The systematics of the Genus *Widdringtonia* Endl., (Cupressaceae).

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ABSTRACT

The Genus *Widdringtonia* Endl., (Cupressaceae) is re-examined for three species of *Widdringtonia*. Tree morphology was obtained in the field for *W. nodiflora*, *W. schwarzii* and *W. cedarbergensis* at six localities in the Western Cape. The fourth species *W. whytei* is briefly discussed.

The morphological data were subjected to a phenetic cluster analysis and principal component analysis. The results of the cluster analysis indicated possible paraphyly for *W. nodiflora* but the principal component analysis indicates that the three species of *Widdringtonia* are distinct. The cophenetic correlation suggested a poor comparison between the two matrices.

Although the three species are distinct, they are separated on numerous overlapping characters and there is an absence of any absolute characters separating the species. Morphological characters that could constitute as fire characters were subjected to a phenetic cluster analysis and principal component analysis. The results indicate that *W. schwarzii* and *W. cedarbergensis* are clearly different from *W. nodiflora*. Different "fire-adaptive" strategies are discussed.

INTRODUCTION

Widdringtonia Endl.

Widdringtonia Endl. is an African genus of the family Cupressaceae currently proposed as having four species : *Widdringtonia nodiflora* (L.) Powrie, *Widdringtonia schwarzii* (Marloth) Mast. and *Widdringtonia cedarbergensis* (Marsh) and *Widdringtonia whytei* (Pauw & Linder,1997). All species occur in Southern Africa with W. *whytei* in Malawi, *W. nodiflora* widespread from Malawi to Cape Town, *W.* *cedarbergensis* restricted to the Cedarberg mountains, and *W. schwarzii* s restricted to the Baviaanskloof and Kouga mountains (Figure 2).

Widdringtonia nodiflora, W. *cedarbergensis* and *W. schwarzii* are protected in South Africa (Hilton-Taylor, 1996), while *W. whytei* is endangered (Pauw & Linder,1997).

Cupressaceae : *Widdringtonia*

The Cupressaceae (Cypress family) has two genera in Southern Africa, *Widdringtonia* Endl. which is restricted to Southern Africa and *Juniperus L* (Kubitzki,1990) which is widespread in the northern hemisphere. *Juniperus L.* has one species, *Juniperus procera*, which is found in Zimbabwe and widespread to the Middle East. The Cupressaceae contain an aromatic and flammable resin which make them susceptible to fire (Coates Palgrave,1984) and their leaves are usually of two types, needle-like in juveniles and small and squamiform in adults (Marsh,1966).

The monophyly of Cupressaceae sensu stricto is well supported with support for the recognition of a southern subfamily (Callitroideae) (Gadek & Quinn,1993). The recent phylogeny of Cupressaceae sensu lato has placed *Widdingtonia* in the sub-family Callitroideae and not in the Cupressoideae (Gadek et al, 2000). It was shown that *Widdringtonia, Diselma, Neocallitropsis* and *Callistris* are related (Gadek et al, 2000).

Widdringtonia Endl. comprises of monoecious and evergreen shrubs or trees with scale-like leaves and fragrant wood. *Widdringtonia* is named in honour of Edward Widdrington, a botanical explorer who made valuable contributions to the knowledge of conifers (von Breitenbach,1974). *Widdringtonia* has dimorphic foliage, in the adult form they are scale-like and tightly appressed to the slender twigs, decussate or alternate. while the juvenile leaves are needle-like and spirally arranged. The male cones are small, more or less 4 mm long, terminal and on short lateral branchlets. Mature female cones are woody, single or clustered on elongated shoots, with normally 4 very thick, woody valves or scales, which are smooth to warty. The valves are of equal size and arranged in one whorl, they are divaricate at time of pollination, then later closing, with several ovules at the base of each valve. The seeds are ovoid with a papery wing (Coates Palgrave,1984).

Widdringtonia nodiflora (L.) Powrie

Widdringtonia nodiflora, so called because it was initially thought to be *Brunia nodiflora* L. of *Brunia*, which ante-date both *W. cupressoides* and *W. juniperus* (Powrie,1972). *Widdringtonia nodiflora* is known as the mountain cedar and is usually a scrubby bush or small tree, 3-6 m high, with a short crooked trunk and a bushy crown. It has a column-like shape, sexes separate on the same plant (Coates Palgrave,1984). *Widdringtonia nodiflora* is easily inflammable, but capable of resprouting at the base after fire. *W. nodiflora* is a widespread species and is found in a narrow belt from southern Malawi to the south western Cape (Coates Palgrave 1984). *Widdringtonia nodiflora* has a higher allelic diversity and genetic polymorphism than its more endemic congeners, *W. cedarbergensis*.and *W. schwarzii* (Thomas & Bond,1997).

Widdringtonia cedarbergensis Marsh

Widdringtonia cedarbergensis is endemic to the Cedarberg Mountains in the South Western Cape. The features which distinguish it from other *Widdringtonia* species are the rough and warty valves of the female cone and large ovoid, 3-cornered and obscurely winged seeds (Coates Palgrave,1984) and it has more of a spreading crown (Van Wyk & van Wyk,1997).

The population of *W. cedarbergensis* is declining in spite of conservation efforts and studies (Manders,1987;Privett, 1994). *Widdringtonia cedarbergensis* is enigmatic as it is extremely fire sensitive while the mesic mountain fynbos communities in which it is found are fire adaptive. *Widdringtonia cedarbergensis* does not resprout after fire and serotiny is absent. Fire causes high adult mortality, which is why *W. cedarbergensis* is mainly found where they are more protected from fire such as on cliffs, rocky outcrops and slopes (Manders,1987). There is some evidence that the restriction to rocky outcrops is related to the inability of the seedlings to regenerate on dry sandy flats (Manders & Botha,1987). Planting and reforestation schemes have met with little success

(Manders,1986). Being a slow grower, *W. cedarbergensis* may only produce its first cones after about 12 years, reaching full reproductive maturity only after about 30 years (Manders,1987).

A decline in numbers of individual *W. cedarbergensis* was noted as early as the beginning of the 19th century, (Manders,1986) and in 1883 approximately 7250 pole stage trees were cut down for the construction of a telegraph line between Calvinia and Piketberg (Thomas,1995). Although Meadows and Sugden (1992), indicate that climatic change is the key causal factor causing the decline of *Widdringtonia cedarbergensis*, the main reasons are over-exploitation and the deleterious effects of fire (Manders,1986).

Widdringtonia schwarzii (Marloth) Mast

Widdringtonia schwarzii , the Willowmore cedar is endemic to the deep and inaccessible ravines of the Baviaanskloof and Kouga mountains. *W. schwarzii* was named by Marloth, in honour of E. Schwarz, Professor of Geology at Rhodes University (Woods,1976). *Widdringtonia schwarzxii* is a rare species with similar cones to *W. cedarbergensis* and has a flattened winged seed.

Widdringtonia whytei Rendle

Woods (1976) questioned the inclusion *W. whytei* with *W. nodiflora* by Marsh (1966) and he describes "the former, though it appears stunted in less favourable conditions, occurs in the tropics as a noble tree of considerable proportions known as the Mulanje cedar, rising occasionally up to 50m; while the latter, the mountain cypress or bergsapree of the Cape, is generally a little more than a shrub, often multiple-stemmed and regenerating by coppicing after being cut down or burnt."

Pauw (1992) found two morphologically and ecologically distinct species present on Mulanje and gave a revised species diagnosis for *W. nodiflora* Powrie and the Mulanje cedar, *W. whytei* Rendle. *W. whytei* differs from *W. nodiflora* having thicker bark, smaller cones, different architecture and differing number of cotyledons (Pauw,1992). *Widdringtonia whytei* was first collected by Alexander Whyte in 1891(Pauw,1992), who was the Principal Scientific Officer to the Administration of British Central Africa and was credited with having discovered the tree (Woods,1976).

Widdringtonia whytei is in danger of extinction and the confusion to between the two species may have lead to the failure of identifying forest potential (Pauw & Linder,1997).

Fire and *Widdringtonia*

The flora of the south-western Cape fynbos have evolved under conditions of low soil nutrients and fire (Cowling,1992) but have a rarity of sprouting shrubs and trees in the overstorey (le Maitre & Midgley,1992). The effects of fire depend on the fire regime (Bond & van Wilgen,1996) and populations respond differently to varying components of the fire regime (Cowling,1992). Fire regimes vary in terms of their frequency, season and intensity (Privett,1994).

In *Widdringtonia* genus, only *W. nodiflora* occurs in montane fynbos. Fires in fynbos are essentially crown fires in the canopies of the shrubs and many adult shrubs are killed or burnt back to ground level. Fires in coniferous forests are surface fires under mild conditions, but under drier conditions, can burn into the crowns of the overstorey trees (van Wilgen et al, 1992). Plants have adopted different survival traits and factors such as thick bark, crown architecture, resprouting from buds and the subterranean position all contribute to fire survival (van Wilgen et al, 1992).

Bond & van Wilgen (1996) refute the concept of forest and fynbos as two distinct and mutually exclusive fynbos types. They postulate that when forest is destroyed fynbos will replace it and the perceived restriction of forest communities to sheltered environments is principally a function of past and present fire regimes (Bond & van Wilgen,1996).

Manders (1987) investigated fire in the *W. cedarbergensis* community. Wildfires have at times devastated vast areas of the Cedarberg mountains. Manders (1987) predicted that an interval of 15 to 20 years between fires is short enough to preempt the occurrence of extremely intense wild fires, with the probability for wild fires becoming high for vegetation over fifteen years (Manders 1987).

Privett (1994) explored the impact of fire intensity on survival and the potential for fire as a management tool and suggested that fire intensity, physiological status, size and height of trees, crown base height, shape and degree of protection by rocks, fuel load and weather conditions all influence the mortality of *W. cedarbergensis* in fire. Privett (1994) emphasized the importance of ensuring low mortalities in the larger tree size classes and concluded that prescribed burning, both inside and outside the reserve, is the only viable management option for the conservation of *W. cedarbergensis*. Attempts have been made to reinstate the species and large numbers of nursery-reared seedlings are planted out each year and monitored (Mustart et al,1995).

This study was set to answer the following questions. Does multivariate analysis of morphological characters retrieve the three species of *Widdringtonia*? Is there any geographical patterning in W. nodiflora? Are there any morphological characters that could be used to key the species? What is the impact of fire on *Widdringtonia* and what 'fire adaptive' strategies are these species employing?

METHODS

Sampling

Widdringtonia species were sampled at six localities: Cedarberg, Bainskloof, Baviaanskloof, Outeniqua Pass, Garcias Pass and Swellendam. Two populations of *W. cedarbergensis* were sampled at Algeria, and two populations of *W. schwarzii* were sampled at Baviaanskloof. *W. nodiflora* has a much wider distribution and was sampled at the remaining three sites (Table 1). The operational taxonomic units (OTU) in this analysis were the individual tree samples and morphological data from ten trees were collected at each population. At each population an attempt was made to sample the full morphological range, from the tallest to the smallest and any odd specimens or environmental peculiarities were collected and noted.

Each sample was given a code of three digits. The first digit indicates the species sampled and is denoted by C – *cedarbergensis*, N – *nodiflora* and S – *schwarzii*. The second digit indicates one of the eight localities, annotated by the letters A to H. The third digit defines the ten samples measured at each locality and is numbered 0 – 9.

Table 1: Locality data for Widdringtonia species

Locality	Species/samples	Description	Position	Altitude	Field notes
1.	*W. cedarbergensis* CA0-CA9	Algeria top of Helshoogte path	32°21.52 'S 19°04. 41'E	807m	recent nearby fire good specimens protected from fire by rocky outcrops signs of juveniles
2.	*W. cedarbergensis* CB0-CB9	Algeria South slope	32° 19.95' S 19° 04.41'E	800m	recent nearby fire cool south facing slope trees appeared healthier also protected by rocks
4.	*W. schwarzii* SD0-SD9	Baviaanskloof Rocky ledge	33° 32' S 23° 40' E	920m	on a rocky cliff face protruding out of cliff ledges and clinging to the rock face not easy to access/loose scree gully with Rhus and Cussonia hot slopes - mostly succulents other WS noticably absent
5.	*W. schwarzii* SE0-SE9	Baviaanskloof River	33 °31' S 23° 48' E	880m	near river & up slope a small stream with WS in it grasses and restionaceae but succulents on higher slopes less dry and exposed, healthier a few 3m juveniles
3.	*W. nodiflora* NC0-NC9	Bainskloof	33°34' S 19°12 'E	588m	near top of the pass down SE slope towards river recent fire opposite side river good signs of re-growth
6.	*W. nodiflora* NF0-NF9	Outeniqua Pass	33°57.24' S 21°12.52' E	700m	few sparse *W. nodiflora* on summit of ridge western side Outeniqua Pass trees small due to suspected recent fire – none on slopes vegetation waist height, thick mainly restionaceae, ericaceae
7.	*W. nodiflora* NG0-NG9	Garcia Pass	33°56.30' S 21°12.59' E	400m	in valley alongside stream - extraordinary diversity - restionaceae, ericaceae and cliffortia, proteaceae higher trees smallish with coppicing shoots - no green branch primordia – very serotinous
8.	*W. nodiflora* NH0-NH9	Clock Peaks	33°57.24' S 21°12.52' E	79m	small & multi-stemmed only south side of the mountain none on summit many Bruniaceae,Restionaceae

Twenty nine characters were used in the analysis and are described as follows:

Tree characters

1. Tree height in metres was estimated in the field.
2. Diameter breast height (*dbh*) in centimeters was measured at breast height using a tape measure.
3. Bark thickness was measured by scraping away the bark until the fleshy cambium appeared. The bark thickness was then measured in millimeters using a pair of Dial^R calipers.
4. Bark description was subjective. Most bark showed definite longitudinal "tiles" which seemed to differ with the age of the tree, some bark was flaking in long narrow strips while other bark appeared flaky.

Juvenile and fire signs

5. Juvenile foliage was easily noted as the leaves differ markedly from the adult trees. Juvenile leaves are needle like and longer than the adult leaves (up to 2 cm).
6. Fire signs were noted only if they were evident on the tree itself. Fire signs were coded as scorch marks or burnt stumps (1), no signs (0). Trees that were suspected to have resprouted after fire but with no fire evidence were not included.
7. Resprouting was noted only if it came from the base of the tree where it is evident as juvenile foliage on small branches or shoots at the base of the tree (1), no resprouting (0).
8. Number of stems was not that easy to ascertain in those areas where a few *Widdringtonia* were growing near each other amongst thick grassy vegetation. It was

difficult to assess whether stems of multi-stemmed trees were part of the same tree or whether they constitute separate trees.

9. Green branch primordia are the green shoots growing from the base of the stems without juvenile foliage (1), no primordia (0).
9. Sequential seeds in years were estimated to give the number of years that seeds were stored on the tree. This was obtained by counting the sequential clumps of cones separated by bare branch lengths along one branch.

