REHABILITATION OF DUNE FORESTS IN KWAZULU-NATAL:

Predicting slow colonisers and vulnerable species based on plant morphology

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ABSTRACT:

Some characters of plants, related to life history, may give an indiction of a species ability to recolonise an area. These include fruit size (related to dispersal), the ability to resprout (related to seed vigour), specific leaf area (shade tolerance) and flower morphology (reproductive specialisation). Birds were also studied to determine their effect on fleshy fruit dispersal. Trends in these plant characters, as rehabilitation time increased, were noted and used to determine the effectiveness of rehabilitation in restoring all the groups. The characters of forest species that were able to colonise the rehabilitating area were compared to that of species that were absent from the mined areas. It was found that large frugivorous birds appear only in old rehabilitating stands, while small fruigivores return more rapidly. This may be related to similar trends in fruit size. Few species with other dispersal mechanisms (excluding wind dispersal), have colonised mined areas. Identification of the primary regeneration mode (seeding or sprouting) proved difficult, however the limited data available suggested that this character did not affect colonisation. Shade tolerance decreased with increasing rehabilitation time. The chance of pollination failure, related to specialised flower structure, also did not directly affect species establishment. Dispersal appears to be the primary factor limiting colonisation of trees. Plants with poor seed dispersal (eg large fruit, or capsules) as well as specialised pollination systems, or poor seed regeneration were hypothesised to be species at high risk of being absent or slow to recolonise mined areas. Trends in all characters tended towards the conditions found in the unmined stands indicating that the rehabilitation program should be successful.

INTRODUCTION:

Mining the coastal dunes near Richards Bay, KwaZulu-Natal for heavy metals involves the removal of all existing vegetation in the mining path (Mentis and Ellery, 1994). This includes indigenous dune forests, which should be of high conservation priority as they have very high species diversity and are of scientific interest (Weisser, 1987). Richards Bay Minerals has therefore been implementing a rehabilitation program since 1977 with the aim of aiding the re-establishment of these forests (van Aarde, Coe and Niering, 1996; van Aarde et al., 1996, Kritzinger and van Aarde, 1996; Mentis and Ellery, 1994).

Briefly the rehabilitation program entails spreading a layer of topsoil (collected before mining) over the reformed dune (Mentis and Ellery, 1994; Camp, 1987). A mixture of seeds is sown, consisting mainly of *Penniseyum americanum* (babala grass), *Crotalaria juncea* (sun hemp), but also including several indigenous species (Camp 1987). Following this the vegetation is left to revegetate naturally (Mentis and Ellery, 1994; van Aarde et al., 1996). Within a month, a dense cover crop of annuals develops. This dies after six to eight months, leaving a cover of indigenous grass. A dense *Acacia karoo* shrubland develops after 18 months (Camp, 1987) and this is believed to be a precursor of dune forest (Weisser, 1980).

The effectiveness of this rehabilitation has been the subject of many studies in which the community structure in a series of rehabilitating stands of known age (assumed to represent different stages in the rehabilitation process) were compared to that of adjacent unmined areas (eg Van Aarde et al., 1996; Kritzinger and van Aarde, 1996, Mentis and Ellery, 1994, Foord et al., 1994). These studies have found that, at least in terms of species richness, composition and density, communities develop towards a state which becomes increasingly similar to the unmined stands, as rehabilitation time increases (Mentis and Ellery, 1994, van Aarde et al., 1996). However, even the communities in the oldest rehabilitating areas (which were 16 years old) were found to be different to those in the unmined forests. This was attributed to the mined areas representing early stages in a successional sequence, while the unmined sites, which are at least 35 years old, represent much later stages (eg van Aarde, Coe and Niering, 1996; van Aarde et al., 1996). The results of all studies so far indicate that the initial stages of rehabilitation are successful, but the process is not complete (eg Mentis and Ellery, 1994, van Aarde et al., 1996, Kritzinger and van Aarde, 1996).

These studies have all based their finding on community structure only - comparing of species richness, similarity and density of the different sites. Rehabilitation should ideally restore the natural dynamic to the communities. Functional characteristics of communities are therefore important in assessing the rehabilitation process (van Aarde et al., 1996; van Aarde, Coe and Niering, 1996; Mentis and Ellery, 1994). Although structure and function are related in ecosystems (van Aarde et al., 1996), interactions between taxa means that all species cannot be considered equal (Howe, 1984). Different suites of species in a community may have differing rates and abilities to recolonise areas (Begon et al., 1996). Studying only the structure of a community gives no indication that any functional groups or biological interactions may be missing, or slow to colonise rehabilitating areas.

The likelihood of a species colonising an area is determined by its chance of being dispersed into the region and the probability of it establishing in that environment (Diamond and Case, 1986, Begon et al., 1990). Once established the species can either increase its density by continual introduction from an outside source or by establishing an actively reproducing community. The life history characters of a species affect its chances of being dispersed and establishing in a new environment (Begon et al., 1990). Succession should therefore not be random in terms of species characters, but occur in a predictable manner.

