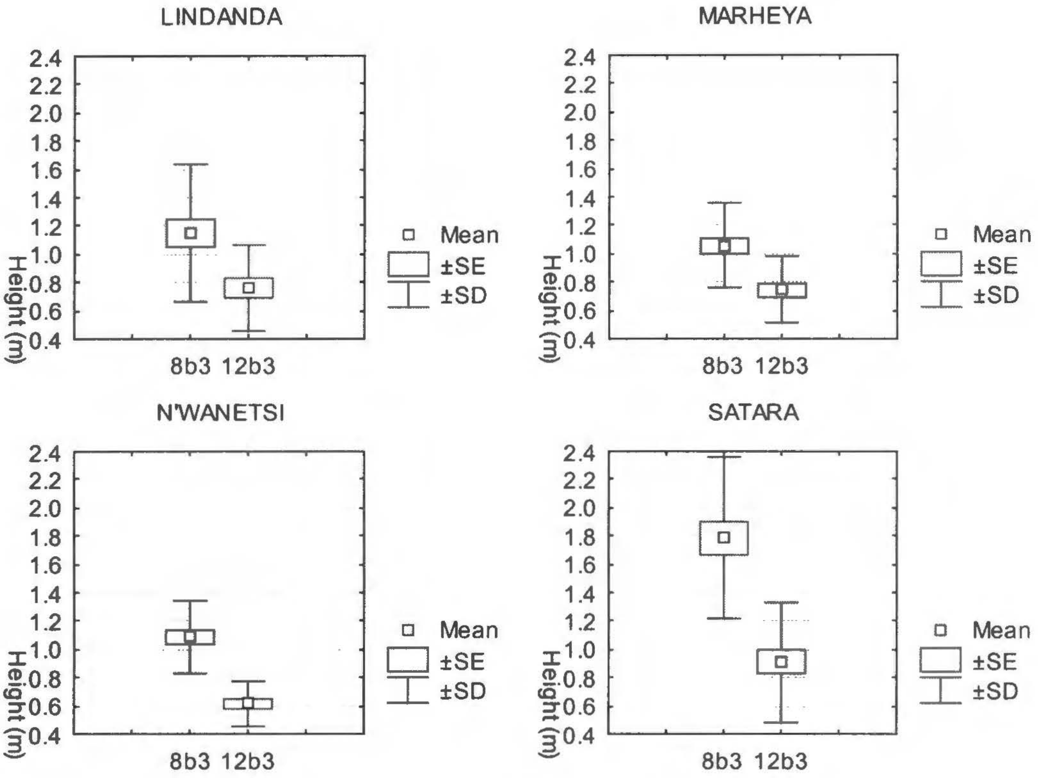

Figure 8: A comparison of the difference in the average height of *D. cinerea* individuals in winter and summer triennial burns for the four strings. T-test showed that for each string there was a significant difference ($p < 0.05$) between the heights of shrubs in the two plots. All assumptions of normality and variance were met (Levene's test $p > 0.05$).

Table 2: The results from t-tests for independent sample means for the mean heights and widths of the plants in the Augb3 and Decb3 plots. *The N'wanetsi width are log transformed.

	Mean Height					**Mean Width**				
	8b3	**12b3**	**t**	**df**	**p**	**8b3**	**12b3**	**t**	**df**	**p**
Lindanda	1.2	0.8	3.197	44	0.003	0.9	0.9	-0.135	44	0.893
sd	*0.5*	*0.3*				*0.4*	*0.3*			
Marheya	1.1	0.8	4.023	47	0.000	1.3	0.9	3.144	47	0.003
sd	*0.3*	*0.2*				*0.5*	*0.3*			
Satara	1.8	0.9	6.196	48	0.000	1.7	1.14	4.407	47	0.000
sd	*0.6*	*0.4*				*0.4*	*0.4*			
N'wanetsi	1.1	0.6	7.615	48	0.000	3.1*	2.9*	4.222	48	0.000
sd	*0.3*	*0.2*				*0.2*	*0.1*			

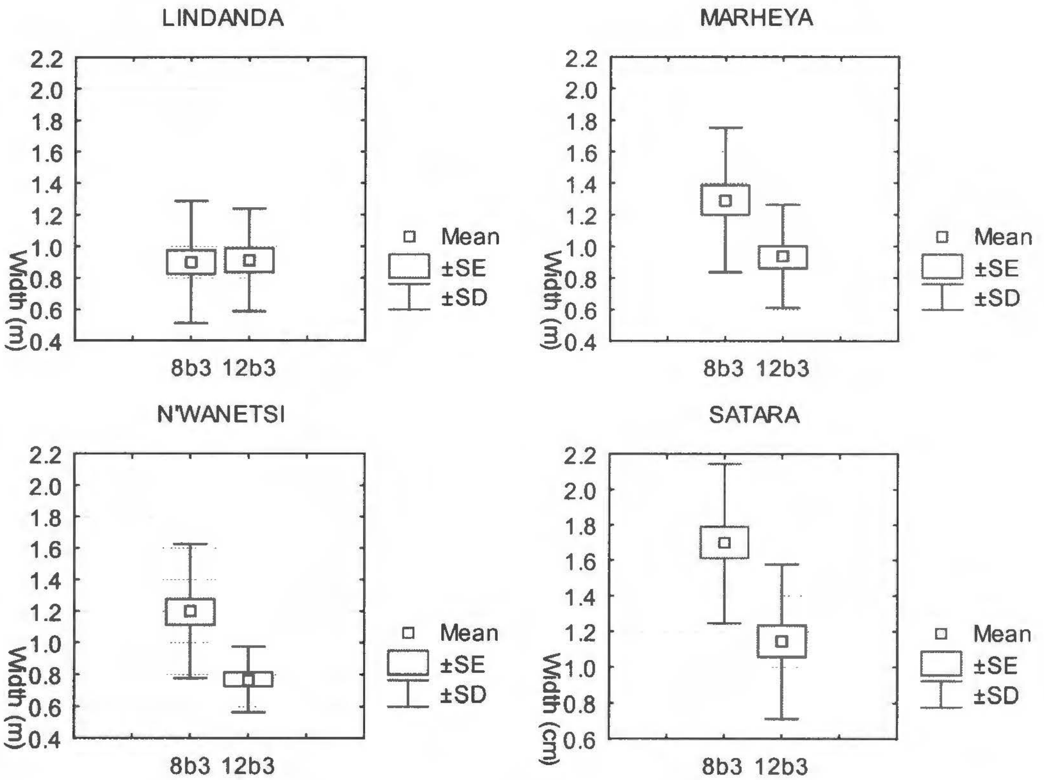

Figure 9: A comparison of the difference in the average width of *D. cinerea* individuals in winter and summer triennial burns for the four strings. T-test showed that for Marheya and Satara there was a significant difference ($p < 0.05$) between the width of the shrubs in the two plots. All assumptions of normality and variance were met (Levene's test $p > 0.05$). There was no significant difference between the width of the shrubs in the two Lindanda plots but note that 8b3 plot was accidentally burnt in 2001 and is in fact younger than the 12b3 plot. The variances for the N'wanetsi data were not homogenous. A T-test of log transformed data showed the two populations to be significantly different ($p < 0.05$).

