THE AUTECOLOGY OF *WIDDRINGTONIA CEDARBERGENSIS* IN RELATION TO ITS CONSERVATION MANAGEMENT

BY

PATRICK TIMOTHY MANDERS

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CONTENTS

ABSRACT

The Clanwilliam cedar is an endangered tree species confined to the Cederberg mountains in the south-western Cape Province. An assessment of the current status of the species is presented as an introduction to the thesis. In the introduction inferences are made from the available evidence on the previous status of the populations. The present status is inferior to that prior to the influence of European settlers. Theories presented by previous authors to account for the decline are examined.

A transition matrix model was developed, based on data from permanent monitoring plots, to model the population dynamics of the species. The methods of dealing with the data and fitting the observations to the transition matrix are presented. An eigenvalue of 1,01444 was calculated for the species, indicating population growth in the absence of fire. Inferences drawn from this model indicate that a minimum interval of 15 to 20 years between fires is necessary for the survival of the species.

An analysis of habitat features obtainable from maps was used to define the general distribution range and the actual distribution of cedars within their range. Altitude is the major factor influencing both the general and actual distribution. Indirect evidence is presented in this analysis to indicate that cedars can grow over a far greater area within their present distribution range.

Sowing experiments were conducted in the field to determine the effects of season of sowing and site features on germination success and seedling survival. Seeds sown in autumn exhibit the best combination of germination and establishment success.

It is concluded that the Clanwilliam cedar can be successfully managed without detriment to the other species in the community and therefore warrants efforts for its conservation. Intervals of 15 to 20 years between prescribed burns are recommended on the grounds that cedar stands will be afforded sufficient time to recover from the mortality of the previous fire, especially with respect to seed production. At the same time, this interval should be short enough to preclude the occurrence of extremely intense wild fires and thus should prevent the associated high cedar mortality.

Prescribed burns should be applied in late summer or autumn coinciding with the natural period of seed release. This will maximise the germination and establishment of the seed released from both the survivors and the trees killed. Where deemed necessary in terms of adult mortality or seedling recruitment, seed should be sown on selected sites as soon after a fire as possible. Cedar mortality will depend more on the conditions under which the prescribed burn is applied than on the season in which the burn is carried out.

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PREAMBLE

In line with recent practices this thesis has been written as a series of papers suitable for publication. This is to avoid duplication of effort and to ensure that the results are published and made available to a wider readership.

The thesis is presented in six parts. In Part one the situation and problems relating to the study are reviewed. In Part two the theory and methods of developing a transition probability matrix are presented, and in Part three this transition probability matrix is used in a transition matrix model. Appendix A is included in Part two as it will be published with this paper. Parts two and three are separated primarily to avoid a bulky and confusing single presentation. It will be requested that they are published together.

Parts four and five are largely aimed at answering questions related directly to the conservation management of the species. Part four deals with the habitat on a broad scale and Part five includes some aspects of more specific habitat requirements. Part six, the general conclusion, serves only to gather the main conclusions together, and is not intended for publication.

As none of these papers has been published yet, they are referred to by part number and paper number within the thesis.

PART ONE : INTRODUCTION

BACKGROUND

The only coniferous tree genera indigenous to South Africa are *Widdringtonia* and *Podocarpus*. *Widdringtonia*, the sole representative genus of the Cupressaceae in South Africa, occurs mainly along the southern and eastern mountain ranges, extending as far north as Malawi (Marsh 1965). Members of this genus are generally known as the 'African Cypresses' (Chapman 1961). Marsh (1965) recognised three species of *Widdringtonia*, namely: *W. cedarbergensis* Marsh (the Clanwilliam cedar), *W. schwarzii* (Marloth) Mast. (the Willowmore cedar) and *W. cupressoides* (L.) Endl. (the mountain cypress).

The Clanwilliam cedar is confined to the Cederberg mountains in the south western Cape Province (Figure 1). The species has been placed in the category 'Endangered', defined as being in immediate danger of extinction if the causal factors continue operating, or with numbers so critically reduced, that a breeding collapse is possible even in the absence of the causal factors (Hall *et al*. 1980).

The decline in cedar numbers has been noted by several observers since the early 19th century. Unfortunately they did not provide accurate descriptions of the distribution and status of the cedars and the first reliable records are very recent. Reasons advanced to account for the decline include over-exploitation and the very apparent deleterious effects of fire. Attempts

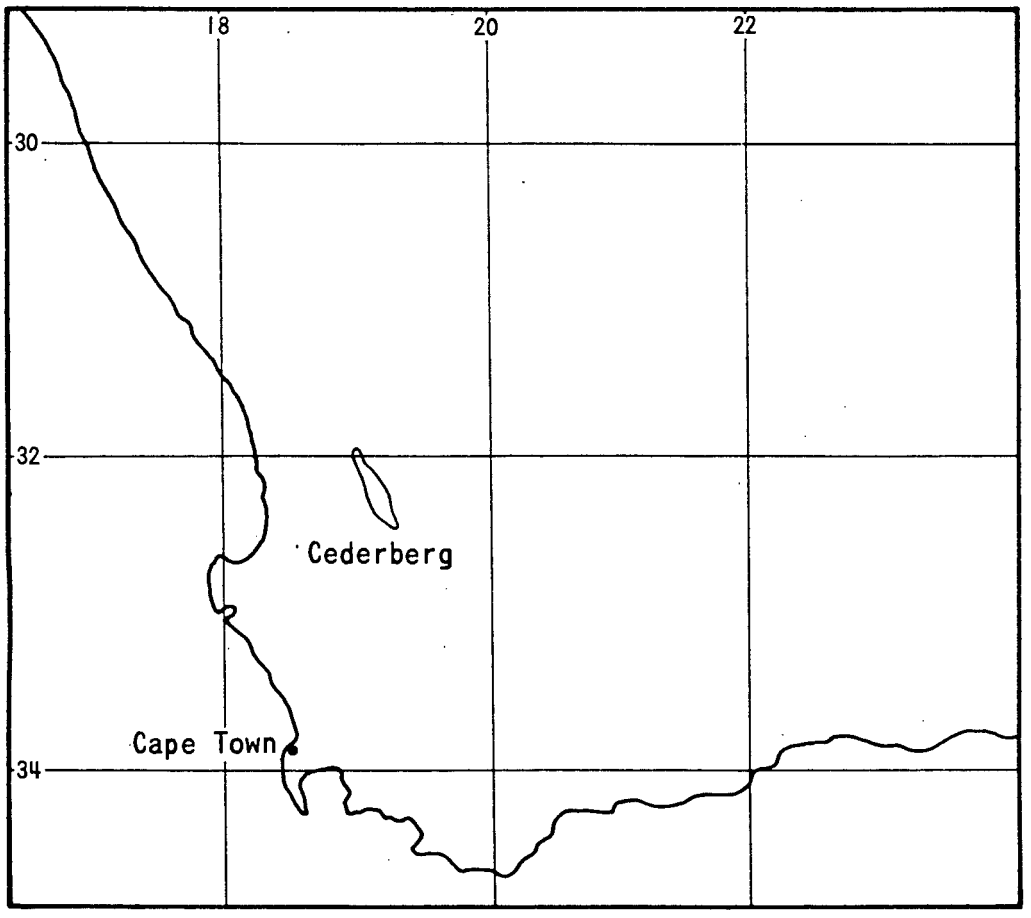


FIGURE 1. Location of the Cederberg

to reverse the decline of the cedars through management of the area and re-stocking have been made since the later years of the last century with questionable success.

The Cederberg is a proclaimed Mountain Catchment Area, and as such is managed primarily to ensure a sustained yield of high quality water (Bands 1977). Secondary objectives include the maintenance of species diversity, the control of wild fires and the preservation of the wilderness character. Fynbos is a fire-adapted vegetation (Van der Merwe 1966, Kruger 1979, Bond 1980, Van Wilgen 1982) and fire is the major form of management (Kruger 1977). Options open to managers in the implementation of fire include variation in the fire season, fire frequency, size of area burnt and the conditions under which the burn is carried out.

The Cederberg, due to the presence of the endangered Clanwilliam cedar on a significant area of the catchment provides a special case. Management of this catchment will have to take cognizance of the requirements of the cedars without proving detrimental to the general vegetation.

HABITAT

The Cederberg lies between latitudes 32° 00′ and 32° 45′ south, and longitudes 18° 50′ and 19° 25′ east, within the winter rainfall region of South Africa. Although the maximum altitudes are not

great, there is pronounced local relief. Citrusdal, to the south-west of the range is approximately 170 m above sea level, and the highest peak of the Cederberg is Sneeuberg at 2028 m, only 19 km away.

Most of the range is composed of sedimentary sandstones of the Table Mountain Group, with some remnants of the older Malmesbury Shales on the lower western slopes (Bands 1981). The dominant vegetation of the Cederberg is mesic mountain fynbos (Moll et al. 1984).

Hot dry summers occur in the Cederberg from October to April, while winters (May to September) are cold and wet. Large differences in altitude over short distances result in a wide range of annual rainfall, which tends to increase with altitude. Night temperatures often drop below freezing in winter and frost occurs frequently. Summer daytime temperatures are in the range of 25 °C to 30 °C, with occasional extremes of over 40 °C.

PRESENT DISTRIBUTION

In general, cedars are found on cliffs, rocky outcrops and very rocky slopes, and not on the sandy flats between rocky outcrops. They occur in low restio shrubland and in some areas are conspicuously associated with Paranomus tomentosus and Protea magnifica (Andrag 1977).

The distribution of W. cedarbergensis, based on black and white aerial photographs taken in 1960 is shown in Figure 2 (Haynes and Van Dijk 1979). The altitude range of the species is 1050 m to 1650 m above sea level, with isolated specimens at lower altitudes, some of which occur next to an old homestead and were probably planted.

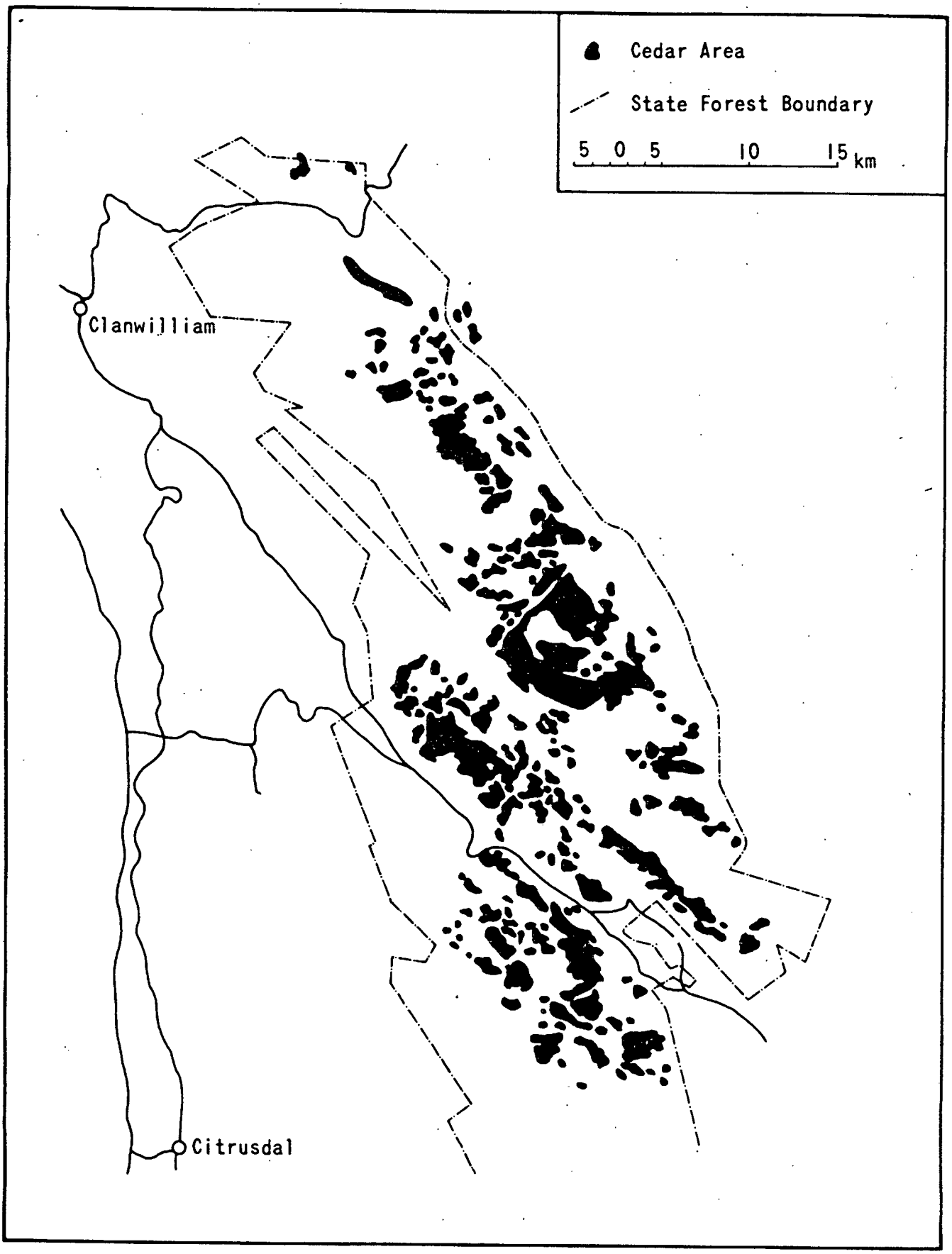
Cedars near the northern limits of the distribution range are not vigorous. The northernmost stand shows no recruitment and may die out (Andrag 1977). Cedars grow mainly on eastern slopes in the northern areas, but elsewhere are not obviously limited to any aspect (Andrag 1977). Most stands occur on the Peninsula Sandstone Formation, with some stands in the east and north-east on the Nardouw Sandstone Formation above the shale band. The only natural occurrence on the shale band is in the east and here they grow prolifically, forming the only remaining closed stand of cedars.

EARLY MANAGEMENT AND CONTROL

The first definite attempt to restrict the exploitation of cedar wood on Crown land came with the appointment of a Forest Ranger at Clanwilliam in 1876. In 1879 the felling of living cedars was banned and only dead and fallen trees were allowed to be utilised (Luckhoff 1972).

Further attempts were made in 1891 to alleviate the pressures

Figure 2. The distribution of the Clanwilliam cedar (Haynes and Van Dijk 1979).


Cedar Area
State Forest Boundary
5 0 5 10 15 km
Clanwilliam
Citrusdal

on the cedars. Grazing in the area was prohibited and more ranger help was supplied in summer to combat fires. The prohibition on grazing was considered ineffective and was lifted in 1910.

Large areas of the Cederberg were proclaimed Crown Forest Reserve in the late nineteenth century to facilitate control, and the sale of dead trees was restricted to recognised sawyers (Luckhoff 1972). A fire policy was introduced early in the twentieth century under which all cedar areas were protected from fire. Burning and the issuing of grazing permits were stopped in all Forest Reserves in 1937.

A policy of burning cedar areas on a four year cycle and protecting all other veld was implemented in 1956, but protection of all areas was re-introduced after one or two years. In 1967 exploitation of dead trees was stopped in a move aimed primarily at preventing supposed deliberate incendiarism to provide a source of dead trees (Luckhoff 1972). Prescribed burning on a 12 year planning cycle was introduced in 1972.

The first records of organised re-establishment are to be found in the annual report of the Conservator of Forests for 1896 (Hutchins 1896). Seeds sown the previous year had developed into seedlings approximately 23 cm high. In the year of the report, 10 ha had been ploughed and sown with 181,5 kg of seed. A further 23 kg had been scattered between rocks in unprepared areas.