The aim of this study is to determine what, if any, trends occur in the characters of dune forest species as succession proceeds following mining. This information should give an indication of the effectiveness of the rehabilitation program in restoring the natural functioning of dune forests and an indication of which factors may be limiting the rehabilitation process. It is ultimately hoped that, based on the findings, it will be possible to predict the probability of woody species colonising mined or similarly disturbed ares by using only a few characters that are easy to measure or obtain from literature.

Factors that may affect seed dispersal:

Since mining involves the clearing of all the living material, regeneration of forest species must result from either the seedbank or dispersal. It appears that very little indigenous forest vegetation germinates from the seedbank after mining (van Aarde et al., 1996 and pers. obs.), so it can be assumed that dispersal is the main source of indigenous forest species in rehabilitating areas.

Bird dispersal:

The most important dispersers of fruit in the dune forests are monkeys and birds (Foord et al., 1994). The movement of birds is affected by areas cleared of forest trees (da Silva et al., 1996; Kritzinger and van Aarde, 1996). Since there may be links between bird movement, seed dispersal and plant succession (da Silva et al., 1996), the large areas cleared by mining may therefore affect the dispersal and colonisation of forest tree species.

Birds may directly aid dispersal (and therefore affect succession) by ingesting seeds while consuming fruit and then regurgitating or defecating the intact seeds away from the parent tree (Debusshe et al., 1982). The abundance of frugivores may therefore affect the rate of colonisation of fleshy fruited trees.

It has previously been observed that small fruited species characterise early seral stages, with species with large fruits appearing later (eg Davidson 1993). This may be related to the similar trends observed in bird size (eg da Silva et al., 1996). Most fruit eating birds typically swallow fruits whole, and reject large fruits only if they cannot be swallowed. The size of fruit consumed (and dispersed) by birds is affected by their gape width (Herrera, 1984). Only birds with large gape width can ingest and therefore disperse large fruits, while small fruits can be consumed by birds of all sizes. Large fruited species therefore have fewer potential dispersers than trees with small fruited (Wheelwright, 1985; Howe and Westley, 1988; Herrera, 1984). This implies that small fruit has a much greater chance of being dispersed into cleared areas than large fruit, which can be expected to be slow to colonised areas.

Other dispersal mechanisms:
The colonization by species with fruits that are not fleshy may depend on their dispersal mechanism, which affects the dispersal distance. Species with seeds dispersed by gravity, for example, are most likely to be poorly dispersed, while those with explosive seed dispersal may be dispersed slightly further. Long distance seed dispersal is likely to occur in species with winged or plumose seeds (Hamrick and Loveless, 1986).

Factors that may affect establishment:
Primary mode of regeneration:
The number and vigour of seeds characteristically produced by a species will affect both its dispersal and probability of becoming established. Many forest species have the ability to resprout. This ability is often associated with a decreased dependence on seeds for reproduction and seedlings that are competitively inferior to those of obligate seeders (Hunt and Loyd, 1987). These persistent (resprouting) species are often found in the later successional stages (Begon et al., 1990). Species that depend largely on resprouting may therefore be slow to recolonise mined areas due to their limited number of competitively inferior seeds and the lack of material for vegetative reproduction.

Shade tolerance:
The ability of a species to survive in the abiotic conditions of an area may also determine whether the species will be able to become established in the area (Diamond and Case, 1986). The amount of light, for example, may be an important factor

affecting species establishment (van Aarde et al., 1996). Shade tolerance can easily be inferred from specific leaf areas (SLA) which also give and indication of the growth rates of plants (Reigh et al., 1991). As succession proceeds (and canopy cover increases) in mined areas, it would be expected that the species would become increasingly shade tolerant and have slower growth rates.

Reproduction:
Once a few individuals have become established, a species can increase in abundance either by dispersal, or by reproduction. If an area is to be considered truly rehabilitated, all biological interactions should be reinstated, this includes pollination interactions. Species with specialised reproductive systems are at risk of pollination failure (Bond, 1994) and therefore may be slow to become well established in mined areas, as limited pollination would mean low seed set (Linhart and Fiensinger, 1980). Specialisation in reproductive associations is indicated by traits that limit access to potential pollinators, for example large size and long corolla tubes (Linhart and Feinsinger, 1980; Faegri and van der Pijl 1979). Dioecious species, which are dependant on pollen dispersal for reproduction, are at especially high risk of not reproducing if they also have specific associations with pollinators (Bond, 1994).

To trends that are expected to occur as rehabilitation proceeds are:

1. Increasing average size of birds and fruit.
2. Increasing abundance of primarily resprouting species.
3. Increasing shade tolerance
4. Increasing abundance of species with specialised reproductive systems.