Table 3: The difference between the mean height and width of plants burnt on a winter triennial basis and plants burnt on a summer triennial basis.

	Mean Height (m)			Mean Width (m)		
	Augb3	Decb3	Difference	Augb3	Decb3	Difference
Lindanda	1.16	0.76	0.39	0.90	0.91	-0.01
Marheya	1.06	0.75	0.31	1.29	0.93	0.36
Satara	1.78	0.91	0.88	1.70	1.14	0.56
N'wanetsi	1.09	0.62	0.47	1.20	0.77	0.43
Average	1.27	0.76	0.51	1.27	0.94	0.33

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Figure 10 shows the predicted growth rate (in height and width) of a *D. cinerea* shrub. The mean heights and widths of the *D. cinerea* shrubs in the different treatments were plotted using the data from all the strings, and ignoring potential affects of the season of burn on subsequent re-growth and seasonality of growth. In Figures 10a and 10c the regression equations was calculated using the data from all the burn treatments, while in Figures 10b and 10d the regression equation was calculated using only the data from the October and August burn treatments. It is clear that data from Decb3 plots deviates the most from the trend-lines. So although the R^2 values are high (~0.8, N=6) in the plots were the December burn data is included R^2 values are greater than 0.98 (N=4) if this data is excluded. At the time of the fieldwork the DecB3 plots had been burnt 30 months ago and the AugB3 plots had been burnt 34 months ago. Using the equations displayed in Figures 10b and 10d one can predict that between the 30th and the 34th month, one would expect the average height and width of a *D. cinerea* plant to increase by 6cm and 5cm respectively. The equations in Figures 10a and 10c predict a change of 5cm for both height and width between the 30 and 34 month.

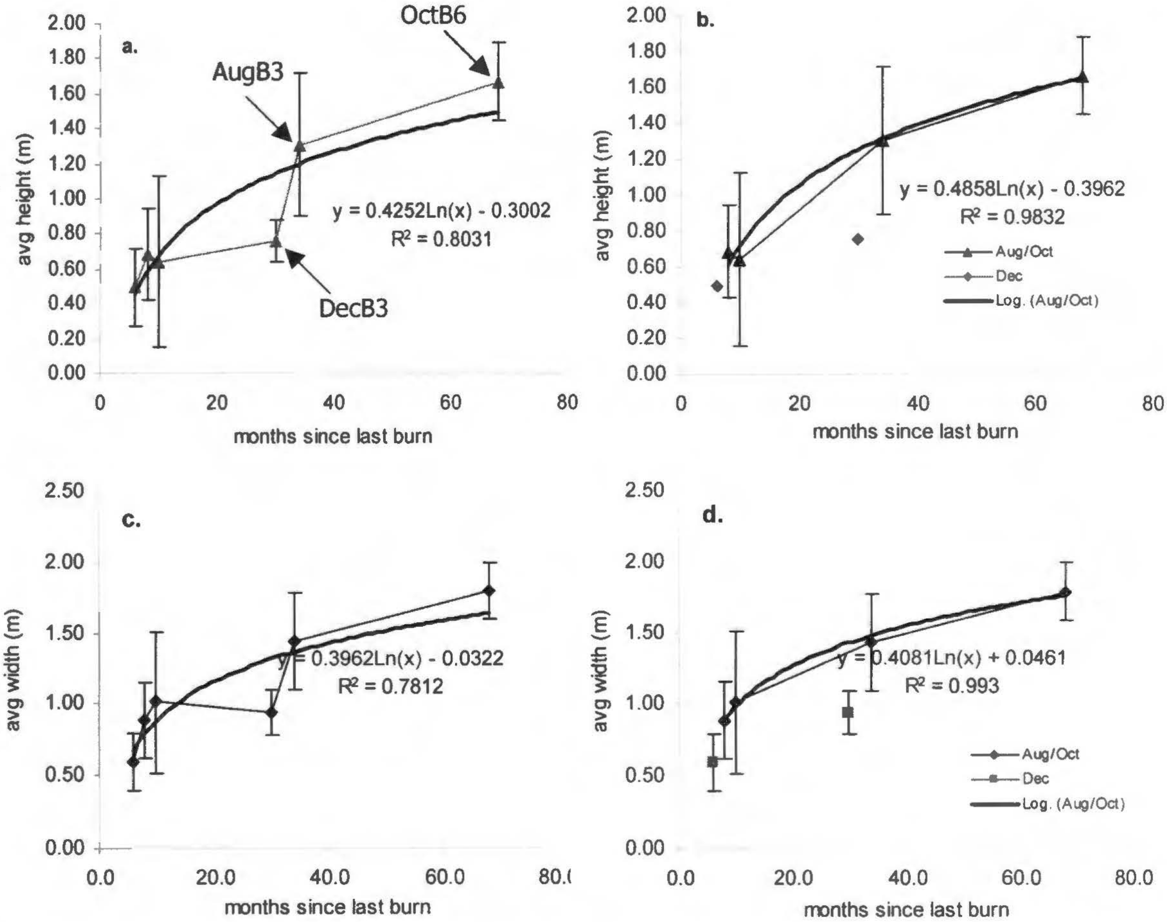

Figure 10: The relationship between the size of an average *D. cinerea* shrub and the time since the last fire, as an estimate of re-growth rates following a fire. The error bars show the standard deviation of the means of the four streams. Each point represents the mean of the mean width in the particular treatment. The regression lines in b. and d. on the left have been calculated excluding the December burns.

Post-burn recovery rates

Figure 11 shows the relationship between pre-burn height and post-burn height for August and December burns. Recovery rates were much greater after August burns than December burns. Ten months after an August fire the regression between pre-burn height and re-growth rate had an R^2 value of 0.65 (N=68), 34 months after the fire the relationship had an R^2 of 0.63 (N=36). The relationship is not nearly as strong in the summer burns with R^2 values of 0.09 (N=77) and 0.22 (N=59), six months and thirty months after the burn respectively. The slopes of the regression equations are much greater for August than December burns, which implies that the plants burnt in winter will have faster re-growth rates than similar sized plants burnt in mid-summer. Figure 12 illustrates this last point in that it shows the predicted growth rate, using the regression equations from Figure 11, of a 1.5m tall shrub burnt in August compared to the same shrub burnt in December. Using the growth rates shown in Figure 12 a 1.5m tall shrub will have a growth rate of 2.8cm/month, between the 30th and the 34th, when month it will increase by ~12cm in height. This is twice the value predicted from Figure 10.