Between 1895 and 1905 an approximate total of 11 700 kg of seed (roughly 12 million seeds) was sown in the Cederberg, mainly in plantations and to a lesser extent in unprepared sites. Occasional references to the success of the plantings were made in subsequent annual reports. By 1903 the seeds planted in 1896 had developed into trees of up to nearly 5 m. Mortality must have been high as a large proportion of the sowings were in gaps in earlier plantations (Hutchins 1903). Seedlings were also raised in nurseries as early as 1897. The only references made to the numbers transplanted into the Cederberg are in 1904 and 1905 in which a total of 78 855 were planted out (Hutchins 1904, 1905).

After 1905 it appears that no further attempts at re-establishment were made until the early 1960's. In 1965 the following report was made: 'Early results of experiments show that seed sown *in situ* is completely destroyed by rodents and that, unless an effective rodent repellant can be found, this method of re-establishment is impracticable. Seedlings planted out in their natural habitat have established themselves well but in many cases have been badly browsed by dassies (rock rabbits)' (De Wet 1965).

Despite these problems, extensive attempts at re-establishment were continued. No effective rodent repellant was found, but it was discovered that two to three year old transplants were most suitable as dassie damage is not serious on plants this

size (Luckhoff 1974). However most attempts over the last 15 years have failed due to granivory, herbivory and the occasional severe drought (Kruger and Haynes 1978).

No transplanting has been carried out recently due to the contamination of the nursery stock at Algeria by the fungus Phytophthora cinnamomi.

EVIDENCE AND INFERENCE ON LEVELS OF EXPLOITATION

The Khoisan peoples who lived in the Cederberg area prior to European settlement were concentrated along the Olifants river and probably had little effect on the relatively inaccessible cedar areas. This inaccessibility also isolated the cedars for over 120 years after the landing of the first settlers in 1652 (Smith 1955). The earliest known record of the cedars is contained in a report by the Livestock and Agricultural Commissioner of an inspection of the area in 1805. The Commission found that sawyers had been living along the Cederberg for some time and making a living by selling timber in nearby districts. The Commission also made the first effort to regenerate the forest by instructing the sawyers to sow seed over the kloofs during April of each year (Smith 1955).

The lack of useful timber trees in the predominant shrublands of the region gave rise to excessive exploitation of the trees in the Cederberg and other forested areas (King 1938). Timber

was required for housing, fortification, shipping, as fuel for domestic and industrial use, and for all wooden products integral to the way of life of the period. Within a decade of the first settlement the Governor of the Cape found it necessary to place restrictions on timber cutting, and much of the timber used at the Cape was imported from Europe (Grut 1977). With wood at such a premium, harvesting practices were likely to have been short-sighted in the extreme.

This is supported by Sir James Alexander who in 1836 reported that no care was taken of the cedars and that the people in the neighbourhood '...cut them down without leave or license, and burn the grass to improve the pasture, by which many old trees and thousands of young plants are consumed annually' (Smith 1955). Soon after Alexander's visit, the German traveller W. von Meyer also mentioned the 'wanton destruction' of the cedar forests through cutting and burning (Luckhoff 1972).

In 1883 a telegraph line was erected between Calvinia and Piketberg, a distance of 290 km. This would have involved the felling of some 7250 pole stage trees (Andrag 1977). Today it would be impossible to find more than a few hundred suitable pole stage trees.

In 1883 the Superintendent of Woods and Forests of the Cape wrote, 'It is deplorable to witness how these valuable trees have been ruthlessly burned and the young trees destroyed by

sheep and goats. All, or nearly all, the accessible cedars of commercial value have gone'. In the same year the Conservator of Forests wrote 'The largest cedar still standing is about 18 feet in girth and about 70 feet in height but it is a dwarf compared with the big trees whose stumps are still standing as evidence of what they were. These past giants must have been nearly double the girth of any now standing' (Hubbard 1937).

Apart from uncontrolled exploitation and farming practices from the late 18th century to the late 19th century, there were several misguided attempts to improve the situation which may well have had a strongly negative effect on the cedars. Seed, for example, was largely planted in inappropriate parts of the Cederberg, resulting in a poor return for the effort involved. The collection of seed in itself also probably had serious deleterious effects. The 2 700 kg collected in 1900 represents the annual seed production of about 500 to 800 ha of good cedar stands. Furthermore it is almost impossible to remove cones from a branch without damaging the branch and it can be confidently assumed that the branches were cut off with the cluster of cones when harvesting the seed. Cedars usually produce cones on branches which have produced cones in previous years (personal observation). As there are three year's crops present at any given time, this means that removal of the branch also removes part of the cone crop for the following two years, as well as having an unknown effect on future cone production. The collection of nearly 12 000 kg of seed around the turn of the last century, therefore, had

a major effect on cedar populations.

EXAMINATION OF THEORIES REGARDING THE DECLINE OF CEDAR POPULATIONS

The hypotheses presented to account for the decline in the status of the cedars, aside from exploitation, include:

1. Excessive granivory and destruction of seedlings by rodents, dassies and baboons (De Hoogh 1968, Andrag 1977).
2. Frequent fires causing high mortality in young trees and seedlings (Haynes and Kruger 1972).
3. Fires occurring too seldom, with intensity and consequent tree mortality being too great (Andrag 1977).

These theories should be examined in relation to known aspects of the biology and population dynamics of the species.

Hubbard (1937) found large differences in the rate of growth of trees. Artificially established trees in plantations grew more rapidly than those naturally regenerated and this was ascribed to lower levels of competition from fynbos which was cleared before planting. This observation was substantiated by the higher growth rate in naturally regenerated plants after about 10 years by which time the competition from the surrounding fynbos was overcome.

Some germination of seed occurs every year, but is most prolific in the first winter and spring after a fire (Kruger and Haynes

1978). Unlike most fynbos species, cedars can germinate in dense fynbos between fires. Success is limited under a canopy of old trees (Kruger 1970), partly due to the litter from the trees in which seedlings tend to become chlorotic and stunted. No seed dormancy is apparent, with the seeds germinating within two weeks in moist sand or vermiculite under experimental conditions (Marsh 1965).

Seed production may begin when the tree is about 12 years old. Early production is minimal, and only after 40 years does it become significant with more than 30 clusters of cones per tree (Andrag 1977). The trees are monoecious, although young trees may bear only male cones at first.

A period of almost 36 months between fertilisation and release is required for the seeds to ripen (personal observation). Seedlings are seldom more than 30 m from the parent tree. If favourable microhabitats are limited then this limited dispersal may increase the probability of the seed landing in a favourable site (Kruger and Haynes 1978).

Baboons readily eat the seed in cones plucked from the tree. Various rodents eat the fallen seed which is aromatic and attracts granivores. De Hoogh (1968) found that the rodent population density in a cedar area on Middelberg was 17 ha^{-1}. In captivity the average consumption of cedar seeds, for which the rodents showed a marked preference, was about 4 g per day. Seed production

was estimated to be 227,1 g $ha^{-1}.year^{-1}$, from which it is evident that the rodent population is capable of consuming the entire annual seed crop in less than 4 days.

There are, however, several possible sources of error in these arguments. Firstly, absolute densities of small mammals are difficult to determine accurately. Secondly, in the estimation of the potential amounts of seed consumed, cedar seed was the sole source of food supplied, and no allowance was made for searching time. In addition, the area in which De Hoogh worked and derived his seed crop estimates has a low density of cedars (personal observation).

Most seed production is by old mature trees. Andrag (1977) derived a seed production index for 38 cedar plots based on the number of cone clusters present. Eleven of the plots were considered to have indices indicating self-maintenance and eleven plots were considered incapable of self-maintenance. The rest of the plots were considered to be of doubtful status. These ratings, however, are based entirely on personal assessment, and there are no data yet available on the seed production required to maintain a population.

A survey carried out in 1966 (Luckhoff 1972) revealed that 75% of standing cedars were dead, although many of these may have been very old. Only 0,78% of the trees enumerated were classed as 'healthy and vigorous without any fire damage', and

15% were 'reasonably healthy with only minor fire scars'. The number of young trees found was very low and averaged 0,88 for each parent tree. Andrag (1977) also claimed that there was insufficient replacement of mature trees killed in fires. The ratio of submature to mature trees in his survey was 0,64 to 1.

Although these assessments show an apparent imbalance in the population structure, trees which may have a mature phase of several hundred years should not require a high recruitment rate. Far more work on the population dynamics of the species is required before an assessment may be made of the recruitment and seed production rates required to maintain cedar populations.

It is the effect of fire on mortality and recruitment which exerts the greatest influence on cedar populations under the present circumstances. It is only relatively recently that fire has been accepted as a natural ecological factor in fynbos ecosystems (Bands 1977, Kruger 1977). Andrag (1977) mapped a total of 53 fires which burnt 35 800 ha of vegetation in the Cederberg between 1958 and 1974, with an average of 675 ha per fire. The majority of the fires occurred in the summer months, and these were by far the largest. He ascribed the causes of 58% of the fires to natural phenomena such as lightning and falling rocks.

<u>Widdringtonia cedarbergensis</u>, unlike most other fynbos species, does not, at first appraisal, appear to have a mechanism for

fire survival. Mortality in hot fires is high, no resprouting occurs and no seed pool is established either in the soil or on the plants. However, Kruger and Haynes (1978) found a high incidence of fire scars on living pole-stage trees, showing that even small cedars are able to survive some fires. This ability to escape fire is unusual in woody fynbos plants, and may be considered a form of mechanism for persisting through fire. In addition, germination after a fire is often prolific and seedlings growing on favourable sites should be large enough to stand a fair chance of survival in the next fire.

Several of the plots enumerated by Andrag (1977) were subsequently burnt. Examination of these plots showed that bigger trees had better survival rates. Factors affecting survival in fire included size of tree, fuel load, terrain and weather conditions.

Low level aerial photography has been used to compare the effects of wild fires and prescribed burns. Following prescribed burns, of the 935 trees assessed, 81,8% were unaffected, 11,7% were scorched and 6,5% killed. Assessment of the effects of a wild fire of January 1979 showed far greater mortality. In this case 56,5% of the trees were unaffected, 11,5% were scorched and 32% were killed (Van Wilgen 1980).

Forsyth (1979) found that the mortality of cedars in summer wild fires, excluding seedlings, was between 81,2% and 97,8%. In prescribed spring burns, mortality was between 6% and 18%. Survival

was again found to be positively correlated with tree size. A germination flush occurred after wild fires, with between 21 and 662 (average 365) seedlings per hectare. In comparison, one plot in the prescribed burn area had only two seedlings and the other plot had none.

Haynes and Kruger (1972) proposed the use of short interval winter burns to improve the survival rate of cedars in fire by decreasing the fuel load, but experimental implementation of this proposal was frustrated by extremely hot wild fires in 1975.

Andrag (1977) also proposed short intervals of ten years between fires, claiming better recruitment than on a 20 year cycle, faster growth as the fynbos would be suppressed, and the reasonably certain survival of mature seed-producing trees. The use of winter burns was accepted as the only alternative in view of the high mortalities in summer fires.

Despite the high mortalities in summer fires, prescribed burns in winter or spring are unacceptable due to unsatisfactory recruitment. Trees killed in a winter or spring burn release their seed in the post-fire environment at a time when germination may not occur until the following autumn. Exposure to granivores is therefore greatly extended and the survival rate of seeds likely to be minimal. Those seeds which do germinate are not sufficiently established to survive the ensuing summer drought.

Similar patterns occur in serotinous Proteaceae (Bond 1984). The seed released in the following autumn by the surviving cedars is possibly the only food source available and granivory appears complete. Recruitment levels remain minimal for some years (personal observation), possibly as a result of detrimental effects of winter burns on other food-producing fynbos species.

Pre-dispersal and post-dispersal granivory are not seen as a cause of the reduction of cedar status, but rather as factors which have become serious only in the present situation. Procedures developed to conserve cedars should attempt to lessen the effects of these factors.

The high mortalities recorded after summer fires have, to date, been the result of wild fires which typically occur in conditions of extreme fire danger, and thus have extreme intensities with consequent high mortality of cedars. Prescribed burns in summer or autumn could be implemented under less severe conditions, closer to the natural period of seed release. This would minimise mortality while maximising seedling recruitment, thus enhancing the status of the populations

Attention up to now has focussed on the striking loss of adult trees in fires. While this is an important component of population dynamics, any management prescription aimed at remedying this aspect without ensuring adequate regeneration will lead to the rapid extinction of the species.

RESEARCH REQUIREMENTS

From a review of the literature and an initial appraisal of the situation, a number of questions are raised which this study attempts to resolve. The first is whether the cedars have been reduced to a level from which recovery is impossible, and secondly there is the question of the species reaction to the season of fire and the interval between fire. This information will provide the basis of management prescriptions for the species.

Related to both these questions is the question of whether it is possible to re-introduce cedars into areas where they previously occurred. This study attempts to test the feasibility of re-establishment and to define potential growth sites.

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PART 2 : APPLICATION OF A TRANSITION MATRIX MODEL TO THE POPULATION DYNAMICS OF THE CLANWILLIAM CEDAR: 1. DEVELOPMENT OF THE MODEL

P.T. MANDERS

SOUTH AFRICAN FORESTRY RESEARCH INSTITUTE

JONKERSHOEK FORESTRY RESEARCH CENTRE

PRIVATE BAG X5011

STELLENBOSCH

SYNOPSIS

This paper describes the derivation of a transition probability matrix for application in a single species model of the population dynamics of the Clanwilliam cedar. The determination of appropriate size classes, dealing with irregular intervals between observations and fitting the observations to the the transition probability matrix are discussed. Seed production and the rate of recruitment from seed are estimated.

INTRODUCTION

The truism of Harper (1977) that the study of tree population dynamics is a study of short cuts is particularly pertinent in the case of the Clanwilliam cedar (*Widdringtonia cedarbergensis* Marsh) where mature trees may reach an age in excess of 400 years. The questions and problems relating to the management and conservation of the Clanwilliam cedar are presented in greater detail by Andrag (1977) and Manders (Part 1).

There are two major questions posed in the conservation of this species. The first is whether the species is capable of expanding its population, or whether it will become extinct regardless of attempts at conservation. The second question is what interval between fires will allow the survival of the species. The application of fire is the major means of managing catchment areas and therefore this second question is of fundamental importance.

There are few examples of transition matrix models being used to simulate the dynamics of tree species in natural situations. An attempt by Bosch (1971) received much criticism for its inaccuracies and misinterpretations (see Enright and Ogden 1979 and Namkoong and Roberds 1974) and may have caused some reluctance to use this method. Hartshorn (1975), in what may be considered the first valid application of the method to a natural plant population, also made a significant misinterpretation (see Enright and Ogden 1979).

Rather more successful attempts to use transition matrix models have been made by Enright and Ogden (1979), Enright (1982) and Usher (1969). They have also been for the dynamics of non-tree species (Bierzychudek 1982) and plant parts (Maillette 1982). Caswell (1982a, 1982b) has used transition matrix models to describe the dynamics of populations with complex life cycles. Multispecies or community models have also been derived, for example Stephens and Waggoner (1970, quoted by Enright and Ogden 1979) and Malanson (1983).

This study aims initially to investigate whether it is feasible to model the population dynamics of the Clanwilliam cedar with the transition matrix method. This paper deals with the derivation of a transition probability matrix for the species. The questions related to the self-maintenance of populations and the effects of various fire cycles will be dealt with in a later paper (Part 3).