If the trends observed during rehabilitation could not conceivably result in the condition observed in the unmined sites, rehabilitation is not as effective as first believed. If certain groups of species show no visible trend towards the unmined condition these species may be slow to recolonise the mined areas if they will colonised there at all.

METHODS:

The species composition and diversity of birds and forest trees has been well documented due to the many studies assessing the rehabilitation program. There was therefore no need to do any direct population sampling. Information concerning the number and abundance of bird species found in rehabilitating areas was obtained from Appendix B in Kritzinger and van Aarde (1996). This information was gathered by using line transects to observe bird species (excluding aerial feeders and birds of prey) in 5 known aged rehabilitated stands and an unmined strip consisting of secondary dune forest dominated by *Acacia karoo* (Kritzinger and van Aarde, 1996).

As it was intended to develop a predictive model based on easily obtainable information, bird weights were used to give an admittedly very rough idea of the a birds gape width because no information on this character was readily accessible. Bird weights and main food sources of species was obtained from Robert's Birds of Southern Africa (Maclean, 1993). The number and abundance of bird species that consumed seeds, fruit, nectar and insects at each rehabilitation stage was calculated. A Chi squared test was used to determine if the bird species that had not recolonised the mined areas consumed different food types (in terms of insects, fruit or "other food") to those that had (the number of species consuming each food type in each distribution was compared). A t-test was used to test if the mean weights of the birds that colonised mined areas and those that had not, differed. For graphical representation the bird species were divided into three categories according to their average weight: small <20g; medium ≥20g but <100g; large ≥100g.

Information regarding the abundance and diversity of tree species found in rehabilitating stands of various known ages, and a disturbed unmined stand (35 years old) were obtained courtesy of the Mammal Research Institute, Pretoria. All these sites were dominated by *Acacia karoo*. The species diversity found in

Mapelane, representing a pristine dune forest, was kindly provided by Rick van Wyk. Unfortunately no density value were available for this area. The sampling method for both information sources is unknown.

The literature used to determine the fruit type and size, and flower structure and breeding system included Pooley (1993), Von Breitenbach, (1965) and Palgrave (1984). No statistical analysis was used to compare the different fruit types that had, or had not, colonised the mined areas due to the small number of species that did not have fleshy fruits.

Species with fleshy fruits were divided into three size class categories, based on the smallest dimension of the fruit (breadth or diameter). This is believed to give the most accurate indication of the potential to be swallowed (eg. a small bird may be able to swallow a long, but thin fruit). If information in the literature regarding fruit size did not correspond, an average of the values was used. Small fruits were classified as having a smallest dimension of less that 10mm; medium fruits $\geqslant 10$, but <20; and large fruits were $\geqslant 20$ mm. A chi square test was used to determine if there were any significant difference in the number of species with different sized fruits found in both the mined and unmined areas compared to those that had not successfully colonised mined areas.

The breeding systems of dune forest species was found to be poorly documented. Flower size and dioecy were the most well documented characters, these were used to make a crude assessment of a species vulnerability to pollination breakdown, based on Bond's (1994) model that predicts that high risk species would be dioecious species with large, specialised flowers.

Information regarding species ability to resprout was also very limited and the field assessment of this character proved to be much more complex than initially expected. In addition to the ability to sprout not being a discrete character (making it difficult to assess with limited sampling time), species that have previously been believed to be obligate seeders, for example

Celtis africana (Midgley, 1996 pers. comm.), were observed to resprout, (including by root-suckering!). This aspect was therefore not pursued further than to note species that clearly depend largely on resprouting for regeneration from limited field observations and suggestions from Rick van Wyk who is very familiar with the forest species in the area.

Midgley et al. (1995) conducted a study of the surface leaf areas (SLA) of some South African forest species. These figures (obtained from Appendix 1) were used as an indication of the shade tolerance of species found in the various stages of rehabilitation. Unfortunately measurements of only a limited number of species were available, most of which are dominant in the pristine dune forest. A t-test was used to determine if species found in both mined and unmined areas had significantly different values for SLA than to those that had not recolonised mined zones.

RESULTS:

Factors that may affect seed dispersal:

Trends in bird populations:

Food preference did not significantly affect the colonisation ability of bird species at the present stage of rehabilitation ($df=2$; $p>0.05$; Figure 1). The total number of bird species was similar both mined and unmined areas, although fewer frugivorous species were found in the rehabilitating forests. The density of birds in all diet groups, with the exception of nectivores, was higher in the unmined forest (Figure 2).

Most of the bird species recorded include insects as part of their diet, so the number and abundance of insectivorous species was very high (Figures 1 and 2). Graniverous species were rare and consisted of few species. The proportion of graniverous birds species was slightly higher in the earliest stage of rehabilitation, but fluctuated little thereafter (Figure 2). the abundance however was highest in the unmined areas and peaked at the 9-12 year old rehabilitating stand (Figure 1).

