Root Suckering in *Dichrostachys cinerea* and a Comparison of Subspecies *africana* and *nyassana*

Julia Wakeling
Plant Ecology - Botany Honours 2004
University of Cape Town
Supervisor: Professor William Bond
A project in part fulfillment of the requirements for a BSc(Hons) degree in Plant Ecology

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Clonal growth has been studied little in Africa, and models of savanna tree-grass interactions have not included vegetatively reproducing trees or shrubs. Root suckering has been observed in both subspecies of *Dichrostachys cinerea* that occur in Southern Africa. This study, performed in Hluhluwe-iMfolozi Game Reserve, KwaZulu Natal South Africa, examines variability in subspecies distribution and the extent of root suckering under different fire regimes, and levels of herbivory. Variations in subspecies distribution are clear. Subspecies *africana*, with greater structural defenses, survives in areas of high herbivory but is rarely seen under high fire disturbance. The opposite is true for subspecies *nyassana*, which is poorly defended against herbivory. There was no difference in vegetative propogation by root suckering in areas of different fire regime, rainfall, soil type or degree of herbivory. The implication is that the management of the species will be a formidable task. A combination of burning during summer, when below ground reserves are depleted, and heavy browsing may aid in the control of this species.

INTRODUCTION

Clonal growth, or vegetative reproduction, is the production of new genetically identical descendants (ramets), which have the potential to become independent of their mother organism. Vegetative progagation may occur via sprouting from roots (root suckers), rhizomes, or stolons or from branch and truck layering (de Kroon & van Groenendael, 1997; Peterson & Jones, 1997). The population ecology of clonal growth has been extensively studied in Europe and North America (de Kroon & van Groenendael, 1997; Peterson & Jones, 1997), and acknowledged in Australia (Lacey *et al*, 1982), but has hardly been studied in Africa (White, 1977). I observed root suckering in *Dichrostachys cinerea* (L.) Wight et Arn (Legume: Mimosoideae), a common invasive savanna shrub, in the Pretoriuskop region of the Kruger National Park (pers. obs., unpublished data). This study explores root-suckering in *D. cinerea*, particularly in relation to disturbance frequency and type.

The abundance of clonal plants varies between ecosystems. In central Europe, clonal plants are more common than non-clonals, and an estimated 70% of plants in the temperate zone are clonal (de Kroon & van Groenendael, 1997). Clonal growth forms in tropical and subtropical forests are common and diversified, but very different from those found in central Europe (de Kroon & van Groenendael, 1997).

Clonal growth has benefits, such as increased opportunity for acquisition of resources; successful establishment of offspring in new environments; the maintenance of genet stability (for example, palm ramets provide mechanical support); and protection from fire, wind and herbivore damage in clonal clumps (de Kroon & van Groenendael, 1997; Peterson & Jones, 1997). However, clonality increases the chance of transmission of disease, and there is a decrease of resources available for reproduction (de Kroon & van Groenendael, 1997).

In Europe, clonal growth is more common under stressed conditions, such as in low nutrient, cold, wet and shaded habitats, but less common in frequently disturbed habitats (de Kroon & van Groenendael, 1997). Clonal plants are more commonly self fertilized, and are rarely insect pollinated, and animal or wind dispersed. de Kroon & van

Groenendael (1997) found that clonal tend to be less invasive, and that very common or very rare species are more often non-clonal.

There are many different types of clonal growth forms (de Kroon & van Groenendael, 1997, Peterson & Jones, 1997). Where fire is pivotal in tropical savannas (and more generally, where plants are exposed to frequent disturbance), many woody species sprout from lignotubers and other underground tissues (Lacey, 1982; Higgins, *et al*, 2000; Roques, *et al*, 2001; Bond & Midgley, 2001). Xylopodia ("geoxylic suffrutices", White, 1997) and lignotubers, large woody underground swellings, have been well documented in Africa (Bond & Midgley, 2003; Bond & Midgley, 2001, Huntley & Walker, 1982; White, 1977, Lawson *et al*, 1968). Root suckering, the production of daughter ramets from root buds, is a clonal growth form that occurs in a large number of herbaceous plants, but only a limited number of woody plants (Jeník, 1994). Root suckering species are rare when compared with the occurrence of sprouting from underground stumps (Lawson *et al*, 1968). It is, however, the most effective form of clonal growth in woody plants in temperate broad-leaved woodlands (Jeník, 1994).

Root suckering has been observed in a number of African savanna trees, such as *Milletia thonningii, Detarium microcarpum*, *Parinari curatellifolia* and *Daniellia oliveri* (Lawson *et al*, 1968; Jeník, 1994) in West Africa; *Maytenus senegalensis*, and *Spirostachys africana* in Southern Africa. It has also been observed in *Eucalyptus tetrodonta* and *Erythrophleum chlorostachys* in Australian savannas (Walker & Gillison, 1982; Lacey *et al*, 1982). *Dichrostachys glomerata* (*Caesalpiniaceae*) has become invasive in Cuba, because of its suckering ability (Jeník, 1994). Individuals of the Genus *Cliffortia* (Rosaceae) in the Fynbos of the South Western Cape, have been found to also root sucker (Bond & Midgley, 2003).

For woody plants, an ortet (the original single ancestor of a clone (Henderson, ****)) is typically at least two years old before it forms daughter ramets. The initiation of ramets is often modified by local conditions, such as burning or clear cutting an area, after which a flush of ramets emerge (Peterson & Jones, 1997). The physiological integration, and thus movement of materials among connected ramets, is poorly studied, but connections within clones can persist from a few years, up to decades, and can exist between large numbers of ramets (Paterson & Jones, 1997). As ramets have better access to belowground resources than seedlings, they have better survival and a greater ability to establish in neighboring vegetation, thus facilitating the invasion and displacement of neighbours (Peterson & Jones, 1997). Self-thinning is, however, common among clonal trees and shrubs (Peterson & Jones, 1997).