DERIVATION OF THE TRANSITION PROBABILITY MATRIX

The principle of the transition matrix model

The approach is based on the Leslie matrix model (Leslie 1945,1948) which is a deterministic model, based on the age distribution of populations, and predicts the distribution of age classes at successive intervals. It was assumed that age-specific rates

such as mortality and fecundity are constant over a period of time (Leslie 1945).

A seminal development in the modelling of tree population dynamics was the modification by Lefkovitch (1965) where populations were grouped into developmental stages rather than age states. This avoids the problems associated with determining the age of an individual and allows for differences in developmental rates as there is no fixed relationship between size and age.

The basic Leslie model places the numbers of individuals in the different classes of the population in a column vector (a) in which the numbers of each class of the population are one unit older each row down the vector. This vector is premultiplied by the transition matrix (A) of fertility rates on the first row, and probabilities on the first subdiagonal which represent the proportions surviving to the next class corresponding to classes in the column vector. The product of the multiplication is the column vector (a_{t+1}), representing the population structure after one unit of time,

$$Aa_t = a_{t+1} .$$

This implicit progression from one age state to the next does not occur in the Lefkovitch (1965) modification. Here the matrix may also contain entries on the main diagonal which represent the probability of surviving in the same class over a unit of time. The entries in a matrix may therefore be defined as the contribution which an individual in a stage makes to any other

or the same stage in a unit time interval.

As the transition matrix is square and irreducible, eigenvalues and eigenvectors exist such that

$$Av = \lambda V,$$

where v (the eigenvector) is a column vector and λ (the eigenvalue) is a scalar (Jeffers 1978). In the case of transition matrix models, a dominant eigenvalue, which is real and positive, exists with its corresponding eigenvector which represents the stable population structure (Williamson 1972).

The dominant eigenvalue is equivalent to e^r in the Lotka equation,

$$N_t = N_0.e^{rt},$$

where r is the intrinsic rate of natural increase (Leslie 1945). Therefore if $\lambda=1$, $er=1$ and $r=0$, and the population neither increases or decreases. Increasing populations are indicated by $\lambda>1$ and decreasing populations by $\lambda<1$.

Sites

A number of permanent plots to monitor Widdringtonia cedarbergensis have been established since 1970. Enumerations were undertaken at irregular intervals until 1978. Certain plots with reliable and complete data were re-enumerated during 1983 and 1984. Details of the plots and the enumerations are given in Table 1. In all plots, all individuals were labelled with numbered steel labels and heights and diameters recorded at the first enumeration. Sub-

Table 1. A summary of the history and enumerations of the permanent monitoring plots.

PLOT AND AREA	DATE AND NATURE OF BURN	APPROX. VEG. AGE AT BURN (yrs)	DATES OF ENUMERATIONS
A (Sneeuberg hut) (1 ha)	13-12-75 wild fire	17	27-3-71
			13-8-74
			2-9-75
			2-2-76
			18-5-83
B (Hoogvertoon) (1 ha)	13-12-75 wild fire	17	29-3-71
			15-8-74
			5-9-75
			2-2-76
			15-9-83
C (Groot koupoort) (3,69 ha)	15-2-75 wild fire	35	10-1-71
			9-11-83
D (Grootland) Plot 1) (?)	?-9-78 Prescribed burn	20	7-2-77
			30-8-79
			18-1-84
E (Grootland Plot 2) (?)	?-9-78 Prescribed burn	20	7-2-77
			30-8-79
			18-1-84

sequently, individuals were re-measured and deaths due to fire and other reasons were recorded. New (recruited) plants were measured and labelled at each visit. At plot C (Groot Koupoort), where the plot was established after a burn, killed plants were also labelled and measured to provide an estimate of fire mortality.

Determination of size classes

Two sources of error in transition probabilities may result from the selection of size class. The first involves the errors of estimation which occur where the number of individuals in a class is low as a result of selecting too small a size class. The second involves the errors of distribution in a size class which is too large, and where individuals may show a skewed distribution within the category. Vandermeer (1978) has suggested a mathematical technique for balancing the two sources of error.

Early enumerations of the permanent monitoring plots divided populations into 5 size categories based on height and growth form (Table 2). Diameters at 1,4 m along the trunk axis (or below a branch swelling at this point) were measured where applicable. Heights were not measured for mature classes (classes 3 - 5) in all instances. With the measurements available from the previous enumerations 13 size categories (Table 3) were arbitrarily selected without mathematical procedures, but taking due cognizance of the possible sources of error.

Table 2. Categories used for the classification of cedars by height and growth form in observations up to 1978.

DEFINITION	TREE CLASS
Seedlings and young plants (no mature leaves)	1
Young saplings <1,4 m with mature leaves	2
Pole stage trees >1,4 m with conical crown	3
Mature trees >2,5 m with spreading crown	4
Dwarfed trees <2,5 m of mature form	5

Table 3. Categories used for the classification of cedars by height and diameter for the transition count matrices.

DEFINITION	CLASS
Seed	1
<= 25 cm high	2
> 25 cm and <= 50 cm high	3
> 50 cm and <= 75 cm high	4
> 75 cm and <= 100 cm high	5
> 100 cm and <= 125 cm high	6
> 125 cm and <= 150 cm high	7
> 150 cm high with diameter <= 5 cm	8
> 5 cm diameter and <= 10 cm diameter	9
> 10 cm diameter and <= 20 cm diameter	10
> 20 cm diameter and <= 40 cm diameter	11
> 40 cm diameter and <= 60 cm diameter	12
> 60 cm diameter	13

Construction of transition count matrices

Transition matrix models are mathematically convenient. The difficulty lies in the logical and mathematical approaches to the derivation of the elements of the transition matrix.

To determine the numbers of a class which move into the next, authors (Enright 1982, Enright and Ogden 1979 and Hartshorn 1975) have hitherto assumed that this number consists of those individuals which would move into the next class if the average growth of the class is added to their actual height or diameter. It was felt that this is an unnecessary assumption in this case, especially as there is no class which does not have promotion in at least one of the observations, and that observations were carried out for up to 12 years on some of the plots. In addition, this method not only adds to the necessary calculations, but will also mask the diversity of growth rates. Actual counts of individuals moving up through classes are therefore used in this study.

Each individual in each plot was assigned to a size category at each enumeration. From this a transition count matrix was developed for each interval between observations in each plot, representing the numbers of each class which stayed in the same class, moved to other classes or died. A transition count matrix was also derived for the fire mortality recorded at the first enumeration in plot C. Transition count matrices for all periods

are presented in appendix A.

Standardisation of transition count matrices

Optimally, a transition matrix model should be constructed from data obtained at fixed discrete intervals of time. These intervals would then be used as the time units of the model, and the data from all observations fitted to the transition matrix using a maximum likelihood method. In this study, this form of model construction was precluded by the form of the existing data and has not been used.

The variation in the intervals between observations necessitated a standardisation of the transition count matrices. From the rates of death, mortality and promotion exhibited over the intervals between enumerations, further transition count matrices were derived to cover one year from the beginning of the interval for the 9 intervals which did not include fire.

An individual in a size class has two alternatives. In the first instance the individual may die (d) or survive (s), and in the second instance the individual may stay in the same class (q) or move to another (p). In both cases the probabilities total to 1, ie.:

(1) $s + d = 1$, and

(2) $q + p = 1$.

Following the individuals in a single class through time, one would arrive at the following:

	Start		Die	Survive	Promote	Stay
Year 1	X	->	dX	sX	psX	qsX
Year 2	qsX	->	$qsdX$	$qssX$	$qspsX$	q^2s^2X
Year 3	q^2s^2X	->	q^2s^2dX	q^2s^2sX	q^2s^2psX	q^3s^3X
					etc.	

If at an observation after N years, the following observations are made for the class:

D (number that have died)

P (number that have promoted)

S (number that have remained and survived in the same class), then:

(3) $D = (1 + qs + q^2s^2 + \ldots\ldots\ldots + q^{N-1}s^{N-1})dX$

(4) $P = (1 + qs + q^2s^2 + \ldots\ldots\ldots + q^{N-1}s^{N-1})psX$

(5) $S = q^N s^N X$

(6) $X = D + P + S.$

The rates s, d, p and q may be calculated as follows:

From (3) and (4),

$$\frac{D}{P} = \frac{d}{ps} = \frac{1-s}{ps}$$

$$\therefore \frac{Dp}{P} = \frac{1}{s} - 1 \quad \text{and} \quad p = \frac{P}{D}.\frac{1}{s} - \frac{P}{D}$$

(7) $$\therefore p = \frac{P}{D}.\left(\frac{1}{s} - 1\right)$$

From (5),

$$qs = \left(\frac{S}{X}\right)^{\frac{1}{N}} = (1 - p)s$$

$$\therefore \left(\frac{S}{X}\right)^{\frac{1}{N}} = s - s\left(P.\frac{1}{D} - \frac{P}{s\,D}\right)$$

$$\therefore D\left(\frac{S}{X}\right)^{\frac{1}{N}} = Ds - P + Ps$$

$$(8) \qquad \therefore s = \frac{D\left(\frac{S}{X}\right)^{\frac{1}{N}} + P}{D + P}$$

From (7) and (8) and the relationships (1) and (2), the rates s, d, p and q for the first year of each interval may be derived.

For cases where no mortality is observed (D = 0) then s = 1 and from (5):

$$q = \left(\frac{S}{X}\right)^{\frac{1}{N}},$$

and p = 1 - q. These equations are then used in place of (7).

Fitting the observations to the transition probability matrix

Two assumptions should be tested in order to have confidence in the predictions of a transition matrix model (Bierzychudek 1982):

1. The transition probability matrix describes a first order Markov process, ie the transition probabilities during the time interval t - t+1 depend only upon the state an individual is in at time t, and not on its state at any previous time. In this case this would entail determining whether an individual's past history exerts an influence on the transition probabilities which is not evident from its present state.

2. The transition probability matrices remain constant with time, ie the transition probability matrices exhibit stationarity or may be considered as homogeneous Markov processes. Bierzychudek (1982) criticises previous authors for not testing these assumptions.

The test devised by Anderson and Goodman (1957) and presented in a biological context by Usher (1979) to test the first assumption is that used by Bierzychudek (1982). However this test makes no allowance for matrices with input through reproduction or output through mortality. Furthermore, in the equation for this test,

$$-2\ln\lambda = 2\sum_{i=1}^{m}\sum_{i=1}^{m} n_{ij}\ \ln(P_{ij}/P_j)$$

where P_{ij} is the probability of transition from state i to state j (Anderson and Goodman 1957), $\ln(P_{ij}/P_j)$ is mathematically undefined for most cases of i and j in transition count matrices, whereas it is usually defined in Markov matrices for which it was derived. In fact Anderson and Goodman (1957) specifically make the assumption that every P_{ij} is greater than zero. Bierzychudek's (1982) criticism, as far as testing of the first assumption is concerned may be rather harsh..

The form of model construction proposed and used here is a method of goodness of fit which rejects the poorest-fitting transition count matrix in a stepwise procedure.

From each of the standardised transition count matrices a contingency table was drawn up for each observation of the possible outcomes (stay promote or die) for each of the classes 2 to 13. For the purposes of the analysis all promotions to higher classes were combined. Goodness of fit was tested using the G test (log likelihood ratio) which approximates the χ^2 distribution (Sokal and Rohlf 1968).

The null hypothesis tested is that outcome is independent of observation (both with regard to plot and time of observation). The best fit for successive combinations of plots is shown in Table 4. The best possible fit is for the observations plot A (1974), plot A (1976), plot C (1977) and plot D (1979) where $0,75 > \alpha > 0,50$. However, for the purposes of the model it was decided to use a different combination, namely plot A (1974), plot B (1976), plot C (1977) and plot D (1979). There is less independence in this combination ($0,25 > \alpha > 0,10$) but the combination includes one observation from each area and most of the observations are in the post-fire period, and thus for the longest intervals. This combination was therefore selected for a presumed wider applicability to cedar growth in general.

Table 4 also shows the results of tests for 'stationarity' in those plots (A and B) where successive enumerations were carried out, using the G test method. The results may be interpreted as showing significant differences in transition probabilities with time. However, they are regarded here as being indicators

Table 4. Results of the G test carried out on the non-fire observations. (The combinations refer to the standardised transition count matrix for each enumeration in each plot, for example A'71 refers to the standardised transition count matrix for 1971 to 1974 in plot A).

NUMBER IN COMBINATION	COMBINATION	DEGREES FREEDOM	G VALUE
9	A'71 A'74 A'76 B'71 B'74 B'76 C'77 D'79 E'79	16	125,116
8	A'71 A'74 A'76 B'71 B'76 C'77 D'79 E'79	14	75,055
7	A'71 A'74 A'76 B'71 B'76 C'77 D'79	12	51,164
6	A'74 A'76 B'71 B'76 C'77 D'79	10	32,117
5	A'74 A'76 B'76 C'77 D'79	8	10,1641
4	A'74 A'76 C'77 D'79	6	4,5781**
4	A'74 B'76 C'77 D'79	6	10,0811*
3	A'71 A'74 A'76	4	26,352
3	B'71 B'74 B'76	4	75,922

** α > 0,50

* α > 0,10

of the high variation between observations within the limited data set available. It will be of interest to test this feature with an extended data set after further observations.

The effects of the fire on the transitions are assumed to be minimal by the beginning of the intervals (up to 23 months after the fire for plot C and plot D). The interval for plot B starts only two months after the fire, however, as the greatest effect of fire is considered to be in respect of recruitment from seeds (class 1) to class 2, and this probability was derived separately, the same assumption was made for this plot as well.

The transition count matrices for the four selected observations were combined (Table 5) and from this transition count matrix a transition probability matrix was derived (Table 6) by taking each entry as a proportion of the column total. No class 12 or 13 individuals died in any of these selected observations. This was considered to be unrealistic as even mature trees die on occasion in non-fire situations (personal observation). The totals of the transition probabilities for these two classes were therefore reduced to 0,999.

Seed production

The seed production of cedars in the various size classes was estimated by counting the mature cones on trees in different areas. Samples from some of the trees were taken to determine

Table 5. Transition count matrix for the combined observations for plot A (1974), plot B (1976), plot C (1978) and plot D (1979).

CLASS

	2	3	4	5	6	7	8	9	10	11	12	13
2	47,56											
3	11,44	33,52										
4	1,00	7,91	19,92									
5		1,22	4,78	33,77								
6		0,96	1,39	1,46	12,74							
7				1,25	0,96	5,17						
8			1,00	2,00	2,25	6,83	62,45					
9							1,22	23,31				
10							0,26	0,92	44,77			
11									2,08	45,56		
12										1,21	19,34	
13											0,65	9,00

Table 6. Transition probability matrix derived from the transition count matrix in Table 5.

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0												
2	.00181	.743											
3		.179	.684										
4		.016	.161	.687									
5			.025	.165	.750								
6			.020	.048	.032	.670							
7					.028	.050	.431						
8				.034	.044	.118	.569	.833					
9								.016	.932				
10								.004	.037	.933			
11										.043	.949		
12											.025	.966	
13												.032	.999

the number of seeds per cone. The average seed production of trees in each size class is given in Table 7. No relationships between seed production and area or between seeds per cone and tree size were apparent.

Recruitment from seed

The rate of recruitment into class 2 from seed (class 1) was estimated for each of the observation periods from the standardised transition count matrix for the period (Table 8). Seed present was calculated from the average seed production of each class multiplied by the number present in that class at the beginning of the interval, and summing the production of all the classes. The over-all proportion derived from all the observations is $8{,}198 \times 10^{-4}$.

CONCLUSION

It has been possible to derive a transition probability matrix from the available data for this species. Although it was necessary to allow some latitude in the statistical procedures, the matrix should provide a means to model the population dynamics of the cedar.