Receptive Cones

10. Female cones receptive (1) means a female cone is with a pollination droplet. This requires close scrutiny of the cone and could be missed. Not receptive (0).
11. Male cones are situated at the tips of the branches and store pollen. Ready to drop pollen (1) and not receptive (0).
13. Average number of female cones was estimated as the average number of cones in a cluster on the tree. The sample picked was often not representative of the average cone cluster, so estimates needed to be made in the field.
14. Position of female cones was where the cones were positioned on the branches relative to the foliage, base (0) tip (1).

Colour

15. Foliage colour was difficult to determine but a definite colour distinction existed between *W. cedarbergensis* and the remaining two *Widdringtonia* species. Leaf colour in *W. nodiflora* and *W. schwarzii* could be described as dark green (2) or grey

green (3) and in *W. cedarbergensis* a more fresh dark green (1). Juvenile foliage is a distinctly more grassy green than the darker green of the adult leaves. Colour was often determined by comparing the sample colours against each other.

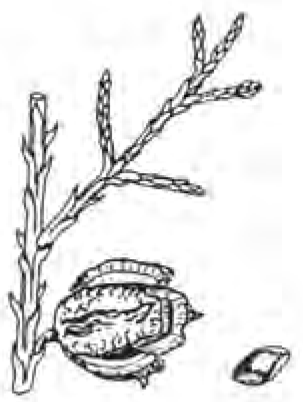
Leaves

Each of the leaf measurements for each OTU is the average of 6 measurements.

16. Tip of leaf to first branch was measured in millimeters using Dial^{R} calipers. A branch was defined as any side branch with at least one leaf.
17. Leaf length 1cm from tip was measured in millimeters using Dial^{R} calipers. As the leaves are small and often indistinct, a magnifying glass was sometimes used. The leaves were measured on the plant as dissection of the leaf was not as successful.
18. Leaf length 6cm from tip was measured in millimeters using Dial^{R} calipers.
19. Branch leaf length was the length of the leaf at the tertiary branch and was measured in millimeters using Dial^{R} calipers.

Cone data

W. cedarbergensis



W. nodiflora

W. schwarzii

Four cones from each sample were collected and measured in millimeters using Dial^{R} calipers. The average data from each sample is used in the analyses.

20. Cone average width is the average measurement of the cone width, measured at the widest point. The horns of the valves were excluded from the measurement.
21. Cone average length is the average measurement of the cone length, measured from the tip to the base of the cone.
22. Mean cusp length is the average measurement of the cone cusp length, measured from the tip of the horn to the base of the valve.

The four cones from each sample were then placed in brown paper packets and left for a few weeks to dry. Measurements for cones and seeds were in millimeters using Dial^{R} calipers and the average measurement was used for each OTU.

23. Cone width at widest point was measured as the widest point between the two open valve tips.
28. Opposite valve size was determined as valves of same size (0), indeterminate (1), unequal size (2)
29. Cone texture was classed very warty and gnarled (3), partially warty (1) or smooth (0).

Seeds

The seed measurements for each OTU were the average of 4 measurements.

24. Seed width was measured in millimeters using Dial^{R} calipers.
25. Seed length was measured in millimeters using Dial^{R} calipers.
26. Approximate number of seeds per cone was determined by counting the number of seeds in the packets in which the cones were dried and double checking this amount with the number of seed scars evident in the open cone.
27. Resin sacs not evident or obscure (0), one resin sac (1), two resin sacs (2).

Phenetic Analysis

In these analyses NTSYS (Version 1.80) (Rohlf,1993) was used for the similarity measurements, clustering and ordination methods.

As the data here are mainly continuous, character variation was overcome by standardizing the data, which reduces the effects of different scales of measurement in different characters (Rohlf,1993). This standardization corresponds to the usual standardization of a matrix used in numerical taxonom, where the mean of each variable is subtracted and the difference is divided by the standard deviation (Rohlf,1993), thus the mean is zero and the standard deviation is equal to 1.

Distance and similarity measures are used to quantify the degree to which samples differ, or conversely how similar they are (Quicke, 1993). A rectangular standardized data matrix is used to create a symmetric matrix. The dissimilarity measure used to create this matrix is the average taxonomic distance (Rohlf,1993). Distance measures the distance between OTU's in a space defined in various ways and is the easiest similarity to visualise (Sokal & Sneath,1973).

In a large average taxonomic distance matrix it is difficult to see which samples are similar and which are different, so relationships between points are summarized by cluster analysis and ordination analysis (Rohlf,1993). The UPGMA (*unweighted pair-group method using arithmetic averages*) is probably the most frequently used SAHN clustering strategy (Sokal & Sneath,1973). UPGMA is a nested set of OTU's being connected at different levels according to the overall similarity (Quicke.1993) and is based on joining an OTU to existing clusters on the basis of their average (mean) distance to the members of that cluster (Quicke,1993). As UPGMA uses mean distances it is not so subject to the effects of aberrant OTU's (Quicke,1993). The FIND option was used for ties which can result in duplicate trees (Rohlf,1993) and the maximum number of tied trees were 25.

A criticism of clustering methods is that they set out by assuming that clusters are present while ordination methods avoid this assumption (Pankhurst,1991). Clustering methods will always cluster data whether or not there are really clusters present in the data, it is important that some check be made for the existence of clusters (Rohlf,1993).

After the SAHN program the COPH program was used to calculate the cophenetic value matrix using the tree matrix produced by SAHN. The MXCOMP module was then used to compute the correlation between the cophenetic value matrix with the original matrix being clustered (Rohlf,1993). If one matrix is a cophenetic value matrix and the other the matrix upon which the clustering was based, then the correlation is called the "cophentic correlation" and it can be used as a measure of goodness of fit for a cluster analysis (Rohlf,1993). The Mantel test statistic, Z, is used to measure the degree of relationship between the two matrices and $0.7 \leq r < 0.8$ is a poor fit.

Ordination methods are useful in finding natural splits between sets of data and is a technique that determines whether the samples represent an homogeneous sample or whether they represent two or more distinctly different groups (Quicke,1993). Principal component analysis or PCA reveals groupings in data based on a set of two or more measurements and was applied to the standardized data, since results are sensitive to the often arbitrary choice of units of measurement used in this study.

The aim of PCA is 'to discover a series of new vectors that are all at right angles to one another such that the normalised data have maximum variance along the first principal component axis. The second principal component is then selected such that it is a right angles to the first and explains the maximum amount of the remaining variance in the data.' (Quicke,1993). The first three principal components usually explain most of the useful variation in the data. Eigenvectors, their percentages and their cumulative percentages were listed. The eigenvector projection matrix plot gave a two dimensional plot of the 29 variables in the PCA. It gives some idea as to which variables are associated with each other.

Cluster analyses and projection matrixes were also produced for ten of the variables considered to be fire characters. Height, diameter and bark thickness were regressed with each other to establish possible differences with respect to fire.

Character variation patterns

Box and Whisker plots were produced for seed, cone and leaf data of the *Widdringtonia* species in order to explore the variation patterns of these characters.

RESULTS

The output of the UPGMA cluster analysis of *Widdringtonia* is given in a dendrogram with a single tree and no ties were found (Figure 3). The UPGMA grouped all *W. cedarbergensis* together and most of the *W. schwarzii*. Three *W. schwarzii* OTU's (SE0, SE9 and SD5) were nested between the *W. nodiflora*, while the remaining *W. schwarzii* nested within *W. nodiflora*, thus separating *W. nodiflora* into two clusters.

Some of the OTU's were indicated as clustering within their localities as well, such as *W. cedarbergensis* localities CA and CB, which nested all ten OTU's together, nine OTU's were nested at SD and NH. Not all OTU's were geographically linked and some outliers existed.

Examination of the PCA is therefore important in showing their relationship to one another. The cophenetic correlation $r = 0.7704$ indicated a poor fit ($0.7 < r < 0.8$) and possibly data loss in the conversion from the distance matrix to the phenogram. Sometimes most of the lack of fit can be due just a few OUT's (Rohlf,1993).

The eigenvector projection matrix plot gave a two dimensional plot of the 29 variables in the PCA (Figure 4). One can see for example that tree height (Var-1), diameter breast height (Var-2), bark thickness (Var-3) and cone texture (Var-29) are all associated, having eigenvectors 6.64, 8.03, 8.00 and 6.44 respectively.

The projection matrix for the OTU's of the *Widdringtonia* spp. clearly separates the 3 species into three clusters (Figure 4). However the outlier SE0 indicates a marginal overlap between *W. cedarbergensis* and *W. schwarzii*. Apart from the NH8 outlier, the OTU's of the *W. nodiflora* are completely distinct. Although the majority of the specimens from the Bainskloof locality (NC) form a distinct cluster, there are outliers. The other OTU's are clustered together but geographic localities are indicated when they are peeled (Figure 5). The CA population appears less divergent than CB while the SD and SE populations are clustered close together, with SE slightly more divergent than SD.

Usually in multivariate analysis the first three characters on the first PCA constitute about 90% of the variation (Quicke,1993) but in this analysis the first three characters only accounted for 46.5 % and thirteen characters constituted 89% of the variation. As so many characters were needed to contribute to the variation, the multivariate analysis was completed in 6 dimensions in order to be able to scrutinize more of the characters contributing to this variation.

Table 2: Eigenvectors for *Widdringtonia* characters

Character						
1	6.64	0.32	3.01	1.51	**3.52**	1.41
2	**8.03**	-0.72	2.24	1.95	1.69	0.65
3	**8.00**	-2.72	1.45	2.48	1.24	0.47
4	**-7.72**	2.85	1.85	-0.62	1.92	-1.18
5	0.50	-0.12	-0.42	0.81	3.06	**-4.14**
6	-3.05	-0.67	-0.65	1.00	1.84	**4.02**
7	**-7.90**	-2.49	-1.56	2.33	-0.63	-2.16
8	-5.78	-2.15	-0.84	1.02	-2.36	2.88
9	**-7.25**	-3.39	-0.04	1.54	-0.76	-2.16
10	-5.59	3.12	-0.72	**4.46**	2.12	2.76
11	1.24	0.51	-0.40	0.48	0.88	-1.80
12	1.22	4.32	4.32	-0.88	-1.37	**4.39**
13	-3.94	**5.26**	2.22	-2.07	2.05	3.02
14	1.80	-0.66	**7.21**	**7.85**	0.88	-2.16
15	-4.14	6.48	3.65	-2.32	1.18	-0.65
16	-4.74	-1.95	**4.74**	1.04	-3.67	-2.22
17	2.20	3.56	2.21	2.41	-3.14	1.76
18	3.88	-1.58	2.01	2.28	**-6.31**	2.03
19	-2.13	-0.47	4.22	-5.47	**-5.20**	-0.42
20	0.86	**-8.23**	1.71	-1.20	1.59	2.66
21	-1.38	**-6.46**	3.88	**-3.87**	2.34	-0.70
22	-2.08	2.38	3.76	-1.07	**4.55**	1.24
23	2.20	**-8.41**	1.59	0.04	0.15	1.91
24	-3.41	-4.66	0.67	-2.55	1.48	**4.03**
25	**-7.21**	-3.79	3.57	1.74	2.53	-1.27
26	-7.40	-2.86	1.17	0.67	-0.89	0.69
27	-1.27	2.42	**5.67**	1.60	-2.28	-0.48
28	-2.45	-0.62	**-5.07**	**4.68**	-1.31	1.91
29	6.44	-0.63	0.93	-3.71	-0.57	-2.80

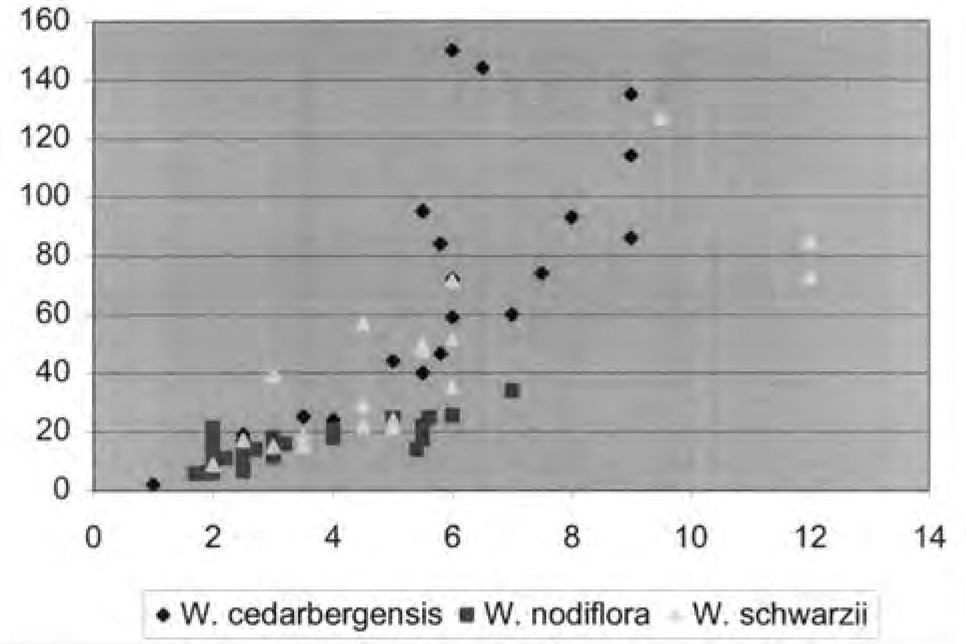
In the eigenvectors results (Table 2) the highest absolute values are highlighted for the first 6 characters of the first dimension (column one) and thereafter for the first four characters in the remaining 5 dimensions (columns). The characters indicating the most variance along the axis of the first principal component (PCA) are in descending magnitude Var-2 (diameter), Var-3 (bark thickness), Var-7 (resprouting), Var-4 (bark description), Var-9 (branch primordia) and Var-24 (seed length). Similarly the characters indicating maximum variance along the second PCA are Var-23 (cone open width at widest), Var-20 (cone width), Var-21 (cone average length) and Var-13 (average number of female cones). The third PCA explains the maximum amount of variance in the data not yet explained by the first two principal components. Var-14 (Position of the female cone) had the highest absolute value in this third dimension. Similarly Var-14 explained the maximum amount of variance in the fourth dimension. Var-18 (leaf length 6 cm from the tip) and Var-12 (male cones receptive) explained the maximum variance in the fifth and sixth dimensions respectively.

The first two variables explaining maximum variation in the first principal component are diameter (Var-2) and bark thickness (Var-3). Diameter and bark thickness are correlated with tree height (Graphs 1a-d). The correlation coefficients are positively significant ($p > 0.05$) for all these regressions (Table 3).

Table 3 : Correlation coefficients * for *Widdringtonia* spp.

