A revision of the genus *Widdringtonia* Endl. (Cupressaceae) occuring in Malawi, Mozambique, Zimbabwe and the Transvaal (South Africa).

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A *Widdringtonia* forest on Mt. Mulanje, Malawi.

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Abstract

Widdringtonia occurring in Malawi, Zimbabwe and the Transvaal (South Africa) were examined in the field. According to the most recent revision of the genus only one species, *W. nodiflora*, occurs throughout these areas. Many aspects of tree morphology were quantified or measured, and seeds were collected. The morphological data was subjected to a phenetic cluster analysis which showed that the specimens can be divided into two distinct groups. Member of the one group are present throughout the areas which were visited, while the other group occurs only on Mulanje. This result confirms my own observation that there are two morphologically and ecologically distinct species present on Mulanje. Revised species diagnoses are given for *W. nodiflora* Powrie and the Mt. Mulanje endemic *W. whytei* Rendle. The Mulanje cedar, *W. whytei*, is the national tree of Malawi and is of considerable economic importance. However, because no distinction was formally drawn between the two species which are present on Mulanje, seeds of the species which is less suitable for silviculture were frequently used in silviculture trials and in the establishment of a plantation on Zomba Mountain (Malawi). The new endemic status of the "Mulanje Cedar" hightens its priority for conservation. Unfortunately, this unique tree with great economic potential is already in danger of extinction.

Introduction

General introduction

Widdringtonia is a small genus of African conifers which occurs from the Cape Peninsula in the South, to Malawi in the North. This study, however, deals with the genus only in the northern half of its distribution range. In this area, *Widdringtonia* is at the same time poorly known, and of great economic importance.

The majestic *Widdringtonia* from Mt. Mulanje is the national tree of Malawi and has been the country's most important source of softwood for almost a hundreds years. Seed collected on Mulanje has been sent all over the world for the establishment of plantations. However, despite the obvious importance of the genus, the alpha taxonomy of the northern Widdringtonias has not been adequately dealt with. The inadequacy of the most recent revision (Marsh 1966) is seriously hampering commercial forestry efforts (Chapola 1990; Venkatesh 1989; Chapman 1992a) and ecological studies aimed at the formulation of a management plan for this valuable natural resource (Chapman 1961 and 1992).

The main aims of this study are 1) to describe, within a geographical context, the morphological variation in *Widdringtonia* occurring north of the Drakensberg; and 2) to simplify these observations into a formal taxonomic treatment which will serve the needs of foresters, conservationists, ecologists, systematists and laymen.

This revision has to serve people that deal with trees at various stages of development and in various habitats. For this reason I have attempted to make the species diagnoses (Appendix 1), which are the product of this study, thorough enough to allow the identification of any *Widdringtonia* north of the Drakensberg, regardless of whether it is a seedling or cone bearing adult and regardless of the particular habitat of the tree. Identification should also be possible from herbarium specimens alone. To achieve these aims, I have considered variation that may be expressed at a wide range of scales, from tree architecture, quantified in meters, through leaf length measured in tenths of a millimeter to allozymatic variation which is dependant on the size and charge of protein molecules.

The genus *Widdringtonia* Endl.

Widdringtonia is a genus of monoecious, African cedars with small scale-like leaves and woody female cones that are about the size of a small plum. Each female cone consists of four thick valves which enclose the winged seeds (Dallimore and Jackson 1954). Widdringtonias occur in a narrow belt extending from the south western corner of the Cape Province along the eastern side of Africa, to Malawi in Tropical Africa (Palgrave 1977)(Fig. 1). Under the right conditions, all the species grow into tall trees, however, throughout the range of the genus, the number of large trees, which provide a durable and aromatic timber, has been greatly reduced through exploitation (Manders *et al.* 1990; Chapman 1990).

Within the family Cupressaceae, *Widdringtonia* is most closely related to the Australian genera *Callitris* and *Actinostrobus* with which it shares a number of derived characteristics (Moseley 1943). It has been suggested that *Widdringtonia*, like *Podocarpus*, had its origin in the Cape, and has migrated northwards, mountain-hopping along the archipelago of temperate "islands" that are scattered along the eastern side of Africa (Kerfoot 1975).

The taxonomic history of the northern Widdringtonias

W. whytei was first collected in October 1891 by Mr Alexander Whyte who lead the first botanical expedition up Mulanje (Fig. 1). According to Mr. Whyte, the cedar is the most striking botanical feature of Mulanje. He describes it as a "magnificent tree, reaching a height of 140 feet, sometimes with a clear straight stem of 90 feet, or giving off long straggling branches nearer the base" (Rendle 1893). The cedars occur in dense stands in the moist, deeply incised gorges of the Mulanje Plateau where they form a super-canopy above an understory of Afromontane forest trees (Chapman and White 1970)(cover picture). Rendle (1893) formally described the new tree from Mr. Whyte's collections and named it *Widdringtonia whytei* Rendle in his honour.

In the first detailed account of the genus, Masters (1905) described a new species, *W. mahoni*, from the eastern highlands of Zimbabwe. However, in 1911, Rendle concluded that these trees also belong to *W. whytei*. Later accounts of the species extended its range even further South to include the Soutpansberg Range in the Northern Transvaal (Burtt Davy 1926; Gilliland 1938; Palgrave 1957; Lewis 1960 and Chapman 1961). According to these authors, *W. whytei* in Zimbabwe is usually a small tree and it is very unusual to find trees over fifty feet in height, while in the Soutpansberg *W. whytei* occurs as a shrub rarely exceeding 10 feet in height. It was not until 1956 that *W. whytei* was first recorded from Mozambique. It was found on the southern slopes of the Gorongosa Mountains and on Mt. Xiroso, where it is only known to occur as a small tree (Chapman 1992)(Fig. 1).

It has often been suggested that *W. whytei* growing in areas other than Mulanje is experiencing suboptimal conditions, and for this reason is a smaller tree (Palgrave 1957; Lewis 1960). Chapman (1961) for example refers to the Zimbabwian and Mozambican forms of *W. whytei* as "a depauperate variation of the typical Mulanje form".

Even within Malawi, there is a great deal of variation in the growth form of *W. whytei*. In the most detailed account, Chapman (1961) described four different forms occurring only on Mulanje. The *typical form* coincides with Rendle's original description of *W. whytei*. The *scaly form*, *dwarf form* and *glaucous form* all differ from the *typical form* in being small shrubs which occur in the open bush, and not in the forests. According to Chapman (1961), the *dwarf form* differs further from the *typical form* in having the ability to coppice vigorously. Palgrave (1957) also refers to a *dwarf variety* of *W. whytei* which is found high up on the Lichenya plateau.

To further complicate the situation, Venkatesh (1987) described *narrow crowned variants* of the Mulanje cedar from the 79-year old plantation on Malawi's Zomba Mountain. The seeds used to establish the plantation were collected on Mulanje, however, the exact origin and habit of the parent trees is not known. The "variants" differ from the typical trees which surround them in having narrow-crowns, thin branches and thin bark. Venkatesh (1987) suggests that the narrow-crowned habit and associated characters could be pleitropic effects of a single dominant allele. In a follow-up study, Chapola (1990) found that the narrow and wide-crowned forms from the plantation on Zomba Mountain differ significantly in their wood properties.

In her revision of the genus Marsh (1966) sunk *W. whytei* Rendle and included it with the cedars from the Drakensberg in *W. cupressoides* (L.) Endl. *W. cupressoides* was originally described from the Cape Mountains where it occurs with *W. cedarbergensis* and *W. schwarzii*, both of which have very restricted distribution ranges. Thus, according to Marsh's (1966) revision there are three species in the genus *Widdringtonia*. Two occur within very restricted areas, and one, *W. cupressoides*, has a drawn out distribution range stretching from the Cape to the Tropics. It occurs from the

Cape Peninsular along the escarpment to the Natal Drakensberg, in the mountains of the northern Transvaal, the mountain range along the east of Zimbabwe, and finally, on Mount Mulanje (Fig. 1).

It invariably comes as a surprise to South African visitors to Mulanje that the 40m tall Mulanje cedars belong to the same species as the shrubby cedars of the Cape Mountains and the Drakensberg (Woods 1976; Burrows 1987). Marsh explains that "although an impression is gained that geographical races can be recognised in *W. cupressoides* (*sens. lat.*), a range of variation is found in characters such as leaf shape, seed and cone morphology. Thus no reliable distinguishing character could be found." In addition, she mentions that some of the cedar specimens on Mulanje *do* have a "stunted" growth form similar to the cedars of the South African mountains. She is referring here to what Chapman (1961) called the *dwarf form* of *W. whytei.*

Subsequently, *W. cupressoides* L. was renamed *Widdringtonia nodiflora* by Powrie (1972) who found that the type of *Brunia nodiflora* L. (Bruniaceae) was a twig of *Widdringtonia cupressoides*. This name change involves no change in the species concepts put forward by Marsh (1966).

During a trip to Malawi in 1990, we began to suspect that there are in fact two species of *Widdringtonia* on Mulanje. The forests of giant Widdringtonias, that so impressed Whyte (Rendle 1893), were truly magnificent and quite unlike anything we had ever seen before. However, within sight of these forests, in the Fynbos-like shrub on the slopes, we found a *Widdringtonia* that looked more familiar. These Widdringtonias had multiple stems which were coppicing from a subterranean tuber. This *dwarf form* bore a striking resemblance to the *W. nodiflora* (Syn. *W. cupressoides*) that we frequently see in the Cape Mountains, where it is usually a multi-stemmed shrub.

It seemed likely to us that the shrubby, coppicing cedar on Mulanje belonged to the same species as the Cape Mountain Cedar, while the giant forest tree belonged to a different species. Although *W. nodiflora* (Syn. *W. cupressoides*) does become a tall single stemmed tree in moist, fire protected conditions in the Cape Mountains, it seemed hard to believe that it could grow into the wide-crowned forest giants so typical of Mulanje. Blackened stumps of forest cedars that had been killed by fire, indicated that these trees, unlike the shrubby cedars nearby (and *W. nodiflora* Syn. *W. cupressoides* from the Cape), were unable to coppice.