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Numerous members of the Jonkershoek staff have assisted in the enumerations of the permanent monitoring plots. I would particularly

Table 7. Average annual seed production of cedars in size classes. (No seed production in classes 2 to 5)

SIZE CLASS	SEED PRODUCTION
6	0,988
7	3,65
8	33,74
9	104,6
10	490,1
11	1215,0
12	2806,0
13	2704,0

Table 8. Recruitment from seed to class 2 in all intervals between enumerations of the permanent monitoring plots

OBSERVATION (* = fire)	PROPORTION OF SEED -> CLASS 2
Plot A (1971)	7,458 x 10-5
Plot A (1974)	1,873 x 10-5
Plot A (1975) *	6,776 x 10-4
Plot A (1976)	1,949 x 10-3
Plot B (1971)	2,286 x 10-4
Plot B (1974)	9,942 x 10-4
Plot B (1975) *	0
Plot B (1976)	3,370 x 10-3
Plot C (1977)	2,712 x 10-3
Plot D (1977) *	0
Plot D (1979)	1,485 x 10-5
Plot E (1979)	0
Plot E (1979)	2,642 x 10-5

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APPENDIX A : TRANSITION COUNT MATRICES FOR ALL INTERVALS ON PERMANENT MONITORING PLOTS (SEEDS NOT INCLUDED)

Plot A (Sneeuberg hut) 1971 - 1974.

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	58	0	0	0	0	0	0	0	0	0	0	0
3	2	14	26	0	0	0	0	0	0	0	0	0	0
4	2	1	6	14	0	0	0	0	0	0	0	0	0
5	7	1	0	7	14	0	0	0	0	0	0	0	0
6	1	0	0	1	4	7	0	0	0	0	0	0	0
7	0	0	0	0	2	4	3	0	0	0	0	0	0
8	2	0	1	0	0	4	2	50	0	0	0	0	0
9	0	0	0	0	0	0	0	0	7	0	0	0	0
10	0	0	0	0	0	0	0	0	2	17	0	0	0
11	0	0	0	0	0	0	0	0	0	0	11	0	0
12	0	0	0	0	0	0	0	0	0	0	0	9	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0
Died	0	7	5	1	1	0	0	0	0	0	0	0	0
Tot.	15	81	38	23	21	15	5	50	9	17	11	9	0

Plot A (Sneeuberg hut) 1974 - 1975

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	47	0	0	0	0	0	0	0	0	0	0	0
3	0	12	29	0	0	0	0	0	0	0	0	0	0
4	0	0	8	16	0	0	0	0	0	0	0	0	0
5	0	0	1	5	23	0	0	0	0	0	0	0	0
6	0	0	1	0	1	8	0	0	0	0	0	0	0
7	0	0	0	0	0	1	4	0	0	0	0	0	0
8	0	0	0	0	0	1	5	47	0	0	0	0	0
9	0	0	0	0	0	0	0	1	7	0	0	0	0
10	0	0	0	0	0	0	0	0	0	19	0	0	0
11	0	0	0	0	0	0	0	0	0	0	11	0	0
12	0	0	0	0	0	0	0	0	0	0	0	9	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0
Died	0	0	3	2	5	3	0	11	0	0	0	0	0
Tot.	1	59	42	23	29	13	9	59	7	19	11	9	0

Plot A (Sneeuberg hut) 1975 - 1976

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	3	28	0	0	0	0	0	0	0	0	0	0	0
3	4	4	31	0	0	0	0	0	0	0	0	0	0
4	3	0	2	16	0	0	0	0	0	0	0	0	0
5	1	0	0	1	19	0	0	0	0	0	0	0	0
6	1	0	0	0	2	7	0	0	0	0	0	0	0
7	0	0	0	0	0	1	2	0	0	0	0	0	0
8	2	0	0	0	0	1	3	50	0	0	0	0	0
9	0	0	0	0	0	0	0	0	7	0	0	0	0
10	1	0	0	0	0	0	0	0	0	16	0	0	0
11	0	0	0	0	0	0	0	0	0	0	11	0	0
12	0	0	0	0	0	0	0	0	0	0	1	9	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0
Died	0	16	8	7	8	1	0	3	1	3	0	0	0
Tot.	15	48	41	24	29	10	5	53	8	19	12	9	0

Plot A (Sneeuberg hut) 1976 - 1983

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	432	1	0	0	0	0	0	0	0	0	0	0	0
3	154	11	2	0	0	0	0	0	0	0	0	0	0
4	56	5	7	2	0	0	0	0	0	0	0	0	0
5	34	4	7	6	7	0	0	0	0	0	0	0	0
6	19	1	5	3	8	3	0	0	0	0	0	0	0
7	3	0	0	0	2	1	2	0	0	0	0	0	0
8	17	0	1	5	4	3	1	36	0	0	0	0	0
9	0	0	0	0	0	1	0	4	1	0	0	0	0
10	1	0	0	0	0	0	0	0	3	11	0	0	0
11	0	0	0	0	0	0	0	0	0	3	5	0	0
12	0	0	0	0	0	0	0	0	0	0	2	5	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0
Died	0	9	17	5	0	2	0	16	3	3	4	5	0
Tot.	716	31	39	21	21	10	3	56	7	17	11	10	0

Plot B (Hoogvertoon) 1971 - 1974

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	41	0	0	0	0	0	0	0	0	0	0	0
3	6	11	19	0	0	0	0	0	0	0	0	0	0
4	14	3	9	14	0	0	0	0	0	0	0	0	0
5	17	0	1	13	30	0	0	0	0	0	0	0	0
6	0	0	0	2	20	25	0	0	0	0	0	0	0
7	0	1	0	0	10	20	10	0	0	0	0	0	0
8	6	1	0	0	43	0	7	139	0	0	0	0	0
9	0	0	0	0	0	0	0	4	16	0	0	0	0
10	0	0	0	0	0	0	0	0	0	10	0	0	0
11	0	0	0	0	0	0	0	0	0	0	18	0	0
12	0	0	0	0	0	0	0	0	0	0	0	8	1
13	0	0	0	0	0	0	0	0	0	0	0	0	0
Died	0	4	3	3	5	4	2	8	0	0	0	0	0
Tot.	43	61	32	32	108	49	19	151	16	10	18	8	1

Plot B (Hoogvertoon)1974 - 1975

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	17	28	0	0	0	0	0	0	0	0	0	0	0
3	22	3	24	0	0	0	0	0	0	0	0	0	0
4	9	1	4	26	0	0	0	0	0	0	0	0	0
5	11	0	2	5	42	0	0	0	0	0	0	0	0
6	1	0	0	0	4	27	0	0	0	0	0	0	0
7	0	0	0	0	0	4	28	0	0	0	0	0	0
8	0	0	0	0	2	0	1	182	0	0	0	0	0
9	0	0	0	0	0	0	0	1	19	0	0	0	0
10	0	0	0	0	0	0	0	0	1	9	0	0	0
11	0	0	0	0	0	0	0	0	0	0	17	0	0
12	0	0	0	0	0	0	0	0	0	0	0	8	0
13	0	0	0	0	0	0	0	0	0	0	0	0	1
Died	0	9	6	9	13	16	12	13	0	1	1	0	0
Tot.	60	41	36	40	61	47	41	196	20	10	18	8	1

Plot B (Hoogvertoon) 1975 - 1976

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	1	0	0	0	0	0	0	0	0	0
5	0	0	0	0	1	0	0	0	0	0	0	0	0
6	0	0	0	0	0	1	0	0	0	0	0	0	0
7	0	0	0	0	0	0	1	0	0	0	0	0	0
8	0	0	0	0	0	0	0	4	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	2	0	0	0
11	0	0	0	0	0	0	0	0	0	0	3	0	0
12	0	0	0	0	0	0	0	0	0	0	0	4	0
13	0	0	0	0	0	0	0	0	0	0	0	0	1
Died	0	45	49	39	59	31	31	181	20	8	14	4	0
Tot.	0	45	49	40	60	32	32	185	20	10	17	8	1

Plot B (Hoogvertoon) 1976 - 1983

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	232	0	0	0	0	0	0	0	0	0	0	0	0
3	227	0	0	0	0	0	0	0	0	0	0	0	0
4	75	0	0	0	0	0	0	0	0	0	0	0	0
5	32	0	0	0	0	0	0	0	0	0	0	0	0
6	6	0	0	0	0	0	0	0	0	0	0	0	0
7	1	0	0	0	0	0	0	0	0	0	0	0	0
8	6	0	0	1	1	1	1	4	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	1	0	0	0
11	0	0	0	0	0	0	0	0	0	1	3	0	0
12	0	0	0	0	0	0	0	0	0	0	0	3	0
13	0	0	0	0	0	0	0	0	0	0	0	1	1
Died	0	0	0	0	0	0	0	0	0	0	0	0	0
Tot.	579	0	0	1	1	1	1	4	0	2	3	4	1

Plot C (Groot Koupoort) ? - 1977

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	5	0	0	0	0	0	0	0	0	0	0
4	0	0	0	4	0	0	0	0	0	0	0	0	0
5	0	0	0	0	13	0	0	0	0	0	0	0	0
6	0	0	0	0	0	3	0	0	0	0	0	0	0
7	0	0	0	0	0	0	1	0	0	0	0	0	0
8	0	0	0	0	0	0	0	6	0	0	0	0	0
9	0	0	0	0	0	0	0	0	12	0	0	0	0
10	0	0	0	0	0	0	0	0	0	14	0	0	0
11	0	0	0	0	0	0	0	0	0	0	13	0	0
12	0	0	0	0	0	0	0	0	0	0	0	1	0
13	0	0	0	0	0	0	0	0	0	0	0	0	3
Died	0	0	31	40	70	44	23	216	74	105	26	4	1
Tot.	0	0	36	44	83	47	24	222	86	119	39	5	4

Plot C (Groot Koupoort) 1977 - 1983

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	217	0	0	0	0	0	0	0	0	0	0	0	0
3	335	0	1	0	0	0	0	0	0	0	0	0	0
4	140	0	1	2	0	0	0	0	0	0	0	0	0
5	45	0	1	0	3	0	0	0	0	0	0	0	0
6	12	0	0	2	2	0	0	0	0	0	0	0	0
7	8	0	0	0	1	0	0	0	0	0	0	0	0
8	14	0	0	0	0	2	1	0	0	0	0	0	0
9	0	0	0	0	0	0	0	3	6	0	0	0	0
10	1	0	0	0	0	0	0	0	2	7	0	0	0
11	0	0	0	0	0	0	0	0	0	4	8	0	0
12	0	0	0	0	0	0	0	0	0	0	1	1	0
13	0	0	0	0	0	0	0	0	0	0	0	0	3
Died	0	0	2	0	7	1	0	3	4	3	4	0	0
Tot.	772	0	5	4	13	3	1	6	12	14	13	1	3

Plot D (Grootland Plot 1) 1977 - 1979

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	5	0	0	0	0	0	0	0	0	0	0	0
3	0	2	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	1	0	0	0	0	0	0	0	0	0
5	0	0	1	0	1	0	0	0	0	0	0	0	0
6	0	0	0	0	1	1	0	0	0	0	0	0	0
7	0	0	0	0	0	1	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	6	0	0	0	0	0
9	0	0	0	0	0	0	0	2	4	0	0	0	0
10	0	0	0	0	0	0	0	0	0	13	0	0	0
11	0	0	0	0	0	0	0	0	0	0	21	0	0
12	0	0	0	0	0	0	0	0	0	0	1	5	0
13	0	0	0	0	0	0	0	0	0	0	0	0	5
Died	0	69	0	0	0	0	0	2	0	1	2	1	0
Tot.	0	76	1	1	2	2	0	10	4	14	24	6	5

Plot D (Grootland Plot 1) 1979 - 1984

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	1	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0
6	1	0	0	1	0	1	0	0	0	0	0	0	0
7	0	0	0	0	1	0	0	0	0	0	0	0	0
8	0	0	0	0	1	1	1	4	0	0	0	0	0
9	0	0	0	0	0	0	0	1	4	0	0	0	0
10	0	0	0	0	0	0	0	1	2	7	0	0	0
11	0	0	0	0	0	0	0	0	0	4	15	0	0
12	0	0	0	0	0	0	0	0	0	0	4	6	0
13	0	0	0	0	0	0	0	0	0	0	0	0	4
Died	0	4	2	0	0	0	0	0	0	2	2	0	1
Tot.	2	5	2	1	2	2	1	6	6	13	21	6	5

Plot E (Grootland Plot 2) 1977 - 1979

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	24	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	1	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	1	0	0	0	0	0	4	0	0	0	0	0
9	0	0	0	0	0	0	0	0	5	0	0	0	0
10	0	0	0	0	0	0	0	0	2	12	0	0	0
11	0	0	0	0	0	0	0	0	0	1	17	0	0
12	0	0	0	0	0	0	0	0	0	0	0	5	0
13	0	0	0	0	0	0	0	0	0	0	0	0	3
Died	0	221	0	0	0	0	0	0	0	0	0	0	0
Tot.	0	248	0	0	0	0	0	4	7	13	17	5	3

Plot E (Grootland Plot 2) 1979 - 1984

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	8	0	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	2	0	0	0	0	0
9	0	0	0	0	0	0	0	2	2	0	0	0	0
10	0	0	0	0	0	0	0	0	1	10	0	0	0
11	0	0	0	0	0	0	0	0	1	4	10	0	0
12	0	0	0	0	0	0	0	0	0	0	5	4	0
13	0	0	0	0	0	0	0	0	0	0	0	1	3
Died	0	23	1	0	1	0	0	1	1	0	3	0	0
Tot.	8	24	1	0	1	0	0	5	5	14	18	5	3

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PART 3 : APPLICATION OF A TRANSITION MATRIX MODEL TO THE POPULATION DYNAMICS OF THE CLANWILLIAM CEDAR: 2. APPLICATION OF THE MODEL

P.T. MANDERS

SOUTH AFRICAN FORESTRY RESEARCH INSTITUTE

JONKERSHOEK FORESTRY RESEARCH CENTRE

PRIVATE BAG X5011

STELLENBOSCH

SYNOPSIS

A transition probability matrix previously derived for the Clanwilliam cedar is analysed and used in a transition matrix model of the population dynamics of this species. An eigenvalue of 1.01444 is arrived at which is consistent with other investigations. This value indicates that cedar populations are theoretically capable of increase in the absence of fire. The model is manipulated to determine the factors required for the growth of stands of the species. A fire interval of 15 to 20 years is inferred for management of the vegetation where this species occurs.

INTRODUCTION

An earlier paper (Part 2) demonstrated the feasibility of the transition matrix approach for the modelling of the dynamics of the Clanwilliam cedar. A transition probability matrix (Table 1) was developed from observations on four permanent monitoring plots (A, B, C and D).

In this paper this transition probability matrix is analysed to determine whether the species exhibits population growth. The transition probability matrix is then used within a transition matrix model to determine the effects of different fire cycles on the species.

ANALYSES OF THE TRANSITION PROBABILITY MATRIX

The eigenvalue and eigenvector of the transition probability matrix were approximated by the power (iteration) method. The eigenvalue derived for the transition probability matrix is 1,01444, reached after 198 iterations. This value is comparable to those of 1,02041 derived for Araucaria by Enright and Ogden (1979) and 1,002 for Pentaclethra macroloba derived by Hartshorn (1975). Enright (1982) also arrived at a range of similar figures for stands of Araucaria.