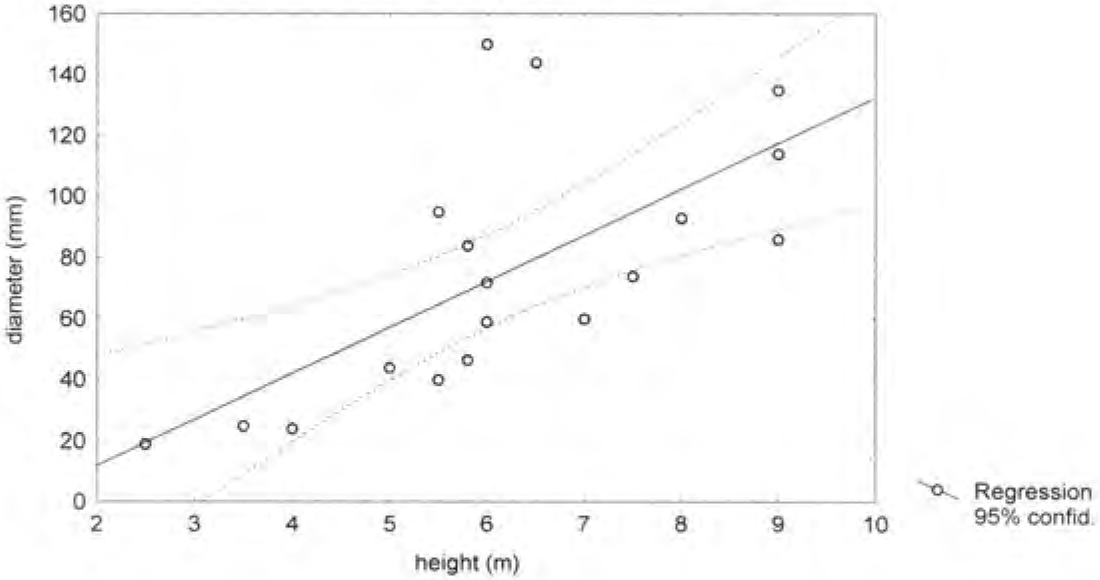
	height vs diameter	bark thickness vs diameter	bark thickness vs height
Widdringtonia spp.	0.78	0.90	0.65
W. cedarbergensis	0.69	0.86	0.74
W. nodiflora	0.80	0.76	0.52
W. schwarzii	0.80	0.90	0.62

*** All significant for $p > 0.05$**

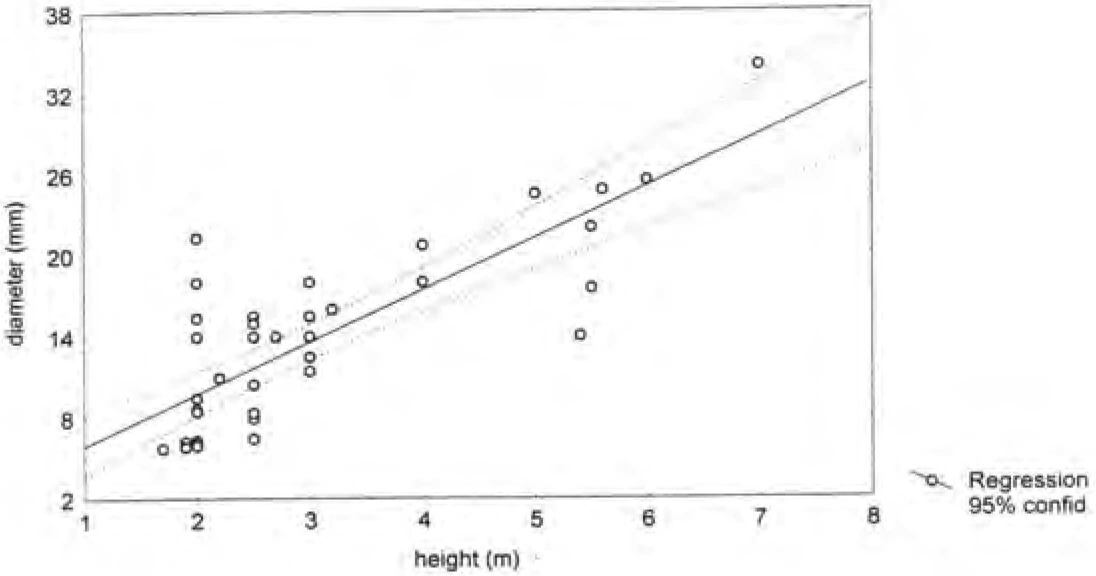


Graph 1 (a) Height vs diameter for Widdringtonia

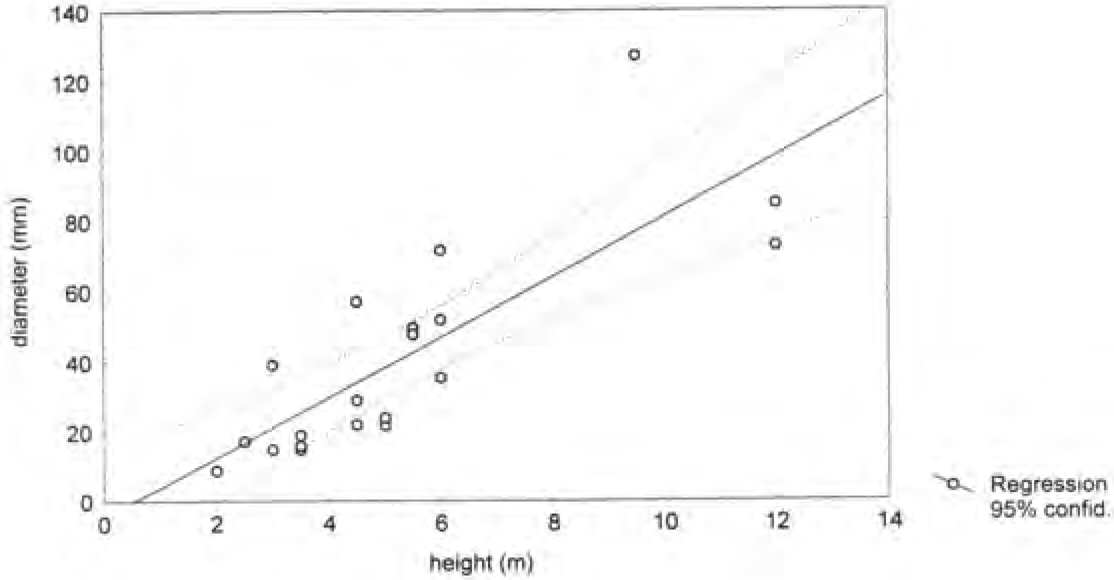
Graph 1 (b) : Correlation of height vs diameter
Widdringtonia cedarbergensis
Correlation: r = .69369



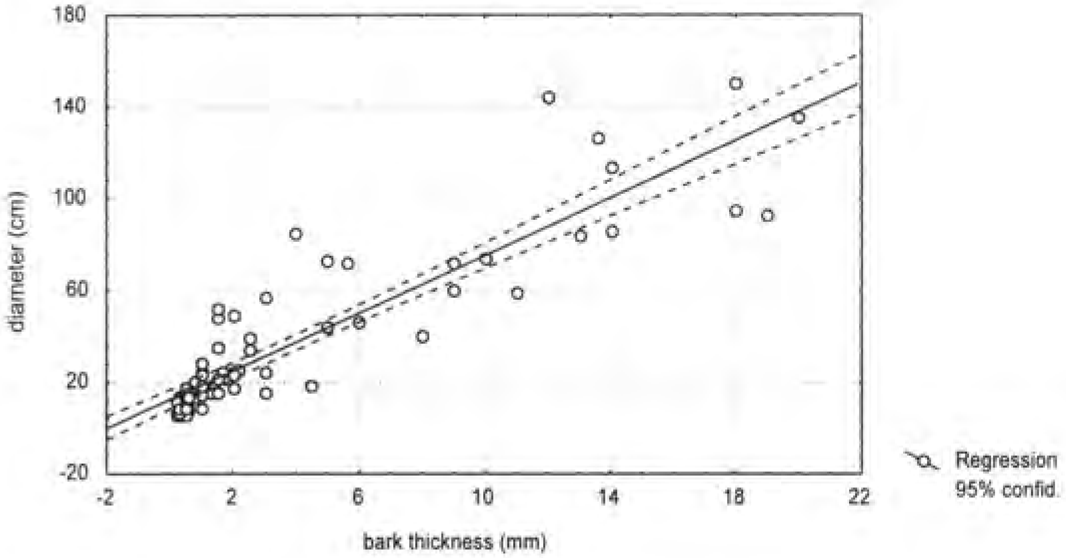
Graph 1 (c) : Correlation of height vs diameter
Widdringtonia nodiflora
Correlation: r = .79772



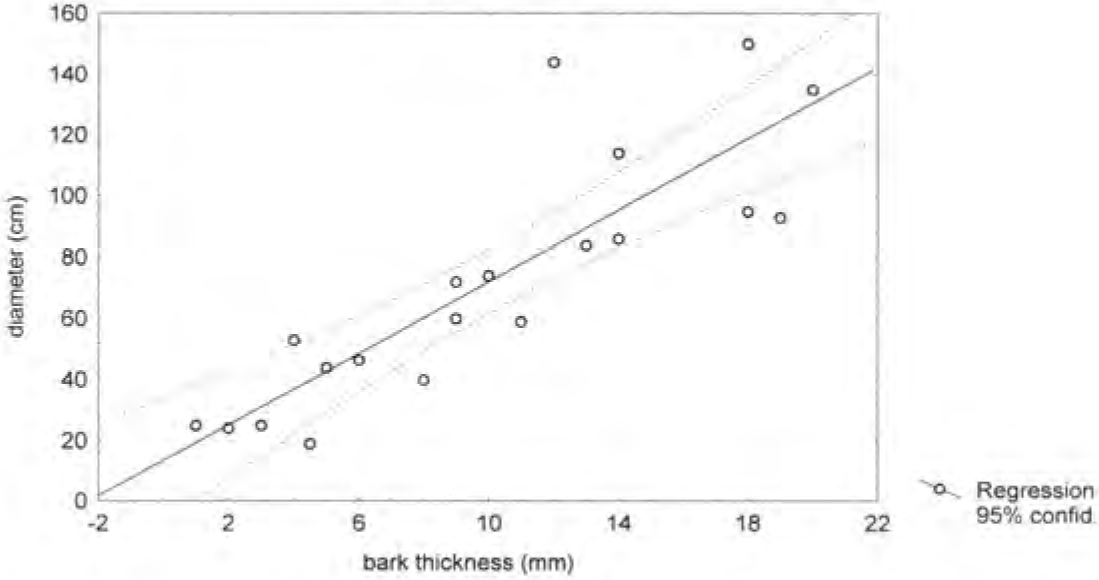
Graph 1 (d) : Correlation of height vs diameter
Widdringtonia schwartzii
Correlation: r = .80596



Graph 2 (a) Correlation of diameter vs bark thickness
All species of *Widdringtonia*
Correlation: r = .90207



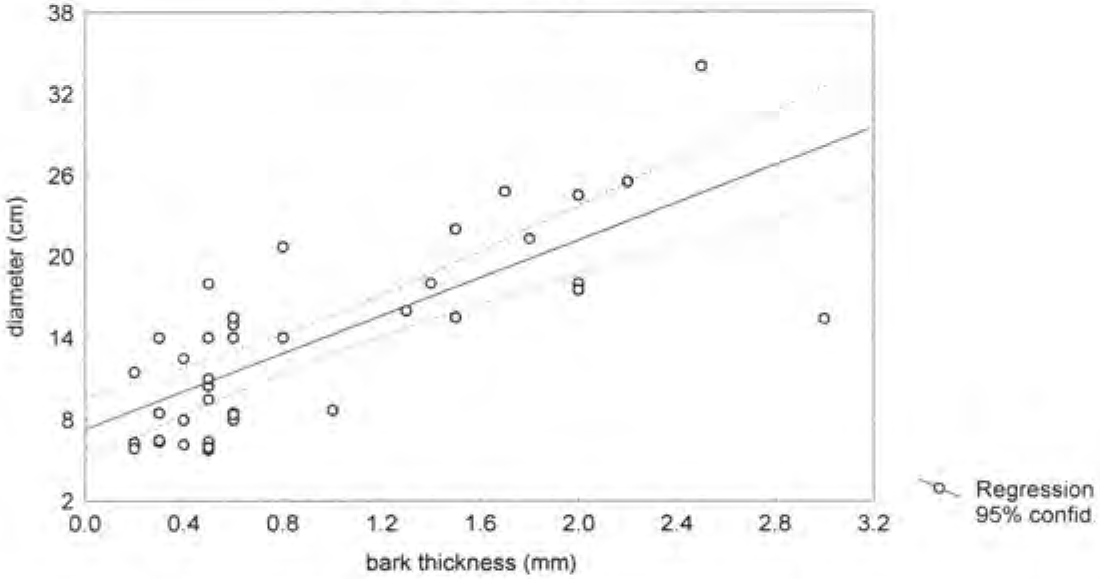
Graph 2 (b) : Correlation of diameter vs bark thickness
Widdringtonia cedarbergensis
Correlation: r = .85607