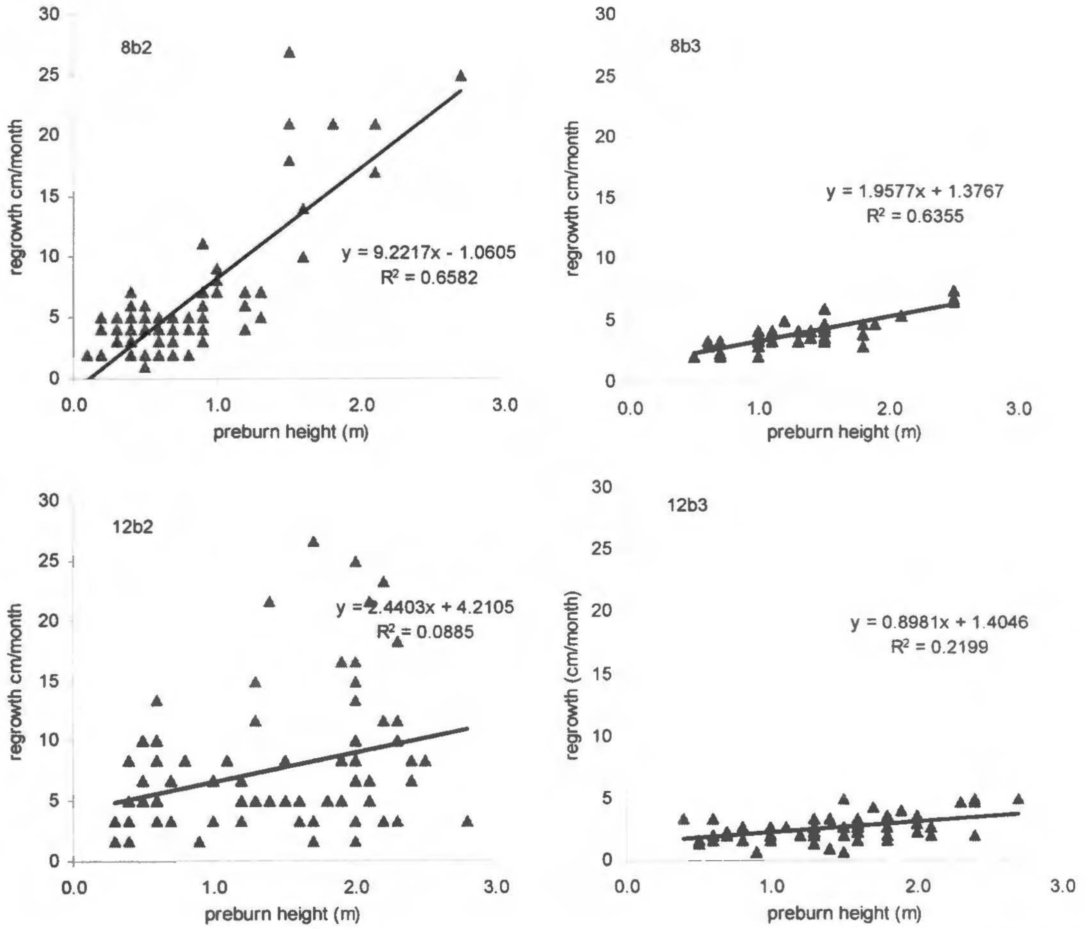

Figure 11: Linear regression analysis showing the relationship between pre-burn height and subsequent re-growth rates, in terms of height, after the fire.8b2 includes plots that were burnt in August 10 months before the census, 8b3 plots that were burnt in August 34 months before the census, 12b2 plots that were burnt in December 6 months before the census and 12b3 plots that were burnt 30 months before the census. All r values are significant at $p < 0.05$.

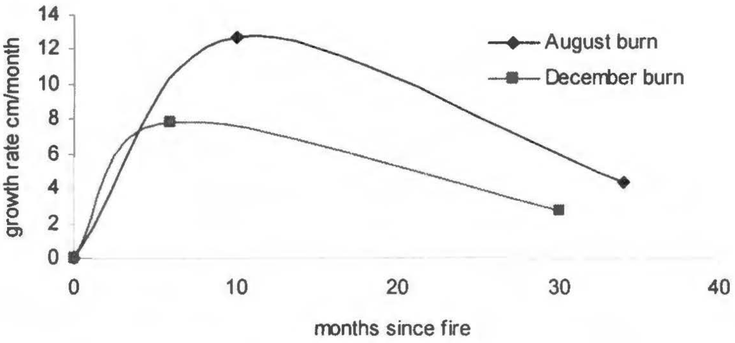

Figure 12: A comparison of the predicted re-growth rates after an August and a December fire of a *D. cinerea* shrub that was 1.5 meters before being burnt.

Foliage density

Figure 13 shows the percentage of plants in the various foliage density categories in the different treatments. In all the treatments most plants were classified as having a foliage density of B. It is not surprising that most plants fell into this category (B) as the data was collected in the middle of the dry season, and highlights the seasonal (deciduous) growth of *D. cinerea*. In both the triennial and the biennial treatments the data was generally normally distributed around B. However the values in the biennial plots were slightly skewed to the left (the sparer side), while the values in the triennial plots were slightly skewed to the right (the denser side). The higher frequency of plants with denser vegetation in the triennial plots re-enforces the concept of a post-burn recovery period. Other than these slight trends associated with different frequency of burns there was no obvious pattern that distinguished the different burn treatments from each other.

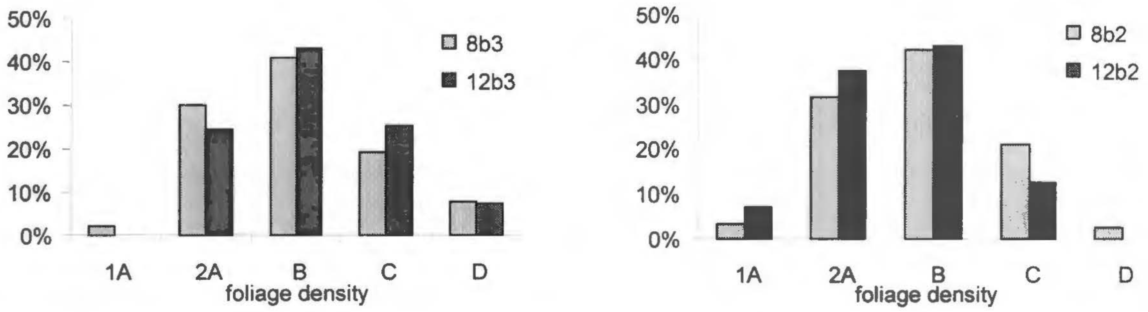

Figure 13:The percentage of plants in the different foliage density categories in the triennial and biennial treatments