We did not know how the variation which we observed on Mulanje fitted into the context of variation in Zimbabwe, Mozambique and South Africa. If *W. whytei* was to be "resurrected", it would be necessary to asses the status of the Widdringtonias in all the mountains within its original distribution range. In particular, I was interested to see whether two sympatric species might also be present throughout these areas.

The possibility of two sympatric *Widdringtonia* species on Mulanje has important implications for plantation forestry. With two species present on Mulanje, it is important to know from which species seeds were collected to establish plantations. One would expect that each species would require unique forestry techniques and yield wood with unique properties.

There are equally far reaching implications for the conservation and exploitation of natural stands. After almost 100 years of intensive cedar logging, this potentially sustainable resource faces extinction (Chapman 1992). The artificially high incidence of fires is another serious threat. In an attempt to curb fire damage to the cedar forests, a very extensive network of fire breaks has been laid out. However, while the losses to fire are still great, there seem to be few seedlings around to replace the felled or burnt trees. An ecological study to determine appropriate conservation measures will not be possible until the alpha taxonomy of the species concerned has been resolved. It seems that there are two ecologically distinct species on Mulanje which currently share the same name. The one species survives fairly regular fires by coppicing, while the other is vulnerable to frequent fires but needs intense infrequent fires for the regeneration of old stands. This duality would certainly confound any attempt at understanding the ecology of the "Mulanje Cedar"(s).

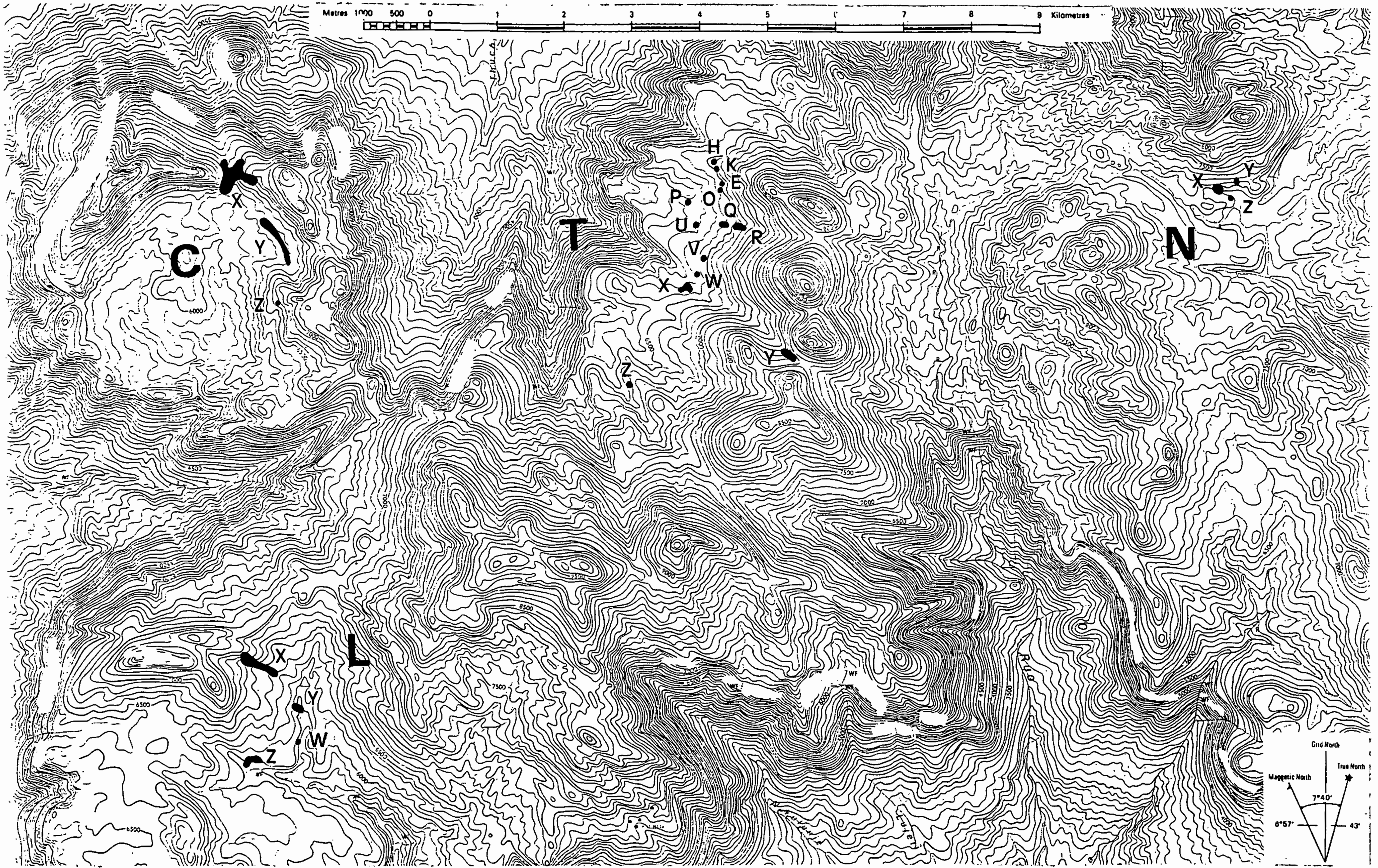


Fig. 2. The distribution of the poplations sampled on Mulanje. L = Lichenya, C = Chambe, T = Tuchila and N = Namasile. Smaller letters refer to specific populations sampled within the four areas.

Methods

Sampling areas

150 trees were examined in the field. Of these 127 are from Mount Mulanje (Malawi), 11 on Mount Inyangani (Zimbabwe) and 12 in the Soutpansberg (South Africa). In all cases, the trees which were sampled come from a wide range of different ages. Herbarium material collected on Mount Gorongosa (Mozambique) and Blouberg (South Africa) was examined in the National Herbarium of Zimbabwe.

The exact locations of the populations which were sampled on Mulanje are indicated in Figure 2. Two populations were sampled on the western slopes of Mt. Inyangani (Zimbabwe) at an altitude of 2100m. Population IA is located at 18°16'48'S and 32°49'45''E, and IB at 18°17'00'S and 32°49'30''E. Two populations were sampled from the top of the Soutpansberg (South Africa) at an altitude of 1500m on the farm Sederkranz. Population ZA is located at 22°58'00''S and 30°00'54''E, and ZB at 22°58'00''S and 30°01'00''E.

Each tree was given a code number. The first letter indicates which mountain it was found on, the second, which general area, and the third, which subpopulation. The number at the end of the code uniquely identifies each tree within a subpopulation.

Mountains

M	Mulanje
G	Gorongosa
I	Inyangani
S	Soutpansberg
B	Blouberg

General areas on Mulanje

C	Chambe Basin
L	Lichenya Valley
T	Tuchila Shelf
N	Namasile Slopes

Although only a small number of trees from the Soutpansberg and Inyangani Mountain were examined in detail, these trees are a representative sample from a very large population of trees which was examined more superficially.

For each new population which was sampled, a few features of the population and its habitat were recorded:

1) Population size
    a) The area, in hectares, occupied by the *W. whytei* (or wide-crowned) populations were taken from Isao Sakai's (1989) map of cedar distribution on Mulanje.
    b) *W. nodiflora* (narrow-crowned) populations are considerably smaller, so the number of individuals per population could be counted or estimated.
2) Distance to next population
    a) Taken from map of Mulanje cedar distribution (Sakai 1989) for "*W. whytei.*"
    b) Estimated or paced where possible for populations of "*W. nodiflora.*"
3) The position of each population was recorded on a map of Mulanje with a scale of 1:30 000 (Malawi Government 1977).
4) Percentage canopy cover
5) Notes on population demographics
6) Fire history, noting the age of proteas and other scrubs and grass in the area, the presence of multi-stemmed forest trees, the presence of charred wood and fire killed *Widdringtonias* and the location of the population relative to fire breaks.

7) A brief community description, noting indicator and dominant species
8) Description of abiotic habitat, noting rock cover, proximity to streams etc.
9) Altitude
10) Aspect of slope, determined with the aid of a compass.
11) An estimate of the slope angle.

Morphological characters

For each of the 150 trees that were sampled, the following was recorded:

1) My assessment of whether the tree looked like *W. nodiflora* (Syn. *W. cupressoides*) from the Cape Mountains or whether it fitted the original descriptions of *W. whytei* (Rendle 1893 which includes a drawing of cones, leaves and growth form).
2) An estimate of tree height in meters.
3) Diameter at breast-height (150 cm) measured as circumference with a tape measure
4) Bark thickness in millimeters at beast height: measured by cutting a small hole in the bark until the cork cambium showed, and inserting the depth measuring pin of a pair of Dial^R calipers.
5) A short description of the bark, noting flakiness / sponginess, colour and splitting pattern
6) Shape of leaf sprays: leaf bearing branchlets forming a short dense blunt ended tassel on the ends of long thin horizontal branches, tassels about as long as wide (0) or, leaf sprays pointed at the tip, long, thin and sparse (1).
7) A small sketch of the branching pattern of the tree, recording the extent of juvenile foliage.

A number of features which relate to fire ecology and reproductive condition were recorded:

8) Signs of fire e.g. blackened bark, burnt branches (1), no signs (0).
9) Resprouting from fire blackened base (0), single stemmed (1).
10) Number of stems if multi-stemmed.
11) Green branch primodia protruding through bark at base of tree, present (1), absent (0).
12) Number of batches (years) of sequential seed stores along a branch.
13) Receptive or very young female cones present (1), absent (0).
14) Male cones present (1), absent (0).
15) Average number of female cones per cluster.
16) Position of female cones on branch relative to foliage.
17) Order of cone bearing branches (order calculated as for rivers).

One to six branches bearing cones and leaves were collected from each tree. The cones of shrubby coppicing trees were usually within reach, and if not the thin, flexible branches could be bent down. The long, bare trunks of the tall timber trees that may rise for 12m without branching, are impossible to climb, but the canopy could sometimes be reached by climbing neighbouring forest trees. Low branches of large cedars growing on steep slopes could sometimes be reached from higher up the slope. If a branch was just out of reach, a long thin pole with a hook at the end was used to haul it down. This method was often employed, but because low branches seldom bore closed cones, many trees had to be scanned with binoculars before a suitable tree was located.