Tree-Grass Interactions and Root Suckering

Savannas are characterized by the presence and coexistence of grasses and trees, which occur in varying proportions, depending on environmental factors.

Grass-tree coexistence in savannas has been attributed to root-niche separation of grasses and trees (Walker & Noy-Meir, 1982), and to demographic bottlenecks in the recruitment of trees (Higgins *et al*, 2000). The demographic bottleneck hypothesis explicitly considers the demography if woody plants and how populations are influenced by fire and rainfall variably. However, this model does not take vegetative propagation by root suckering into account, and this persistence niche (Bond & Midgley, 2001) would have a significant effect on how woody plant populations function.

Aims and Hypotheses

The aims of this study are to establish if disturbance by fire and/or herbivory causes variation in the distribution patterns of the two subspecies and the degree of root suckering of the species as a whole. I hypothesized that root suckering would be more prolific in areas of high fire disturbance, because adults would be consistently burnt before reaching maturity, and would thus not be able to set seed, and would have to revert to asexual means of reproduction.

Species Description

Dichrostahys cinerea is distributed throughout Africa, Australia, Burma and India (van Wyk, 1972; Coates Palgrave, 1984; Pooley, 1993). *D. cinerea* was introduced and has become invasive in Cuba (Codd, 1951; Jeník, 1994). It displays much phenotypic variation throughout its range and has been broken down into 10 subspecies and a sum of

11 varieties (Coates Palgrave, 1984). This paper deals with the two dominant subspecies in Southern Africa: subspecies *africana* and ssp. *nyassana*. Van Wyk (1972) recognizes two varieties of ssp *africana*, namely var. *africana* and var. *pubescens*, in the Kruger National Park. These two varieties are not differentiated in this paper.

D. cinerea occurs in bushveld, and can form impenetrable thickets (Codd, 1951; van Wyk, 1972; Moll, 1981; Coates Palgrave, 1984; Pooley, 1993), where the grass has been weakened by overgrazing (Codd, 1951), and it is taken as an indication of overgrazing (Coates Palgrave, 1984). It can become invasive, and is difficult to eradicate by mechanical means because, even when the main stems are dug out, many young plants regenerate from the rootlets remaining in the ground (Codd, 1951; van Wyk, 1972). Researchers do not agree on the causes or prevention of the intrusion of *D. cinerea* (van Wyk, 1972). In Kruger National Park it has been noticed that there is a tendency for *D. cinerea* abundance to increase in the absence of fire (van Wyk, 1972).

The pods, leaves and stems of both subspecies are highly nutritious, and eaten by domestic stock and game, as well as some grazers that have been observed to eat *D. cinerea* during the dry season (van Wyk, 1972, Pooley, 1993).

Ssp *africana* branches more frequently than ssp *nyassana*, and thus has a much denser architecture (van Wyk, 1972; Pooley, 1993), whereas ssp. *nyassana* has a wide-spreading canopy (van Wyk, 1972). The flowers of *D. cinerea* are made up of pink sterile staminodes, and yellow, bisexual flowers (van Wyk, 1972; Moll, 1981; Coates Palgrave, 1984; Pooley, 1993). There is a savanna myth that *D. cinerea* is apomictic. However, I was unable to trace any published study referring to its apomixis.

Study Site Description

This study took place in the 900Km^2 Hluhluwe-iMfolozi Game Reserve, KwaZulu Natal, South Africa. It is a mesic savanna, made up of three broad vegetation types, namely a) grasslands and forested hilltops, b) narrow riverine forest strips and c) a mixture of fine-leaved Acacia savanna with areas of closed broad-leaved woodland (Balfour & Howison, 2001). Balfour and Howison (2001) showed that mean annual rainfall is strongly correlated to altitude in the reserve (rainfall = 0.995 (altitude) + 522.6 ($R^2 = 0.80$, $p < 0.001$)). Thus, the higher areas in the north west have a mean annual rainfall of 990mm, and the low lying southern end of the reserve has a rainfall of less than 635mmpa (Balfour & Howison, 2001).

The Reserve is divided into three major areas, which have fairly different characteristics, namely Hluhluwe in the North, the Corridor in the centre and iMfolozi in the South. Hluhluwe is made up of rolling hills with all three habitat types. The Corridor also consists of rolling hills, dominated by grasslands, fairly high rainfall and thus high fuel loads, with frequent and intense fire. iMfolozi is fairly flat and dominated by the latter two vegetation types. It has lower mean annual rainfall and thus a low fuel load and so fires are typically less frequent and less intense.

Fire frequency maps have been compiled from individual fire area data that has been recorded since 1956 on 1:50 000 maps, by park rangers. The accuracy is variable and in general it is not precise as to which areas, within a mapped fire, actually burnt. However, it gives a good indication of general fire frequency. The original maps were digitized, and the polygonal data rasterised into 1ha ($0.01Km^2$) pixels (Balfour & Howison, 2001).

METHODS

Comparison of Subspecies

Both subspecies occur in Hluhluwe iMfolozi Park. As the ecology of the subspecies, and their sprouting behaviour may differ, I explored subspecies differences, first of all in terms of relative proportions of subspecies at each study site. For this, I performed a wandering quarter transect, and recorded the subspecies of 30 plants, at eleven sites (see below).

I also explored architectural differences, by comparing the ratio of average leaf length to number of spines between individuals of the two subspecies. Leaf length was determined by averaging the length of ten randomly chosen leaves, measured using a tape measure to the nearest millimetre. A branch was marked where it was 10mm in diameter, and the number of spines on it counted. Five plants of each subspecies were sampled from the Maqanda site. Five ssp. *africana* and two ssp. *nyassana* were sampled from Gqoyeni (it was difficult to find ssp. *nyassana* here), and three ssp. *nyassana* were sampled from Muntulu.