Mortality and Recruitment

Figure 14 shows the percentage of plants that were classified as having died or survived the last fire and the percentage of newly recruited plants in the different treatments. In all the treatments mortality rates were low but highest in the Decb2 plots at 5% and lowest in the Augb3 plots at 0%. These classification schemes were flawed in that neither actual mortality or recruitment rates were recorded but only evidence of these rates that was observable. However the mortality data was likely to be more reliable than the recruitment data. The skeletons that showed no post-burn re-growth one were definitely dead however the plants that had no skeleton were not definitely new recruits. A plant's skeleton could have been completely burnt away in the last fire; it could have fallen over and rotted or the fire could have skirted around the plant. To illustrate the difficulties of deciding which plants had survived previous fires more precisely, one can consider the percentage of plants that seem to be too large to be new recruits or the plants that have many stems, which is a sign of resprouting. In the Augb3 and Decb3 plots, respectively, 64% and 50% of the plants that were classified as new recruits were either taller or wider than 1.5m or had more than three stems. Ignoring these difficulties one can note that for the biennial plots, there was not much difference between the December and August burns. Both seem to rely heavily on persistence rather than recruiting new individuals as the number of plants that persist through burns is almost 80%. In the triennial plots apparent recruitment was greater there seems to be more opportunity to recruit new individuals, especially in the August treatment where the percentage of new recruits (52%) was even slightly greater than the percentage of persisting individuals (48%).

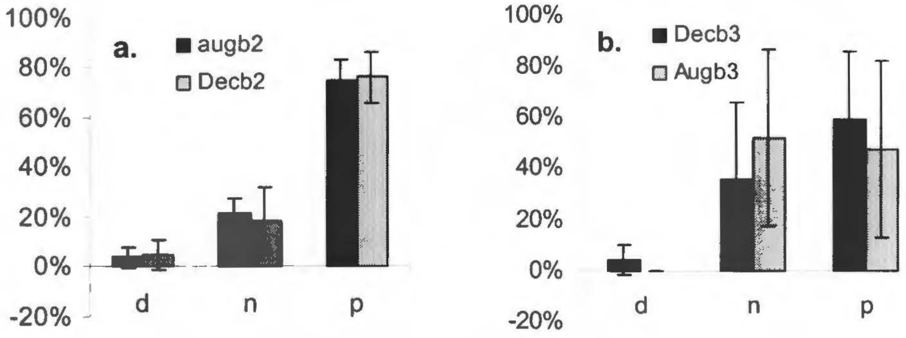

Figure 14: A comparison of the percentage of shrubs that had no re-growth (d), had no visible skeleton (n) and had a skeleton and re-growth (p), i.e. persisted. A Chi-squared test showed that the frequency in the categories, d, n and p did not differ significantly within a particular frequency of burning (p>0.05).

Demographic effects of burn treatments

Figure15 shows the change in the density of *D. cinerea* and *A. nigrescens* and the change in their contribution to the total woody community in the EBP, averaged for all the Satara strings between 1954 and 1998. Figures 15a and 15b show that between 1954 and 1998 both *D. cinerea* and *A. nigrescens* have increased in numbers in the plots. However *D. cinerea* has increased in density in the plots to a much greater extent than *A. nigrescens*. The density of *D. cinerea* has increased the least in the December biennial (Decb2) plots (207 plants/hectare) and the most in the August triennial (Augb3) plots (515 plants/hectare). This means that in the Augb3 plots there are now roughly an extra five *D. cinerea* individuals in every 10m by 10m grid. The density of *A. nigrescens* has increase the most in the October biennial plots (153 plants/hectare) and the least under the August triennial (Augb3) burns (74 plants/hectare). Figures 15c and 15d show the percentage of plants in the diagonals in 1954 and 1998, that were either *A. nigrescens* or *D. cinerea* individuals. Whereas the percentages have remained fairly constant for *A. nigrescens* they have increased across all the treatments for *D. cinerea*. This implies that between 1954 and 1998 *D. cinerea* has become more prolific throughout the plant community regardless of the different burning treatments. The critical observation in regard to this project however is how the increase in *D. cinerea* relates to the season of burn. Averaged across the Satara streams *D. cinerea* has increased the most, in terms of both plant density and percentage of the community, under August burning treatments and the least in plots with December burns.

Figure 16 shows the increase the density of *D. cinerea* over 1954 and 1998 in the different strings. For the triennial burns Satara and Lindanda fit the hypothesis well in that the number of *D. cinerea* plants in the Augb3 diagonals have increased more in the Augb3 plots compared to the Decb3 plots. At N'wanetsi the opposite of what was predicted has occurred in that the density of *D. cinerea* has increased slightly more in the Decb3 plots compared to the Augb3 plots. At Marheya the Decb3 and the Augb3 values are very similar. For the biennially burnt the density of *D. cinerea* has increased more under spring (October) burning compared to mid-summer (December) burning across all four strings. Compared to the other two biennial burns the August burn would probably the most intense. August is in the middle of the dry-season when there is a relative abundance of dry fuel. Thus repeated frequent hot burns might be too much for a plant to survive regardless of the state of its carbon reserves at the time. As a whole the number of all woody plants has increased the least between 1954 and 1998 in the Augb2 plots and was ~6plants/m^2 in 1998. The Decb2 plots had the second lowest woody plant density in 1998 at ~8 plants/m^2. The anomaly to this pattern is the N'wanetsi value where in its case the density of *D. cinerea* plants has increased the most under the Augb2 treatment.