The final resort was to throw a line over a low branch. If the line passed over a thin branchlet, it was hauled down and the cones collected. If the line passed over a sturdier branch, a forty meter (11mm) rock climbing rope was attached to the line and pulled over. The one end was tied at ground level and the free rope was used to prussic into the canopy with two 4mm slings. It was more time effective to search for trees with accessible canopies, so the latter method was seldom used.

A tree can be accessible for many different reasons, usually related to its proximity to other climbable trees and slopes and to its age (size). As these variables are independent from the genotype, the selection of accessible trees would not have introduced a sampling bias.

The leaf and cone material was kept in labeled brown paper bags. The following properties were usually measured on the same day:

Foliage:

17) Foliage colour: light green (0); dark green (2); intermediate (1).
18) Length of ultimate branchlets measured to the nearest millimeter with calipers: Branchlets were selected at random and measured from the tip to the first node. Buds and very small branchlets (< 3mm) which were sometimes present near the tips of the branchlets were not regarded as nodes. About 6 replicates were measured per individual and averaged. This character attempts to quantify the differences that were observed in the fine branching structure of the leaf sprays.
19) Leaf tips closely appressed to the leaf bearing branchlets, or even curving inwards towards the branchlet axis, ultimate branchlets with a smooth appearance (2); leaf tips not closely appressed, standing at an angle to the branchlet axis, ultimate branchlets appear rough (0); intermediate (1).
20) A drawing of the leaf shape 3cm from the tip of the branchlet.
21) A drawing of the crossectional shape of the leaf.
22) Leaf length 1cm from the tip of branchlet, measured with calipers to the nearest tenth of a millimeter. Average for about 6 branchlets selected at selected at random.
23) Average leaf length 3cm from the tip of the same 6 branchlets.
24) Maximum size of large green leaves on 4th order branches. The leaves on elongating branches that are eventually to become main branches, in some individuals grow with the branches becoming unusually large while staying green, and in others die sooner and become shrivelled hard scales which persist on the branch for a few centimeters along its length.

Foliage data was always collected from mature foliage, distant from the apical meristem. However, to test a hypothesis concerning leaf ontogeny, additional data was recorded for the young leaves of the growing tips on six individuals. For these trees, the metric characters listed above were measured on both mature and young foliage.

Female cones:

25) A sketch of the lateral view of a female cone.
26) Average length of female cone, about four replicates, measured to the nearest millimeter.
27) Average width of the same female cones measured across widest diameter.
28) Number of valves per cone.
29) Relative size of valves: In some individuals one set of apposing valves is much broader than the other set (0), in others, the valves are all of equal size (2); intermediate (1).
30) Position of cusps on the set of broad apposing valves: tip of cusp protruding beyond central apex of cone (1); subapical (0).
31) Position of cusps on the set of narrow valves: tip of cusp protruding beyond central apex of cone (1); subapical (0).
32) Texture of valves: smooth (0); covered in large warts and longitudinal folds to the extent that the cusps are obliterated (3); (1) and (2) intermediate.
33) Colour of cones

About 6 cones from each individual were kept in brown paper packets and allowed to dry next to the fire or in the sun. Once the cones had opened all the seeds from the cones were collected and transferred to small waxpaper envelopes.

In the center of most open cones, at base of the four scales there are one or two hard pyramid shaped protuberances about 4mm in height. These structures contain liquid resin. In some unusual cones these structures are replaced by narrow greatly reduced valves. It seems that these resin sacs are vestiges of an additional set or sets of valves that have been reduced by the shortening of the cone axis. Before the empty cones were discarded, extent of the development of these structures was recorded for each individual.

34) Resin sacs: two distinct pyramids (3); a continuous twin peaked structure (2); a single pyramid (1); absent (O).

Back in the lab, an average sized seed was selected from the pooled seed collection of each individual and measured to the nearest millimeter with calipers.

35) Seed length including wing to the nearest 0.1mm
36) Seed width at widest part of wing

To give an indication of the variation in seed size within one individual, all the seeds in the seed collections from four trees were measured. The trees were selected to show the range in the degree of variability. Prior to measuring all the seeds, an "average" sized seed was selected as usual from each of these four individuals. A comparison of the four calculated averages and the estimated averages suggests that the estimations are a good approximation of the true mean (Fig. 3).

The seeds collected from the cones of each individual were counted. In some individuals, a substantial proportion of the ovules were aborted. These seeds are predictably found along the four extension of the central seed mass most distant from the center of the cone. They are a few millimeters long, have no endosperm and can easily be distinguished from seeds which grew to maturity but have no endosperm as a result of predation and fungal attack. Because predictable abortion of seeds in a specific part of the cone is a character with systematic value, while predation is only of ecological interest, aborted seeds were not counted while attached seeds were simply counted with the rest of the seeds. The seed totals which varied from 680 to 16 were divided by the number of contributing cones to give:

37) Average number of seeds per cone

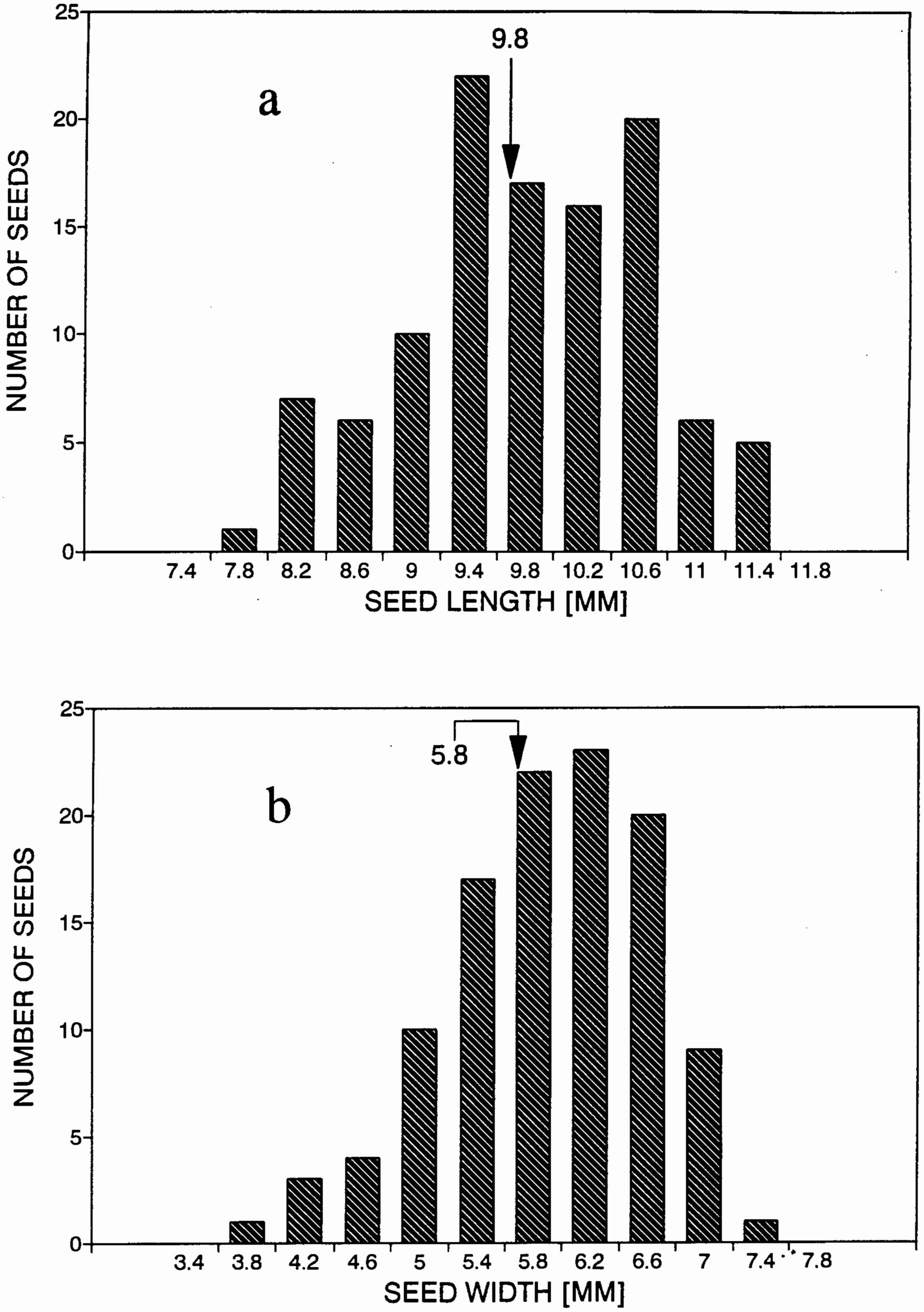


Fig. 3. The frequency distribution for the length (a) and width (b) of the the seeds collected from specimen number MTK10. An "average sized" seed was picked and measured. The length and width the "average" seed falls close to the peak of the distribution functions, indicating that the estimate is a good approximation of the true median. "Estimated mean values" fell equally close to the true median for three other specimens.

From each individual five to twenty large seeds were selected for germination. The seeds from each individual were placed in a separate Petri^R dish on filter paper soaked in Benelate^R solution ($1g.l^{-1}$) - a commercial fungicide [which contains?]. The Petri^R dishes were enclosed in plastic bags to limit evaporation, and placed in an environmental chamber [make, humidity settings ?]. The environmental settings were: 14hrs at 20°C in the light; 10hrs at 10°C in the dark.

After 50 days the following data was collected from each Petri^R:

38) Fraction of seedlings with 2 cotyledonary leaves.
39) Fraction of seedlings with 3 cotyledonary leaves.
40) Fraction of seedlings with 4 cotyledonary leaves.
41) Fraction of seedlings in which the radicle {spell] has emerged, but the cotyledonary leaves are still hidden.
42) Fraction of seedling in which the radicle has not yet emerged.
43) The cotyledonary leaf length of a representative seedling was measured to the nearest millimetre.
44) The cotyledonary leaf length of the same seedling.

If there was variation in the number of cotyledonary leaves within a Petri^R dish (seed collection from one individual), a representative seedling of each type was measured. At this stage of development, none of the seedling had euphylls.