Root Suckering and Population Demography Data

I observed root suckering in both subspecies. As it was sometimes difficult to differentiate between subspecies when individuals were very young, and there were too few ssp. *africana* at the selected study sites, for the purpose of this project, root suckering was not differentiated between the two subspecies.

Sites were selected in regions of different fire frequency, and several grazing lawns were also sampled to examine the impact of heavy grazing/browsing on root suckering (Figure 1). Sites of high fire frequency were Nyalazi, Centenary and Masundwini. Intermediate sites were Muntulu and Le Dube, and those of low fire frequency were Hilltop, Mansiya Loop and Maqanda. The grazing lawn sites were Crossroads, Seme Gulliver and Seme Exclosures.

Exploring Alternative Methods for Assessing Root Suckering

I performed a pilot study to test if the use of a systemic herbicide ("Access") would aid in establishment of presence of root suckers between plants (Grundy et al., 1994). Although very successful in killing 'mothers' or ortets, this method did not work. One reason is because the connecting root breaks down over time.

As we could think of no other viable method of assessing root sucking, I resorted to the dirtier method of excavating roots of "juveniles" (height < 50 cm) plants. Once excavated, juveniles were classed into one of five categories, as follows.

Definite Seedling	Typically has a single or dominant vertical taproot, which often tapers.

Potential Seedling	Does not necessarily possess the single vertical taproot of a 'definite seedling', but appears more like a seedling than a root-sucker.
Unsure	Some specimens were very difficult to classify, because they had very peculiar root structures, or they had been broken during excavation, and it was impossible to tell.
Definite Root-Sucker	Did not have a dominant taproot. The dominant root was horizontal with no distinctive tapering. The sucker either formed a T-junction with this root, or an L-junction. T-junctions are the classic root-suckering structures. L-junctions could be formed when the root breaks down on one side of the sucker, but remains on the other. (See Appendix 1)
Potential Root-Sucker	Similar to 'Potential Seedlings', this class refers to specimens which I could not confidently record as definite root-suckers, but they are more likely to be suckers than seedlings.

Transects

At each study site I set out a 25m by 4m transect and recorded the heights of all the *D. cinerea* individuals, to give an indication of population size structure.

All the *D. cinerea* less than 50cm in height (a general juvenile classification) were marked and excavated carefully, so as to not break the roots. Each juvenile was classified into one of the above classes. I stopped excavations once a juvenile could be placed into one of these classes. In general, I did not have to dig deeper than 30cm, as this is where most roots involved in root suckering occur (pers. obs.) Lawson *et al* (1968) found the greatest concentration of tree and shrub roots of suckering species in a reserve in Ghana, to be between 20 and 30cm deep, when they excavated to a depth of 70cm.

For each site, I set out to excavate 30 juveniles (less than 50cm in height). If there were less than 30 juveniles in the transect, then another transect was marked out, and more specimens were found and excavated. This was repeated until at least 30 juveniles were excavated at each site. In some sites there were more than 30 "juveniles" in the transect, and in these cases, all the individuals were excavated (e.g. Le Dube). There were some sites where less than 30 individuals were excavated. This was due to time constraints, and the number excavated in each case was usually the number found in the first transect.

To assess if sites predominantly consisted of lawn or bunch grasses, 25 disc pasture meter (DPM) readings (Bransby & Tainton, 1977) were taken randomly from within or adjacent to each area. The dominant grass species was recorded for each DPM reading taken. Soils were classified as sand or clay by W.J. Bond from manipulation of moist soil. A quick vegetation survey was made at each site. Each species was classed as common, frequent or rare. Shrubs were assessed within a 25m radius of the centre of the plot, and trees within a 50m radius.

Data Analysis

The five categories of juveniles were reduced to two for analysis: suckers and potential suckers, and seedlings and potential seedlings. These results are treated as proportions of the total, and the category of uncertainties is not used in analysis.

I used regression analysis to explore the relationships between the proportion of ssp. *africana* per site and amount of rainfall, the number of times sites have burnt in the last 46 years, and the proportion of lawn grass at sites, as well as between proportion of ssp. *nyassana* and proportion of bunch grass at sites. I also used regression analysis to explore the relationships between the proportion of root suckering as the predicted variable and the proportion of lawn grass, annual rainfall and soil type, as well as the number of times sites have burnt in the last 46 years and the last 12 years as independent variables.

I transformed proportion data with an arcsine transformation for the following statistical tests, and statistical significance was taken as $p < 0.05$. The proportion of root suckering was found to be normal (Lilliefors $p > 0.2$), but there was heterogeneity of variances (Levene's Test: $F = 71.63$, $df = 20$, $p < 0.05$), and thus non-parametric statistical tests were performed.

I used Mann-Whitney U-Tests to compare the proportion of ssp. *africana* and the proportion of root suckering at sites with different soils; the variation in leaf size between the two subspecies, and spine density between the two subspecies. I also used this test to compare the ratio of leaf length to spine density between the subspecies, and this ratio for ssp. *africana* between two different sites (Gqoyeni and Maqanda). I evaluated the difference between the proportions of roots suckering in areas classed into different fire frequency categories (e.g. high, intermediate and low fire frequency, and grazing lawns) using a Kruskal-Wallis Test. I compared the proportion of adults and the proportion of juveniles in areas of different fire regime (high, intermediate, low and grazing lawn) using ANOVA.

RESULTS

Part 1 – Subspecies Ecology and Distribution

The leaves of ssp. *africana* were significantly shorter than those of ssp. *nyassana* (means of 5.9 cm versus 13.1 cm respectively; $p < 0.01$, Mann-Whitney U-Test), and there were significantly more spines on ssp. *africana* than on ssp. *nyassana* (means of 242 and 57 respectively; $p < 0.01$, Mann-Whitney U-Test). Thus, the ratio of leaf length to number of spines was significantly smaller for ssp. *africana*, than for ssp. *nyassana*, for all areas combined (Figure 2, $p < 0.01$, Mann-Whitney U-Test). There was a significant difference between the ratios of leaf length to spine density of ssp. *africana* at Gqoyeni and at Maqanda ($p < 0.01$, Mann-Whitney U-Test).