The density and proportion of frugivore species (Figure 1 and 2

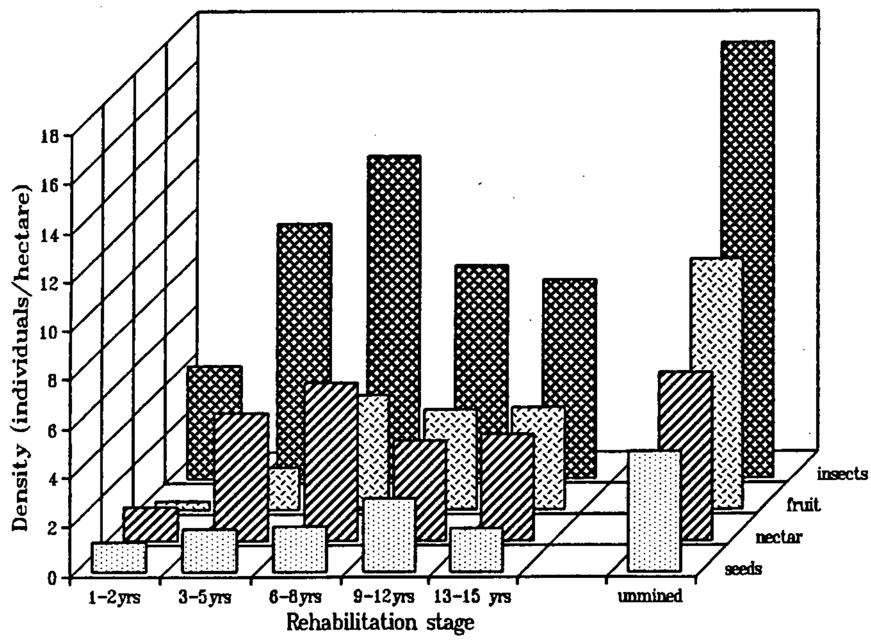

Figure 1: The density of birds with different diets in rehabilitating stands of different ages and an unmined site disturbed 35 years ago.

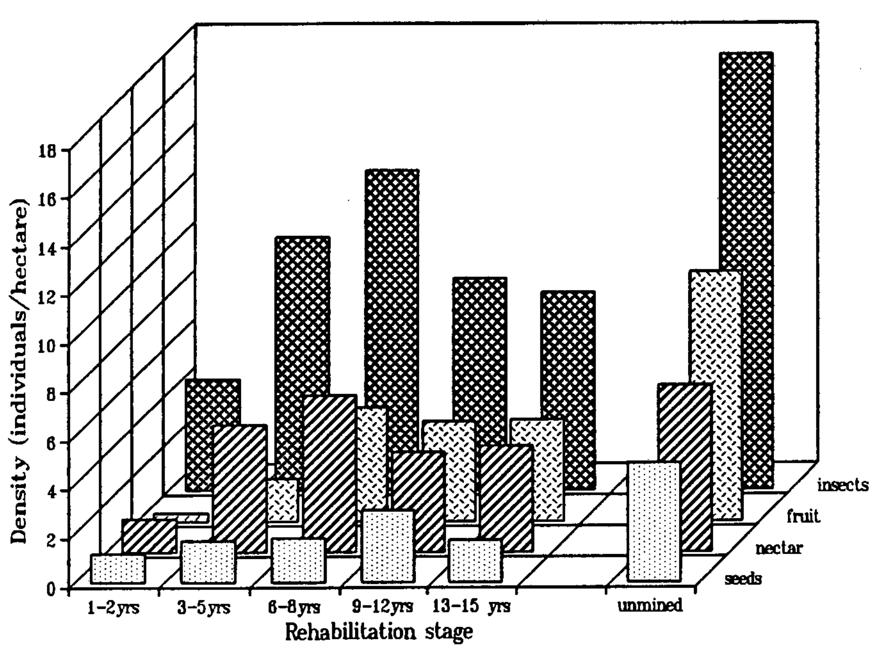

Figure 2: The number of bird species with different diets in rehabilitating stands of different ages and an unmined site disturbed 35 years ago.