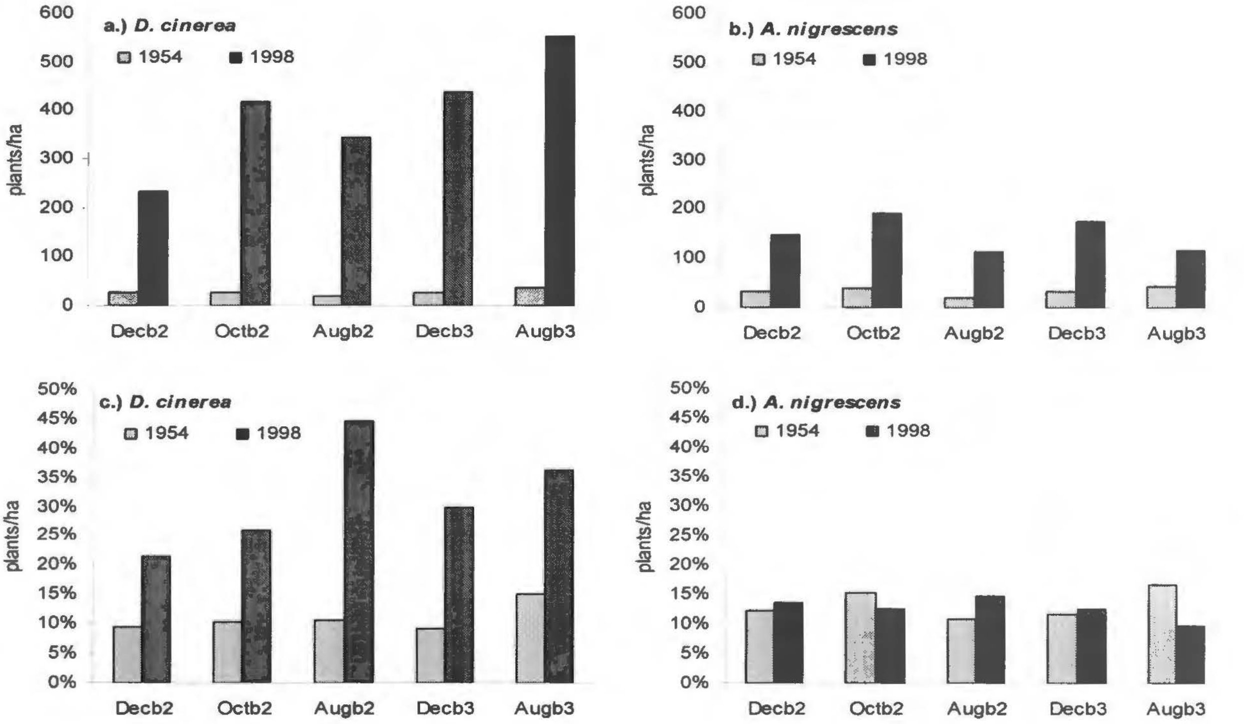

Figure 15: The demographic effects of 40 years of burn treatments on the woody plant communities of the EBPs - a. and b. show the change in population density of *D. cinerea* and *A. nigrescens*, respectively; c. and d. show the change in the contribution of the species to the total woody plant community

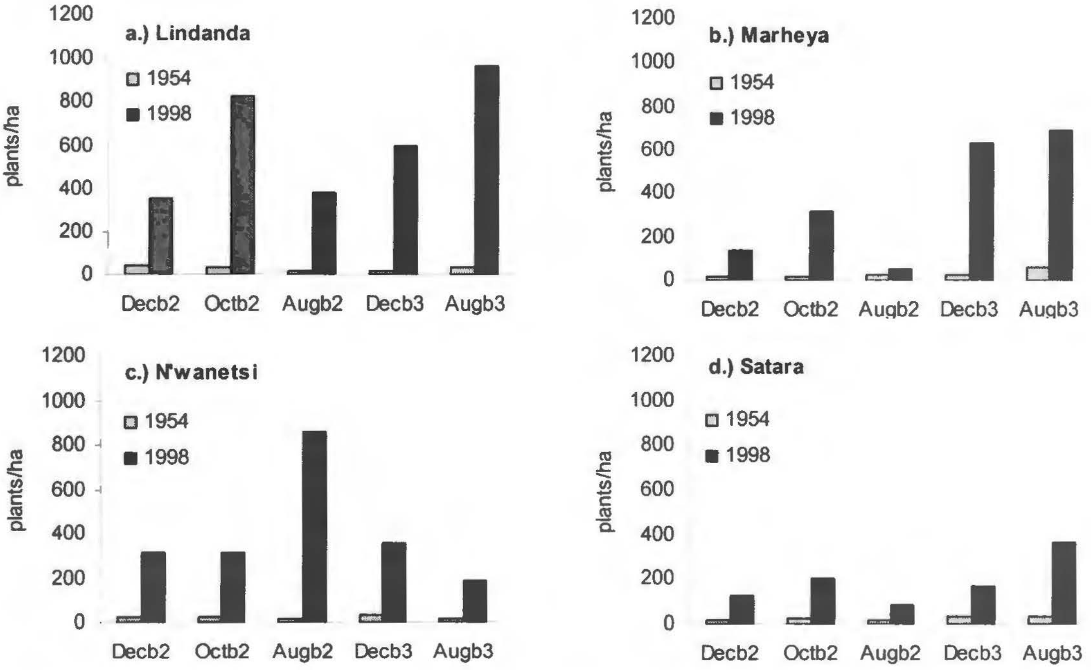

Figure 16: The change in population density of *D. cinerea* between 1954 and 1998 on the EBP in the four Satara strings.

Life-History Differences: *Acacia vs. Dichrostachys* (Gulliver vs. non-Gulliver)

Figure 17 shows the relationship between size and seed production for *D. cinerea* and *A. nigrescens*. Unlike *A. nigrescens D. cinerea* is reproductive within the flame zone, which is the zone in which plant topkill occurs and is considered to extend to between 2.5-6m off the ground depending on the intensity of the fire. *D. cinerea* plants as small as 1m tall have the capacity to produce pod, however on average plants only start producing pods at heights of about 1.5m. On average *D. cinerea* shrubs between 2.5m to 3.0m are at their most fertile stage and can produce on average 1800 seeds per plant per season. Above this height plants seem less fertile and the average seeds per plant drops to below 1000 seeds per season. *A. nigrescens* individuals have the potential to produce pods at heights above 4m but on average only start producing pods once they are taller than 6m. There was no decline in fertility above a certain size in the *A. nigrescens* individuals. The largest *A. nigrescens* individuals produced the most seeds with an average of 3600 seeds per plant per season. These values predict that one mature A. nigrescens individual can on average produce twice as many seeds as a mature *D. cinerea* individual, however the maximum lines indicate that despite their smaller size mature *D. cinerea* can potentially produce more seeds than the largest of the *A. nigrescens*.