The seedlings which were not used in the electrophoretic analysis were planted in trays filled with potting soil and kept on a mist-bed for two weeks. After removal from the mist-bed, the seedling were watered once a day. After seven months the length and width of the leaves was measured, and the colour of the leaves was recorded.

Before analysis could begin, a number of data transformations had to be performed:

a) For many characters, multiple measurements were taken from one individual (e.g. the length of about six leaves and six cones from each tree were measured). For these characters, the average value for each tree was used.

b) Some metric characters which are dependant on the developmental stage of the individual tree, are best expressed as relative, rather than absolute values. Bark thickness, for example, is best expressed as the ratio of bark thickness to stem diameter. Similarly, the ratio of tree height to circumference is a more informative measure than either of the two absolute values.

c) The **number** of seedling per parent with 2, 3 or 4 cotyledonary leaves was converted to the **fraction** of seedlings with 2, 3 and 4 leaves. This was done because the number of seeds selected for germination was not equal throughout all parent plants.

d) Tree circumference at breast height was converted to tree diameter at breast height.

e) The character "signs of fire damage; 1 = yes, 0 = no" was combined with the character "coppicing; 1 = yes, no = 0" to give the character "response to fire damage; 1 = coppicing, 0 = not coppicing, not damaged = no data." A formula containing a conditional statement returned the value for the new composite character. A tree will coppice only if it a) has the ability to coppice, and b) is damaged. The composite character considers only those trees which **are** damaged and so is dependent only on the genotype of the tree, and not on whether or not the tree is damaged.

Electrophoretic methods

If there are two species present on Mulanje, these may well be distinguishable on the basis of an electrophoretic marker. For example, one or both of the species may be characterized by the presence of an unique locus or allele. I looked for such a markers by comparing the banding pattern for the groups of specimens which in the field had been assigned to the two species. I hoped that the electrophoretic analysis would clarify the relationship between the Mulanje Widdringtonias and the Widdringtonias further South.

The recently germinated seedlings were removed from the environmental chamber after 50 days. One seedling from each Petri^R dish (maternal parent) was used in the electrophoretic analysis. The analysis followed the methods outlined by Conkle *et al.* (1982). Only minor modifications were necessary.

The addition of bovine albumin (40 mg/100 ml) and 2-mercaptoethanol (1 drop/100 ml) to the Tris-maleate extraction buffer improved the resolution of enzyme bands. The albumin binds phenolics and free fatty acids, while the 2-mercaptoethanol reduces the effect of resins. The best results were obtained using a morpholine citrate buffer (pH 6.1) for both the gel and the tray.

Analytical methods

Phenetic analysis:

The first step was to objectively test the hypothesis that the morphological variation on Mulanje could be divided into two groups. This was done by running a computerized phenetic analysis of the morphological data collected on Mulanje. The software package, NTSYS-pc (Numerical Taxonomy and Multivariate Analysis Systems for personal computers), was used to perform this task. Those characters which were found to be useful in the field were selected for analysis; they include:

Ratio of height to diameter
Ratio of diameter to bark thickness
Buds or juv. foliage at base [1=yes; 0=no]
Response to fire damage [1=coppicing; 0=not coppicing]
Foliage colour [2=light; 1=intermediate; 0=dark]
Avg. leaf length 3cm from tip [mm]

Avg. leaf length 1cm from tip [mm]
Avg. length of ultimate branchlets [mm]
Leaf angle to axis [2=closely appressed to 0=free standing]
Number of cones per cluster
Max. leaves on 4th order branches
Shape of leaf sprays [2=poined to 0=blunt ending]
Avg. female cone length [mm]
Avg. female cone width [mm]
Position of cusps on broad valves [1 = always apical]
Position of cusps on narrow valves [0 = always subapical]
Number of seeds per cone
Length of average seed [mm]
Width of an average seed [mm]
Ratio of seed length to width
Average length of juvenile leaves [mm]
Fraction of seedlings with 2 cotyledonary leaves
Fraction of seedlings with 3 cotyledonary leaves
Fraction of seedlings with 4 cotyledonary leaves

Before the phenetic analysis was conducted, the data were standardized to reduce the effect of different scales of measurement in different characters. If this was not done, characters with large mean values, such as "tree height" would strongly influence the outcome of the phenetic analysis; while character with small mean values, for example "leaf length" would be insignificant in the grouping process. The standardization was performed using an option within NTSYS-pc which subtracts from each datum the mean value for that character, and then divides this difference by the standard deviation in the character. For example, to standardize the character "average cone width" for individual number MCX1, the mean cone width across all individuals was calculated and subtracted from the datum being standardized; this difference is then divided by the standard deviation in "average cone width" across all individuals (Rohlf 1992).

The standardized data matrix was subjected to a phenetic analysis which computes the level of overall similarity (or dissimilarity) among the individual trees. On this basis, the trees can later be divided into groups of similar trees. There is a wide range of coefficients of dissimilarity to choose from. The nature of the data determines the relative ability of these various algorithms to detect groups within the data. I experimented with a selection of dissimilarity measures, including the Bray-Curtis distance measure, Canberra metric coefficient of dissimilarity, chi-squared distance measure, average taxonomic distance, Euclidean distance and average Manhattan distance.

The Manhattan algorithm (also called the city block algorithm) was the most suitable algorithm to use because it deals well with presence-and-absence data in combination with metric data (Sneath and Sokal 1973). The character "cusp position" which was coded as 0 for subapical and 1 for apical, is an example of a presence-and-absence character used in the analysis. The formula used to calculate the average Manhattan distance is

$$M_{ij} = \frac{1}{n} \Sigma_k \mid x_{ki} + x_{kj} \mid$$

where i and j are two trees being compared; k is the character and n is the total number of shared characters. Missing values are taken into account. For a pair of trees, i, j only those values for k are used for which x_{ki} and x_{kj} are both present. This means that different elements of the resulting dissimilarity matrix may be based on different sample sizes. Thus, average coefficients deal well with incomplete matrices. Although there were few missing data values in the data matrix, this is an added advantage of the average Manhattan distance coefficient.

The Manhattan distance analysis produces a triangular data matrix listing the level of dissimilarity among all the individual trees. In order to visualize this matrix of dissimilarity the data was fed into a clustering program. All clustering programs (sometimes called greedy algorithms") basically work in the same way (Rohlf 1992):

1. Search the input matrix for a pair of objects (tree *i*, and tree *j*) that are the most similar (or least dissimilar).

2. Merge these objects into a new cluster.

3. Update the matrix to reflect the deletion of the pair of objects (trees), *i* and *j*, that were merged and the addition of a new "object" corresponding to the new cluster. Similarities or dissimilarities have to be computed between the existing objects and the new cluster (the different clustering methods differ only in the formulas used at this step).

4. Go back to step 1 if the size of the new matrix is greater than 2 X 2 - else stop. Note that two objects are deleted and one is added at each step so this algorithm must terminate.

The dissimilarity matrix was clustered using the unweighted pair-group method with an arithmetic average (UPGMA). This is the most commonly used clustering method (Sneath and Sokal 1973). The output of the program is in the form of a "tree matrix". A phenogram is also displayed in which similar trees are clustered together.

These objectively produced clusters were compared with my subjective classification of the trees in the field.

The next step was to see how the groups which were detected on Mulanje fit into the general pattern of morphological variation in those mountain ranges which were included in the distribution of the former *W. whytei*. The data collected from cedar trees growing in these mountains was added to the data matrix of the Mulanje trees and the phenetic analysis was rerun.

To test the hypothesis that young leaf-sprays of *W. whytei* are similar to the mature foliage of *W. nodiflora*, another phenetic analysis was conducted. However, this time, only foliage characters were considered and previously excluded data, collected from the growing tips of *W. whytei*, were included in the data matrix.

Once groups in the data had been detected, I individually assessed the characters which had been used to conduct the phenetic analyses. By considering the characters individually, I could determine which characters were the most useful for assigning an tree to a particular group. If it was decided that the groups represent different species, useful character for the identification of these species could be evaluated in this way. I drew frequency histograms for each metric character to determine the extent of overlap between the two "species". Separate histograms for each group (species) were draw on the same axes to allow a direct comparison.

A section of the data matrix was imported into Statgraphics (Statistical Graphics System; Statistical Graphics Corporation 1991) and a regression analysis was run with "bark thickness" as the dependent variable and tree diameter as the independent variable.

Results

Field identification

Of the 127 trees examined on Mulanje, 56 fitted the description of *W. whytei* (Rendle 1893). The remaining 71 trees had the same general habit and detailed morphology as *W. nodiflora* (Syn. *W. cupressoides*) with which I am familiar from the Cape Mountains. The 11 trees which were examined in detail on Mount Inyangani all belonged to the "*W. nodiflora* (Syn. *W. cupressoides*) group." The 12 trees from which data was collected in the Soutpansberg were also assigned to this group.

Phenetic analysis

The phenetic analysis of the 127 Mulanje trees revealed that the trees could be separated into two distinct groups on the basis of the characters which I recorded (Fig. 4). The trees which were identified as *W. whytei* in the field, were clustered together, while those which I had assigned to the "*W. nodiflora* (Syn. *W. cupressoides*) group" made up the other cluster. There was however one exception, tree number MLY9 had been identified as *W. whytei*, but was clustered with trees which had been identified as *W. nodiflora*. This was the first member of the *W. nodiflora*-group which I had (unknowingly) come across on Mulanje. It is 2m tall and single stemmed, however, looking at my sketch of the tree and the data which was recorded, it is obvious that I had misidentified it. I changed the identification of the tree to *W. nodiflora* (Syn. *W. cupressoides*) so that the analysis of individual characters would not be confounded.

A phenetic analysis of the entire data set, this time including the data collected from Inyangani and the Soutpansberg, again yielded two distinct clusters (Fig. 5). The trees from the Soutpansberg and Inyangani Mountain all fall into the "*W. nodiflora* (Syn. *W. cupressoides*)" cluster, while the composition of the "*W. whytei*" cluster is unaffected.