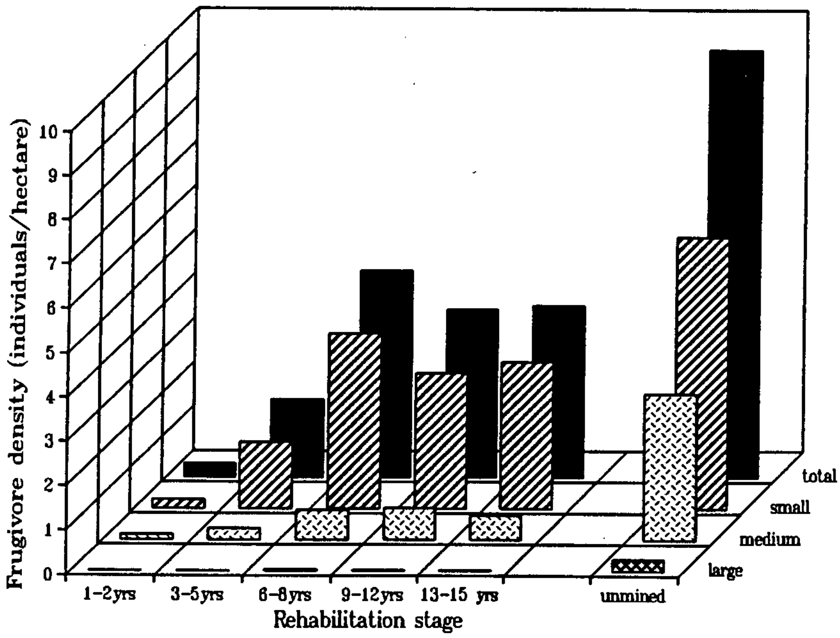

Figure 3: The density of species deferent sized of frugivores in rehabilitating stands of different ages and an unmined site disturbed 35 years ago.

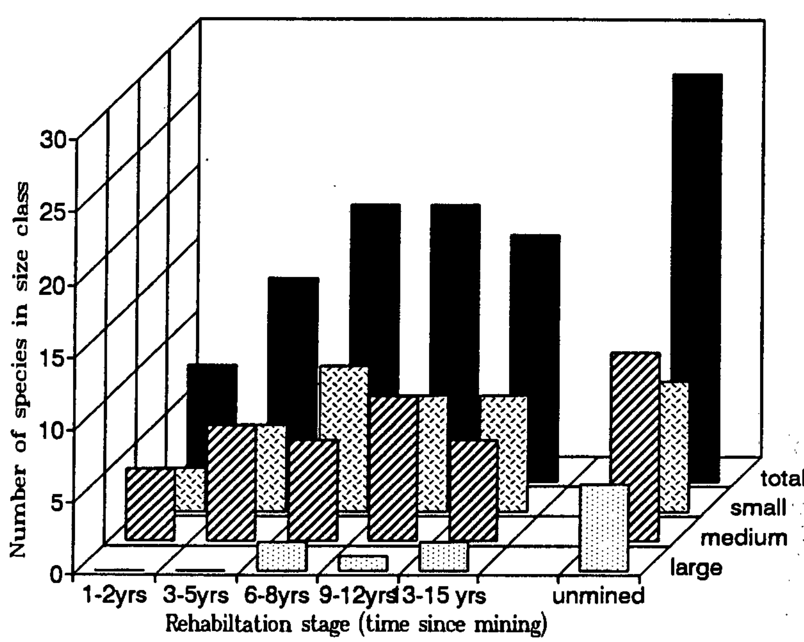

Figure 4: The number of species different sized of frugivores in rehabilitating stands of different ages and an unmined site disturbed 35 years ago.

respectively) was lowest in the early stages of rehabilitation. Following an increase between the 2-5 and 6-8 year old stands, the proportion and abundance of frugivorous species changed little over the rehabilitation periods. The proportion of species consuming fruits was highest in the unmined sites.

The size of the birds that colonised the rehabilitating areas was not significantly different from that of the birds absent from these regions ($t=1.885$; $df=25$; $p> 0.05$). Large birds were rare in terms of number of species (Figure 4) and density (Figure 3) in both the rehabilitating and natural areas, with the values being higher in the latter for both cases. The density of large birds was exceptionally low, with the a maximum density occurring in the unmined site being less than one individual per two hectares. Although low, the number of large bird species was high enough for changes to be apparent. Large species were absent in the early rehabilitating stages from 1-5 years after which about 10% of bird species were large bodied (Figure 4).

The number of small and medium sized birds were similar (Figure 4), although small species were far more abundant (Figure 3). In terms of species number, small birds show no difference between the mined and unmined stands, although, as for all other size classes, the abundance in the unmined sites was higher. The abundance and diversity of medium sized birds fluctuated little in the rehabilitating areas, in which the values were lower than those in the unmined forest.

Trends in fleshy fruited species:

The total number of fleshy fruited species was much higher in Mapalane than in all other sites including the unmined site dominated by *Acacia karoo* which had a similar density and number of fleshy fruits to the mined sites (Figures 5 and 6). The size of fleshy fruits did not significantly affect the number of species that colonised the mined area ($df=2$, $p>0.05$). The number of all size classes of fruit increased with increasing age, while the proportion of species with different size classes incresed in similarity with increasing age (Figure 6). Large fruited species were the least abundant and were also the last to appear

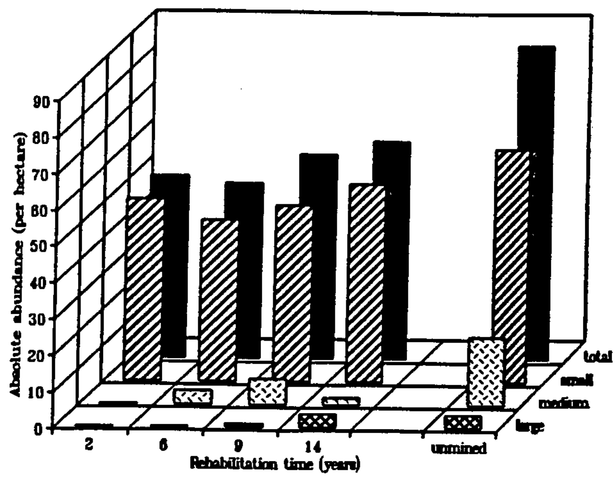

Figure 5: The density of fleshy fruited trees of different sizes in rehabilitating stands of different ages and an unmined site disturbed 35 years ago.