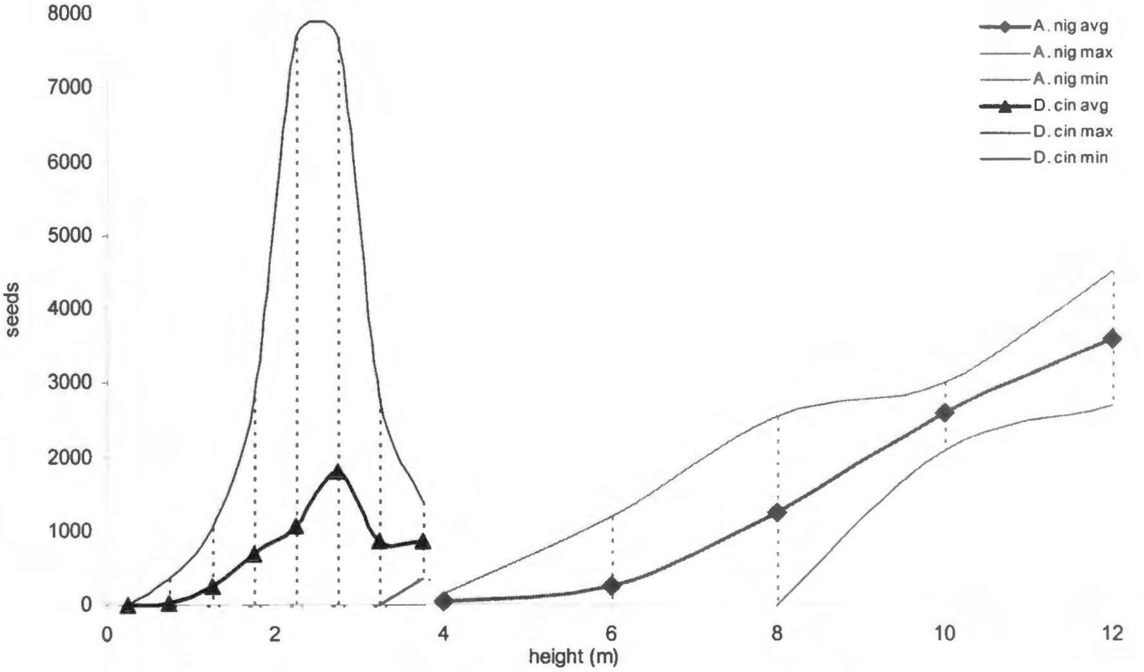

Figure 17: The relationship between the height of *A. nigrescens* and *D. cinerea* individuals and their seed output. The bold lines in the represent the average seeds produced for a plant in a particular size class. The lighter lines show the maximum and minimum number of seeds found on plants in a particular size class.

The data for *A. nigrescens* shown in Figure 17 is based on plants that were growing in Satara's Tourist campsite and its compound. Data from the EBP was not plotted as out of 62 *A. nigrescens* individuals that were taller than 4m and recorded only 3 of them had any pods. All 17 of the *A. nigrescens* individuals that were taller than 4m and recorded in either the campsite or the compound had pods.

DISCUSSION

Burn treatment effects on fertility, growth and persistence

The project aimed to determine the effects of fire season on the persistence, growth and fertility levels of *D. cinerea*. Average pod counts in populations that were subject to winter triennial burns were greater than the average number of pod clusters per plant in populations treated with summer triennial burns. However the plants in the summer triennial treatments were four months younger than the plants in the winter triennial plots, and thus it was possible that the difference in the average number of pod clusters per plant could be explained by the time elapsed since the last burn rather than the season of last burn. Furthermore the plants in the summer treatments would have four months extra growth after the plants in the winter treatments were burnt. But this does not in fact give an advantage in terms of seed production to summer populations because any investment into reproduction by the summer burnt populations in the four months after the august populations were burnt would literally go up in smoke. *D. cinerea* begins to flower in early summer and the seeds are ready to drop in the following winter thus burning in summer interrupts the plants reproductive (phenological) cycle, so regardless of post-burn fertility effects which was what was measured in the field summer burns effectively waste a season's reproductive effort. Populations burnt in winter seemed to recover faster than populations burnt in summer. After a similar period since the last fire the winter burn populations' fertility levels were much closer to that of a population that had had twice as much time to recover from the last fire than the summer burn populations were.

To tackle the problem of whether the observed difference in fertility levels of the populations burnt in different seasons was a function of time elapsed sine the last fire or the effect of a particular burning treatment we compared the average size of the plants in the different plots. By extrapolating a growth rate for the plants we were able to predict by how much the average size of plants in the Decb3 plots would increase over four months, thereby effectively removing the age gap. We found that at all the strings surveyed plants in plants in the augb3 populations were significantly taller than plants in the Decb3 populations even the Lindanda trees which were in fact burnt after the Lindanda Decb3 fires because of an accidental burn. The fact that on average the Lindanda Augb3 plants were taller than the Lindanda Decb3 plants together, even though the above ground growth of the Decb3 plants was older already implies that the time since last burn is not as important as the period since the last burn (see Maze 2001). To re-enforce this point consider that the average width of plants in the Augb2 plots was greater than the average width of the Decb3 plants despite the fact that the Augb2 plots were burnt twenty months after the Decb3 plots.

The predicted increase in height over the four months for the Decb3 populations was 6cm compared to mean difference in height of 50cm between the Augb3 plants and the Decb3 plants. The predicted increase in width was 5cm compared to a mean difference in width of 45cm between the Augb3 and Decb3 populations, if the Lindanda Augb3 values were excluded. Based on these values it is justified to say that the difference between the mean plant size of the populations is an effect of the season of burn and not the time elapsed since the last burn. Maze (2001) came to a similar conclusion in her studies of the re-growth patterns after of *D. cinerea* individuals were clipped at the base. As a strong positive relationship was found between the size of a plant, especially crown diameter, and seed production we can say that based on the above the difference between the number of pods per plant in the populations burnt in different seasons is the result of the season of burning and not the result of the time since the last burn.

Direct counts of pod clusters and defining the relationship between size and seed output were not the only ways in which fertility levels were quantified. The potential photosynthetic capacity of the different populations was also considered, however no pattern was found across the treatments and thus did not prove to be a fruitful measure of future productivity levels and therefore fertility levels. In fact the lack of a trend between foliage density across the treatments justified the use of size alone as plant characteristic that could predict future fertility levels. If the foliage density had differed across substantially across the treatments then it would warrant its inclusion as a predictor of future productivity alongside size. Recruitment rates were also quantified by recording the percentage of shrubs in a sample that exhibited no evidence of being in a previous fire. Such evidence was taken as the lack of a plant skeleton however this limited means of distinguishing between plants that had potentially survived previous fires and plants that had only emerged since the last fire was problematic as described earlier. Thus the recruitment levels recorded in the field were subsequently abandoned as a true reflection of the populations' fertility levels. However they did indicate that on average there was a greater opportunity to recruit mew individuals in triennial burns compared to biennial burns and within the triennial burns there is a greater opportunity to recruit after winter burns.

Actual pod counts and plant size proved to be the best indicator of a populations current and potential fertility levels as a response to different season of burning. Summer burns were found to suppress the fertility levels of a population for up to at least three years after a fire.

Post-burn recovery

Generally we found that plants with a similar pre-burn height will have faster post-burn re-growth rates if they are burnt in winter, as indicated by the slope of the linear regression lines in Figure 11. The correlation co-efficients in Figure 11 show that pre-burn height is a much better predictor of post-burn growth in plots burnt in winter than plots burnt in winter. . One expects that a plant that was larger before a fire to have had a larger root structure and therefore larger root carbon reserves than a smaller plant burnt at the same time. Root carbon reserves are needed to produce the initial coppicing shoots but can also potentially support re-growth even once the new coppice shoots become photosynthetically self-sufficient. Therefore re-growth rate of a plant after a fire is bounded by its root carbon reserves. In summer, plants irrespective of their size will have depleted their carbon reserves on the latest season's growth and the relationship between pre-burn height and root carbon reserves breaks down. Consequently the relationship between pre-burn height and subsequent growth also breaks down. Figure 11 also shows that as growth is cumulative, the season's growth that is lost after a summer burn cannot be recovered, hence the discrepancy in the mean size between the plants burnt in different seasons.. The slow initial re-growth rates of plants burnt in summer will also affect future fertility levels as these plants will take longer to reach maturity than plants burnt in winter. Slow initial re-growth rates also have a compounding effect in that if the fire interval is short the plants will still be small by the time of the next fire and thus will still have slow re-growth rates after the second fire regardless of the season of the fire.