The power method tends to produce eigenvectors with inconveniently large or small components which have no biological meaning. The

Table 1. Transition probability matrix for the Clanwilliam cedar derived from available data (Part 2)

CLASS

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0												
2	.00181	.743											
3		.179	.684										
4		.016	.161	.687									
5			.025	.165	.750								
6			.020	.048	.032	.670							
7					.028	.050	.431						
8				.034	.044	.118	.569	.833					
9								.016	.932				
10								.004	.037	.933			
11										.043	.949		
12											.025	.966	
13												.032	.999

eigenvector (Table 2) therefore, has been reduced proportionally according to the smallest component. The eigenvector thus shows the proportion of the numbers in the classes in a stable population structure and not the actual numbers.

Examination of the eigenvector can give some indications of the logic of the size class limits. It appears that classes 7 (125 to 150 cm high) and 8 (greater than 150 cm higher with a diameter less than 5 cm) are too small and too large respectively. This imbalance is also apparent in the actual situation in the monitoring plots (Part 2, Appendix A) It may be that the majority of individuals in class 7 are established and in a period of rapid growth. Class 8 on the other hand could possibly be split into two classes. This situation probably also reflects anomalies created by the change-over from height criteria to diameter criteria. However, as this is a stage projection matrix, and not based on age categories, differences in the length of time spent in any class will not affect the outcome of the model.

The greater number of class 13 compared to class 12 in the eigenvector is contrary to what one would expect. Again this could be remedied simply by splitting class 13, especially as a diameter of 60 cm is not at all large for a mature cedar. However this was precluded by the data available from the permanent monitoring plots.

Table 2. The eigenvector (proportional population structure) derived from the transition probability matrix (Table 1).

CLASS	NUMBER
1	13280
2	88
3	48
4	28
5	22
6	9
7	2
8	22
9	4
10	3
11	2
12	1
13	2

DEVELOPMENT OF THE MODEL

Recruitment

The over-all proportion of seeds developing to class 2 plants is $8,198 \times 10^{-4}$ (Part 2). Initial seed crops for each transition count matrix were calculated from the number of trees in each seed producing class. The proportions developing to class two plants were derived from the number of class two plants in the transition count matrix and the estimated number of seeds. Grouping those transition count matrices covering a fire into prescribed burns and wild fires shows a dramatic difference in recruitment (Table 3). No recruitment occurred after the prescribed burns (Plots D and E), even though the enumerations were a year after the burn. Furthermore there was virtually no recruitment in either of these plots in the period 1979 to 1984. Dividing the observations which covered wild fires into before-fire observations and after-fire observations again showed a difference in recruitment. In the before-fire observations (Table 3) the proportion of seeds developing to class 2 plants is $3,290 \times 10^{-4}$, whereas after the fires this proportion increased to $1,814 \times 10^{-3}$.

For the transition matrix the proportion of $1,814 \times 10^{-3}$ was included as a 'standard' probability of recruitment from seed. As the figures derived for the post-fire observations are for periods of 5 to 7 years after the burn, the standard value was applied for 5 years after fire in the model. Thereafter the value of

Table 3. Proportions of seed totals which developed to class 2 plants in all observations, in observations of spring burns and wild fires, and in observations before and after fires.

SOURCE OF MEAN	MEAN PROPORTION
ALL OBSERVATIONS	$8,198 \times 10^{-4}$
SPRING FIRES	0
WILD FIRES	$3,388 \times 10^{-4}$
BEFORE FIRES	$3,290 \times 10^{-4}$
AFTER FIRES	$1,814 \times 10^{-3}$

the probability was reduced by a function of time to approach the lower value of $3,290 \times 10^{-4}$ after 15 years, and remained at this value for the duration of the period before the next fire. The figure of 15 years was selected as this is the youngest approximate age of vegetation present in the surveys (plots A and B) before the fires.

This decrease in the probability of recruitment with vegetation age follows the trend expected with increased interspecific competition for growth sites in older vegetation, and possibly increased granivory by small mammals.

Preliminary studies have indicated dramatic effects of seed rain density on the levels of potential granivory (S.A. Botha personal communication, 1984). Insufficient data is available as yet for inclusion in the model, however this aspect is seen as an important future component of the model.

Potentially the most variable component of the transition probability matrix is the proportion of seeds developing to class 2 plants. Reduction of this proportion from $1,814 \times 10^{-3}$ to $1,814 \times 10^{-4}$, a reduction far greater than that employed in the model, reduced the eigenvalue to 1,00129 (after 212 iterations), which still indicates an increasing population.

Mortality in fire

The estimation of mortality in a fire presented a considerable problem. It is considered appropriate to apply prescribed burns to cedar areas in late summer (January to March) (Part 5). All prescribed burns in this study were conducted in spring when there is virtually no mortality in higher classes (Part 2, Appendix A, plot D (1977) and plot E (1977)) and wild fires in summer where mortality in all classes is very high (Part 2, Appendix A, plot A (1975), plot B (1975) and plot C (1976)). No data is available for prescribed burns in summer, where the mortality may be presumed to be intermediate as no prescribed burns would be undertaken in the extreme fire hazard conditions under which both the wild fires occurred.

A reasonable assumption is that mortality in fire will increase with vegetation age as the fuel load increases around the cedars. This is supported both by the data available for the wild fires and by the findings of Andrag (1977). Unfortunately the data in the latter case is not for compatible size classes and could not be included in the analysis.

The wild fires occurred in vegetation approximately 17 years old (plots A and B) and 35 years old (plot C). An arbitrary survival rate of 0,999 was included for a vegetation age of up to 4 years as there is little or no chance of fynbos vegetation burning younger than this. To derive an estimate of the function relating mortality to vegetation age, the survival rates of each class in the fires were regressed against time, using the

model fitting procedure NONLIN of the OXFORD statistical package.

In all classes the best fitting regression model for the 3 points is

$$Y = A + BX + CX^2,$$

where Y is the proportion of the population surviving and X is the time since the last fire in years. An example of the function is given in Figure 1. As this is a parabolic function, correction factors were introduced to maintain the minimum survival rate for values of X greater than that at which the minimum occurred in the function for each class.

RUNNING THE MODEL

The model was run using the derived mortality rates and the population structure present in plot A at the beginning of the post-fire period (1976) as this plot has the best stand of cedars. The initial population structure and that simulated every 20 years for 100 years without fire are given in Table 4 to demonstrate the rate at which the population is theoretically capable of expanding in the absence of fire. After 100 years the population structure is approaching the proportional structure of the stable population structure, with the same patterns in classes 7, 8 and 13 as seen in the eigenvector.

The quantity of seed present on a plot may be regarded as a function of the population of trees in that it reflects the

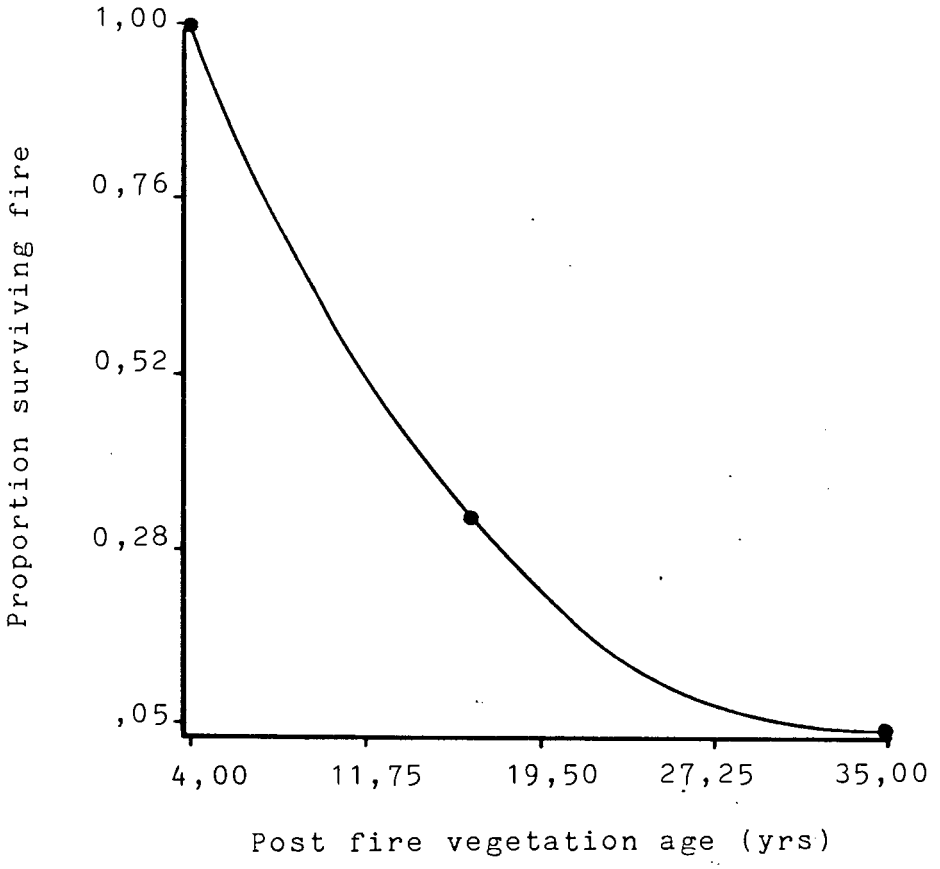

FIGURE 1. Survivorship rates of class 2 plants in fires in different post fire vegetation ages.
Plot of the model $Y = A + BX + CX^2$
$A = 1,28$; $B = 0,07$; $C = 0,001$; $R^2 = 1,000$

Table 4. Theoretical population development of the cedars present in plot A (1976).

CLASS	POPULATION STRUCTURE					
	INITIAL	20 YRS	40 YRS	60 YRS	80 YRS	100 YRS
1	38369	47814	54683	59694	63890	67933
2	31	65	71	78	83	89
3	39	42	39	43	47	49
4	21	32	23	26	28	30
5	21	32	19	21	23	25
6	10	12	7	8	9	10
7	3	3	2	2	2	2
8	56	38	22	22	24	26
9	7	9	7	6	6	6
10	17	9	7	5	4	4
11	11	10	8	6	5	4
12	5	4	7	6	5	4
13	0	4	8	12	15	18

numbers and sizes of trees on the plots. For convenience and brevity therefore, the effects of different fire cycles are demonstrated here by the resultant numbers of seed only.

A number of different fire cycles were tested (Figure 2) by running the model for the stipulated number of years between fires and then reducing the population according to the survivorship rates calculated by the method described above. In all cases the population decreased considerably.

One of the possible management options for the cedars is to 'boost' stands by sowing seed in the area, for which it is assumed that the immediate post-fire situation will be the most appropriate. To simulate this in the model, a figure of 50000 was added to the number of seed present after each fire in a 20 year cycle, using the original transition probability matrix. This had a negligible effect in the long term (18118 seeds after 200 years compared to 16718 without the addition of seeds).

The addition of seeds to assist stands should not be ignored however. The lack of success in this simulation may be attributed to the excessive mortality rates, and gives further indication of the unacceptability of this mortality. In the short term, within the fire intervals there were noticeable effects of the addition of seed. Class 8, for example, increased from 4,66 individuals after the fire at 21 years to 33,31 at 40 years with the addition of seed. Where no seed was added the number

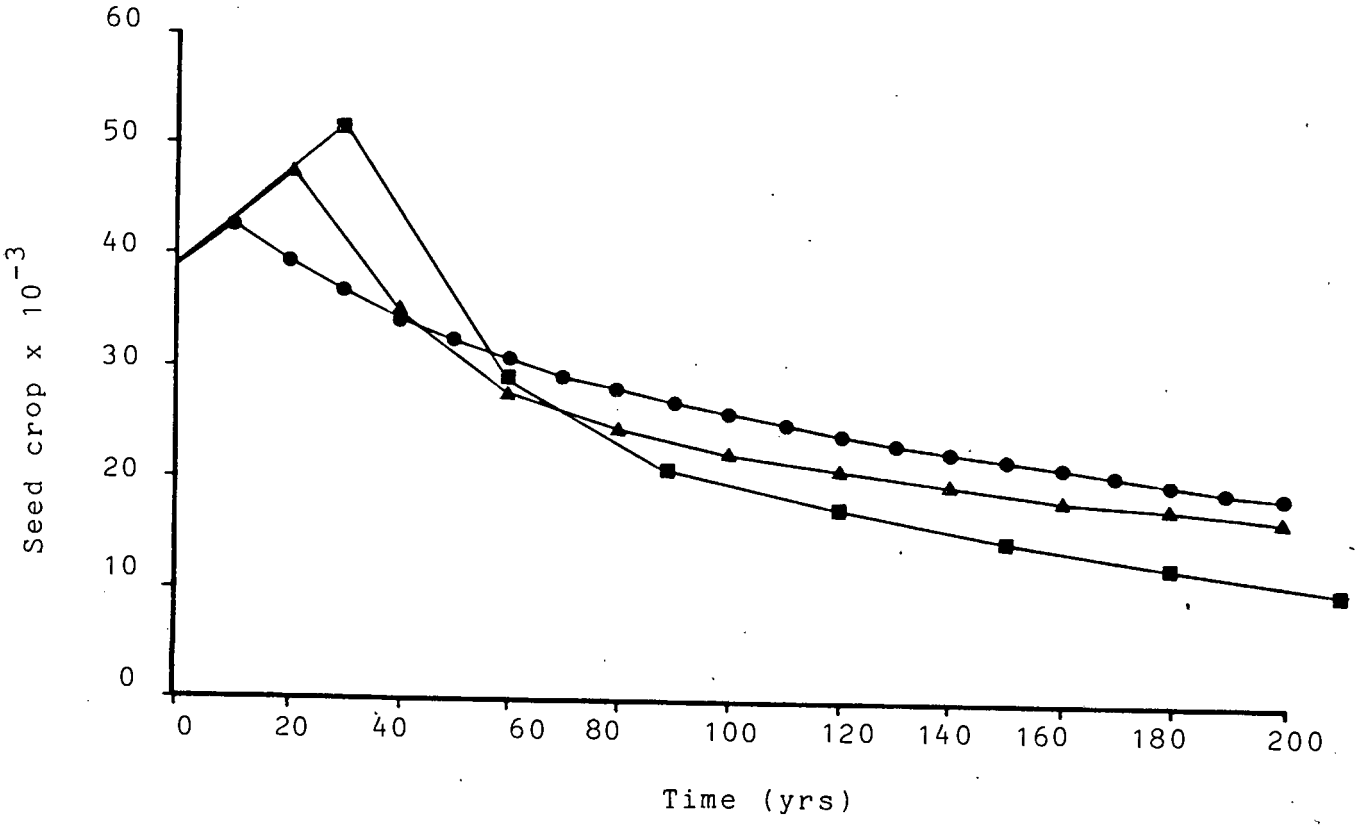

FIGURE 2. Simulated effect of different fire cycles on the cedar stand present on Plot A in 1976. ● = 10 year cycle; ▲ = 20 year cycle and ■ = 30 year cycle.

increased to 28,56 over the same 20 year interval.

This simulation also gives some indication of the considerable efforts required to achieve a modicum of success with this method, as 50 000 seeds represents an extensive collection from the available sources, and the data here only represents a stand on one hectare. The alternative of planting as opposed to sowing the seed to augment stands requires investigation when the problems concerning disease in the nurseries are resolved.

Inference on the optimal interval between burns

To be able to estimate the effects of different fire cycles on the cedar populations, a number of modifications were made to the transition probability matrix and the model. Firstly, examination of the transition probability matrix showed a high mortality rate for class 8 (column total = 0,8524 compared to 0,9999 for class 7 and 0,9691 for class 9). This is due to unusually high mortality in the 1974 observation in plot A.