Graph 2 (c) : Correlation of diameter vs bark thickness

Widdringtonia nodiflora

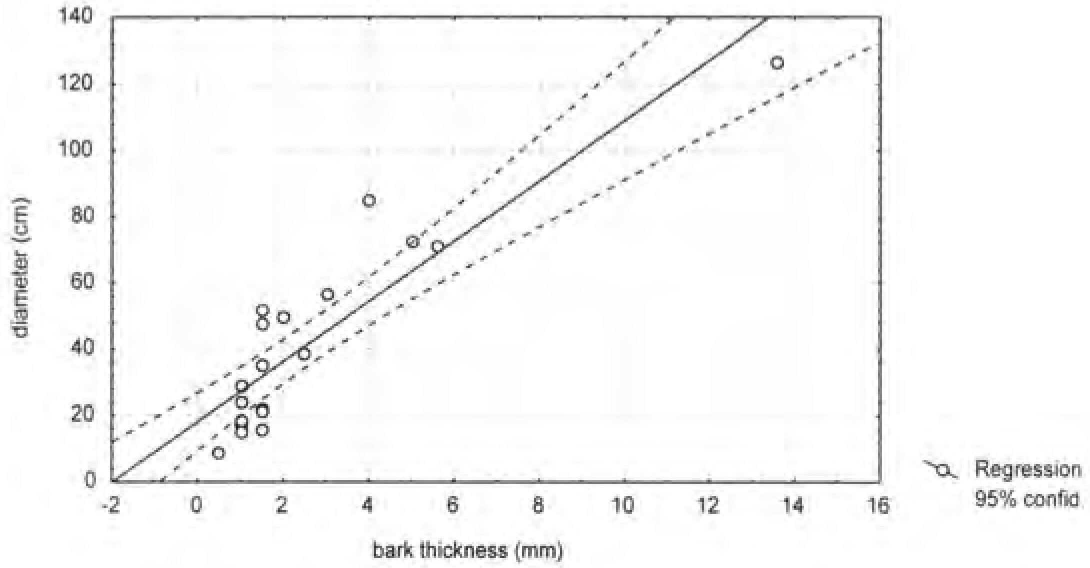
Correlation: r = .75700



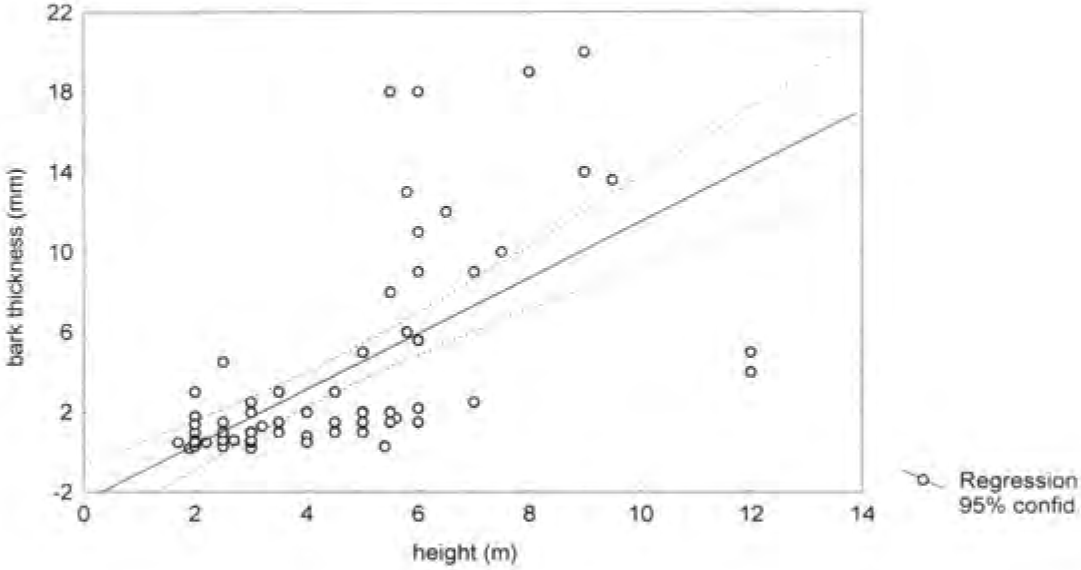
Graph 2 (d) : Correlation of diameter vs bark thickness

Widdringtonia schwarzii

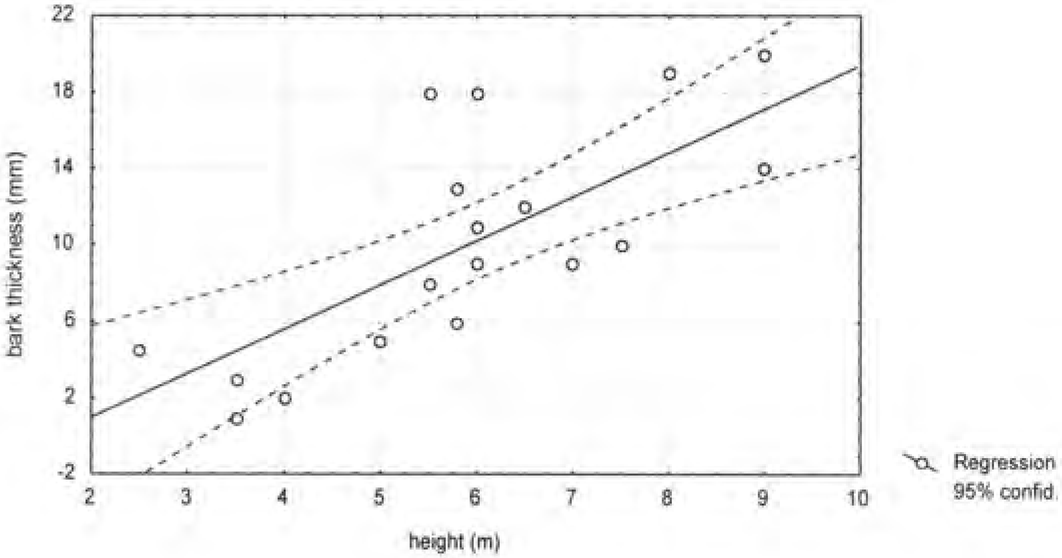
Correlation: r = .89617



Graph 3 (a) : Correlation of height vs bark thickness
All species of *Widdringtonia*
Correlation: r = .65383



Graph 3 (b) : Correlation of height vs bark thickness
Widdringtonia cedarbergensis
Correlation: r = .74152



Graph 3 (c) : Correlation of height vs bark thickness

Widdringtonia nodiflora

Correlation: r = .51810

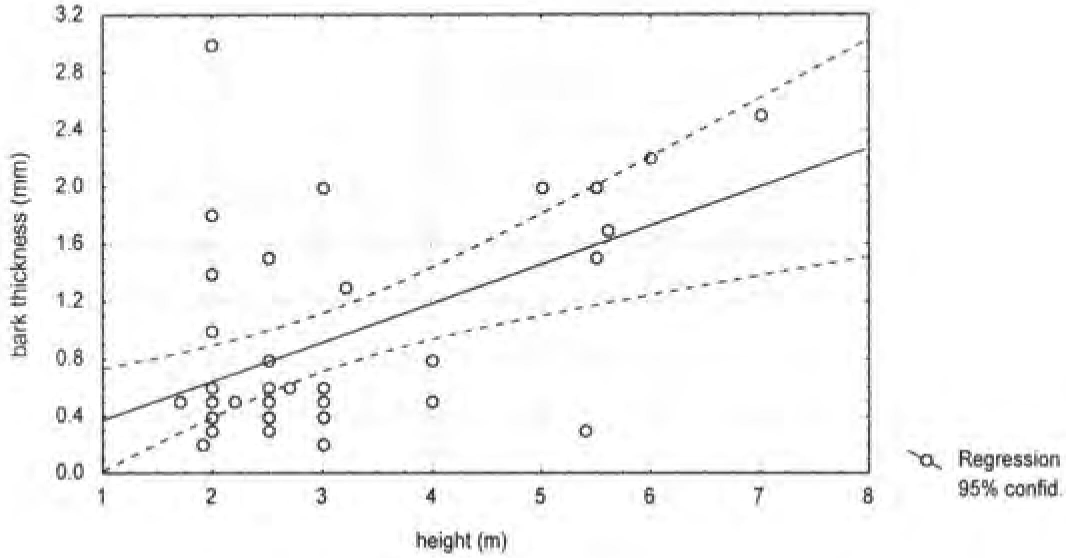
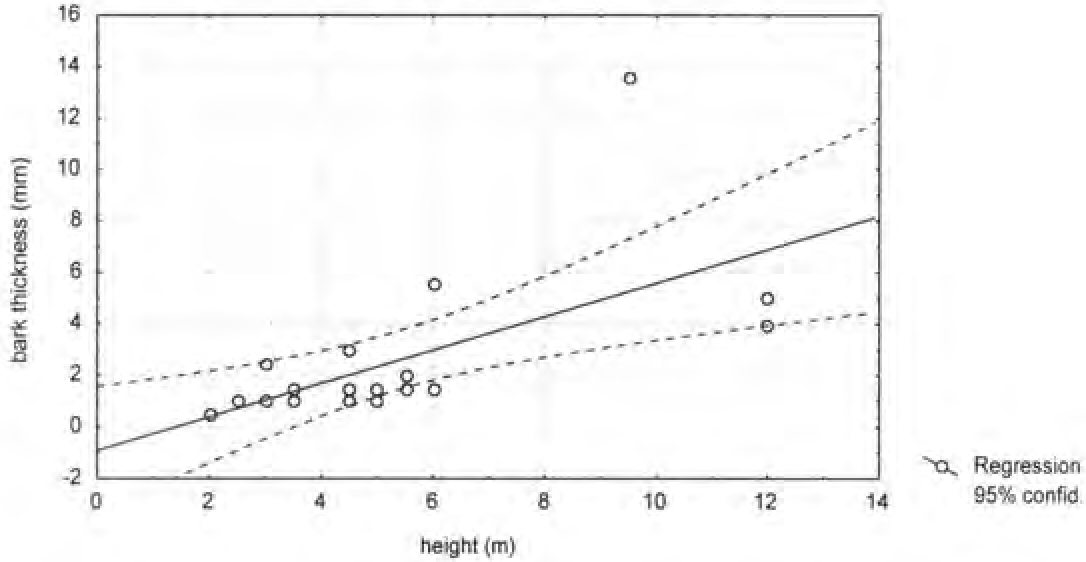


Table 3 (d) : Correlation of height vs bark thickness

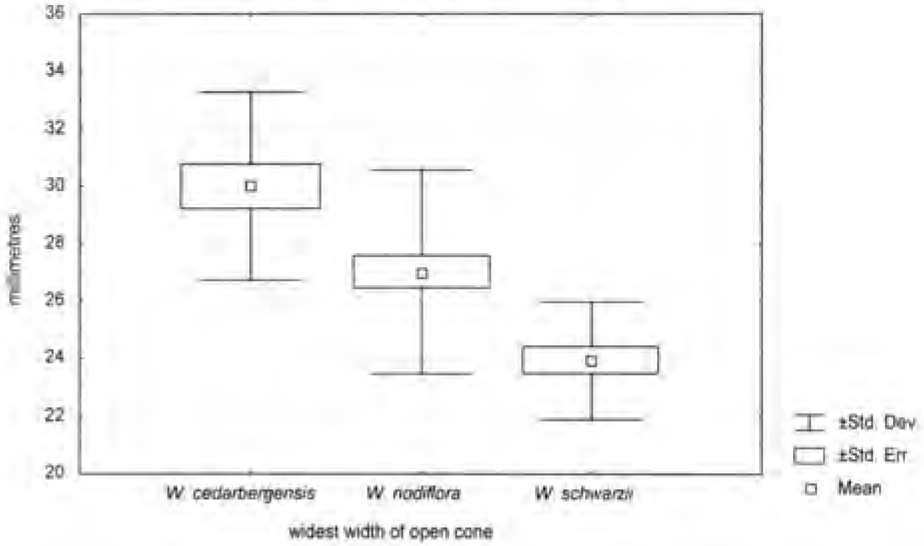
Widdringtonia schwarzii

Correlation: r = .62001



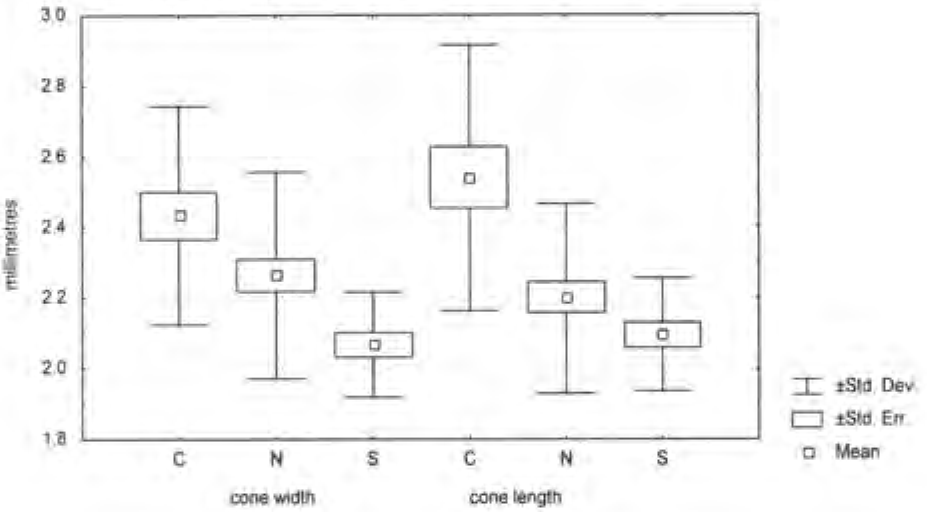
The highest absolute value on the second PCA was the character 'cone open width at the widest point'. One can see that *W. cedarbergensis* has a higher range of 'cone open width at the widest point' with a range of 24.96 – 30 – 36.66 mm (Graph 4). *W. nodiflora* has a range from 20.90 mm – 27.01 – 34.76 mm while *W. schwarzii* has a range from 20.24 – 23.93 – 20.20 mm. The average open cone widths are 30 mm, 27.01 mm and 23.93 mm respectively.

Graph 4 (a) OPEN CONE - WIDEST WIDTH for *WIDDRINGTONIA SPP.*

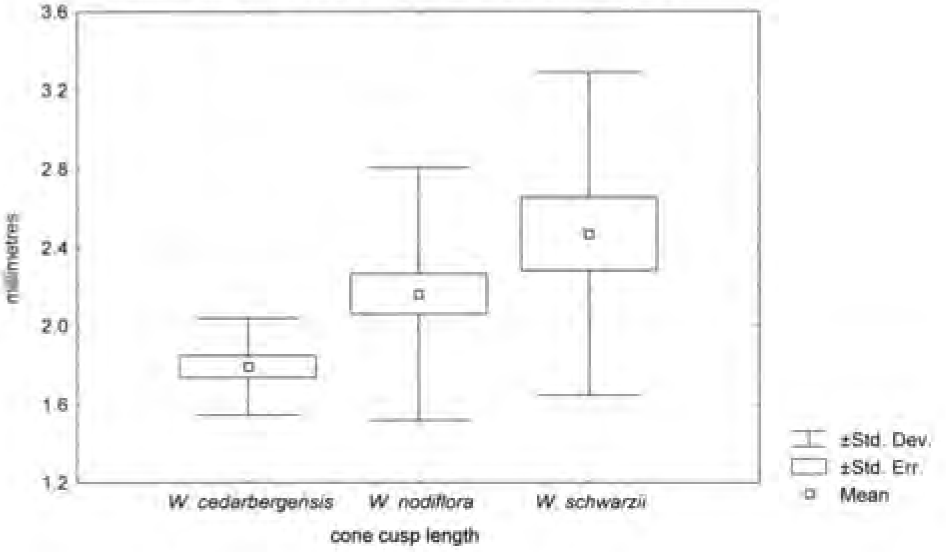


The remaining cone data shows that cone width and cone length are largest in *W. cedarbergensis* and smallest in *W. schwarzii*, indicating that they have the biggest and smallest cones respectively (Graph 5). In the cone cusp length the converse is true with *W. schwarzii* showing extreme variation and ranging from 1.59 – 2.47 – 3.72 mm.