Persistence and mortality

Unlike fertility and re-growth rates we were unable to determine any substantial effects of the season of burn and mortality rates. Partly this was due to the manner in which mortality rates were quantified. Mortality rates were calculated as a percentage of plants in the sample that exhibited no new growth, however this method was inherently flawed as it relied on the assumption that all plants killed in the last fire would still be present in the plots as plant skeletons. This assumption is problematic in that we had no data about the probability of plant skeletons surviving through fires and how this was affected by pre-burn height. One would expect that are measurements of mortality rates were an under-estimate as it failed to include plants whose stems were completely burnt away in the last fire. Despite these problems the data indicated that mortality rates are low across all treatments but nevertheless lowest in the Winter triennial burns and slightly lower in the August biennial burns compared to the December biennial burns. The fact that the mortality rate of the populations burnt in winter is lower than those burnt in summer fits into the hypothesis that summer burns will constrain *D. cinerea* population growth.

Demographic effects of burn treatments: Gullivers vs non-gullivers

The initial prediction of the phenology hypothesis the paper is built on was that repeated summer burning would limit the growth of *D. cinerea* populations. Between 1954 and 1998 the density of *D. cinerea* plants has on average increased across all treatments regardless of the season or frequency of burning. However the degree of increase is different in the different treatments. The pattern of increase in *D. cinerea* density under the different treatments, using the data combined across all the strings, fits nicely into the predictions of the current hypothesis. For plots burnt at equivalent intervals *D. cinerea* plant density has increased more in plots burnt in winter or late spring than plots burnt in mid-summer. A similar pattern can be found with regard to the increase in the percentage of plants in the EBP that were *D. cinerea* individuals.

Based on the above findings, particularly regarding higher fertility rates and re-growth rates in populations burnt on a winter triennial basis compared to plants burnt on a summer triennial schedule, the higher number of *D. cinerea* individuals in the winter EBPs can be adequately explained by the effect of the season of burning on population growth dynamics of *D. cinerea*. Interestingly winter triennial burns were the adopted burning strategy of the park for about 40 years up to about ten years ago (Enslin *et al..*. 2000, Woods *et al..*. 2002). If the phenology hypothesis holds over all ecozones in the park one could argue that bush encroachment in the park by *D. cinerea* has been exacerbated by the Park's previous fire management strategy.

The fact that both *D. cinerea* and *A. nigrescens* have increased in density across all the treatments over the last four decades implies that fire alone is not sufficient at controlling the growth of tree populations, regardless of whether the plants follow a Gulliver life history or a non-gulliver life history. Such a radical increase in the numbers of plants indicated in Figure 15, remembering that an in crease in 100 plants per hectare is equivalent to an increase of 1 plant in a 10m by 10m grid, begs the question of what has prompted such increases in both tree densities and shrub densities. One possible mechanism that has been suggested is that with increasing CO_2 concentrations in the atmosphere C_3 plants become effectively more water use efficient (Bond *et al..*. 2003). Increased $C0_2$ concentrations allow plants to retain small stomata apertures that reduce the amount of water transpired and still attain sufficient levels of CO_2 for photosynthesis (Bert *et al..*. 1997). Such massive increases in the number of *D. cinerea* individuals in the plots is consistent with Roques *et al..*.'s (2001) findings in the lowveld savanna of north eastern Swaziland but surprising as Enslin *et al..*. (2000) reported no significant change in the woody species between 1954 and 1998 in and around Satara. Roques *et al..*. (2001) found that in the last half century shrub cover by *D. cinerea* had increased by approximately 25%. Based on the data shown in Figure 9 if one takes the average width of a *D. cinerea* shrub to be 1.2m, with a cross sectional area of 4.5 m^2, then an increase in shrub cover by 25% is equivalent to an extra 5 shrubs in a 10m by 10m grid, or 500 plants in a hectare. Figure 15 shows that between 1954 and 1998 the increase in the population density of *D.cinera* in the AugB3 plots was also ~500 plants/hectare. This implies that when investigating bush encroachment in the Park it would be more useful to take a species based approach than simply looking at the change in the density of all woody species combined.

The difference in the levels of increase for *A. nigrescens* compared to *D. cinerea* in the EBP is interesting in light of the relationship between size and fertility of the two species. Between 1954 and 1998 the density of *D. cinerea* plants in the EBP has increased more than the density of *A. nigrescens* has increased. Figure 17 indicates the different life-histories of *A. nigrescens* and *D. cinerea*. The relationship between size and height of *A. nigrescens* is typical of a Gulliver type life history, the *A. nigrescens* individuals only start producing seeds at heights greater than that of the flame-zone considered to be approximately 5m above the ground. On the other hand on average a *D. cinerea* shrub that is 3m tall will produce as many seeds as an *A. nigrescens* tree that is approximately 9m tall. The advantage of a Gulliver type life-history, as shown in Figure 17 is that one large *A. nigrescens* individual is able to produce twice as many seeds as one large *D. cinerea* individual. However the maximum lines in Figure 17 show that a mature *D. cinerea* plant of about 3m in height can potentially produce more seeds than the largest of the *A. nigrescens* individuals. At this point is necessary to point out that although the conversion of the number of pods and pod–clusters, on *A. nigrescens* and *D. cinerea* respectively, to total number of seeds facilitated a enabled a direct comparison of the seed output of the two different species direct these values were subject to a large degree of error. The number of pods or pod-clusters was multiplied by a median of seeds per item and because we were dealing with large numbers any error was subject to the same multiplication. In the case of *D. cinerea* the median number of seeds per pod-cluster was 69, however the mean was 80 with a standard deviation of 76, thus it is apparent how variable this value could be and how the difference of just ten pod-clusters was equivalent to a difference of 700 seeds using the median number of seeds per pod-cluster. However if the mean value minus one standard deviation was used the difference between 10 pod-clusters would only be 30 seeds while if the mean plus one standard deviation was used a difference of 10 pod-clusters would amount to a difference of ~1400 seeds. In the case of *A. nigrescens* the values shown in Figure 17 are probably under-estimates especially for the taller trees as the taller a tree the more difficult it was to see and count the pods on the highest branches. The number of pods in the largest trees was estimated to be in the thousands. This value was then multiplied by the median of seeds per pod in a sample, which was three and seemed relatively low based on the author's personal experience. In fact a second sample of 20 *A.nigrescens* pods had a median of 4 seeds per pod. (These pods were not included in the main sample as they came from trees outside of the study area.) If it was found that if one had a larger sample of pods and the mean number of seeds per pod was closer to four then the average number of seeds produced by the tallest *A. nigrescens* individuals would increase by 1000 seeds. Nevertheless ignoring the potential for error in these estimates of seed output they do provide a relatively simple explanation of why *D. cinerea* densities have increased at a faster rate than *A. nigrescens* densities in that *D. cinerea* seems to be incredibly capable of producing high numbers of seeds. This can partly be explained by the fact that by producing pod clusters as opposed to isolated pods, a *D. cinerea* plant requires much less structural architecture or support to hold an equivalent amount of seeds. The median number of seeds supported per petiole in *D. cinerea* out of 16 samples was 69 while it was 3 for *A. nigrescens* out of thirteen samples. If one takes into account that the data for *A. nigrescens* used to produce Figure 17 is based solely on plants in either the Satara tourist campsite or the Satara worker's compound and that less than 5% of the plants encountered on the EBPs supported pods, whereas on the same EBPs ~50% of the *D. cinerea* individuals supported pod-clusters then the superior fertility of *D. cinerea* compared to *A. nigrescens* is even more startling. *D. cinerea* plants that have had only three years re-growth can produce pods. Although the growth rates and fire-trap release rates were not quantified it seems unlikely that an *A. nigrescens* individual can escape the fire-trap and grow taller than six metres in just three years, when gullivers have been reported to persist within the fire-trap for 40 years or more (Bond & Maze, unpublished). *A. nigrescens* plants within the fire trap do not carry the seasonal burden of flower and seed production and Figure 15 shows that contrary the patterns seen in *D. cinerea*, the population density of *A. nigrescens* increased the more in summer and spring burns than in winter burns. This pattern matches the predictions of Higgins *et al..*. (2000) with regard to the release bottleneck that Gulliver type plants experience. As the veld is dry in winter, winter fires are usually more intense than summer burns, when the foliage is green, (Maze 2001) and thus repeated winter burning provide Gullivers with fewer opportunities to escape the fire trap. The difference in the population growth bottlenecks that the two species with contrasting life-histories experience and the dramatic potential for *D.*