To rationalise the transition probabilities for class 8, these were independently derived from all 9 non-fire observations, giving a proportion of 0,9374 remaining in the class and 0,0081 and 0,0005 moving to classes 9 and 10 respectively. This in effect reduced the eigenvalue from 1,01444 to 1,01437 due to the reduction in the probabilities of promotion.

Estimations were then made of likely mortalities in prescribed summer burns for each class. To achieve this, the derived survival rates were increased by 0,3 for the smaller classes to 0,6 for the larger classes, with maximum survivorship defined for each class (Table 5). With these modifications, the model was run for the same cycles as previously. Table 6 shows the resultant number of seed at the end of each run. The first significant increase in the seed crop occurs with a 20 year cycle.

Similar increases were found with this cycle, using the same transition probability matrix and the population structures of the other plots (Table 7). Although this indication of the acceptability of a 20 year cycle is hardly tenable on this premise alone, some indication is given here of the levels of survivorship in fire which must be attained in order to allow populations to develop.

Another approach used was to run the model using the original transition probability matrix with a population consisting of a number of seeds and no other plants (Table 8). There is no significant contribution from the resultant plants to the seeds until after 10 years. This is doubled by 15 years and after 25 years the seed production is roughly equivalent to that of one class 9 individual.

This situation does not realistically reflect the situation one would find after a fire, as in the actual situation the

Table 5. Theoretical survivorship rates applied to the population structure in the event of fire.

CLASS	MINIMUM	INCREASED BY	MAXIMUM	ACTUAL AT 20 yrs
2	0,05	0	0,2	0,2
3	0,1389	0	0,2	0,2
4	0,0909	0	0,2	0,17
5	0,1516	0,2	0,3	0,3
6	0,0638	0,3	0,4	0,4
7	0,0417	0,5	0,6	0,56
8	0,0270	0,5	0,7	0,62
9	0,1395	0,6	0,8	0,76
10	0,1176	0,5	0,8	0,8
11	0,3333	0,5	0,9	0,9
12	0,1500	0,4	0,95	0,95
13	0,7500	0,4	0,95	0,95

Table 6. Seed crops projected from the cedar stand on plot A in 1976 with revised transition probability matrix (see text) and mortality rates as in Table 5. Original seed crop = 38369.

FIRE CYCLE (YRS)	FINAL SEED CROP	LENGTH OF RUN (YRS)
10	20384	200
15	39016	210
20	51017	200
25	55868	200
30	51656	210

Table 7. Predicted seed crops with 10 fire cycles of 20 year intervals, using the revised transition probability matrix and mortality rates in Table 5.

PLOT	ORIGINAL SEED CROP	FINAL SEED CROP
A (1976)	38369	51017
B (1976)	18693	20585
C (1977)	35039	46813
D (1979)	63078	74816
E (1979)	51565	62373

Table 8. Hypothetical replacement by the developing population of the initial population consisting of 10 000 seeds.

YEAR	SEED CROP
1	0
2	0
3	0
4	0,41
5	2,10
10	30,66
15	65,39
20	89,22
25	107,04
30	123,88
40	157,09
50	185,41

survivors would continue to produce seed annually. It does however give some idea of the time scale required for a population of seeds to replenish itself after fire by recruitment rather than by the growth of the survivors. Reliance on the latter process must inevitably result in the loss of the stand after repeated fires.

The most direct method of determining the optimal interval between fires would be to project the development of the survivors of a prescribed summer burn and determine the length of time to regain pre-fire status. In the absence of data for such an event, the stable age structure of the eigenvector was taken as the initial population structure and the model run for 40 years without fire, using the original transition probability matrix.

Figure 3 shows the rate of percentage increase in seed production for 5 year intervals. This rate rapidly increases for the first 10 years, after which there is a rapid decline to 20 years, followed by a more gradual decline. The inference possible from the change in rates of increase of seed production is that prescribed burns should not be carried out for at least 10 years and preferably not before 20 years after the previous fire to allow the population's recovery to achieve full momentum.

The conclusion drawn from these inferences is that the optimal interval between fires for cedars is 20 to 25 years. There are however certain practical limitations to the interval between

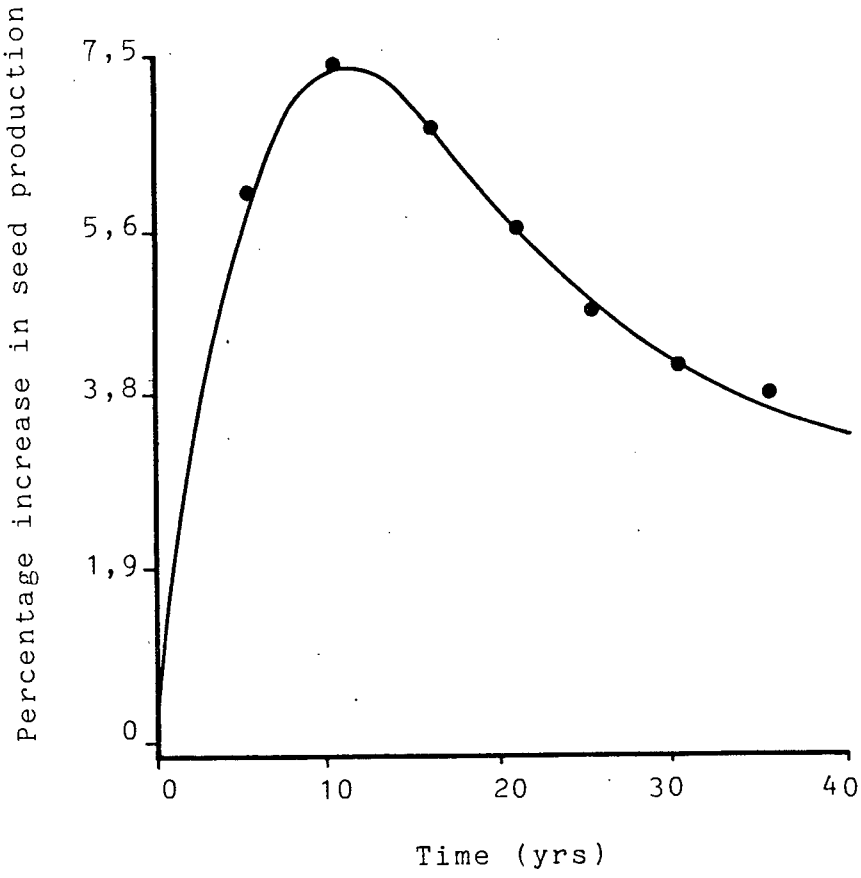

FIGURE 3. Simulated change in the rate of seed production with time. Initial population structure equal to that of the eigenvector (Table 2).

fires in that the probability of wild fires, with the associated extreme mortalities, becomes high for vegetation over 15 years old in the Cederberg. On these grounds it would seem wisest to implement a rotation between 15 and 20 years until there is data available on mortality in summer prescribed burns.

CONCLUSION

The model appears to lose credibility as soon as the lack of appropriate mortality data prevented the direct application of the model to answering one of the most important aspects of the conservation of this species,- the optimal interval between fires. It is therefore appropriate at this stage to examine the benefits derived by attempting to model cedar population dynamics.

Firstly, the exercise has provided an answer to the conundrum as to whether the cedars are merely a vestigial remnant of a species which is rapidly approaching extinction, irrespective of the influence of man. The answer is provided by the derived eigenvalue being greater than 1. This indicates that cedar populations are, in fact, theoretically capable of increase in the absence of fire.

Some inference has been possible on the most appropriate interval between fires, and it has also been demonstrated that, given hypothetical limitations on mortality, cedar populations are

theoretically capable of increase in the presence of fire. Although there is no factual basis for the establishment of these limits on fire mortality, they appear reasonable as mortality is more likely to be determined by fire intensity than fire season and it is possible that mortality in prescribed summer burns may approach that of the prescribed spring burns. If this proves to be the case, then the cedar populations will be able to increase almost as rapidly in the presence of fire as without fire.

A paradoxical situation is presented by the results of the model in that wild fires - the natural situation - are found to be unacceptable in terms of the excessive cedar mortality in these fires. This is most probably due to radical differences in the status of the cedars in the recent past which have altered aspects of their population dynamics, such as seed density and the consequent recruitment to class 2 plants. Mortality in fire could also be affected by reduction in the status of the cedars. Mature cedars suppress fynbos and closed stands have little or no vegetation beneath them. Closed stands may be self-protecting from fire to a certain extent. Exploitation and other negative influences of man in the recent past might have destroyed this self-protection by breaking up the stands of cedars.

Perhaps the most important positive aspect is that it has been shown to be feasible to derive a model from the existing data on cedar population dynamics. As the bulk of the cedar habitat is of much the same post fire age (c 10 years), it should be

possible to collect more appropriate data in a few years time, and use the model with modified fire mortalities to make more concrete prescriptions.

The model as it stands may be criticised for not introducing the concept of density and self-thinning principles. It was felt that this was not necessary at the present levels of cedar populations as even with considerable increases in density are possible without intra-specific competition. There are indications, however, that density will negatively affect recruitment and the development of trees (personal observation) and this element may have to be built into the model at some later stage.

ACKNOWLEDGEMENTS

I wish to thank Brian van Wilgen for useful comment on the text.

This report is based on work undertaken as part of the catchment conservation research programme of the South African Forestry Research Institute and is published with the permission of the Deputy Director General of the Directorate of Forestry.

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PART 4 : A CARTOGRAPHIC ANALYSIS OF THE FACTORS INFLUENCING THE DISTRIBUTION OF THE CLANWILLIAM CEDAR

P.T. MANDERS AND W.M. BRINK

SOUTH AFRICAN FORESTRY RESEARCH INSTITUTE

JONKERSHOEK FORESTRY RESEARCH CENTRE

PRIVATE BAG X5011

STELLENBOSCH

SYNOPSIS

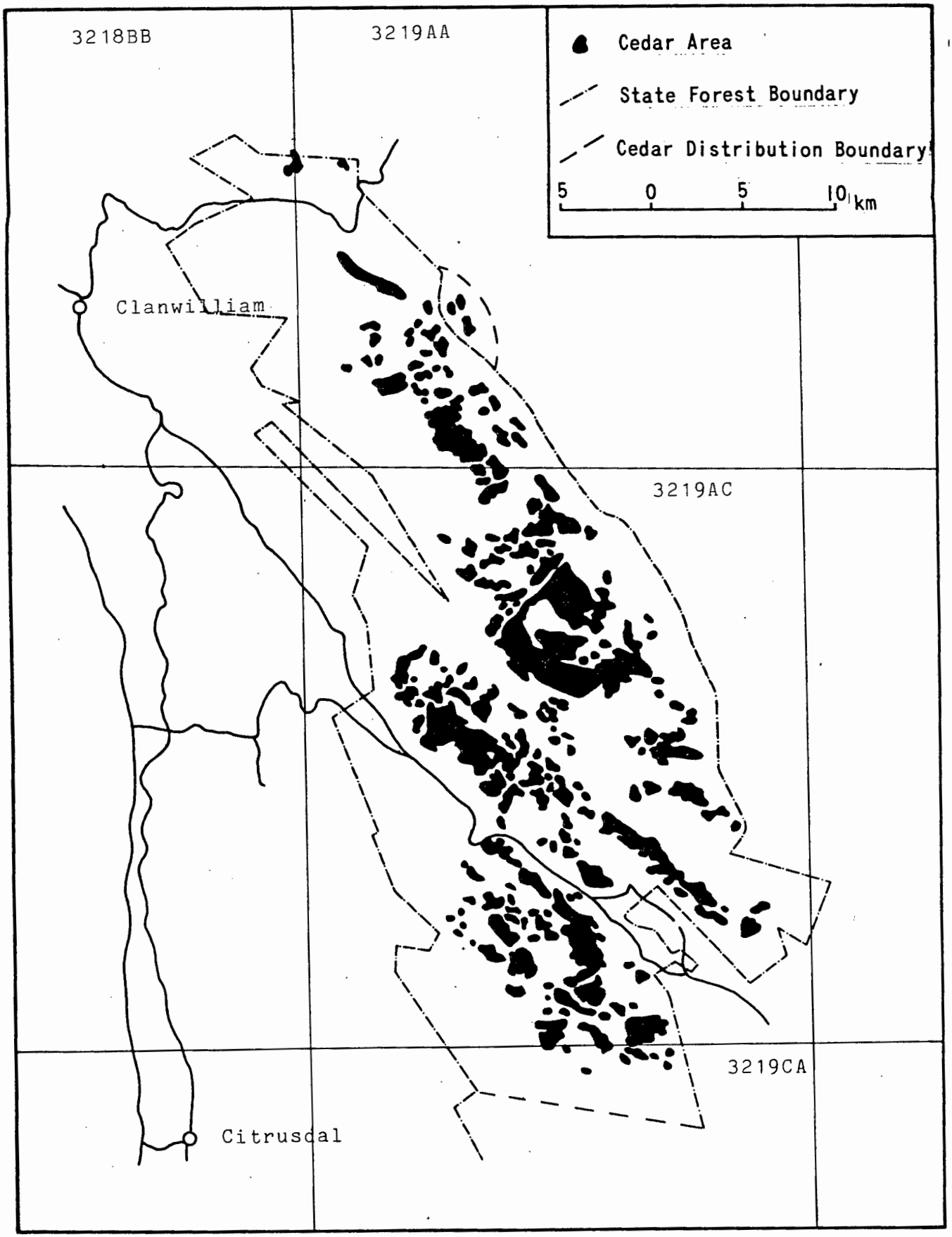
Features of the habitat of the Clanwilliam cedar were obtained from various maps and used to determine which factors were important in determining the general distribution range and the actual distribution within the general range. Analyses consisted of a G test (log likelihood ratio) of contingency tables. The factors studied are altitude, aspect, slope, geological formation and rainfall. Altitude proved to be the major limiting factor in both the general and actual distribution. Rainfall was also significant, but this may be due to the relationship with altitude. The results indicate that cedars can grow in many more areas within the Cederberg, reflecting the decline of the species in the recent historical past.

INTRODUCTION

The Clanwilliam cedar (*Widdringtonia cedarbergensis*) is an endangered species (Hall *et al.* 1980), confined to a range of approximately 250 km^2 in the Cederberg mountains in the western Cape Province. The distribution of the species (Figure 1) was mapped by Haynes and Van Dijk (1979) from black and white aerial photographs taken in 1960. Cedar areas were defined as containing cedars in a more or less continuous distribution, even if widely scattered. The boundaries of these areas were usually aligned with major habitat changes such as valley bottoms.

The question arises as to why the species is so restricted in its range and why, for instance, it does not occur southwards along the Kouebokkeveld mountains as there are no obvious physical or environmental barriers present. Within the distribution range, too, the occurrence of cedars is not uniform. As procedures to conserve the species are being developed, it is important to determine the reasons for this disjunct distribution to be able to define the cedar habitat and to include these factors in conservation management prescriptions. It will then be possible to determine whether the restricted occurrence is a result of environmental limitations. It will also be possible to define areas which potentially can be re-stocked with cedars, and areas in which the poor status of the cedar populations can be attributed to the marginal habitat.

Figure 1. Distribution range of the Clanwilliam cedar (Haynes and Van Dijk 1979), showing the relevant 1:50 000 topographical maps involved and the defined cedar distribution range.


3218BB
3219AA
Cedar Area
State Forest Boundary
Cedar Distribution Boundary
5 0 5 10 km
Clanwilliam
3219AC
3219CA
Citrusdal

This study describes a broad scale definition of the species' habitat using information available from various maps of the region to answer the above questions and to complement efforts being made to determine the habitat on a smaller scale. Mapped information for the area includes rainfall, geology, altitude, aspect and slope.