GRAPH 4 (b) : CONE WIDTH & LENGTH for *WIDDRINGTONIA* SPP
C= *W. cedarbergensis* , N= *W. nodiflora* , S= *W. schwarzii*



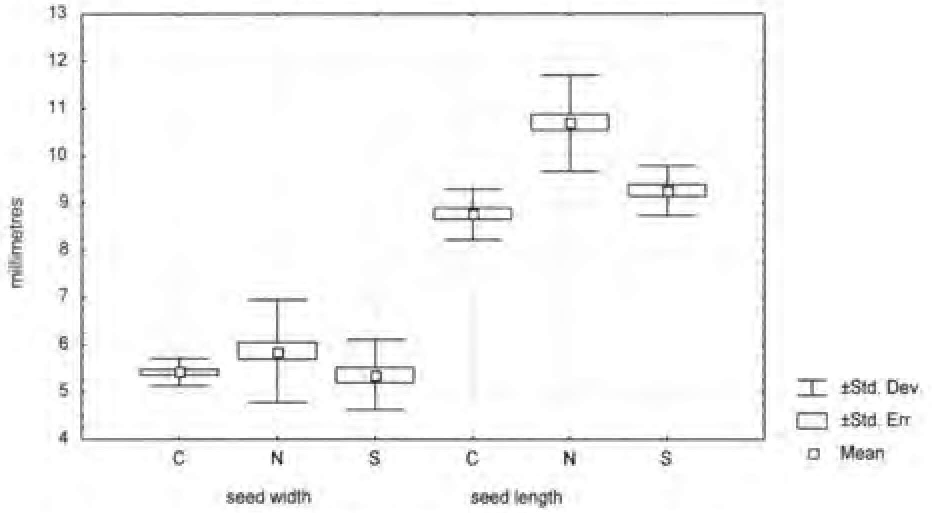
Graph 4 (c) : CONE CUSP LENGTH for *WIDDRINGTONIA*SPP



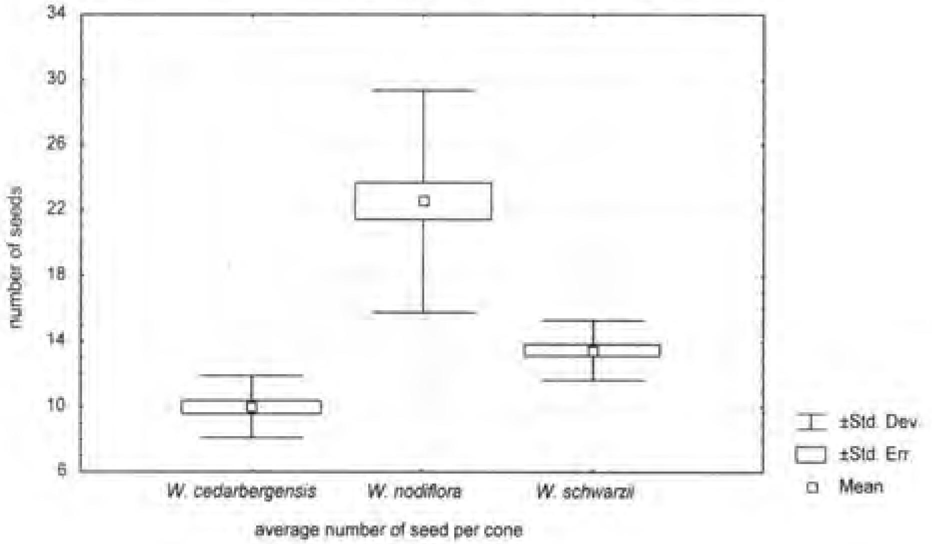
Seed length variation was also examined and the measurements were *W. cedarbergensis* ranging from 7.85 – 8.78 – 9.65mm. *W. nodiflora* ranged from 8.52 – 10.78 –12.19 mm, while *W. schwarzii* ranged from 8.46 – 9.15 –10.39 mm (Graph 5a). Similarly the seed width indicated *W. nodiflora* as only marginally having the widest seed, with the means for *W. cedarbergensis, W. nodiflora* and *W. schwarzii* being 8.76,10.68 and 9.3 mm respectively. The number of seeds per cone vastly differed with *W.nodiflora* having an average of 23.05 seeds as opposed to the averages of to 13.48 and 9.99 for *W. schwarzii* and *W. cedarbergensis* respectively.

Graph 5 (a) : SEED WIDTH & LENGTH for *WIDDRINGTONIA* SPP

C= *W. cedarbergensis* , N= *W. nodiflora* , S= *W. schwarzii*

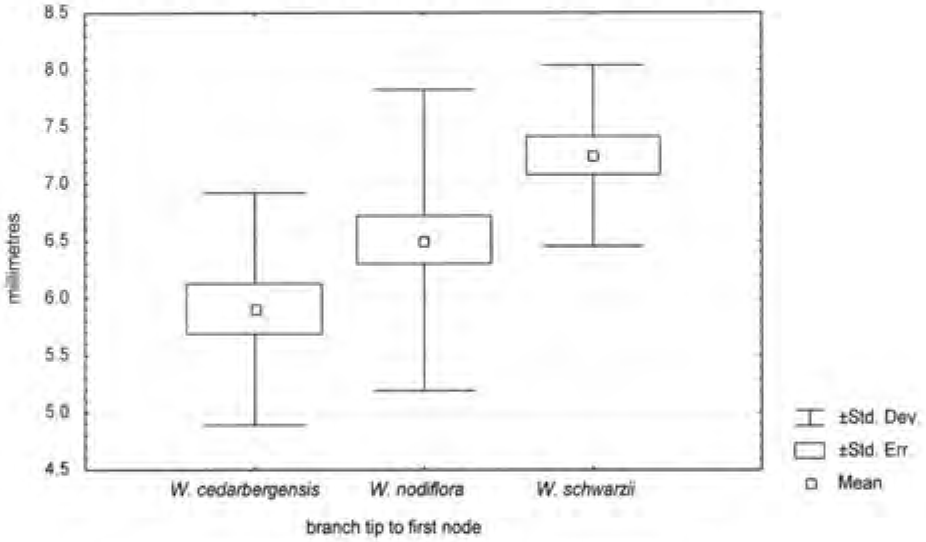


Graph 5 (b) : NUMBER OF SEEDS PER CONE for *WIDDRINGTONIA* SPP

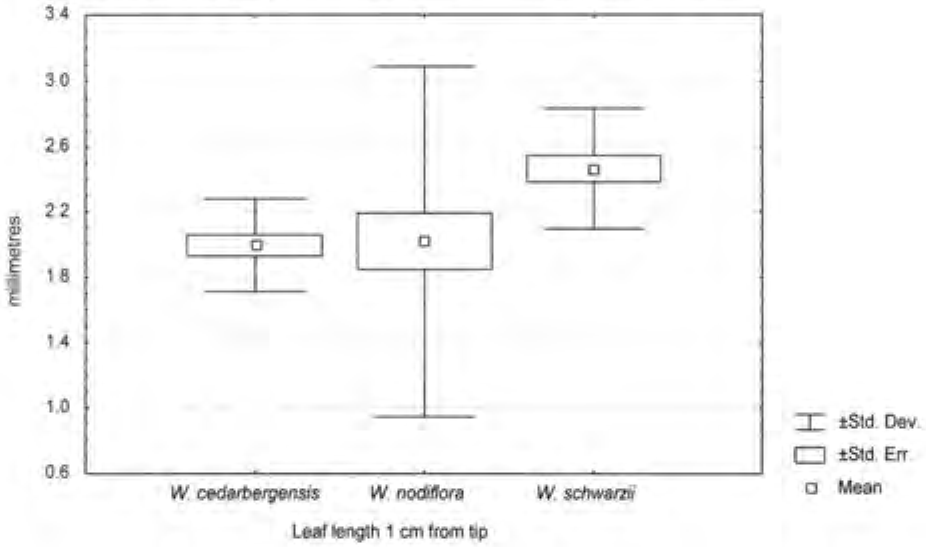


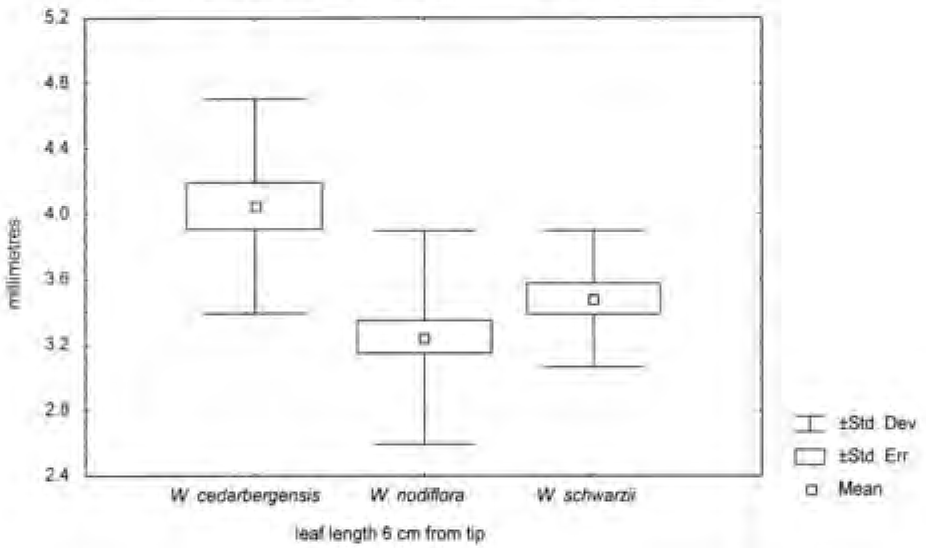
Leaf data measurements indicate that *W. nodiflora* has the shortest leaves but that *W. cedarbergensis* buds nearest to the tip.

Graph 6 (a) : BRANCH TIP TO FIRST NODE for *WIDDRINGTONIA* SPP.



Graph 6 (b) : LEAF LENGTH 1cm FROM TIP for *WIDDRINGTONIA* SPP.




Graph 6 (c) LEAF LENGTH 6 cm FROM TIP for *WIDDRINGTONIA* SPP

In the second part of this analysis only the fire characters were examined and the UPGMA cluster analysis matrix (Figure 6) places the majority of the *W. nodiflora* together, the *W. cedarbergensis* and *W. schwarzii* are mainly nested in two groups but with some OTU's interspersed.

The matrix plot for the fire characters indicates that the first three variables, tree height, diameter and bark thickness are closely linked (Figure 7). The eigenvectors for the fire vectors are given for four dimensions and the maximum absolute values are highlighted (Table 4).

The character displaying maximum variation in the first PCA is Var-5 (juvenile foliage), with the second highest absolute value being Var-2 (diameter), and with Var-3 (bark thickness) and Var-7 (resprouting) displaying maximum variation for the third and fourth highest characters respectively (Table 4). In the second PCA, Var-7 (resprouting) and

Var-6 (fire signs) explain the maximum variation. Likewise Var-5 (juvenile foliage) and Var 3 (bark thickness) explain maximum variation in the third PCA, while Var-2 (diameter) again explains the most variation in the fourth PCA.

Table 4 : Eigenvectors for fire characters for four dimensions

Character				
1	7.49	4.06	1.22	2.13
2	**8.74**	3.49	-2.25	**-9.98**
3	**8.34**	3.41	**-5.25**	-2.55
4	-7.30	2.46	1.58	3.59
5	**9.48**	1.26	**9.33**	7.14
6	-3.46	**6.55**	-2.63	3.25
7	**-8.03**	**7.97**	1.24	-4.18
8	-5.77	4.45	-1.39	-3.94
9	-7.27	2.91	2.01	-2.89
1	-5.89	2.19	-2.06	4.51

The projection matrix for the *Widdringtonia* spp. fire characters indicates a distinct separation between *W. nodiflora* and the other two species (Figure 6). However *W. cedarbergensis* and *W. schwarzii* had OTU's that were quite interspersed. Again no locality differentiation seems to have been made.

DISCUSSION

Does multivariate analysis retrieve the three species?

Is *W. nodiflora* paraphyletic?

Three of the four species of *Widdringtonia* were studied in these analyses and the aim was not to arrange them into hierarchies but to find the best way of distinguishing them from one another. In the UPGMA cluster analyses, four distinct groups of OTU's were evident, with *W. schwarzii* embedded in *W. nodiflora* and splitting this group in two. This does not provide good evidence for the existence of three distinct species and it suggests that *W. nodiflora* could be paraphyletic. The three species would have been resolved if *W. schwarzii* nested between *W. nodiflora* and *W. cedarbergensis* in the UPGMA analysis. The OTU's namely SEO, SE9 and SD5 were not clustered within their species in the UPGMA analysis but were all clearly well separated in the projection matrix, with one exception, NH8, which appears to be an outlier.

The question of how good the ordination is when compared to the cluster analysis is indicated by the co-phenetic correlation that measures the goodness of fit between the two analyses. The co-phenetic correlation was poor ($r= 0.7704$) suggesting that there is a substantial distortion when calculating a phenogram from the distance matrix.

The OTU outlier, NH8, cannot be discarded as an attempt was made to sample the full range of the species. These sample sizes are also fairly small and all evidence must be carefully examined. On closer inspection NH8 appears to have data comparable to the other NH samples. However NH8 is the tallest sample at that locality with a very thick bark, but with only an average diameter and this could account for its outlier behaviour. The PCA projection matrix, however, provides good support for three phenetic species.

Diagnosis of species

In principal component analysis the variation in any one original variable of the raw data may not reveal the true diversity of the sample population (Quicke,1993) and thus the search for eigenvectors. It was hoped to reveal some characters that could more easily distinguish the variation in these three populations of *Widdringtonia*. Usually most of the variation is explained by the first three principal component variables, however in this analysis the first three principal component variables only explained 46.5% of the variation and thirteen principal component variables only explained 89% of the variation. The analysis using 6 variables fitted to the component was therefore calculated in an attempt to reveal all those characters that contribute to the variance.

Diameter, bark thickness and tree height are all closely linked and indeed diameter and bark thickness contributed the most variance for the first two characters of the first principal component. Resprouting, bark description and branch primordia could be considered fire signs and are discussed in the second part of this analysis. Seed length has the sixth highest absolute value contributing to variation in the first PCA and although variation does vary between the species, there is a significant overlap in their seed lengths making a key feature difficult.

The second principal component indicated that the open cone width at the widest point, closed cone-width and cone average length, respectively contributed to the most variance. It would appear that the data differ for the open cone width at the widest point (Graph 4a) but not significantly enough to make it a distinguishing morphological feature. The depth to which the cone split may be related to the degree of serotiny. One would expect a non-serotinous plant to have a wide cone width as in *W. cedarbergensis* (average 30 mm) and a serotinous cone to only partially open as in *W. nodiflora* (average 23.93 mm). Similarly from the evidence one would expect *W. schwarzii* (average 27.01 mm) not to be serotinous.

The character 'position of the female cone' in the third and fourth principal component. contributes to the most variance. However it is felt that as the raw data had missing values this is not a reliable character in this data.