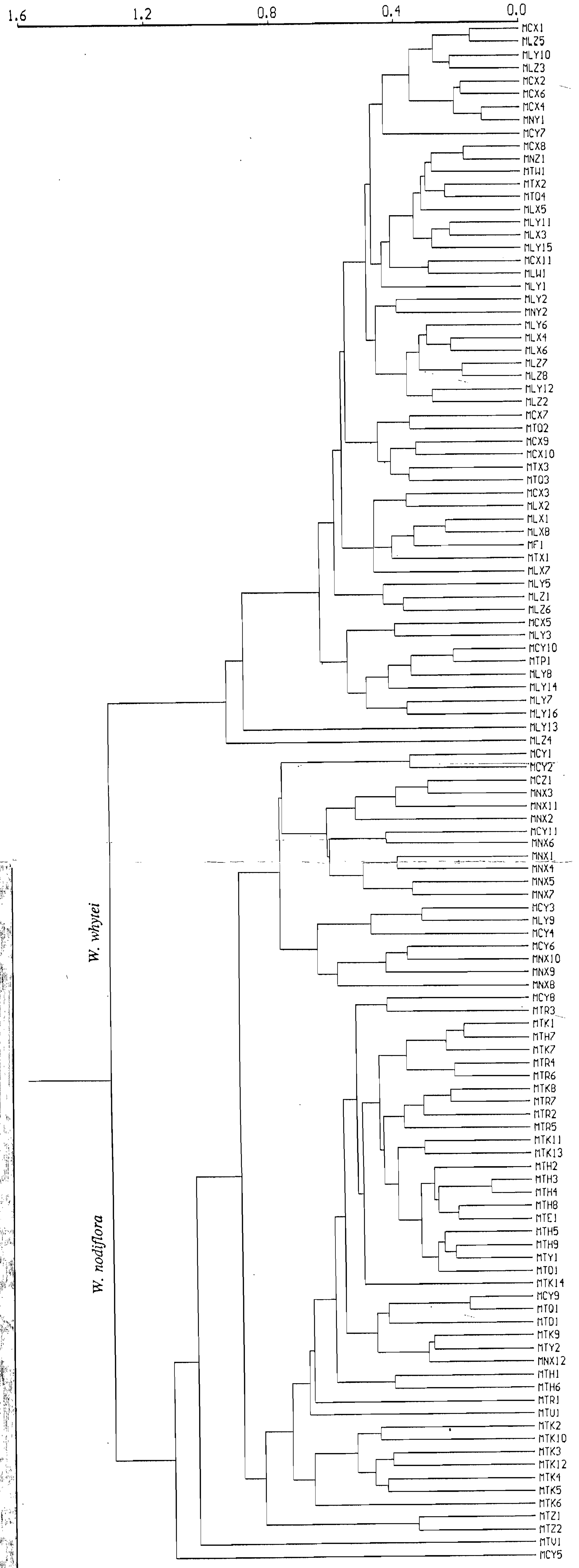


Fig. 4. The phenogram depicts the relationship between 127 Widdringtonias occurring on Mt. Mulanje. The Average Manhattan Distance was used as a measure of dissimilarity between organisms. A phenogram was produced from this data using the unweighted pair group method. Subsequently, the two major groups were assigned to taxa. L = Lichenya, C = Chambe, T = Tuchila, N = Namasile.

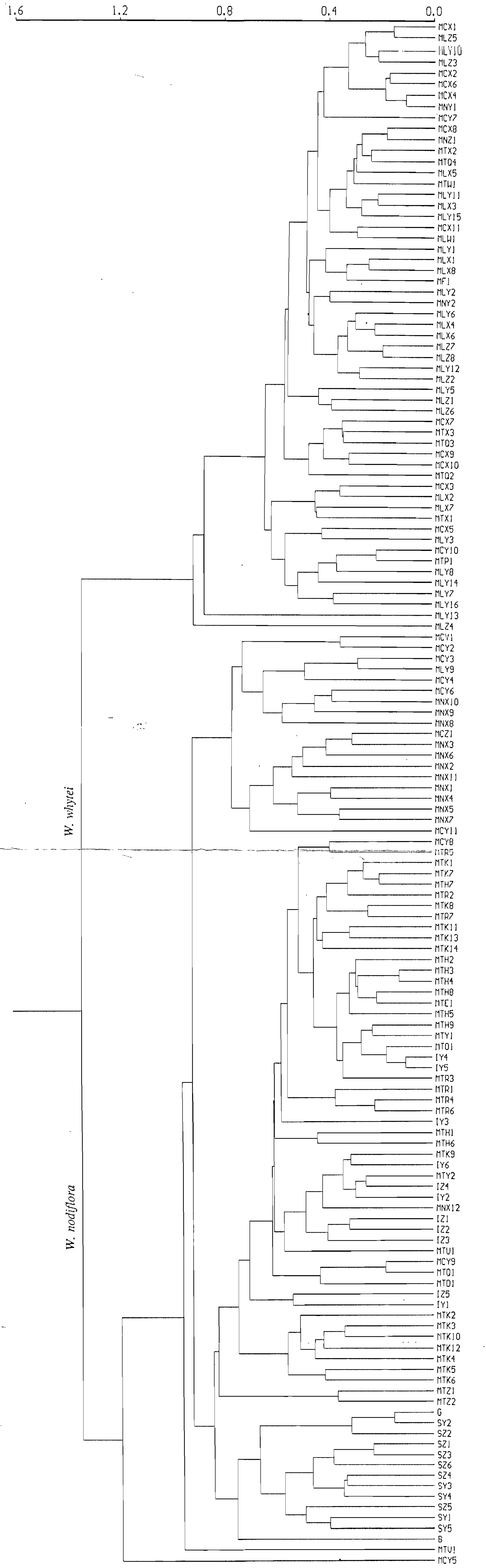


Fig. 5. The phenogram depicts the relationship between 150 Widdringtonias occurring on Mt. Mulanje (M), Mt. Inyangani (I), Mt. Gorongosa (G), the Soutpansberg (S) and Blouberg (B). The second letter of each code refers to specific populations.

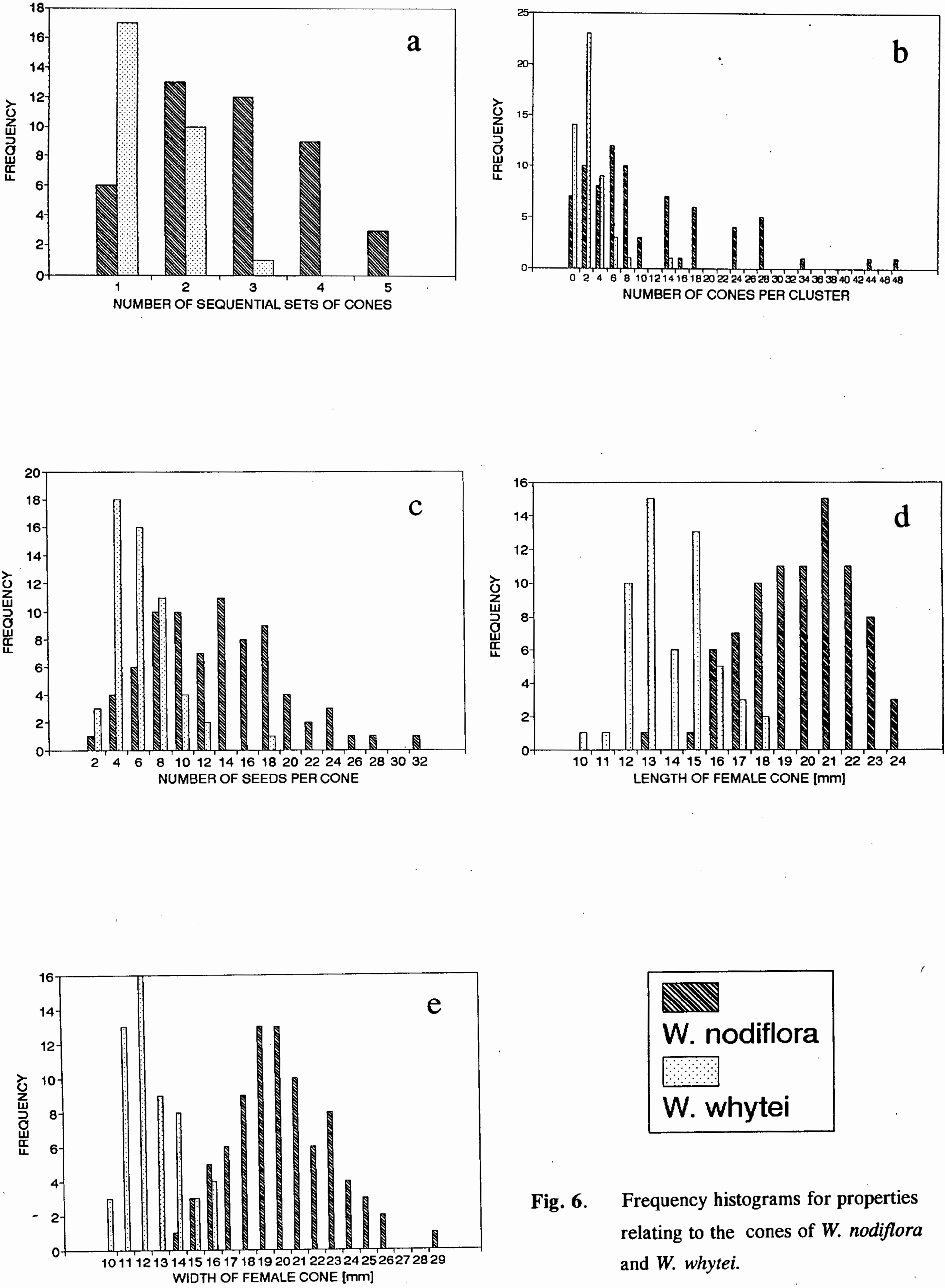


Fig. 6. Frequency histograms for properties relating to the cones of *W. nodiflora* and *W. whytei.*