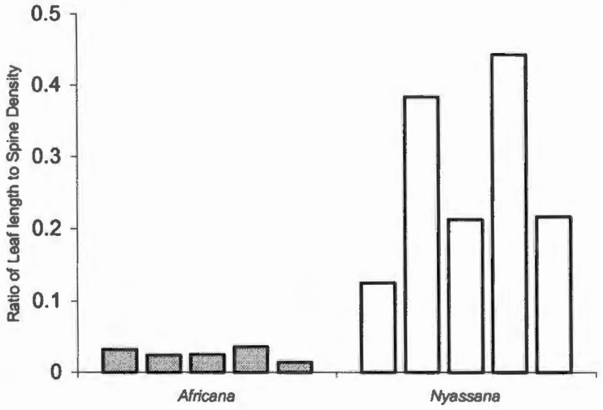


Figure 2: Ratio of leaf length to spine density for the D. cinerea subspecies. All sampling was done at Maqanda

The subspecies were broadly segregated in the park, with ssp. *nyassana* more common in Hluhluwe and ssp. *africana* more common in iMfolozi (pers. obs.). As the study sites were selected primarily in Hluhluwe, ssp. *nyassana* was the main study subspecies. However, ssp. *africana* was found to occur in specific areas in Hluhluwe. It occurred primarily at only three of the study sites, namely Crossroads, Seme Exclosures and Maqanda (the grazing lawns), rarely at a number of other sites, and was not observed at three sites, as shown in Figure 3.

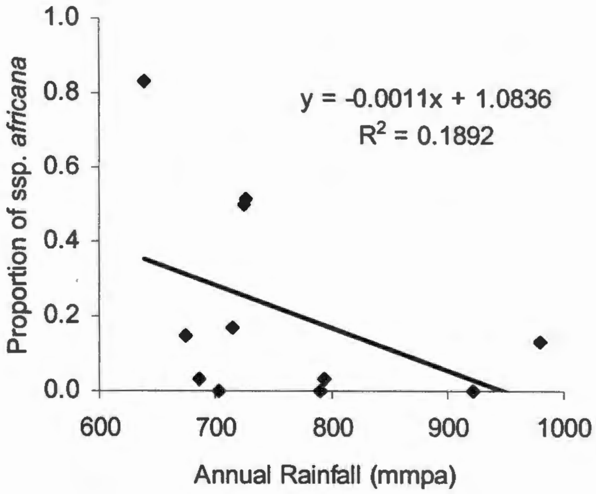


Figure 3: Distribution of ssp. *africana* along a rainfall gradient

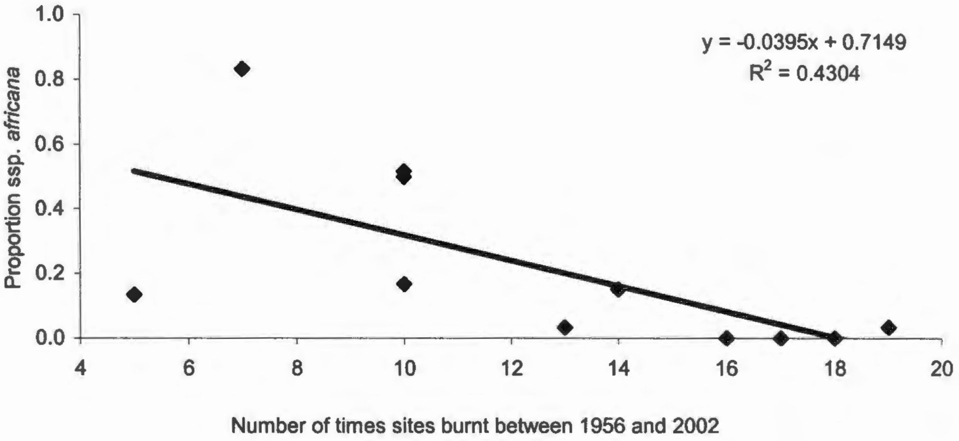


Figure 4: Proportion of ssp. *africana* in areas of different fire frequency

Ssp. *africana* was more common in areas of lower rainfall, and ssp. *nyassana* in areas of higher rainfall, but the regression was not significant (Figure 3, $r = -0.43$, $R^2 = 0.19$, $p > 0.05$). Ssp. *africana* was more common in areas that were less frequently burnt (Figure 4, $r = -0.66$, $R^2 = 0.43$, $p < 0.05$). It was also most common in areas dominated by lawn grass (Figure 5), although a correlation between the proportion of ssp. *africana* and proportion of lawn grass was not significant ($r = 0.46$, $R^2 = 0.21$, $p > 0.05$). Ssp. *nyassana* is more frequent in areas dominated by bunch grass ($r = 0.54$, $R^2 = 0.29$, $p > 0.05$). Ssp. *africana* was found mainly on clay soils, and rarely on sandy soils ($U = 5.5$, $Z = 1.61$, $p = 0.11$, Mann-Whitney

U-Test), whereas ssp. *nyassana* was found in large numbers on both clay and sandy soils (Figure 6).