An analysis of all the different combinations of the six dimensions was run and revealed that when compared to the first dimension, dimensions 2 – 5 revealed a distinct separation of the species with *W. schwarzii* clearly an intermediate. In the second dimension the species distinction was not as distinct when compared to the other 4 axis and eventually there was no distinction.

An attempt was made to produce a key to the species (Figure 9). The morphological characters used would not distinguish herbarium specimens from one another. There is considerable overlap in all the morphological characters assessed, making a key virtually impossible. The characters used are the best characters to distinguish the species and it is evident that they are very inadequate.

Figure 9 : A key to the species of Widdringtonia Endl.

Female cones woody, 4 scales (valves) rarely 5 or 6
Male cones small, terminal on short lateral branches
Leaves very small, scale-like (adults), needle-like (juveniles)

Stem, usually many, slender symmetry, narrow crown, longer than wider.................................. 1
Stem, usually single 2

1. branches, emerge down trunk, sprays not dense 3
3. cones, usually smooth, sometimes rough 4
cones, usually rough, sometimes smooth 5

4. cone cluster, 2 to 48 cones per cluster .... *W. nodiflora*
seeds 6

5. cone cluster, 2 to 20 cones per cluster .... *W. schwarzii*
seeds 6

6. seeds, numerous, small wing .... *W. nodiflora*
seeds, flattened with conspicuous wing .... *W. schwarzii*
seeds, 3-cornered (minute wing) or without wings .... *W. cedarbergensis*
seeds,usually 3-8, 2-14 per cone, 6-12 mm long, 3-8 mm wide.................................. *W. whytei*

2. stem, usually single, large spreading crown 6
stem, usually single, no spreading crown 1

6. branches, shedding lower down
cones, very rough and warty, (open cone widest width 20 – 35 mm) .... *W. cedarbergensis*
seeds 6

branches, multi-tiered, branches lower down trunk support secondary platform of foliage
leaves, dark, serrated appearance, tips of leaves stand free from central axis
cones, smooth to rough (open cone widest width 20 – 30 mm)................................... *W. whytei*
seeds 6

Geographic differences

Although the analysis indicated a separation on the basis of species some OTU's were nested within their localities as well. A good geographical connection for *W. nodiflora* was indicated at Swellendam. The OTU's at Bainskoof appear the most diverse.

Geographical patterning for *W. nodiflora* was emphasized by the projection matrix where 'peeling' revealed geographic separation. Pauw and Linder (1997) in their study of the Mount Mulanje cedar, provide evidence to indicate that two species co-occur. These two species are *W. nodiflora* and *W. whytei*. *W. whytei* is not a mature form of *W. nodiflora* as previously thought.

Fire survival in *Widdringtonia*

Enright & Hill (1995) state that all four species require fire for successful regeneration. Manders (1987) sates that *W. cedarbergensis* show poor recruitment in the inter-fire period. While little is known about recruitment without fire in *W. cedarbergensis* and *W. schwarzii* , *W. cedarbergensis* has been noted to recruit without fire (P. Linder, pers comm.). It can be argued that *W. cedarbergensis* does not require fire for successful regeneration.

Widdringtonia cedarbergensis, W. whyteii and to some extent *W. schwarzii* occur in forest patches. Forests can be on granite, shale and sandstone in sheltered ravines, stream banks and patches of rock scree (Bond & van Wilgen,1996). *W. nodiflora* is found in fynbos and montane grasslands.

All four species of *Widdringtonia* are "fire adapted" but in different ways.

A model is proposed for three different 'fire adaptive' strategies.

Strategy - fire response	Locality	Vegetative response
Fire survivors survive surface fires killed by intense fire	forests patches rocky outcrops	thick bark, single stem, tall trees, sparse crowns, fast grower drops branches, non-sprouting, no serotiny, fewer seeds
Fire recruiters 100% leaf scorch -adults survive (fire recruiters)	mountain fynbos montane grasslands	thin bark, multi-stemmed, shrub-like trees, no crown, slow grower, retains branches, resprouter, serotiny, many seeds
Fire-reseeders attempts to prevents burning	forest patches steep rocky habitats	thick bark, single stem, tall trees, reseeds, non-sprouting, weak serotiny, reasonable seed quantity

The first 'fire-adaptive' strategy is fire-survival and occurs in forest trees. Forest canopies have higher moisture contents, sparser crowns, and are more separated from the litter layer than fynbos canopies and are therefore less likely to burn (Bond & van Wilgen,1996). Their survival depends both on the extent to which the live crown is scorched and the survival of stem tissue. The cambium is insulated from fire heat by bark and it is the thickness of the bark, more than its type, that confers most fire resistance (van Wilgen et al, 1992). Fire-survivors should therefore have thick bark, long bare trunks (by dropping branches) and canopies high above the ground to avoid defoliation (crown scorch) by fires. Fire-survivors attempt survival through avoidance and are therefore expected to have no serotiny and not to resprout.

The second 'fire-adaptive' strategy is fire-recruitment. In this strategy mature plants with 100% leaf scorch can survive by resprouting from the basal stem. One would expect fire-recruiters to be serotinous (accumulation of the seed bank in the canopy) but serotiny can vary greatly within and between species (Bond & van Wilgen,1996). One would expect fire-recruiters to have multi-stems, no crown, short branches, no branch shedding and to produce numerous small seeds.

The third 'fire-adaptive' strategy is fire-resistance, where there is some attempt to resist fire. If fire occurs the tree is killed but reseeds after fire. A fire-reseeder attempts to resist fire but if a fire does occur it has some strategies to survive. One could describe this strategy as an intermediate between the fire-recruiters and fire-survivors. A fire-resister should have thick bark, a single stem and shed some branches. One would expect a fire-reseeder to reseed but not resprout, and weak serotiny would be evident.

The survival of *Widdringtonia* in fire is discussed in light of these three strategies. The UPGMA for the fire characters does not have *W. schwarzii* embedded in *W. nodiflora* but indicates *W. schwarzii* and *W. cedarbergensis* as quite distinct. Similarly multivariate analysis of the 'fire' characters indicate that *W. nodiflora* is clearly separated from *W. cedarbergensis* and *W. schwarzii. Widdringtonia nodiflora* is suggested as being a 'fire recruiter'. It is serotinous and a resprouter. *Widdringtonia cedarbergensis* is not serotinous and does not resprout after fire and could be considered to be a 'fire survivor', while *W. schwarzii* which is weakly serotinous, also reseeds and does not resprout after fire and could be considered to be a 'fire-resister'.

As in the UPGMA for fire characters, the projection matrix clearly separates the three species into two clusters. *W. nodiflora* which survives fire by resprouting is clustered in one group and *W. schwarzii* and *W. cedarbergensis* which attempt to resist and survive fire are clustered into the other group. *Widdringtonia schwarzii* and *W. cedarbergensis* are not separated but are interspersed.

As a fire recruiter, *W. nodiflora* has the thinnest bark with respect to its diameter and height, while *W. cedarbergensis* and *W. schwarzii* respectively have thicker bark. Small differences in bark thickness can produce large differences in fire resistance (van Wilgen et al,1992) and it would be interesting to examine bark thickness in another genus with different species that are fire recruiters, reseeders and survivors.

The shape of the tree is also 'fire adaptive'. Fire recruiters can resprout from the base forming many new stems as in *W. nodiflora,* they grow to fractionally above the vegetative height and can remain as scraggly shrubs with a 'Christmas tree' shape. Fire survivors such as *W. cedarbergensis* need to get tall fast to survive surface fires. They are self pruning, have a single stem and retain their leaves mainly in their crown. The fire resister *W. schwarzii,* although it shares similar strategies to *W. cedarbergensis,* does employ some survival strategies (weak serotiny) and is thought to grow with branches increasing in width at the top.

A tree shape can be assumed when comparing height with diameter (Graph 1a). *W. cedarbergensis,* expend more energy in growing taller and have a wide diameter as in a 'k-selected' strategy. Here one would expect a tall thick stem to support a canopy, providing protection for seedling regeneration. *W. schwarzii* increase their diameter with their height, they have narrower trees than *W. cedarbergensis* but taller trees than *W. nodiflora*. *W. nodiflora* does not expend much energy on growing tall or increasing its diameter. A short thin stem supports a small shrub-like tree. *W. nodiflora* and to some extent *W. schwarzii* have a 'r-selected' strategy.

It was hoped that some of the seed and cone characters such as 'approximate no of seeds per cone', 'valve texture' and 'resin sacs' would have provided evidence for more variation between the species and although slight variation does exist, it is not significant. On the whole the evidence generally indicates *W. nodiflora* as being very different to *W. cedarbergensis* and *W. schwarzii,* with *W. schwarzii* as possibly an intermediate between the other two species. On average *W. cedarbergensis* produced 3.7 cones per cluster, while *W. nodiflora* produced 7.2 cones per cluster. *Widdringtonia schwarzii* surprisingly, produced 9.6 cones per cluster. This high number of cones in *W. schwarzii* could be due to sampling, as although attempts were made to collect the full range of morphological differences, the *W. nodiflora* sampled tended to be younger trees. The number of seeds produced per cone was 9.9 for *W. cedarbergensis*, 13.48 for *W. schwarzii* and 23 for *W. nodiflora*. This is more in accordance with the model where *W. nodiflora* is a fire recruiter following the resprouter strategy of large seed production, thinner bark and space grabbing by new plants.

W. cedarbergensis is thought to be a fire survivor having thicker bark, poor seed investment, no serotiny, taller single stemmed trees and crown spreading. *W. schwarzii* is thought to be an intermediate between the other two species but showing more of *W. cedarbergensis* features in having strategies to survive fire. *W. cedarbergensis* seedlings germinate very easily but have a poor survival rate owing to herbivory (Manders,1987) The model proposed here for fire survivors, fire reseeders and fire recruiters follows the reseeder/resprouter strategies, with *W. nodiflora* following the resprouter strategy. The reseeder strategy of *W. cedarbergensis* and *W. whyteii* is one where "space grabbing" is achieved by crown spreading, which creates an area under which seedlings can grow in good conditions. In the fire survivor strategy it was felt that the spreading crown was a fire-survival strategy and not a space grabbing strategy.

Coates-Palgrave (1984) distinguishes the three species in his key by a description of the valve of the female cone and the adult leaves on the branchlets narrowly oblong. It is interesting to note that neither seed size nor cone texture provided the expected variation in this analysis. The wings on the seeds are a conspicuous morphological character but no other seed variation was significant.

The absence of any absolute morphological characters separating the species makes a herbarium key impossible. The species are separated by numerous overlapping characters and yet they are all distinctly different.

CONCLUSION

It was hoped that phenetic analysis would help to ascertain some distinguishing characters that would help to easily identify the differences between the species in the *Widdringtonia* genus. However although no single character appeared to make a major contribution to the variation, multivariate analysis of the morphological data, suggests that the three species are clearly separated.

The UPGMA analysis indicates possible paraphyly of W. nodiflora but as the co-phenetic analysis reveals a weak correlation, this was not explored further. On the basis of morphology and fire ecology, *W. schwarzii* is possibly indicated as an intermediate between *W. nodiflora* and *W. cedarbergensis* but this was not subjected to cladistic analysis.

W. cedarbergensis and *W. schwarzii* seem to be anachronisms, they are clinging on in fire refugia unable to penetrate grasslands or survive frequent fires (Enright & Hill, 1995), yet morphological analysis does indicate that they have 'fire adaptive' strategies. Further exploration of these strategies in other genera would be interesting.

Widdringtonia is one of the only two conifers genera in Southern Africa and all are threatened and yet our knowledge about these endangered species is still very limited.

ACKNOWLEDGEMENTS

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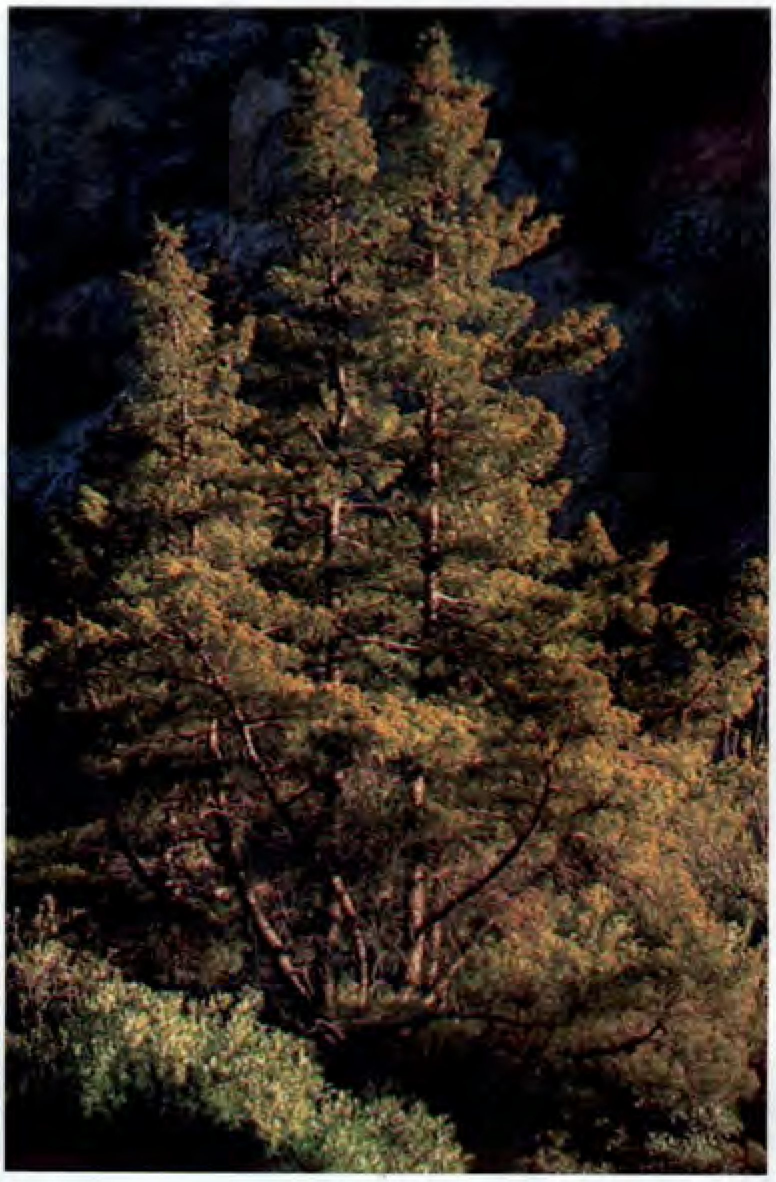
1→

1. ***W. nodiflora***: females cones 2. ***W. nodiflora***: male cones
3. ***W. nodiflora***: slender trees growing in ideal conditions.