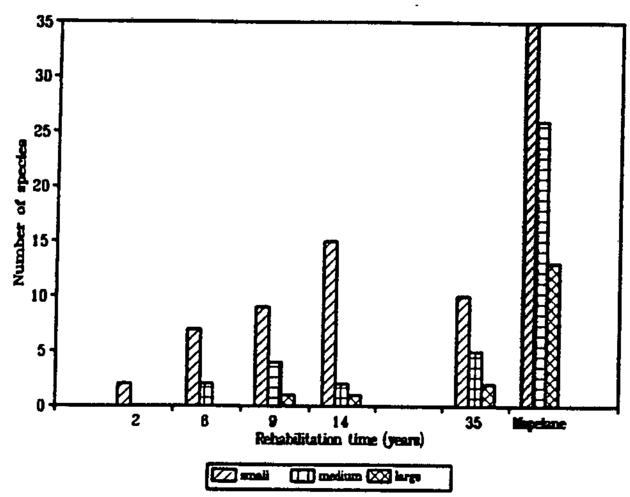

Figure 6: The number of tree species with small, medium and large sized fleshy fruits in rehabilitating stands of different ages, an unmined site disturbed, 35 years ago, and Mapelane, representing a pristine dune forest community.

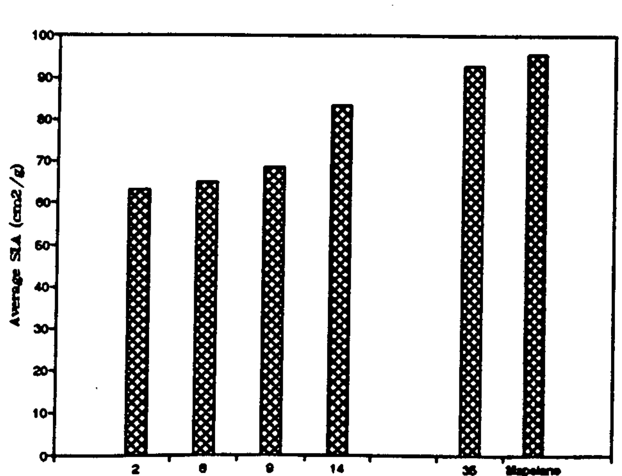

Figure 7: The average specific leaf area of trees found at different stages of rehabilitation, a disturbed unmined that was 35 years old and Mapelane, representing a mature dune forest.

in the rehabilitating sites. Small fruited species were present and abundant from the earliest stage of rehabilitation (Figure 5).

Trends in other types of fruit:
Species with large, hard fruits, like those of *Strychnos*, were absent in mined areas and most probably distributed by monkeys (Pooley, 1994). *Brachylaena discolor*, whose fruit is a nutlet that is wind dispersed (it has a pappus) was found in both mined and unmined sites. Most species with capsules, including those with arils, had not colonised the mined areas. Exceptions were *Dodonae angustifolia* and *Trichillia emietica*.

Factors that may affect the species establishment:
Regeneration/persistance:
There appeared to be no trend in the distribution of species that were thought to be strong resprouters. About 70% of trees that had colonised the mined areas were believed to have a strong capacity to resprout (several multi-stemmed individuals were observeds, and suggestions from van Wyk, pers. comm.). Approximately 65% of species absent from mined areas showed a similar tendency.

Shade tolerance:
There was no significant difference in the SLA of species found that were able to recolonise the mine areas and those that could not ($df=27$; $p>0.05$). The SLA increased with rehabilitation time, with the highest values occurring in the unmined sites (Figure 7).

Breeding system/reproduction:
Most of the flowers of dune forest species were unspecialised and had a low risk of pollination failure. Many species had small, dioecious flowers. Species that were thought to have specialized breeding systems (large dioecious flower), made up roughly 10% of species that colonised mined areas and similarly 10% of those that were specific to the unmined areas.

DISCUSSION:

The trends in the most of the species traits observed in rehabilitating stands indicate that rehabilitation could conceivably result in a community whose biological functioning is very similar to that of the unmined stands. None of the characters investigated differed significantly in species that had colonised rehabilitating areas compared those unique to the unmined sites. This implies that the rehabilitation process, although not complete, will most probably be successful in restoring the mined dunes to dune forests, supporting the findings of all other studies.