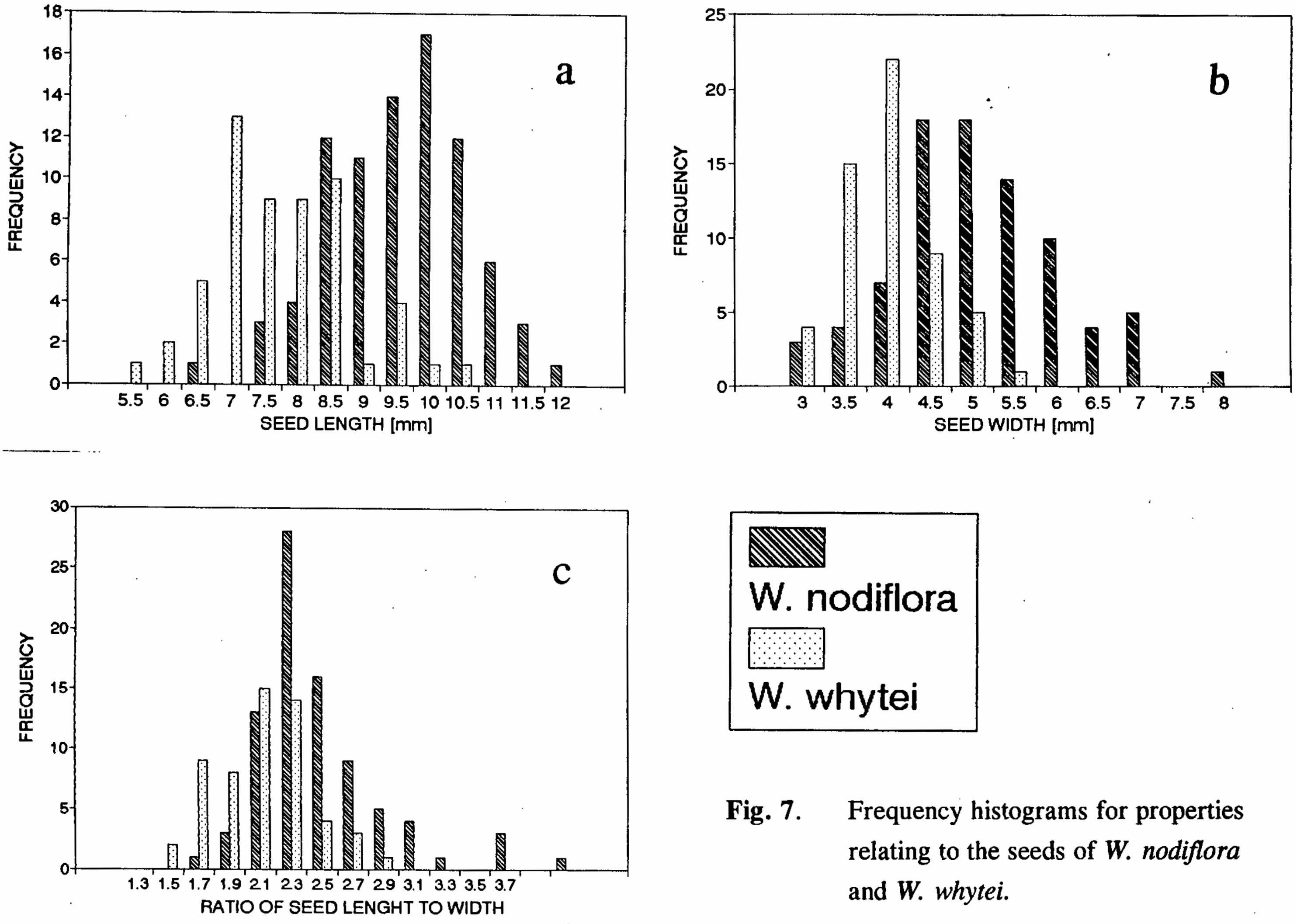


Fig. 7. Frequency histograms for properties relating to the seeds of *W. nodiflora* and *W. whytei.*

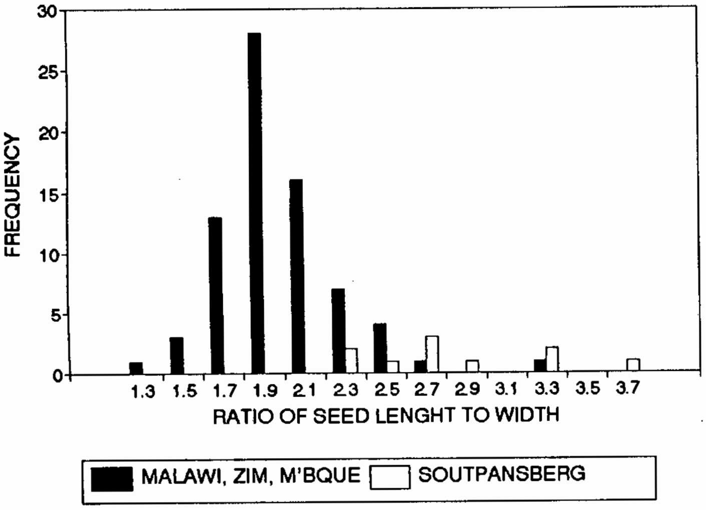


Fig. 8. *W. nodiflora* occurring in the Soutpansberg has long thin seeds.

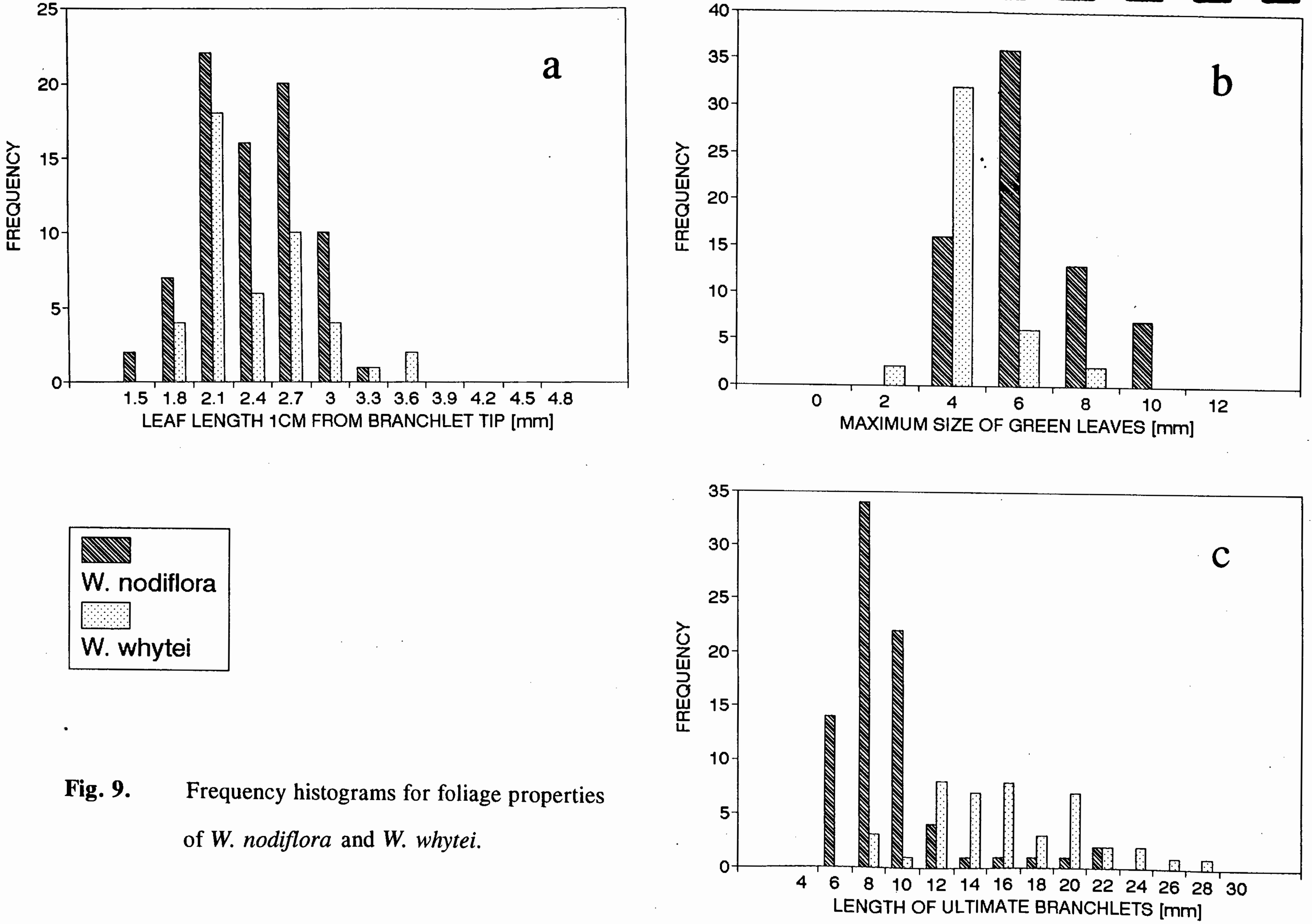


Fig. 9. Frequency histograms for foliage properties of *W. nodiflora* and *W. whytei*.