2↓

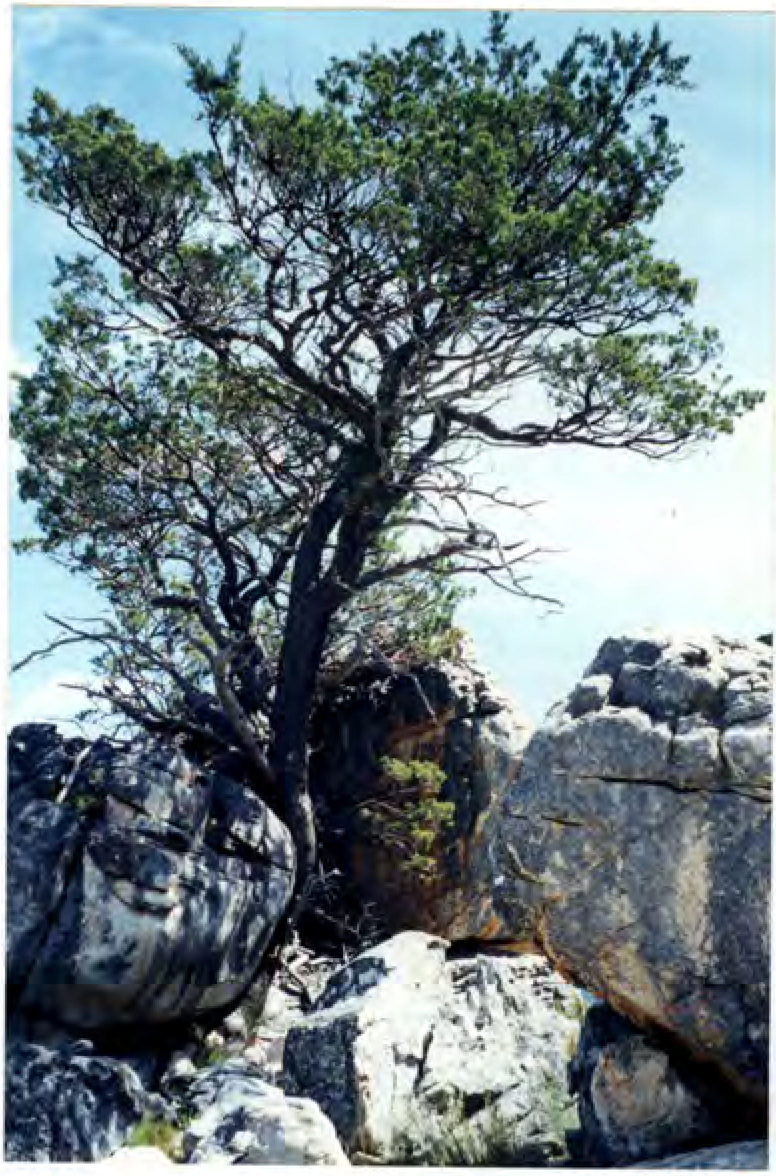
3↓

1.→
W. schwarzii: no spreading crown



← 2.
W. cedargergensis: surviving fire

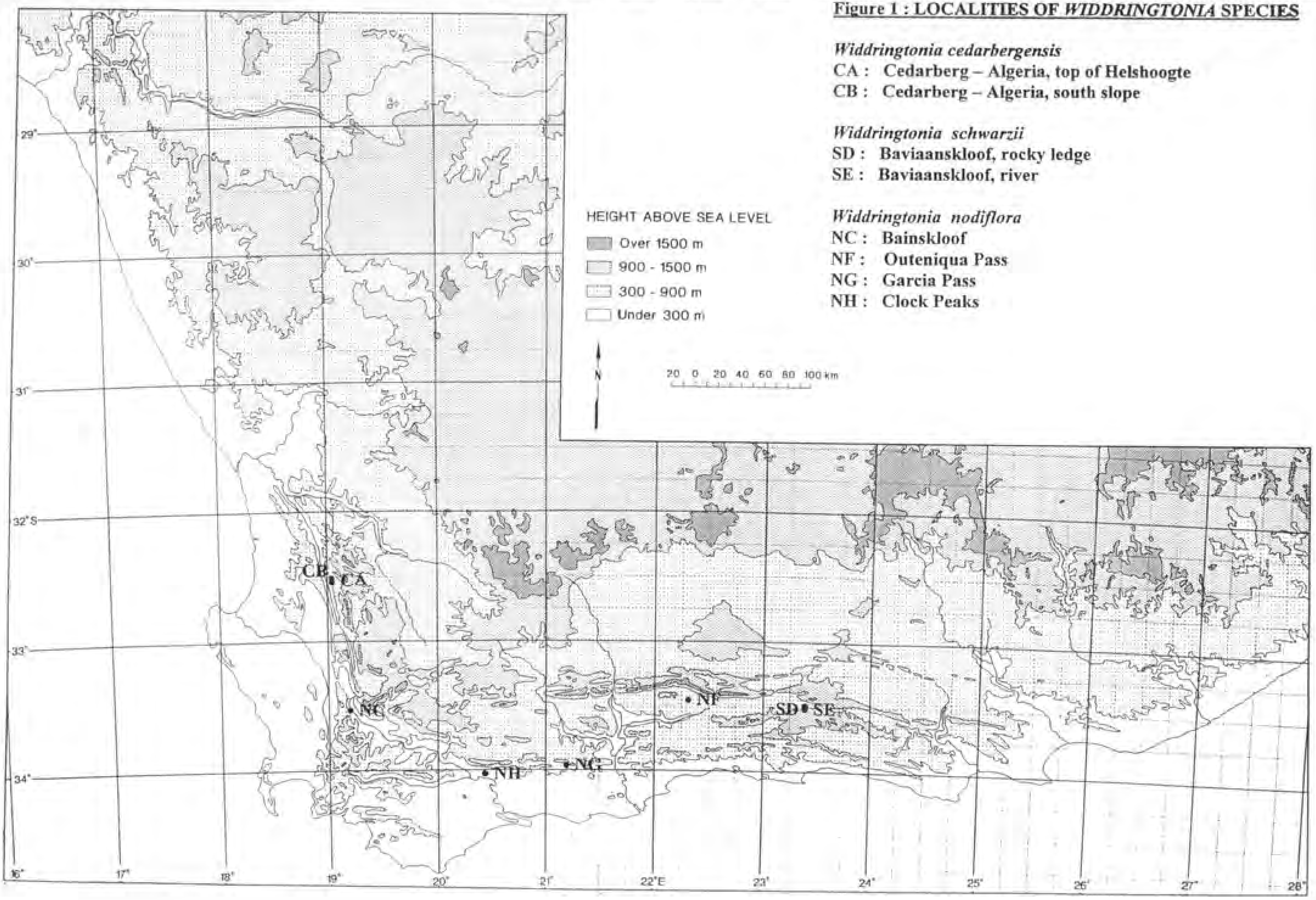
1→



1. ***W. cedarbergensis:*** growing among rocks protected by fire
2. 2. ***W. cedargergensis:*** killed by fire

2 ↓

Figure 1 : LOCALITIES OF *WIDDRINGTONIA* SPECIES



Widdringtonia cedarbergensis
CA : Cedarberg – Algeria, top of Helshoogte
CB : Cedarberg – Algeria, south slope

Widdringtonia schwarzii
SD : Baviaanskloof, rocky ledge
SE : Baviaanskloof, river

Widdringtonia nodiflora
NC : Bainskloof
NF : Outeniqua Pass
NG : Garcia Pass
NH : Clock Peaks