cinerea to increase in density provides incentive to revise existing models of savanna plant communities based primarily on the gulliver strategy of typical, but not all, savanna woody plants.

Future research

A number of questions were raised by the data collected for this project similarly much of the data collected for this project would be better collected over an entire year and include population counts before and after particular fires. By being able to sample a population before and after a burn accurate recruitment and mortality rates could be determined season as one would be able to distinguish between bona-fide new recruits and small resprouting individuals that were known to exist before the fire and all plants that perished in the fire could be accounted for. A longer period of fieldwork would also enable one to measure features of the plants in the different treatments at equivalent times since the last burn, and build up a larger data set that specifically looks at fluctuating root reserves.

Changes in atmospheric CO_2 concentrations was put forward as a possible mechanism driving increases in tree and shrub population densities. This was explained as function of C_3 having improved water use efficiency (WUE) with higher atmospheric CO_2 concentrations. As changes in WUE of plants is expressed in the $\delta^{13}C$ levels of plant matter and preserved in the structural components of the plant (Pate 2001) there is the potential to track changing WUE of plants over time, using a gradient of cores drilled the stem of a tree or a shrub, which represent different stages in the plant's history, and relate this to changes in atmospheric CO_2 concentrations. Normally this would not be feasible in the case of *D. cinerea* as one would not expect many old stems to exist as the shrub which usually experiences complete topkill in fires. Due to the inclusion of fire exclusion as one of the treatments in the EBPs there is the potential to locate *D. cinerea* with relatively old above ground growth, and it is the heartwood of these individuals that could be used to compare the WUE of *D. cinerea* shrubs in previous decades compared to the WUE of plants now. If increased CO_2 levels can explain increased growth levels in *D. cinerea* it would be especially interesting to quantify how allocation of resources to reproduction is affected in light of the massive potential for seed production of *D. cinerea* populations observed during the study.

As second question that could possibly be answered using isotope analysis is the dilemma of why *A. nigrescens* individuals in the field produced so few pods compared to *A. nigrescens* individuals in the tourist campsite. Inside campsites mature *Acacia nigrescens* individuals, i.e. trees taller than 6m, were covered by hundreds and sometimes even thousands of seed pods whereas outside of campsites, out of more than a hundred trees observed, even the tallest had normally less than 10 seed pods. Several hypotheses could potentially explain this stark difference. The hypotheses all focus on lower levels of stress inside the campsites compared to outside the campsites but call upon different primary agents of stress namely fire, browsing and water stress. Campsite trees do not experience fire and browsing stress as naturally fires and browsers are kept out the campsites. The lawns and gardens within the campsites are also watered thus campsite individuals experience less water stress compared to their non-campsite counter-parts. The first two hypotheses share a flaw in that that above a certain height trees became impervious to such causes of disturbance. Giraffes, the tallest browsers in the park with male heights at roughly 5m (KNP Visitors' Map 2000), can only browse to height of about 6 metres. Depending on the intensity of the fire trees taller than 3-4 metres are out of the so-called fire-trap or flame-zone, and fire for them is no longer a severe disturbance causing negligible shoot damage (Archibald & Bond, 2003). (Note that savanna fires are typically ground fires (Bond & van Wilgen, 1996). The tallest trees observed in the field were more than 14m tall and even these bore very few pods, i.e. usually less than ten seed pods. The third hypothesis relating to water stress is thus the most likely of the three hypotheses. Using stable carbon isotopes of phloem sap or newly laid down xylem one could test whether trees have been water-stressed recently or within the last season (Pate 2001). If the non-campsite trees were in fact more water-stressed than the campsite tress one would expect higher WUE by the non-campsite trees, as they are forced to use more conservatively. If a large enough difference exists between the WUE of trees inside and outside the campsites then this difference should also be manifested in the $\delta^{13}C$ values of newly laid down xylem or phloem sap of the trees.

CONCLUSION

This project showed that burning in summer can constrain *D. cinerea* population growth as summer burns negatively affects the fertility levels and re-growth levels of *D. cinerea* shrubs. This negative response is associated with seasonal fluctuations in the root carbon reserves of *D. cinerea* plants. Reserves are lowest in summer and therefore burning at this stage hampers the plants' ability to recover from the fire, which is expressed in lower re-growth rates and fertility levels. Although long term data of *D. cinerea* densities on experimental burn plots showed that regardless of the season of burn *D. cinerea* densities had increased between 1954 and 1998, for a particular fire interval the increases were on average greater in the plots that were burnt in winter as predicted. The high fertility levels of *D. cinerea* compared to *A. nigrescens* a tree which grows to almost three times the height of *D. cinerea*, and is characteristic of the savanna in the study area, and its increasing prevalence on the savanna landscape provides great incentive for the inclusion of *D. cinerea* and other shrubs with similar life-histories into existing models that attempt to explain savanna plant community dynamics.

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