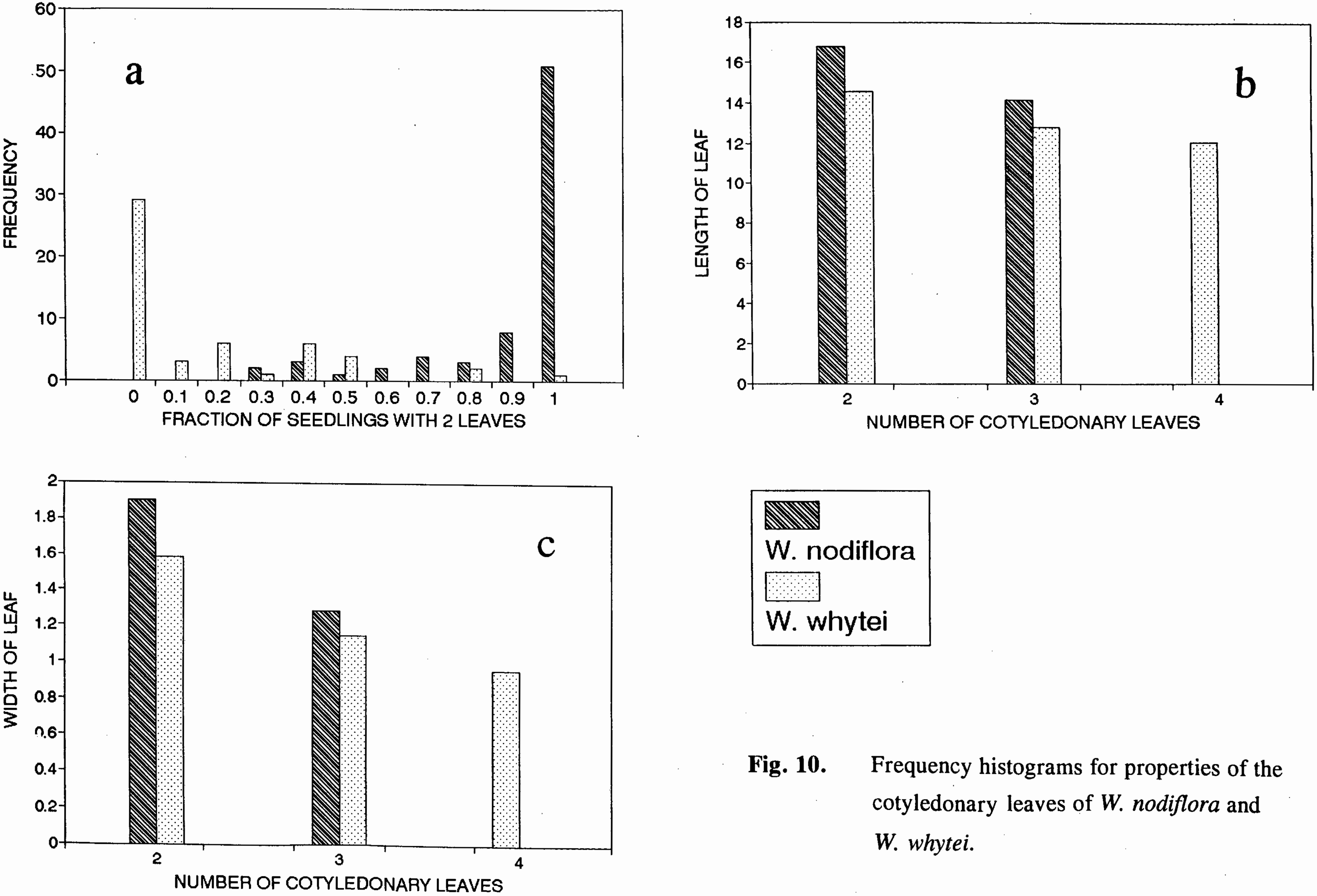


Fig. 10. Frequency histograms for properties of the cotyledonary leaves of *W. nodiflora* and *W. whytei*.

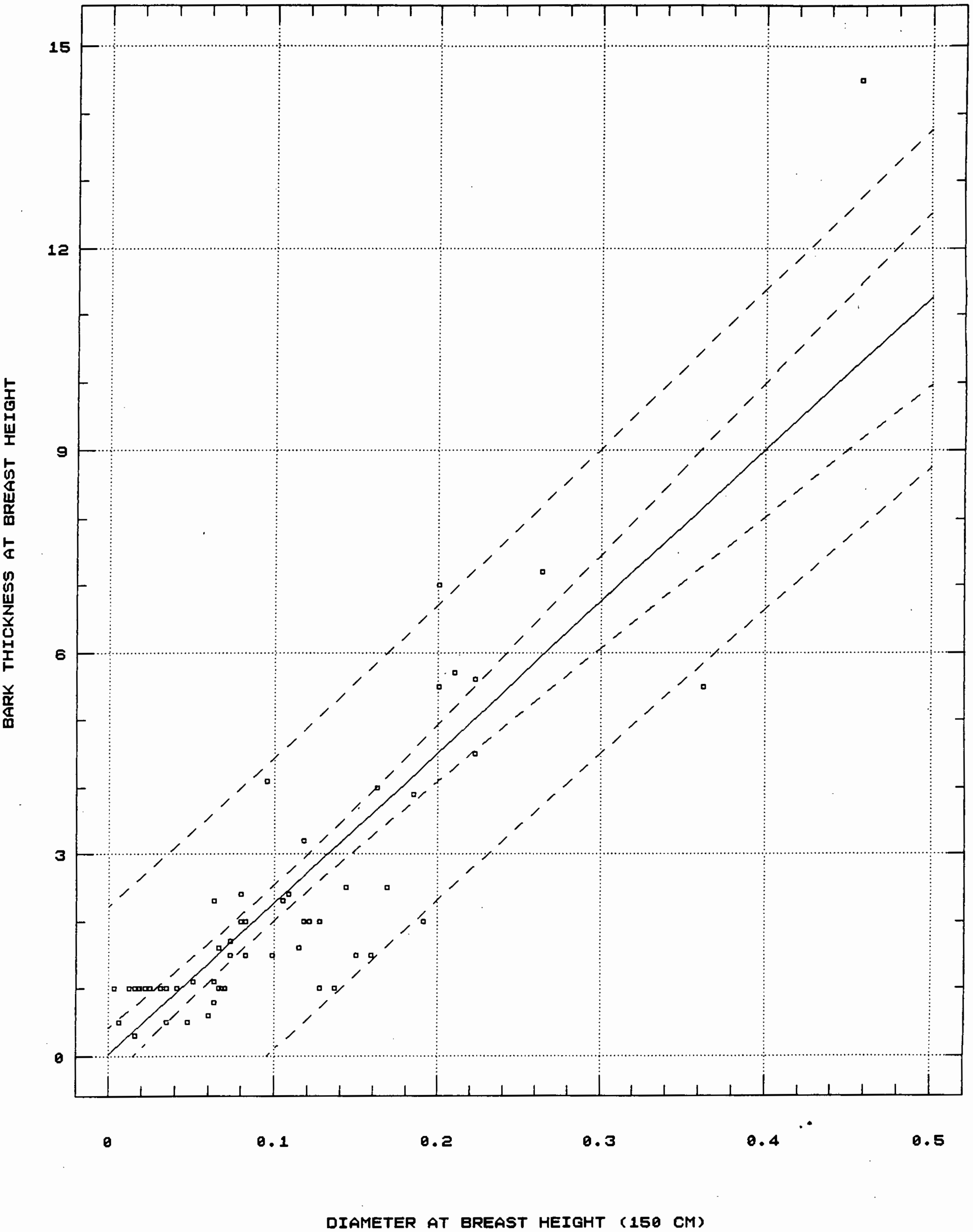


Fig. 11. *W. nodiflora*: a plot for the regression of bark thickness on trunk diameter at breast height (140 cm).

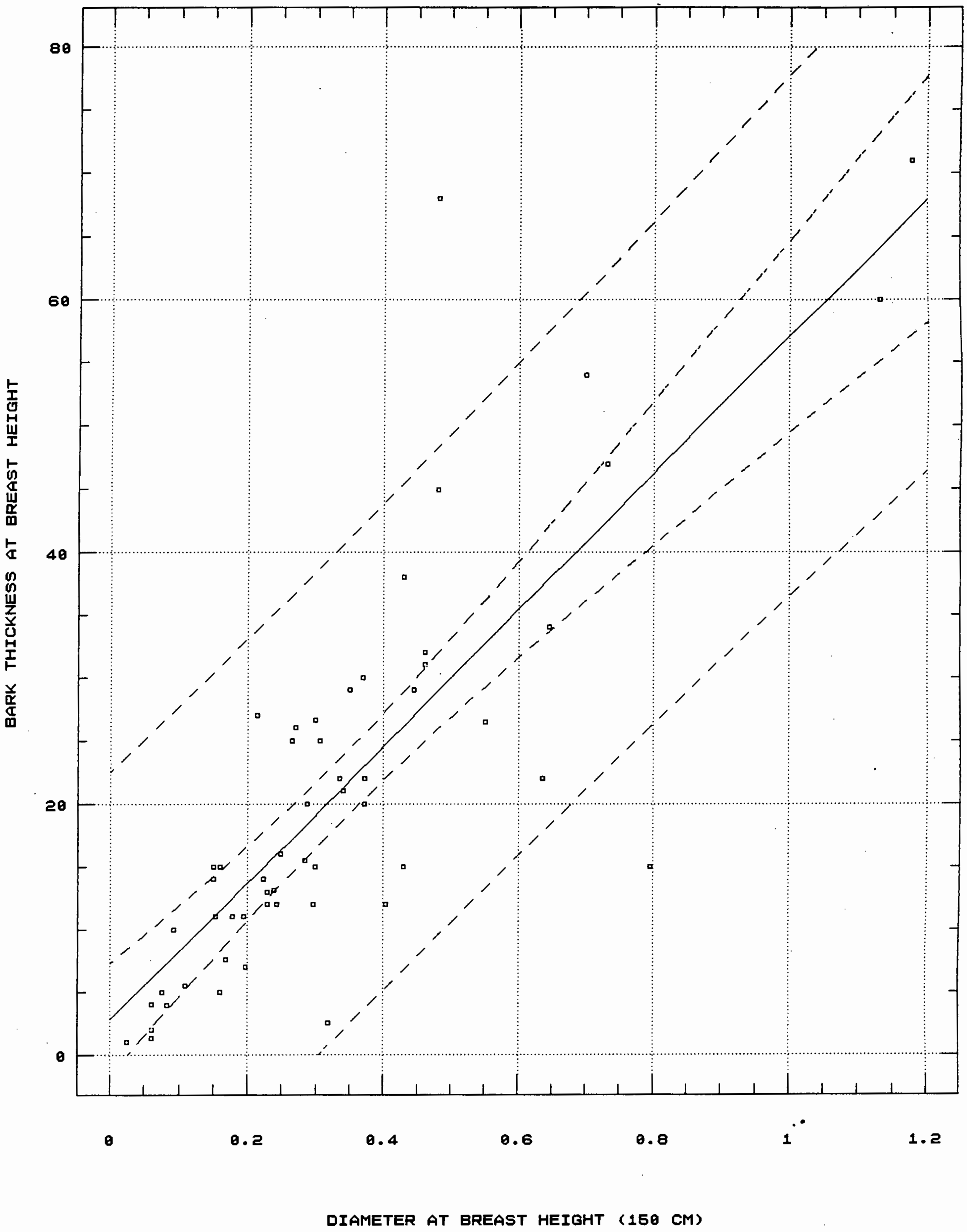


Fig. 12. *W. whytei*: a plot for the regression of bark thickness on trunk diameter at breast height (140 cm).