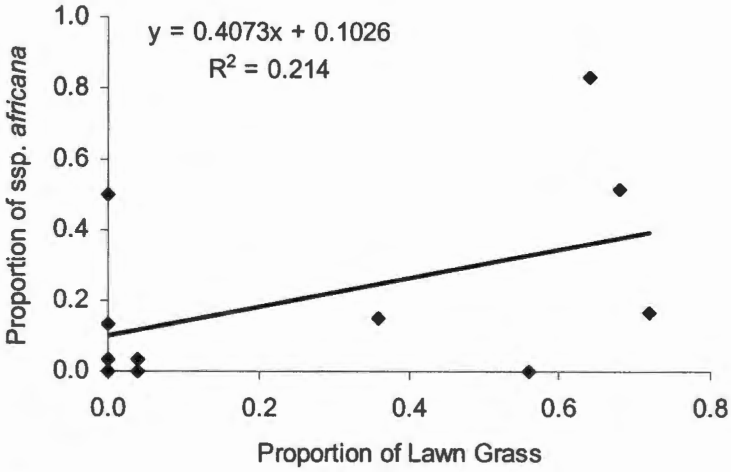


Figure 5: Proportion of ssp. *africana* in relation to proportion of lawn grass

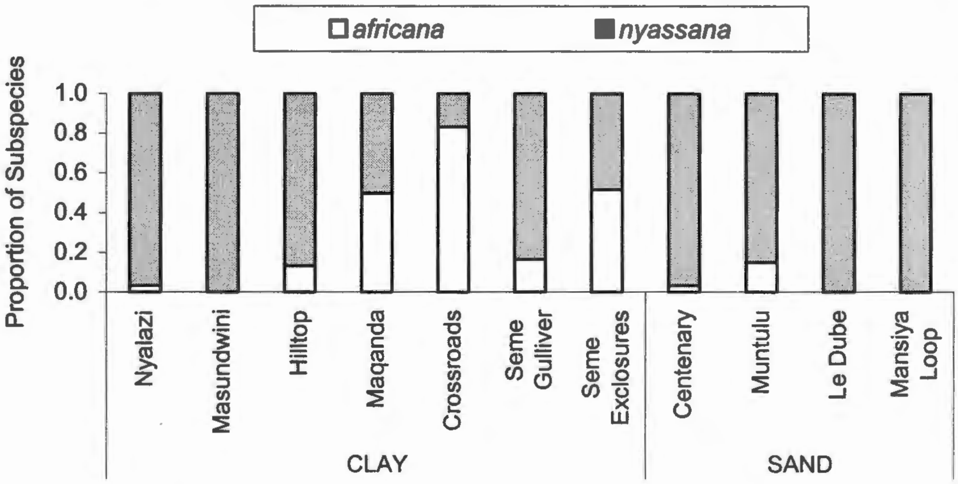
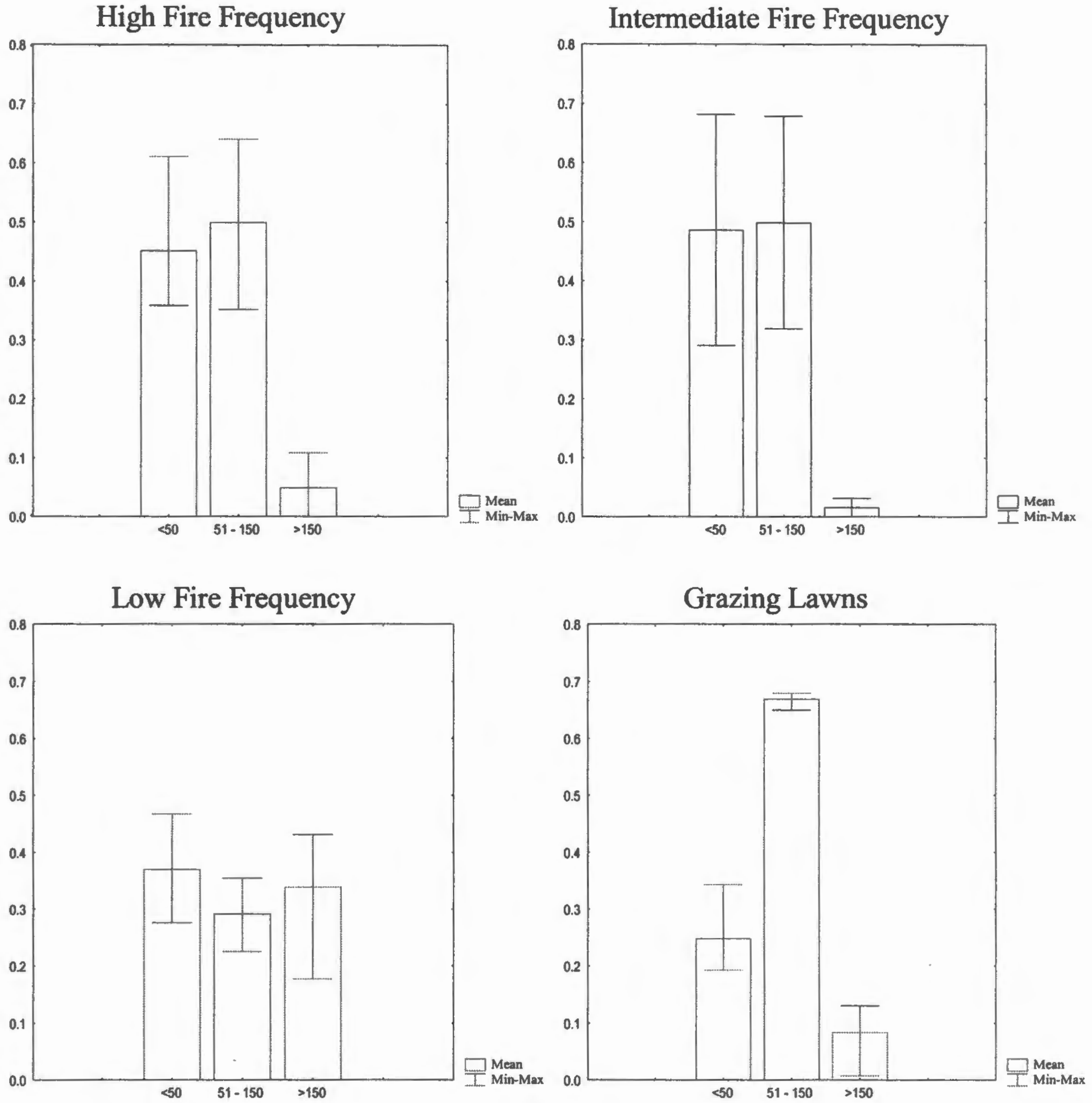