It is hoped that more can be gained from this study than a confirmation of previous findings. By increasing the understanding of the successional process involved in dune forests, species that are most likely to be slow to colonise the mined areas can be identified. If necessary, steps can be taken to actively introduce these species and thereby increase the rate at which succession (and therefore rehabilitation) will take place.

Factors affecting dispersal:

The diet of birds changes little over the rehabilitation period. This may be largely due to the generalised nature of the diet of most bird species in the area. Most species that consume seeds, nectar and fruit also eat insects, possibly to increase the amount of protein in thier diet (Howe and Westley, 1988). Graniverous birds were the least affected by mining while nectivorous and insectivorous birds recovered rapidly to a similar state as observed in the unmined sites. The ability of graniverous species to recolonise areas at early stages of rehabilitation may be due to the large initial cover of grass and annuals which may produce an abundant food source for these birds. Frugivorous bird were the slowest to recover in terms of relative abundance and number. There was a large difference in the number and abundance of these species in the mined and unmined sites, and the trends within the mined areas indicate that recovery of these species will be slow.

The low density of birds in the early successional stages may limit fruit dispersal and therefore could explain the low diversity of the trees with small fleshy fruits in the early stages of rehabilitation. (The abundance of small fleshy fruited species was relatively high in these early stages of rehabilitation, largely as a result of high densities of pioneer species such as *Rhus nebulosa* and *Apodytes dimidiata*). Following the low initial values, the number of small fruited species increased rapidly with rehabilitation time, corresponding to the high abundance of all birds. The rapid recovery of small fruited species can be attributed to the fact that all frugivorous birds are able to disperse small fruits, as gape width (indicated here by bird weight) does not limit the minimum size of fruit that can be ingested, and therefore dispersed (Herrera, 1984, Howe and Westley, 1988; Wheelwright, 1985).

The colonisation of large and medium fruited species was much slower and these species only established after 6 - 9 years of rehabilitation. This may simply be because large fruited species occur in low densities, even in the unmined sites, and therefore have less chance of being dispersed. Furthermore large fruited species have fewer potential dispersers than small fruited plants as only birds as with large gape widths can ingest, and therefore disperse, large fruits (Wheelwright, 1985; Howe and Westley, 1988; Herrera, 1984). The probability of large fruits being dispersed is further reduced as large birds, like large fruited species, are rare, and only appear in the mined areas after 6-8 years. In addition, while large fruited species are dependant on large birds for dispersal, large birds are not dependant on large fruits for food (Wheelwright, 1985, Howe and Westley. 1988). The potential for large fruit to be dispersed into the mined areas is therefore very low and the extent to which these large fruited species have recovered is surprising.

While it seems clear that the dispersal of large fruited species is limited by the abundance of potential dispersers, the relationship between the abundance of birds and small fruited species is less clear. Is the succession of small fruited species dependant on dispersal by birds, or is the colonisation of birds affected by the abundance of fruit in the mined areas? There does not seem to be any clear answers to this question.

The small fruited species that had high densities in the initial stages were probably not introduced by bird dispersal as the abundance of birds at this stage was low. Da Silva (1996) noted that frugivorous birds in Amazonia were probably not important dispersers of early successional plants into abandoned fields, as their movements into these area appeared to be closely linked to foraging for fleshy fruits. It is possible that a similar situation is occuring here. Once the succession is initiated however, the trends are probably maintained by a positive feedback between the abundance of birds and dispersal of fleshy fruited trees. This may work as follows: fruiting pioneer trees act as nuclei for further deposit of seeds (Debusshe et al., 1982), the resulting increased abundance of fruiting species attract more birds to the rehabilitating area and so on ...

Birds are most likely the driving force behind the relationship between bird abundance and seed dispersal, as changes in the movements of birds are more rapid than the colonisation of plants, which once dispersed into an area, would still take time to reach reproductive maturity and produce the fruit that would attract the birds.

Since large birds can consume all sizes of fruit, what is limiting recovery of these birds? Habitat specificity may be important. Kritzinger and van Aarde, (1996) concluded that the overall trend in bird abundance was related to the structure of the rehabilitating forest. It is possible that frugivorous birds, which spend most of their time in the canopy, are more selective than other guilds in terms of the habitat they inhabit. The low canopy in the early successional stages may therefore inhibit the recolonisation of frugivorous birds. This cannot however explain the large difference in number and abundance of frugivores in the mined and unmined sites as the habitat structure in these regions is probably similar as they are both dominated by *Acacia karoo*. The large areas of these *Acacia* stands that follow mining, compare to those that follow farming (unmined site) may be important.

Whatever the reasons, the trend is clear - large fruited species (and large birds) are the most likely species to be slow to recolonise disturbed areas. The results however showed that, although large fruited species were slow to be introduced, they showed a greater recovery than those with medium fruits. This may be as a result of dispersal by monkeys which have been observed to forage in both mined and unmined areas (Foord et al., 1994). If these animals show a preference for large fruits, this could explain why species with large fruits recover more rapidly than species medium sized fruits.