FEATURES OF THE CEDAR HABITAT

Climate

The Cederberg lies between latitudes 32° 00' and 32° 45' south and longitudes 18° 50' and 19° 25' east, within the winter rainfall region of South Africa. The summers between April and October are hot and dry, and rainfall is sporadic and unreliable. The winters are cold and good rains fall from May to September. Precipitation tends to increase with altitude and decreases eastward and northward.

The climate of those parts of the Cederberg in which cedars occur is considerably different to that of the surrounding lowlands. To illustrate this, Walter diagrams for Citrusdal and for a typical cedar area are presented (Figure 2). Citrusdal data is from the Weather Bureau, Department of Transport. The data for the cedar area is derived for an altitude of 1250 m , using a lapse rate of 0,36 °C per 100 m altitude (mean altitude vs mean temperature, Fuggle 1981), subtracted from each average

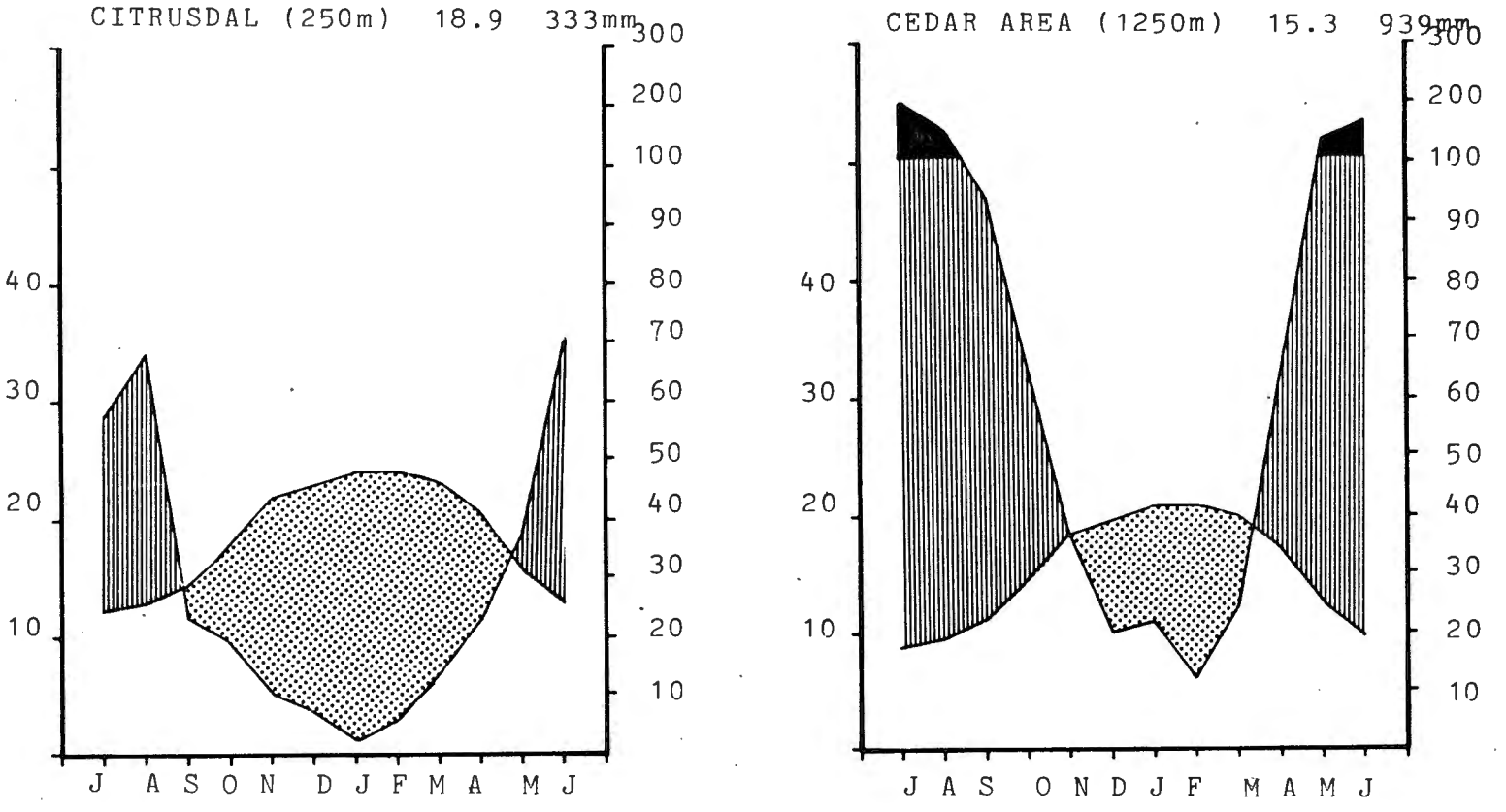


FIGURE 2. Walter diagrams for Citrusdal and a hypothetical cedar area

monthly temperature for Citrusdal. Rainfall figures are from the Weather Bureau, Department of Transport's data from a gauge on Middelberg (altitude of 1219 m) in the central Cederberg for the period 1914 to 1925.

Geology

The geological formations of the Cederberg consist almost entirely of sedimentary rocks of the Table Mountain Group, of which there are four formations present (Rust 1967). The uppermost formation is the Nardouw Formation, composed of coarse-grained quartzitic sandstones with occasional quartz pebbles. Under the Nardouw Formation is the Cedarberg Formation (the 'shale band') which consists of shales and mudstones, interbedded with fine-grained sandstones. The Pakhuis Formation is a thin layer of glacial mudstone with random sized pebbles, which is not uniformly present. The lowest formation is the Peninsula formation, a very thick deposit with the same composition as the Nardouw Formation. It is predominant in the Cederberg.

METHODS

Haynes and Van Dijk (1979) traced the areas in which cedars occur on to 1:50 000 topographical sheets. The four sheets involved in the study are 3218BB Clanwilliam, 3219AA Pakhuis, 3219AC Wuppertal and 3219CA Citrusdal (Figure 1). The great majority of the cedars occur in the areas covered by the 3219AA and 3219AC

sheets. A 30 second grid was drawn on each of the four sheets, providing a total of 961 intersections per sheet. For each sheet 50 intersections were randomly selected and the following details recorded for each intersection:

1. Cedars present or not. This was defined as whether the plotted intersection fell within a cedar area as defined and mapped by Haynes and Van Dijk (1979).

2. Cedar area or not. This area was roughly defined as the State Forest as this boundary more or less coincides with the distribution range of the cedars. The area to the south indicated in Figure 1 was excluded, and the area in the north east included.

3. Altitude. This was determined from the contour lines at the plotted intersection.

4. Slope. This was estimated by the number of contour lines intercepting a 4 mm line drawn perpendicular to the slope and centred on the intersection.

5. Aspect. This was estimated by measuring the angle in degrees from true north of a line drawn perpendicular to the contour line nearest the intersection and extended downslope. Eight categories of 45 degrees were used, N, NE, E, SE, S, SW, W and NW. N was defined as any bearing from 337,5 to 22,5 degrees.

6. Geology. This was obtained from a detailed geological map of the Cederberg Mountain Catchment Area (Bands 1981). Points outside the mountain catchment area were recorded as 'non-defined' for geology as the standard geological map is not of the same degree of detail.

7. Rainfall. This was estimated by superimposing the point on a 1:250 000 rainfall map for the area 3218 Clanwilliam. Isohyets of mean annual rainfall for the period 1921 to 1960 were compiled and drawn by the Hydrological Research Division, Department of Water Affairs from data obtained from the Weather Bureau, Department of Transport.

Of the 200 points on the four sheets, only 9 strikes were positive for the occurrence of cedars. To increase the number of positive strikes extra points were taken on the maps 3219AA and 3219AC. This was achieved by including the details for all intersections of each 30 second line of latitude and each one minute line of longitude where cedars are mapped as present on these maps. This brought the total number of positive strikes for the presence of cedars to 57 and the total number of observations to 248.

Analyses consisted of the formulation of two-way contingency tables which were then analysed using the G test (Sokal and Rohlf 1968).

RESULTS

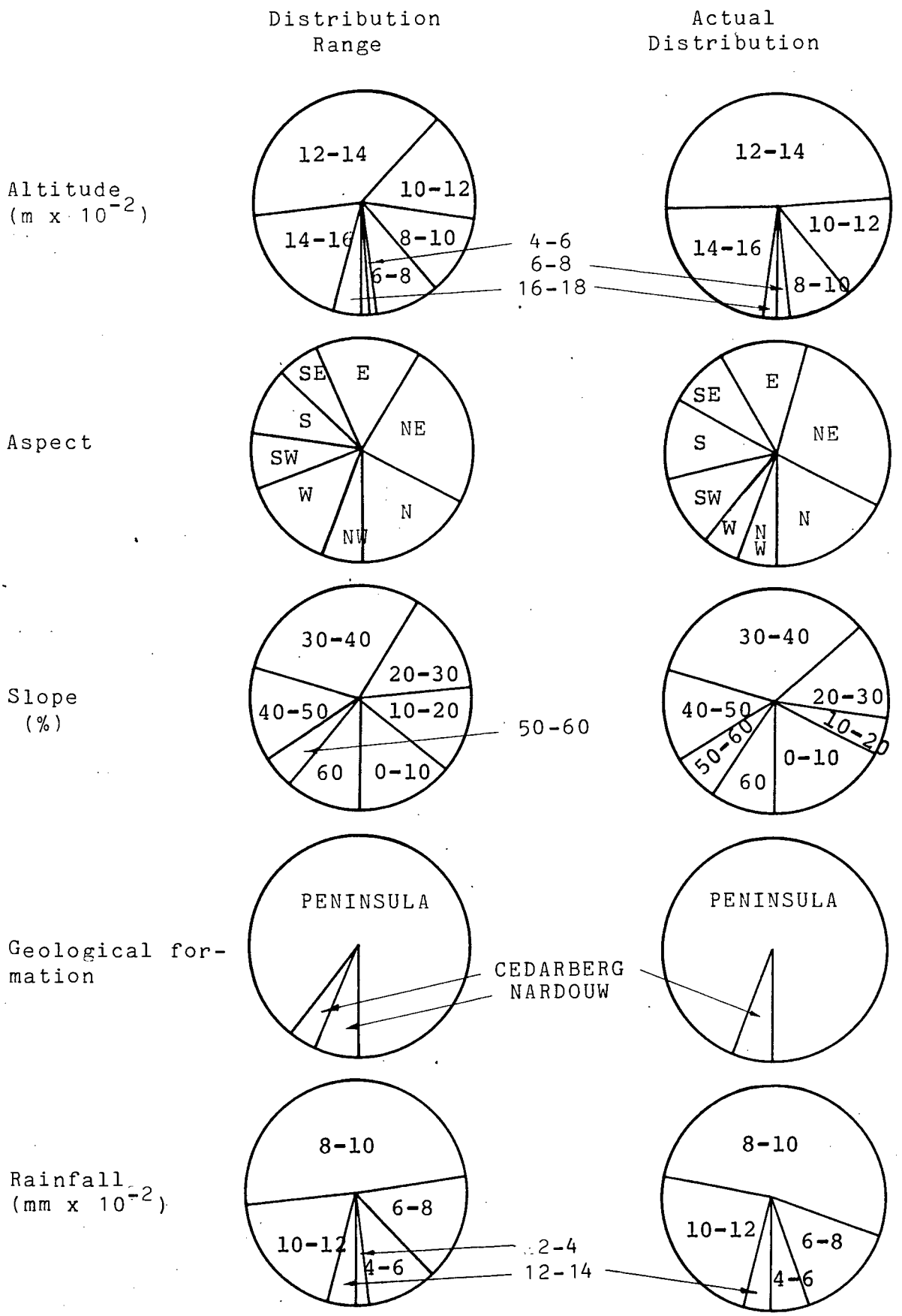
The first analysis was carried out on all observations and discriminated between points which landed in the defined cedar distribution range and those outside the cedar distribution range, with respect to the factors recorded (Table 1). In all analyses the null hypothesis is that there is no relationship between the categories of the factor and the distribution of cedars. Table 1 shows a strong relationship between altitude and the distribution of cedars, with 89,1% of positive strikes occurring in altitudes greater than 800 m. No relationship was found with aspect. Strong relationships exist between the distribution range and slope, geological formation and rainfall.

The second set of analyses (Table 1) tested the relationships between the presence or absence of cedars and the categories of the factors measured. In this case only the points which occurred in the defined distribution range were considered. The differences in the relationships between the factors and the distribution range and the actual distribution are shown in Figure 3.

Table 1. Results of the G tests for relationships between the distribution range and the actual distribution and the factors studied. ** = significant at P = 0,001, * = significant at P = 0,01, NS = not significant.

FACTOR	DISTRIBUTION RANGE		ACTUAL DISTRIBUTION	
	D.F.	G VALUE	D.F.	G VALUE
Altitude	8	160,34 **	7	19,23 *
Aspect	7	8,06 NS	7	10,46 NS
Slope	6	57,08 **	6	10,17 NS
Geology	2	15,71 **	2	7,06 *
Rainfall	6	123,11 **	5	9,19 NS

Figure 3. Distribution (percentages) of the positive strikes for the defined distribution range and the actual distribution of the Clanwilliam cedar within the categories of the factors measured .


Distribution Range
Actual Distribution
Altitude (m x 10-2)
12-14
10-12
14-16
8-10
6-8
4-6
6-8
16-18
12-14
10-12
14-16
8-10
Aspect
SE
E
S
NE
SW
W
N
NW
SE
E
S
NE
SW
W
N
NW
Slope (%)
30-40
20-30
40-50
10-20
50-60
60
0-10
30-40
20-30
40-50
10-20
50-60
60
0-10
Geological formation
PENINSULA
CEDARBERG
NARDOUW
PENINSULA
Rainfall (mm x 10-2)
8-10
6-8
10-12
4-6
2-4
12-14
8-10
10-12
6-8
4-6

DISCUSSION

Relationships between the distribution range and the recorded factors

The relationship between the distribution range and altitude is seen as being a reflection of moisture requirements. At the upper end of the scale it is possible that the occurrence of severe frost or heavy snow is sufficiently regular to preclude seedling establishment. The lack of relationship between aspect and the distribution range demonstrates that the cedar distribution range is spread throughout the Cederberg mountains, and not confined to any general aspect. The significant relationship between the distribution range and slope arises from the lowlands surrounding the distribution range being much flatter than the mountains within the distribution range.

The distribution also coincides largely with the Peninsula Formation. As this formation predominates in the Cederberg, this relationship should be seen as a reflection of this and the low number of strikes in the Cedarberg formation, and not as indicating any environmental pre-requisite. The altitudinal sequence of formations also means that this relationship may only be a reflection of the relationship with altitude.

The relationship between the distribution range and the amount of rainfall is very similar to that with altitude. This is largely

because rainfall as depicted on the climate map used in this study is dependent on altitude. Although this relationship between rainfall and altitude cannot be accepted universally (Fuggle 1981), it does generally apply and is accepted as confirmation that the relationship between the distribution and altitude reflects moisture requirements.

Relationships between the presence or absence of cedars and the recorded factors

The significance of the relationship with altitude is reduced compared to that seen in the test with the distribution range, but still significant. The drop in significance is despite the fewer degrees of freedom caused by no observations occurring under 200 m. Of the positive strikes, 87,8% fell in the altitudinal range of 1000 to 1600 m, confirming Andrag's (1977) observation that most cedars grow within the altitudinal range of 1050 to 1650 m.