Figure 6: Proportion of subspecies in areas of different soils

Part 2 – Effects of Disturbance on Population Structure and Clonality

Population Structure

There were significantly more adult *D. cinerea* in areas of low fire frequency, compared to areas of high and intermediate fire frequency (Figure 8, (ANOVA) SS = 0.20, df = 3, MS = 0.07; F = 7.71, p = 0.01). Grazing lawn populations had similar size structure to areas with high and intermediate fire frequency. There were fewer juveniles on grazing lawns, in comparison to areas of high, intermediate and low fire frequency. However this was not statistically significant ((ANOVA) SS = 0.09, df = 3, MS = 0.03, F = 1.44, p = 0.31).


High Fire Frequency

Intermediate Fire Frequency

Low Fire Frequency

Grazing Lawns

Figure 7: Graphs to show structure of *D. cinerea* populations in areas of different fire frequency and on grazing lawns. The y-axis indicates proportional contribution of each size class to the sampled population.

Clonality

A total of 370 juveniles were excavated, with approximately 30 excavated per site (range: 26 to 61 per site). The fieldwork took 6 people 3 weeks, in comparison to the data collected for the differentiation of subspecies, which took the equivalent of one person, two days. There was a mean proportion of 0.55 suckers per site (standard deviation = 0.11), and 0.36 seedlings per site (standard deviation = 0.15), as shown in Figure 7. The maximum proportion was 0.74 and the minimum was 0.39, recorded at Hilltop and Maqanda respectively. There was no relationship between the proportion of root suckering juveniles and the number of times areas have burnt in the last 46 years ($r = -0.07$, $R^2 = 0.005$, $p > 0.05$), nor with the number of times an area has burnt in the last 12 years ($r = -0.34$, $R^2 = 0.12$, $p > 0.05$). There was no significant difference in the amount of root suckering in areas classified with different fire frequencies (Figure 7, Chi-Square = 2.93, df = 3, p = 0.40, Kruskal-Wallis test: H (3, N = 11) = 0.64, p = 0.89).

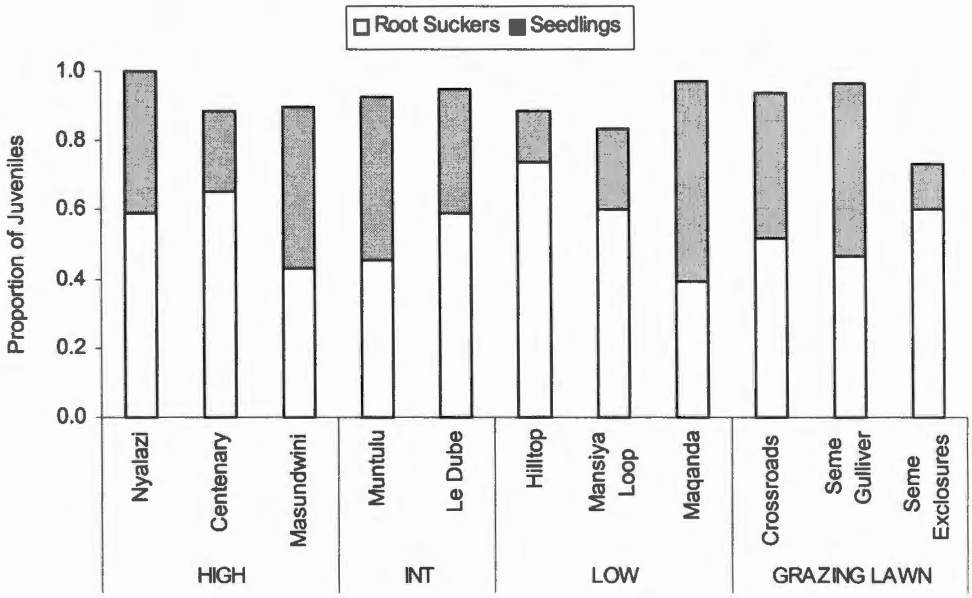


Figure 8: Proportion of suckers and seedlings at each site

Since fire frequency appears to have no influence on the amount of root suckering in *D. cinerea*, there may be another factor influencing variation in root suckering, such as rainfall, soil type or herbivory.

There was no significant relationship between proportions of suckering and proportions of lawn grass ($r = -0.14$, $R^2 = 0.02$, $p = 0.68$). There was a slight increase in suckering with rainfall, but the relationship was not significant ($r = 0.31$, $R^2 = 0.10$, $p > 0.05$). There was no significant difference in the amount of root suckering in clay and sandy soils ($U = 10.5$, $Z = -0.66$, $p = 0.51$, Mann-Whitney U-Test).

Density dependence might affect root suckering by influencing resources available for vegetative propagation. Where there were up to 10 adults (taller than 150cm) per transect, root suckering was variable. However, where there are numerous adults (25 per transect), root suckering was least extensive (39% of juveniles) (Figure 9).