Another related factor that might affect the colonisation rates is the size of seeds. While fruit size is has immediate importance in determining if a fruit will be dispersed at all (as birds generally swallow the fruit whole) seed size may affect the distance that propagules are dispersed. Small seeded species are generally dispersed further than large seeds as small seeds are usually ingested and defecated away from the parent tree. Large seeds are not always swallowed, but if ingested they are often regurgitated and so are not usually dispersed such great distances (Levey, 1986). This may have important consequences in the colonisation of the vast areas that are disturbed by mining and should be investigated further.

The type of fruit of a species, which gives an indication of its seed dispersal mechanism, seems to have a definite affect on the species colonisation ability. The wind dispersed seeds of *Brachylaena discolor* are probably well dispersed and may explain this species rapid colonisation in the mined areas. The hard fruited species which are absent from rehabilitating stands will be slow to recolonised mined area. *Strychnos gerrardii,* for example has a poor dispersal mechanism as these fruits generally gather at the base of the parent (pers. obs). Although these fruits are consumed by monkeys, which are found in both mined and unmined areas (Foord at al., 1994) it is unlikely that species will be dispersed far, as their seeds may be to large to be ingested.

Establishment in the new environment

Shade tolerance:

The trend in shade tolerance (measured by SLA) was unexpected. It was assumed that the average shade tolerance of a community would increase as succession increases, as it was expected that canopy cover increased with age. However, the overall decrease in the shade tolerance of the community may be due to the fact that most of the trees in this region have a high SLA relative to trees in other parts of the country and therefore most probably require gaps for regeneration (Midgley et al., 1995). The dense canopy of *A. karoo* that develops early on in the rehabilitation may inhibit the regeneration of these gap requiring species. As the community ages, more of these species may be able to establish as the *A. karoo* canopy begins to thin and some trees become senescent.

Another consideration is that the SLA figures used were only for species that were typical of the forest at its climax state. No pioneer species were included, and since this is the group expected to have a low shade tolerance the results may have been different if these measurements were included. This trait is easy to measure so the possibility of using this as an indication of the probability of colonisation should be investigated further with more thorough sampling.

Regeneration and breeding system:

Neither breeding system or primary regeneration mode showed any trends in colonising ability. This may be due to the fact that the classification of these systems were very rough and did not give an accurate indication of the real situation. While the idea of using ability to resprout is tempting, in reality it is difficult to measure. It would perhaps be more expedient to study the seed production and vigour more directly, although this is also a large undertaking. More detail on the breeding systems of plants could be obtained from herbarium material.

The lack of any clear trend in regeneration or reproductive specialisation may also be due to these factors having only secondary importance in the colonisation of species. A well dispersed plant (small fruit) that has a specialised breeding system, or depends largely on resprouting for regeneration, has a good chance of colonising an area as the chances for becoming established will be increased, and need for reproduction in the rehabilitating area will be decreased due to the continual input of new propagules. In comparison the chance of a large fruited species becoming established is already low due to their naturally low abundance and poor dispersal of these fruits. Any factor reducing these species chance of survival and reproduction will have a marked effect on the colonisation ability of these plants. It is in these species that reproductive specialization and poor regeneration by seeds may be important.

CONCLUSION:

Seed dispersal appears to the primary factor limiting colonisation of dune forests. While shade tolerance seems to have little effect on the colonisation of species no conclusion can be drawn as data used was probably biased. Although no trends were observed in either primary mode of regeneration (which affects seedling vigour) or pollination system, it is hypothesised these factors, when combined with traits that limit dispersal, may result in a species with little chance of colonising mined, or similarly disturbed areas. This species could be considered as "high risk species".

The validity of this, classifying species as "high risk" or low risk" in terms of their colonisation ability, as hypothesied above, is difficult to assess as 80% of all indigenous species found in unmined forests have not colonised the rehabilitating sites. This means that many "low risk" species are not found in the rehabiliating areas. However, only one "high risk" species has colonised the mined areas - *Carissa macrocarpa* (which has large fruits and specialised flowers). Very few species in the dune forest fall into the "high risk" category which, if the hypotheses is correct may be a further indication that rehabilitation will most likely be successful.

There are increasing demands on ecologists to develop generalisations that can be used to anticipate the long term impact of disturbances and aid restoration of natural ecosystems (Davidson, 1993). It has however become apparent from this study that, while it is likely that predictions can be made concerning the probability of species recolonising mined area, few short cuts exist. A flaw in this study was to try and create generalisations based on generalisations and a more thorough study is needed to test some hypotheses. If these are shown to be correct, it may be possible to make predictions, but, due to the limited information on most species, this may require more field work than originally anticipated (which is not necessarily a bad thing!)

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