Andrag (1977) also observed that cedars did not generally grow on any specific aspect and this too is confirmed. Removal of the observations in the flatter surrounding areas resulted in there being no significant relationship between slope and the presence of cedars. The relationship with geological formation also shows a drop in significance. This relationship is treated with caution for the same reasons detailed above.

The relationship with rainfall became non significant, despite the decrease in the degrees of freedom resulting from no observations occurring in the category of less than 200 mm. Again this pattern is considered to be no more than a reflection of the situation with altitude.

No attempts were made to analyse any three-way contingency tables in this study. This is because all the factors involved in the study are related to altitude to some degree.

CONCLUSION

The negative discussion of many of the results allows positive conclusions to be drawn. The decreased significance when testing the presence or absence of cedars as opposed to the distribution range indicates that there is no reason why cedars are not capable of growing over far greater areas of the Cederberg, as they are believed to have done in the past.

Apart from altitudinal constraints, there are no limits, on this scale of investigation, to potential areas suitable for re-stocking with cedars. In this regard, cognizance should be taken of the geological formation to confirm or substantiate the selection of sites, but this constraint should not be regarded as absolute.

As far as the limits to the species' range are concerned, altitude again appears to be the over-all limiting factor, influencing rainfall and being correlated with geological formation. The strength of the relationship with altitude, and the species' limited capacity to disperse suggest that small scale barriers such as those created by valleys may prove to be insurmountable. Beyond this, it must be surmised that the present distribution is a result of climatic shifts in the past, and that it is maintained largely by current climatic conditions.

ACKNOWLEDGEMENTS

We would like to thank Brian van Wilgen and David Le Maitre for useful comments on the text.

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PART 5 : SOME EFFECTS OF SEASON OF PLANTING AND SITE FACTORS ON GERMINATION AND SURVIVAL OF THE CLANWILLIAM CEDAR

P.T. MANDERS

SOUTH AFRICAN FORESTRY RESEARCH INSTITUTE

JONKERSHOEK FORESTRY RESEARCH CENTRE

PRIVATE BAG X5011

STELLENBOSCH

SYNOPSIS

The influence of the season of planting and the site factors of moisture, terrain and post-fire vegetation age on the germination of the Clanwilliam cedar is studied. The influence of season of planting on the survival rates of the seeds germinating in the autumn and winter plantings is also investigated.

Germination is found to be more successful on sandy plains than in the more typical cedar habitat of rocky areas. The restriction of cedars to rocky areas is interpreted as being a function of requirements for seedling survival rather than germination. Post-fire vegetation age and moisture availability are not identified as factors affecting germination in this study.

Seed sown in autumn exhibits the most success with respect to both germination and survival.

INTRODUCTION

The Clanwilliam cedar (*Widdringtonia cedarbergensis*) is an endangered species endemic to the Cederberg range of mountains in the south-western Cape Province.

Seeds are released from the parent plants mainly during March and April of each year, and on the death of the parent plant (usually as a result of fire). The seeds begin to germinate within 20 days if sufficient moisture is present. No germination cues appear to be required as germination can occur in any season (personal observation), and there is no seed dormancy (Marsh 1965).

Large numbers of seed may be released after a fire as fire mortality is often high, and recruitment after fire is often greater after a wild fire than in other years. On the other hand, recruitment after a prescribed burn may be negligible (Forsyth 1979). The major differences between wild fires and prescribed burns in the Cederberg are the season and intensity of the burn. Extensive wild fires usually occur in mid-summer, whereas prescribed burns have been carried out in winter or spring to reduce the intensity.

The season of prescribed burning is probably critical in determining the regeneration success by influencing establishment success of seeds released from dead trees after the fire. This effect

will be in addition to and independent of any other effects there may be on the germination and establishment of the seeds through effects on rodent populations and other vegetation.

The effect of season of planting is of particular interest in the conservation of this species as efforts will have to be made to re-stock areas where it has recently become extinct or where population levels are low. If sowing seed *in situ* in the correct season proves successful then this will be more convenient than re-stocking with young plants qrown in nurseries.

The first site attribute considered to be important in the selection of sowing sites is soil moisture availability, as personal observations indicate that regeneration is often better in wet areas than the general cedar habitat.

The Cederberg is characterised by rocky outcrops and ridges between many of which deep sands have developed to form flat sandy corridors and plains. Cedars are conspicuously confined to the rocky outcrops and ridges which has been attributed to protection from fire by earlier authors (for example Andrag 1977). This explanation is not totally acceptable as it does not explain the absence of regeneration in the sandy flats. Furthermore, on the rare occasions where cedars do occur on the sandy flats, they are usually associated with boulders or seepage zones (personal observation). I hypothesise that the restriction to rocky outcrops is a result of regeneration requirements rather

than escape from fire, especially as many of the mature trees which occur on the rocky outcrops appear to be as exposed to fire as individuals on the flats.

Vegetation age may also affect the success of regeneration . This has implications for the choice of site for re-stocking, and will give an indication as to whether it is worthwhile continuing to re-stock an area by sowing over consecutive years.

This study was aimed at experimentally determining the effect of season of sowing and site factors (moisture, terrain and vegetation age) on germination success. This experiment is also intended to examine the effect of the season of sowing and site factors on the survival of the germinated seed. This aspect will be of greater importance than germination *per se* as seedling survival may be independent of germination success.

The final data on survival will not be available until mid 1985 when all the seedlings will have survived at least one full year.

METHODS

Site selection and description

Two areas were selected, one in vegetation of approximately 7 years post fire age, situated about 1 km north of Sneeuberg

hut (19° 09' 12,2" east and 32° 29' 09,7" south) and the other in vegetation of approximately 2 years post fire age situated about 2 km due east of Sneeuberg hut. In each area six plots were established, three on a sandy flat, and three on a nearby rocky slope. In each case the three plots were placed so that one was on a dry site, one on a wet site and one on an intermediate site. These soil moisture categories were chosen subjectively, based on factors such as the vegetation, slope and drainage.

Experimental design

In each of the twelve plots, 100 numbered plastic tags were planted. On the sandy flats the pegs were placed at 1 m intervals in a 10 X 10 m grid. On the rocky sites the pegs were placed randomly between the boulders. The numbered tags in each plot were randomly divided into four groups, one group for each season. Sowings, of four seeds per numbered peg, were carried out on one group of 25 pegs in each plot in each season. Thus, in each season 100 seeds were sown in each of the 12 plots. Each set of five consecutive pegs in each sowing was regarded as a replicate, giving 5 replicates of 20 seeds in each sowing.

Procedure

The dates of the sowings were 2 March 1983 (late summer/autumn), 16 May 1983 (winter), 13 September 1983 (spring) and 7 November 1983 (summer). To facilitate relocation of each seed's position

and to remove some of the subjectivity in sowing, the four seed at each peg were sown at the corners of a hardboard template placed over the peg. The seed used for the sowings was collected in January 1983 and stored under normal room temperature and humidity between sowings.

The sites were visited at intervals of approximately two months until March 1984, and thereafter in September 1984, by which time all sowings had been exposed to at least one winter and the autumn and winter sowings had been subjected to one summer drought after germination. At each visit the position in which each seed had been sown was examined for signs of germination. If the seed had germinated since the last visit and the seedling had died before the present visit, this was also recorded to give a complete representation of the different rates of germination and mortality of seedlings.

Data analysis

Germination in each replicate was expressed as a percentage of the 20 seeds and transformed using the arcsine transformation. Analysis, including the variables of percentage germination, season of sowing, moisture availability, terrain and vegetation age, was carried out using the NESTED procedure of the SAS statistical package. This procedure performs a hierarchical analysis of variance (Zar 1974)

The incomplete data on seedling survival were analysed by a one way analysis of variance. For the autumn and winter sowings the seedlings from each season's sowings surviving the summer in each of the twelve plots were expressed as a percentage of the numbers which had germinated. The percentages were transformed using the arcsine transformation.

RESULTS

Table 1 shows the mean percentage germination within the different categories. The results of the hierarchical analysis of variance are presented in Table 2. Two significant relationships are apparent, The null hypothesis that there is no difference in germination between seasons and the null hypothesis that there is no difference in germination on the sandy flats compared to the rocky slopes are both rejected. There is no evidence in these data to suggest that vegetation age or moisture availability have any effect on germination rate.

The mean percentage of germinated seedlings from the autumn sowings which survived the ensuing summer drought was 7,69 from the winter sowings 1,86%. The null hypothesis that there is no difference in survival between the sowings is rejected at P = 0,05 (Table 3).

Table 1. Germination of cedar seed as grouped by the different factors in the experiment.

Factor	Category	Germination (%)
Season	Autumn	17,58
	Winter	15,00
	Spring	11,92
	Summer	8,33
Moisture availability	Dry	14,25
	Intermediate	10,75
	Wet	14,62
Terrain	Rocky slope	9,00
	Sandy flats	17,42
Vegetation age	Young	11,29
	Old	15,12

Table 2. Results of hierarchical analysis of variance of the variable germination percentage. Significant F ratios are shown, * = significant at P=0,025 and ** = significant at P=0,0005.

Variance source	D.F.	Sum of squares	Mean squares	F
Total	239	43362,16	181,43	
Veg age	1	553,25	553,25	
Terrain	2	6493,13	3246,56	
Moisture	8	3659,72	457,46	7,10 *
Season	36	17832,10	495,34	
Error	192	14823,96	77,21	6,42 **

Table 3. Results of analysis of variance of survival of seedlings between autumn and winter sowings. F ratio is significant at P=0,05

Variance source	D.F.	Sum of squares	Mean squares	F
Among groups	1	575,61	575,61	
Within groups	22	1570,07	71,37	7,92

DISCUSSION

Sowings in autumn, winter and to a certain extent in spring are within the period when sufficient moisture is available for germination. This is reflected in the average germination (Table 1). All the seed sown in summer and some of those sown in spring are exposed to granivory for an extended period before suitable conditions for germination occur. This may account for the lower germination success as has been shown for Cape proteaceae (Bond 1984). These differences are shown by the hierarchical analysis of variance to contribute significantly to the variation in the results.

Moisture availability was included in the experiment primarily to gauge the effect on survival. As far as germination is concerned, the rates in the different environments are similar. The major reason for this is that the area experienced good rains in the winter of 1983. Moisture availability is likely to have a more significant effect on germination in years of below average rainfall. In addition, the subjective site selection in the autumn inaccurate as the seasons progressed. The dry sites remained dry, but the wet and intermediate sites either remained dry or became waterlogged to the extent that seeds may have rotted.

Germination is shown to take place readily on the sandy flats. In this study the rate was significantly higher than germination in the rocky areas. However the reasons for the absence of cedars

on these sandy flats are considered to be effective during the establishment of the seedlings rather than in the process of germination, especially as cedar seed predators do not often occur on the flats (S.A. Botha, unpublished data). In early summer the sandy flats rapidly dry out, so that moisture is beyond the reach of the seedlings' roots, leading to their death. Rocky areas, on the other hand have more shade and moisture retained under the boulders, providing more suitable regeneration environments. The lack of success on the flats is already apparent and this hypothesis should be clarified when the experiment has run its full term.

CONCLUSION

It is apparent that late summer/autumn is the the most appropriate time to distribute seed, either by prescribed burning or by direct sowing. Prescribed burns should therefore be carried out as late as possible before the winter rains. In fact, during the experiment good rains began the day after the autumn sowings were completed, possibly largely accounting for the better germination.

When sowing to improve populations, it would appear advisable to restrict the sowings to to rocky areas as there have been no benefits demonstrated in the establishment of seedlings on the sandy flats. Although no advantage in using moist areas has been demonstrated in this experiment, there are certainly

no negative effects shown, and this factor may well be very important in the establishment phase. Sowings should therefore be concentrated in wetter areas, especially where seed supplies are limited. The selection of moist sites should become more accurate with experience.

It appears that vegetation age does not have a great influence on the success of germination, and in fact many seeds in the older vegetation appeared to benefit from the mulching effect of the thicker litter and prostrate vegetation. However, vegetation age may be more important in establishment as the seedlings begin to compete for resources with the other vegetation. Andrag (1977) found that survival in fire increased in bigger trees. Therefore although sowings may be successful in older vegetation, the earlier sowings will be bigger and thus more likely to survive by the time the next prescribed burn or wild fire occurs. Sowings should thus be restricted to the first three to five years after the fire.

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PART 6 : CONCLUSION

CONCLUSION

The questions concerning the Clanwilliam cedar may be summarised as whether the species has declined, whether it is capable of recovery, and what form of management is likely to promote this recovery. Examination of early records and inference from details of seed crops and pole harvests indicate that the numbers of cedars have decreased since the arrival of European settlers. The extent of this reduction will never be quantified and it will never be known just how many of the early reports were valid observations and how many consisted of flights of imagination. There is, however, considerable direct evidence of a decline currently available. High mortality has been exhibited in some recent wild fires and there has been an almost complete lack of regeneration in some areas.

The prescription of a suitable form of management presents the greatest problem. High mortality has been exhibited in some recent wild fires and there has been an almost complete lack of regeneration in some areas. Fire is a natural phenomenon in the Cederberg, and it must be accepted that an inflammable plant such as the cedar has always been at risk in a fire. The sight of trees killed in fire appears to have clouded the vision of those concerned about cedars for the last century, in that it is this aspect of fire that has received almost exclusive attention.

Efforts to prevent mortality by totally excluding fire or by burning in winter have generally been disastrous. In the first instance, it seems that the greater the efforts to exclude fire, the more extreme the intensity of the eventual (and inevitable) fire, leading to extremely heavy cedar mortality. Secondly, burning in winter and spring has resulted in little or no regeneration. The lighter mortality in these fires, although initially more aesthetically acceptable, will therefore lead to the extinction of the species as surely as the extreme wild fires.

An attempt to model the dynamics of sample stands of cedars with a transition matrix approach proved reasonably successful. It is not possible to provide direct evidence to demonstrate the capacity to increase in numbers or the effects of different management options in a species with such a long juvenile period, such a potentially long life span, and where the intervals between applications of management options are so extensive.

The use of models of population dynamics enables estimations of population developments based on the study of a comparatively very short segment in the development of the population. It seems a reasonable assumption that the reality achieved by the model will be a reflection of the length of the segment studied as much as the mathematical background to the model. Therefore, although statistical problems were encountered due to the manner in which the data had been collected, the effort in solving these was offset by the value of the observations which covered

periods of up to 12 years.

Using this model, evidence has been produced to show that existing stands of cedars are capable of expanding even with the periodic influence of fire, providing the mortalities are not excessive. Prescribed burns will therefore have to be applied to prevent the occurrence of extreme wild fires. It is inferred from the predictions of the transition matrix model that an interval of 15 to 20 years between fires is short enough to preempt the occurrence of extremely intense wild fires while providing sufficient time to allow the population to recover from the mortality incurred in the burn.

It is of paramount importance that these prescribed burns are in the appropriate season. Evidence has also been presented to show that seeds released in the natural period of seed release (late summer/autumn) have the best chance of establishing. Seeds released from trees killed in winter and spring fires, as well as the seeds released later from the survivors seldom contribute to the next generation, prescribed burns should therefore be undertaken in late summer/autumn only.

Some success was achieved in sowing trials and it appears that the planting of seed in the correct season and in suitable sites is a feasible method of re-stocking cedar areas. Although the proportion of seeds which grow to established seedlings is very low, the effort required is minimal and this method of re-stocking

should be undertaken after fires. No absolutely restricting habitat factors required for planting sites were identified either by sowing trials or by cartographical analysis. It also appears that within their present distribution range, cedars may be introduced to many areas within the approximate altitudinal range of 1 000 to 1 600 m. Furthermore, as it appears that successful management of stands is possible, efforts to re-stock areas should prove to be worthwhile in the long term.