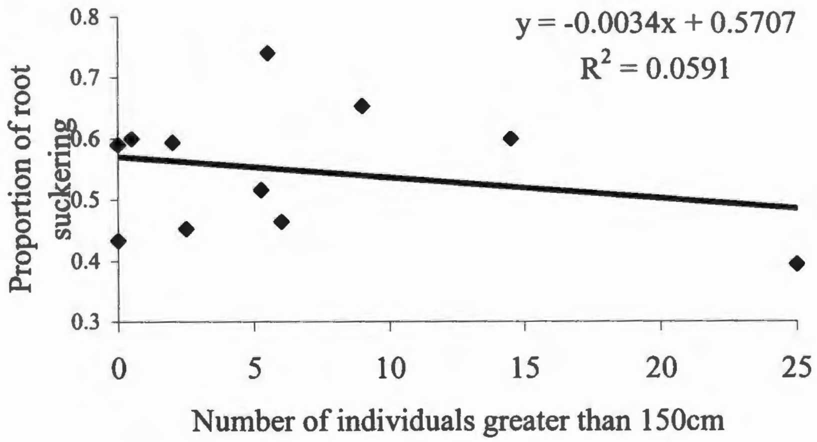


Figure 9: Proportion of root suckering in relation to number of adults (> 150cm)

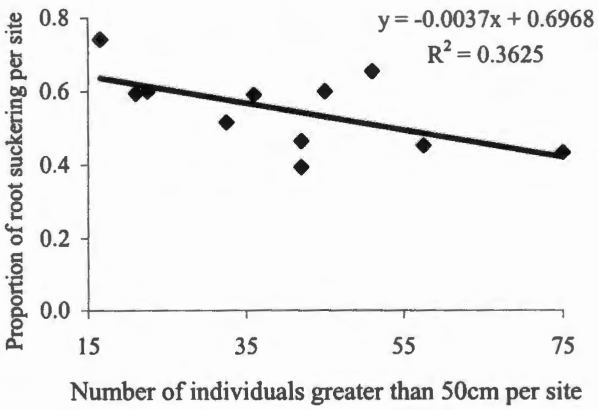


Figure 10: Proportion of root suckering in relation to number of large individuals (> 50cm)

The proportion of root suckering juveniles was, however, negatively related to the number of plants greater than 50cm in height (adults and sub-adults) (Figure 10, $R^2 = 0.36$, $p < 0.05$).

There is no significant relationship between the density of larger individuals (taller than 50cm) and that of juveniles (Figure 11, $R^2 = 0.06$, $p > 0.05$).

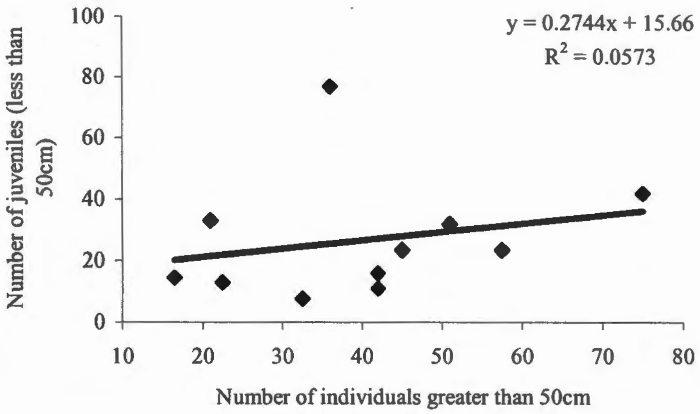


Figure 11: Density of juveniles compared with individuals greater than 50cm

DISCUSSION

Part 1 – Subspecies Ecology and Distribution

The general trend in Hluhluwe-iMfolozi Game Reserve is high densities of ssp. *nyassana* in the northern mesic area, where fire is frequent, and high densities of ssp. *africana* in the arid south where fire is infrequent. However, I also found ssp. *africana* in high densities in certain high rainfall areas, namely grazing lawns. This implies that subspecies distributions are more influenced by disturbance type than rainfall. This is supported by my data on structural defenses. According to structural defense theory (Milewski *et al.*, 1991; Gowda, 1996), the difference in spine density and leaf size should better protect spp. *africana*, than ssp. *Nyassana* from herbivory. It has been shown for *Acacia karroo* that structural defenses are greater in heavily browsed areas, in comparison to areas dominated by frequent fires (Archibald & Bond, 2003).

This is also supported by the fact that the ratio of leaf length to spine density for ssp. *africana* was significantly different between Gqoyeni and Maqanda. Gqoyeni, in iMfolozi is an open area subjected to heavy browsing, whereas the dense thicket at Maqanda would restrict animal movement, and thus reduce browsing (pers. obs.). Comparably, these ratios were lower for ssp. *nyassana* at Gqoyeni than at Muntulu, where browse pressure is likely to be lower. However, only two ssp. *nyassana* individuals were sampled at Gqoyeni, because they were difficult to find. This in itself is interesting, as it shows that ssp. *nyassana* is less frequent in heavily browsed areas.

Archibald and Bond (2003) also found significant differences in A. karroo architecture in forests, savannas and arid shrublands. This has also been observed for *D. cinerea*. Ssp. *nyassana* generally has longer and straighter branches, and a more upright architecture, compared to ssp. *africana* which has a cage-like appearance with much branching (pers. obs., van Wyk, 1972, Pooley, 1993).

Although referred to as "Grazing lawns", these areas also experience heavy browsing. Animals are attracted to these open areas where they can see greater distances and thus are more aware of predators (Underwood, 1982); and plant nutrients are higher (Melton, 1987). A number of grazers also switch to browsing during the dry season months (June to August), when grass is in short supply (van Wyk, 1972).

Ssp. *africana* is more common on clay rather than sandy soils. However this relationship was not statistically significant and the sampling was biased, because the three grazing lawn sites were all on clay soils.

Even though this species is dominant in many areas of Southern African, and its wood is used extensively in rural areas (van Wyk, 1972; Pooley, 1993), it has been very poorly studied, and little is known about its life history and reproduction. The subspecies differences reported here suggest that *D. cinerea* would be an ideal study species for answering questions relating to plant trait differences between fire and herbivory disturbances. It would be useful to know how long each subspecies persists after a change in disturbance type, as subspecies density could be used to read the history of disturbance changes in an area. For example, high densities of ssp. *nyassana* on a lawn grass would imply that the lawn grass was formed recently, and presence of ssp. *africana* in bunch grass areas (or where lawn grass has not been controlled by grazers) implies that the area was recently a grazing lawn.