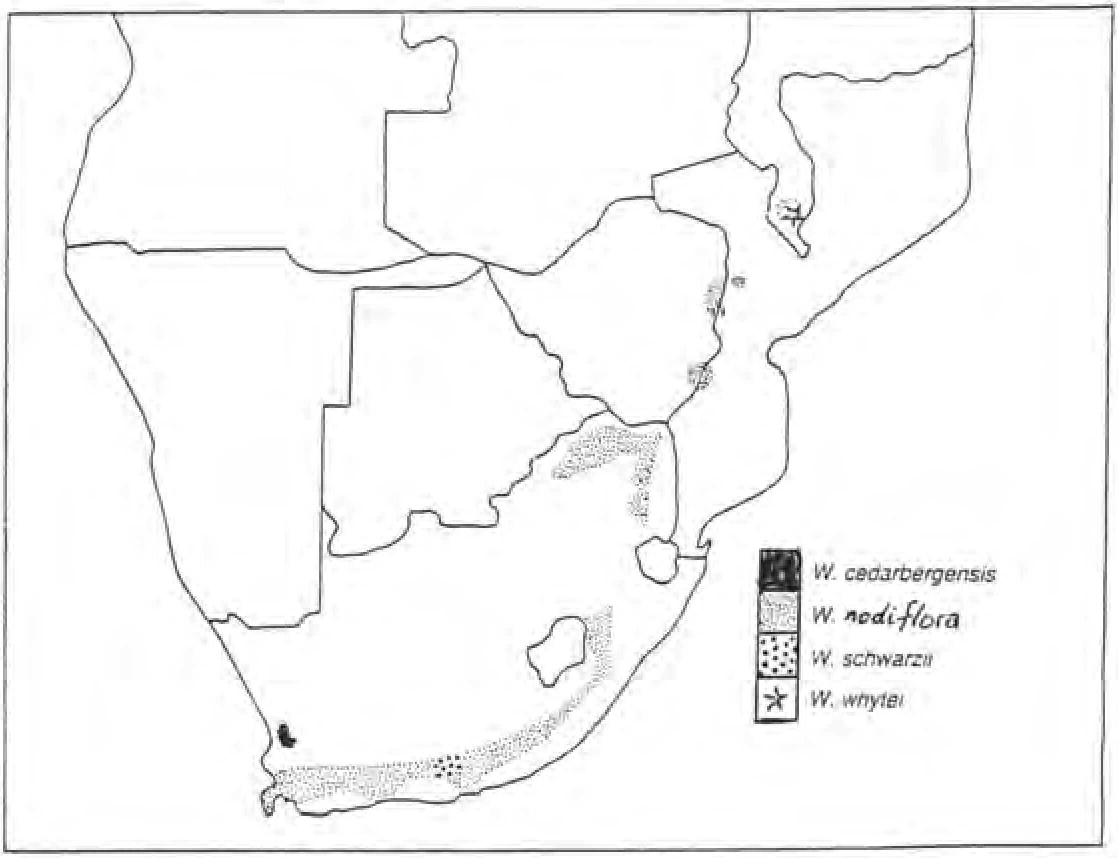


Figure 2 : Distribution of Widdringtonia

Figure 3 : UPGMA for Widdringtonia species

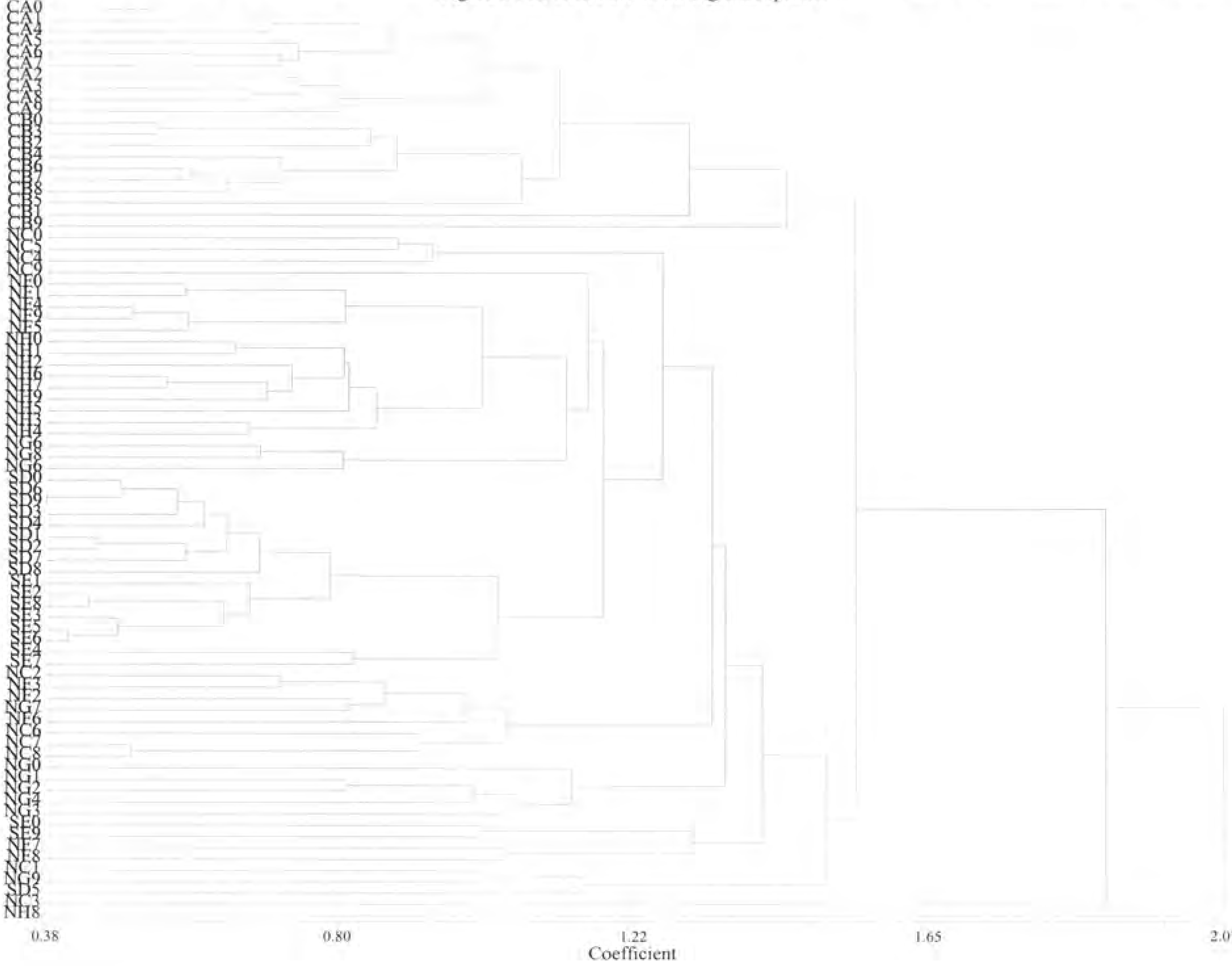


Figure 4 : Eigenvector plot for Widdringtonia species

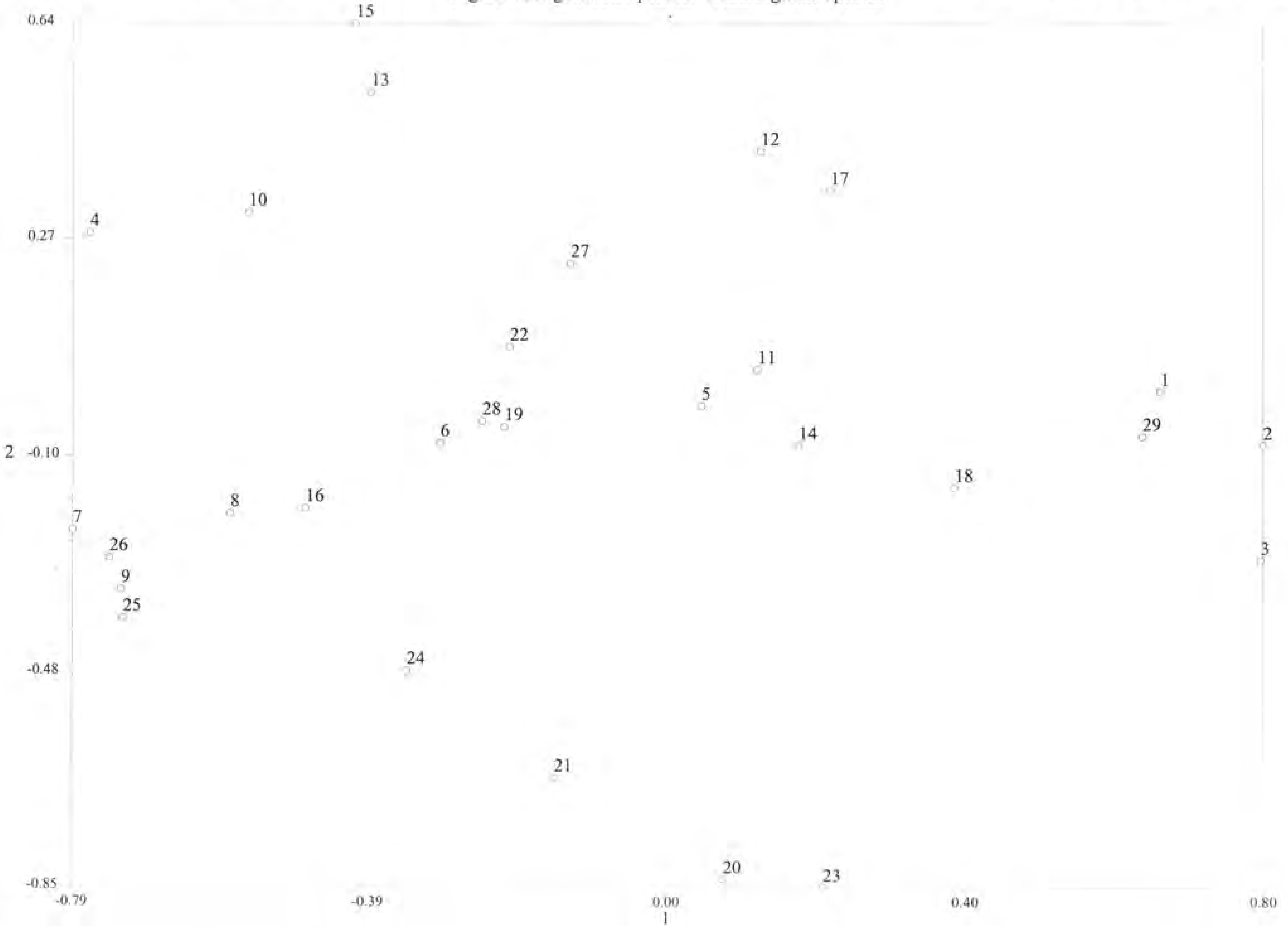


Figure 5 : Projection matrix for Widdringtonia species

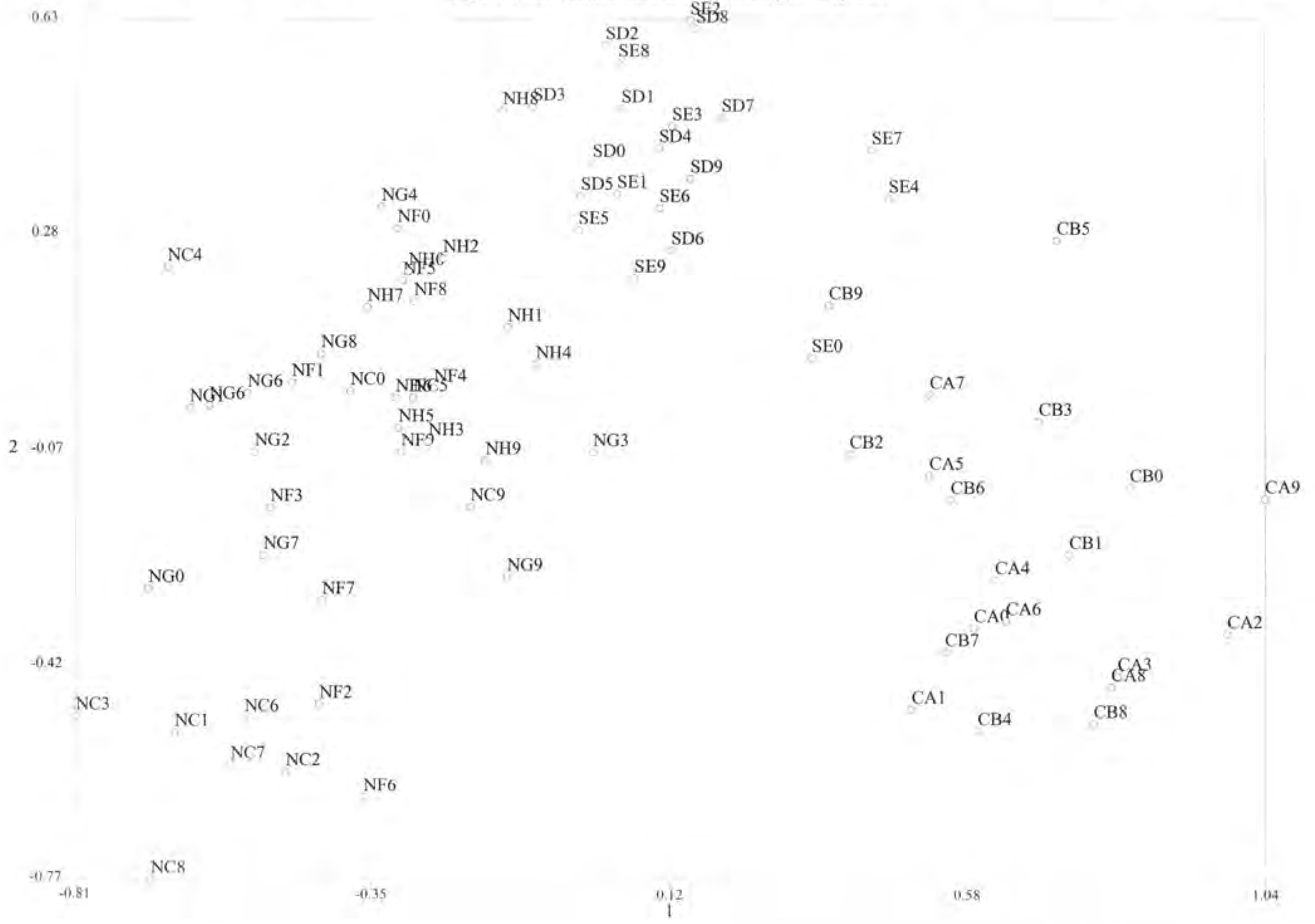


Figure 6 : UPGMA for Widdringtonia fire characters

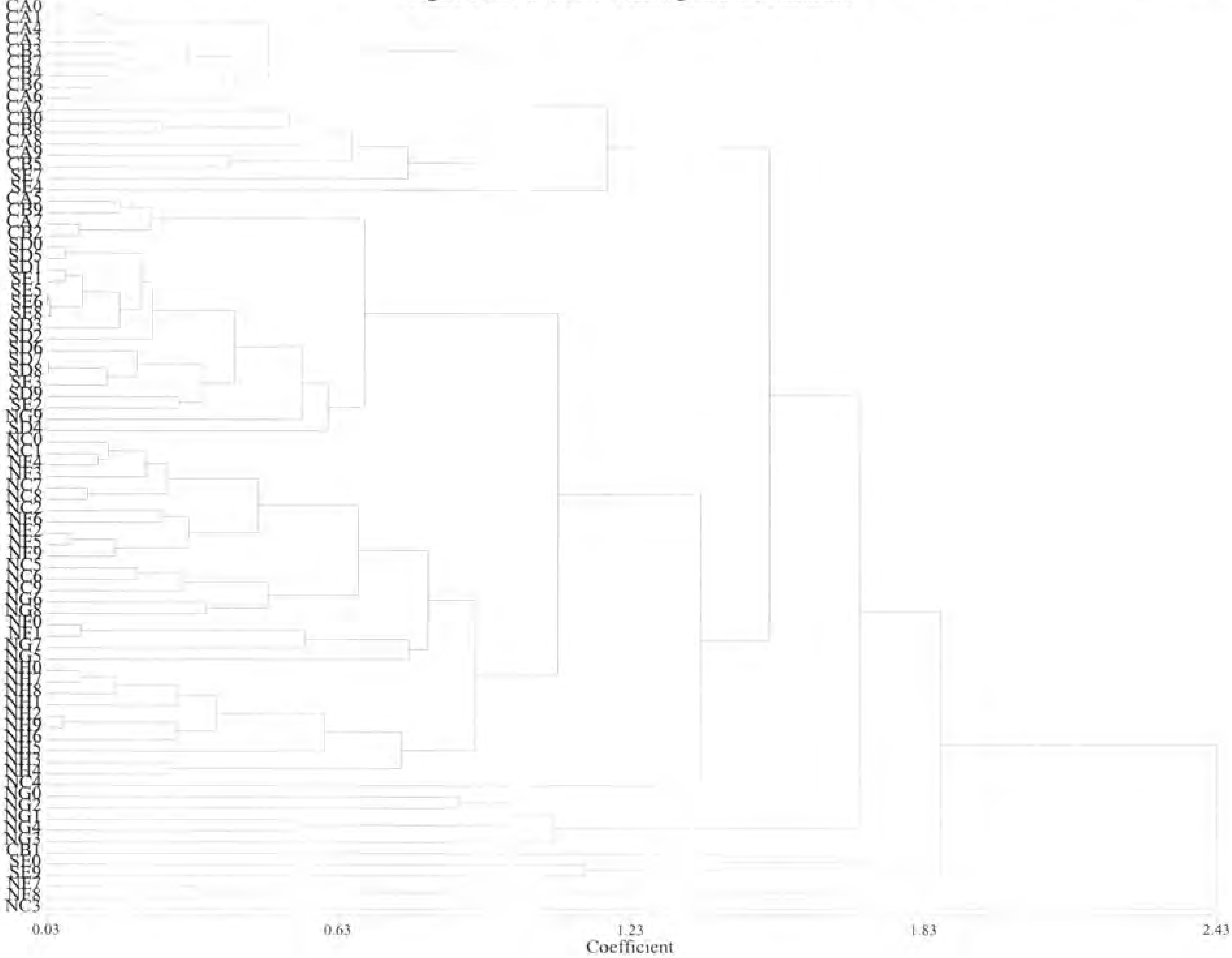


Figure 7 : Eigenvector plot for fire characters of Widdringtonia species

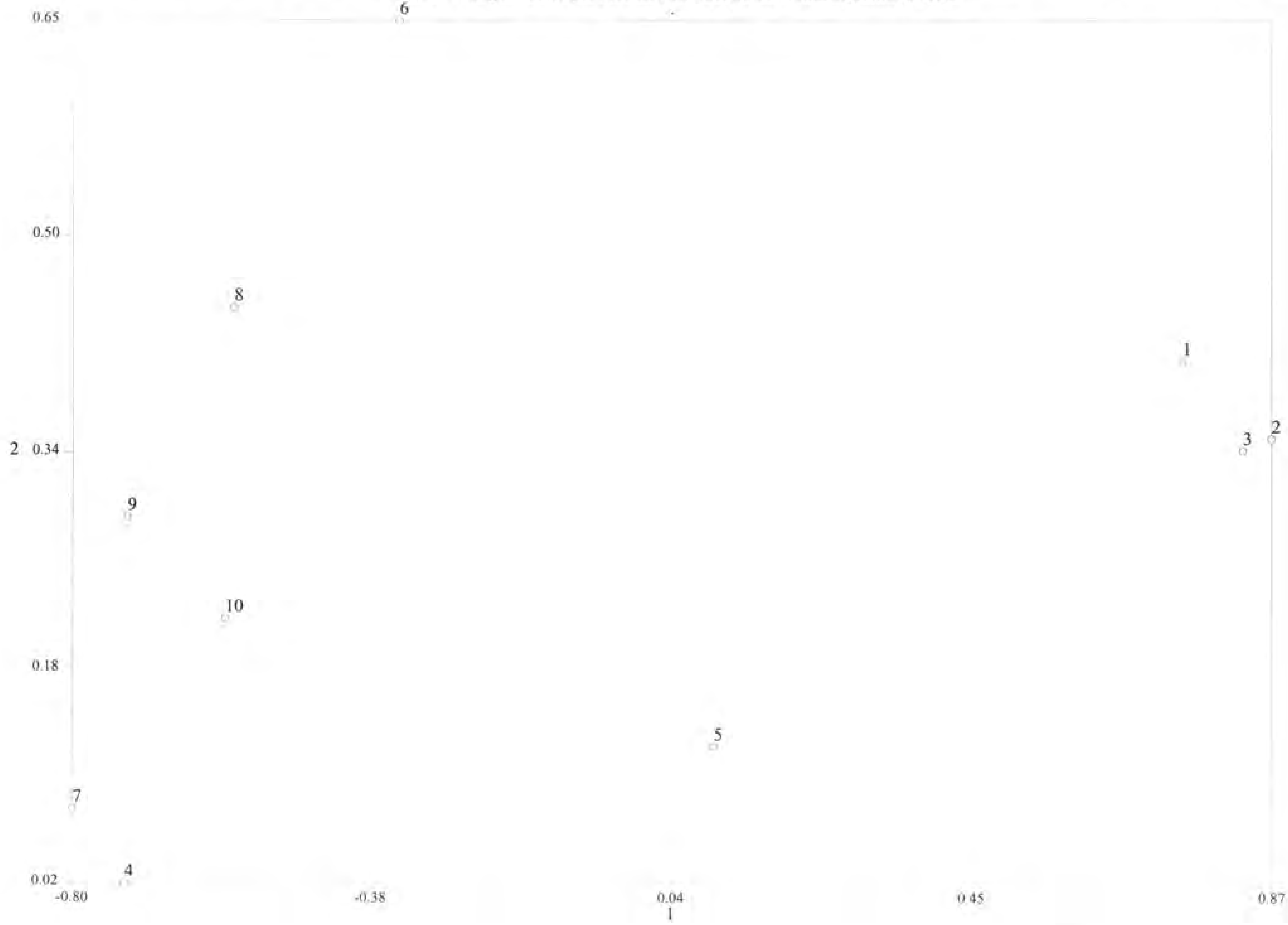


Figure 8 : Projection matrix for fire characters