Unfortunately, due to time constraints, I was unable to compare root suckering in each subspecies. Both subspecies do definitely root sucker. Since there were no outstanding differences in amount of root suckering in grazing lawns and non-grazing lawns, I suspect similar levels of root suckering in both subspecies. More work would need to be done in iMfolozi to get the sample sizes of ssp. *africana* large enough for subspecies comparison.

Part 2 – Effects of Disturbance on Population Structure and Clonality

Population Structure

There were fewer adults (of height greater than 150cm) in areas of high and intermediate fire frequency. This is presumably because individuals are top-killed before they get large. There are also few large *D. cinerea* on grazing lawns. This is presumably because they are eaten by browsers, and are kept small. The proportion of juveniles was fairly high (approximately 0.4) in high, intermediate and low fire frequencies, but slightly lower (0.26) on grazing lawns, suggesting that these too may be experiencing browsing pressure.

D. cinerea in semi-arid areas of Kruger National Park was large enough to produce seeds when plants were greater than 150cm (Schutz, Hons project, unpublished). In areas where fire is frequent, there are very few adults, and thus one would expect suckering to be the major means of reproduction. However, there was no difference in the amount of suckering in areas with different fire frequencies. Instead, root suckering was surprisingly consistent with regards all sites and all frequencies and types of disturbances. Even when burnt almost every year, *D. cinerea* still had the ability to root sucker. One may have thought that its resources would be depleted if it had to invest much resources into sprouting and suckering after each burn. Where fire was replaced by grazing/browsing as the dominant disturbance, on grazing lawns, the proportion of clonal juveniles was still much the same.

Clonality

There seems to be some evidence for density dependent variation in root suckering. Where populations are dense, there is little space for vegetative propagation, and so root suckering would be expected to be less extensive, than in less densely populated areas.

There are two different strategies of clonal growth (Peterson & Jones, 1997). Plants can either form thickets that protect the interior ramets from fire, wind or herbivory damage. Or, root suckering could be aimed at production of many ramets, and thus risk spreading, which is advantageous for fitness of the genotype. For example, in forest tree species a "sprout bank" is formed, where ramets may maintain connections to the genet that promotes the existence of the ramet in highly shaded environments, so that when a gap is formed, the ramet can grow into the canopy (Peterson & Jones, 1997).

The length of time the ramets are connected to the genet may influence clonal strategies. If spatial expansion of the genet is the main aim, then connections may be maintained for as short a time as possible, so that resources can be put into new ramets. If protection of the genet is the main aim, then connections may last much longer, to ensure the survival of the whole thicket.

In Kruger National Park, *D. cinerea* has successfully formed thickets, and excluded grass, so reducing fire spread (van Wyk, 1972). Adult *D. cinerea* were observed to have large root connections in the Pretoriuskop region of Kruger National Park. In contrast, small root suckers in Hluhluwe iMfolozi Game Reserve had often already broken away from their mother ortets. It would be interesting to explore the physiological integration between ramets in this species, in different settings within savannas, to test these preliminary observations.

Part 3 – Implications for Management

Root suckering allows greater persistence and resilience to disturbances such as fire and herbivory. It may have contributed to *D. cinerea* becoming a major problem in certain areas where it has formed dense thickets that shade out grass, and exclude animals. This project has shown that fire alone cannot be used as a management tool to reduce population density of *D. cinerea*, as the degree of root suckering is not influenced by fire. However, growth rates and recovery have been reported to be reduced in populations burnt in December, rather than any other time of year, as seen in the experimental burn plots in Kruger National Park (Schutz, Hons. Thesis, Unpublished). Also, as seen in the variations in population structure, fire generally reduces the height of populations. Thus, fire can be used to reduce the size of plants and growth rates of populations, which would reduce their negative impacts of grazing.

Since the two subspecies have different strategies, they should be managed in different ways. Heavy browsing may be effective in controlling populations ssp. *nyassana*, and freqent fires may be effective in control ssp. *africana*.

Conclusion

Root suckering results in species that are remarkably resilient to disturbance by fire and herbivory, and yet clonality has rarely been examined in African ecosystems. One reason for this is that much of the effects of clonality occur underground. Fieldwork is arduous and time consuming. However, it is hard to make sense of population ecology in savanna trees without more consideration of the ecology of root suckering species.

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Appendix 1

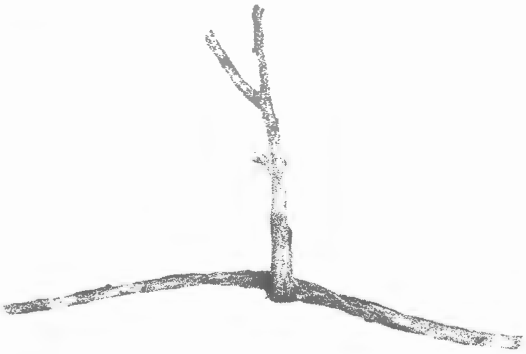

Figure A: A typical T-junction where both roots are healthy

Figure B: An older sucker where the root on the right is breaking down, and the one on the left is still healthy

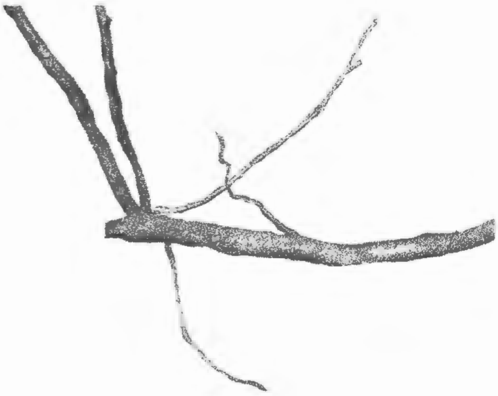

Figure C: A typical L-Junction remains after the root in one direction has broken down.

In all photographs above, roots are horizontal and stems vertical.