The two individuals which were known only from Herbarium specimens collected on Mount Gorongosa (Mozambique) and Blouberg (Northern Transvaal) respectively, were grouped within the Soutpansberg "subcluster" of the "*W. nodiflora* (Syn. *W. cupressoides*)" group.

Unlike the Soutpansberg trees, the trees from Inyangani did not all fall into one neat subcluster, but are scattered among various subclusters of "*W. nodiflora* (Syn. *W. cupressoides*)".

Generally, the individuals from different subpopulations do not form distinct groups, however, 7 of the 14 individuals from population MTK do form a tight subcluster with in the "*W. nodiflora* (Syn. *W. cupressoides*)" cluster.

The phenogram based only on foliage characters did not show a neat dichotomous division. Most of the trees which were assigned to the "*W. whytei*" group in the field still clustered together; however, this cluster of 42 trees is contained within a diffuse cluster of trees which were identified in the field as *W. nodiflora* (Syn. *W. cupressoides*). What is more important though, is the placement of foliage specimens from the growing tips of four trees which were identified as *W. whytei*. These foliage specimens are shown to be more similar to the mature foliage from trees of the "*W. nodiflora* (Syn. *W. cupressoides*)" group than to mature foliage of the "*W. whytei*" group.

Histograms depicting the distribution frequencies for metric characters are shown in Figures 6 to 10. The distribution functions for the two groups have in each case been drawn on one set of axes to allow direct comparison.

The results from the regression analysis of bark thickness (mm)(dependent) on tree diameter (m)(independent) are tabulated below:

Hypothetical group	*"W. whytei"*	*"W. nodiflora"*
Intercept	2.80	0.027
Slope	54.30	22.45
Correlation coefficient	0.81	0.87
R-squared	65.01%	76.49
Degrees of freedom	55	66
Probability level	<0.0005	<0.005

On the basis of these analyses and field observations, I put forward a revised alpha taxonomic treatment for *Widdringtonia* north of the Natal Drakensberg. The species diagnoses are given in Appendix 1.

Electrophoretic results

Good band resolution was obtained for the following enzymes: malic dehydrogenase, esterase, alcohol dehydrogenase, malic enzyme, glucose-6-phosphate dehydrogenase, leucine aminopeptidase, peroxidase, phosphoglucose isomerase and shikimic acid dehydrogenase (Fig. 27). It was found that there is so much allozymatic variation within each "species" that no unique locus or allele is consistently present in all of the individuals which belong to one group. Thus, no diagnostic character, by which individuals can be identified, could be found.

Discussion

General discussion

The results of this study suggest that there are two species of *Widdringtonia* on Mount Mulanje. This conclusion has not been reached in the last revision of the genus (Marsh 1966) or any previous study. I agree with Marsh that the Widdringtonias in the Soutpansberg and the highlands of Zimbabwe bear a strong resemblance to *W. cupressoides* (Syn. *W. nodiflora*) from the Cape. While I agree with her decision to include the Widdringtonias from these two areas in *W. cupressoides* (Syn. *W. nodiflora*), I do not agree with her decision to extend this name to **all** the Mulanje Widdringtonias.

My results suggest that one of the two species on Mulanje does belong to *W. cupressoides* (Syn. *W. nodiflora*), and bears a strong resemblance both to specimens from Zimbabwe and the Soutpansberg (Fig. 5) as well as to those from the Cape (informal observations). However, the other species on Mulanje is a distinctly different tree (Fig. 4), and should not be included with other species from Mulanje or trees further South. This species fits the original description of *W. whytei* (Rendle 1894).

The change of name from *W. cupressoides* (L.) Endl. to *W. nodiflora* (L.) Powrie did not involve a change in the species concept put forward by Marsh (1966). Thus, the name *W. nodiflora* can simply be substituted for *W. cupressoides* in the above discussion; the argument remains the same: This study concludes that, of the two species of *Widdringtonia* present on Mulanje, one is endemic to that mountain and fits the original description of *W. whytei* (Rendle 1893). The other belongs with the Widdringtonias from the eastern highlands of Zimbabwe, Mozambique, the Soutpansberg and Drakensberg to the species *W. nodiflora* (L.) Powrie (Syn. *W. cupressoides* (L.) Endl.), which occurs all the way down to the Cape. The other two species occurring in the Cape Province, *W. cedarbergensis* and *W. schwartzii* are not affected by these changes. In the rest of this discussion, the names *W. whytei* and

W. nodiflora will, unless otherwise stated, refer to the revised species concepts which have been outlined above and which are described in detail in Appendix 1..

Other botanists have in varying detail described different "forms" of *Widdringtonia* from Mulanje. Palgrave (1957) and Marsh (1976) refer briefly to the presence of a "dwarf form" which grows side by side with large timber trees on Mulanje. Chapman (1971) gives a detailed description of the "dwarf form", which he describes as a multistemmed, coppicing shrub which attains a height of 15 feet. These descriptions all fit my diagnosis of *W. nodiflora* (Appendix 1).

Venkatesh (1989) describes "narrow-crowned variants of the Mulanje Cedar" from the plantation on Zomba. These trees have thinner bark, shorter branches and narrower crowns than the other Widdringtonias in the plantation. From Venkatesh's description it is clear to me that these variants also belong to *W. nodiflora*. The trees which Venkatesh (1989) describes are, like the "wide-crowned" trees which surround them 30m tall. Given that these trees are single stemmed and very tall, it is not surprising that Venkatesh (1989) failed to see the link between the multistemmed "dwarf form" (Chapman 1961) and the "narrow-crowned variants".

According to Venkatesh (1987) the characteristic features of the two "variants" are probably determined by the presence or absence of a single gene with pleiotropic effects. Chapman (1992) suggests a similar system of heritability. He describes an isolated Mulanje Cedar of the *"typical form"* with 26 saplings at its base. "Of these, 23 were true to type Mulanje cedars, retaining still a proportion of juvenile foliage and not yet coning. The other three had scale leaves only and bore many cones."

If the results of this study indicated that the "narrow-crowned variants" (*dwarf form*) and the "wide-crowns" (*typical form)* were part of the same breeding population, as suggested by Chapman (1992) and Venkatesh (1989), I would certainly not have decided to describe them as two different species. However, the distribution of morphological variation in the cedars on Mulanje suggests that is not the case. For almost every character considered, there are two median values, the two peaks in the frequency distribution correspond to the median value for each of the two species. The variation within each of the groups is invariably normally distributed around the median value (Figs. 6-10). The fact that there is a normal distribution for each group, and that these distributions are shifted relative to each other, indicates that the measurements were derived from two distinct collections of individuals. These groups would soon become similar and have entirely overlapping frequency distributions if there was gene flow between them. Thus, the only explanation for the distribution of variation on Mulanje is that two non-interbreeding, sympatric groups of individuals must be present. These two groups of individuals seem to fulfill even the stringent criteria of the biological species concept (Mayr 1942).

In a reply to Denis Woods (1976), who expressed alarm at Marsh's decision to reduce of the number of species in *Widdringtonia* from 6 to 3, Marsh writes, "[i]t is all a matter of one's personal opinion" (Marsh 1976). When dealing with allopatric differentiated populations, this, to an extent, is true. For example, if it is shown that all the Widdringtonias from the Soutpansberg differ from other Widdringtonias in having long bent seeds (Fig. 8), these trees may be given a different name by botanists who follow the modern trend of describing "minimum diagnosable units" as species (Cacraft 1991; Donoghue 1985). Other botanists may feel that the features which distinguish this group of trees are not significant enough to warrant a new name. These botanists would be using a different species concept. However, when two groups of organisms are morphologically distinct, ecologically differentiated, non-interbreeding and sympatric, all species concepts concur that they should be recognized as different species. This study suggests that this is the case on Mulanje.

W. nodiflora and *W. whytei* may be prevented from interbreeding on Mulanje because they are sexually active at different times of the year. In a number of *W. nodiflora* populations on Mulanje, I found individuals with recently fertilized female cones which measured 3.5mm across. These cones were probably less than a few weeks old (observations made around 30 Nov.). On the other hand, the smallest cones which I came across on *W. whytei* were already closed and brown. These cones must have been at least one and a half months old. I could find no male cones on either *W. nodiflora* or *W. whytei*. The male cones in *Widdringtonia* drop off soon after shedding their pollen, so I would have been unlikely to find male cones even if I had just missed the period of pollen shedding in *W. nodiflora* (W.J. Bond pers. com.). This area needs further investigation.

The evaluation of characters for use in taxonomy

Although the two species of *Widdringtonia* on Mulanje do look quite similar in some habitats, they can always be distinguished. In the following section, I discuss characters useful in the identification of *W. whytei* and *W. nodiflora*.

Tree architecture:

The two species have strikingly different tree architectures. These differences partly determine the relative success of the two species in different habitats. *W. whytei* is always a single stemmed tree which does not have the ability to coppice. In contrast, *W. nodiflora* on Mulanje, and elsewhere in its extensive distribution range, is usually a multistemmed shrub or tree. Each stem (or trunk) had its origin as a shoot coppicing from a swollen base after the above-ground parts of the plant were destroyed by fire. On the slopes of Mount Inyangani I found a specimen of *W. nodiflora* with a lignified subterranean tuber 3.5m in diameter. Fifteen trunks emerged from this blackened base, the largest of which was 30cm in diameter.

Single stemmed specimens of *W. nodiflora* are rare, and occur only in habitats protected from fire. Even in such habitats, there is usually some sign of coppicing near the base of the tree, or there are buds present which can intiate coppicing (Fig. 23).

The trees most difficult to assign to a species were large single stemmed individuals of *W. nodiflora* which did not have buds or juvenile foliage near the base. However, even in these cases, tree architecture is a reliable character for identification.

Young *W. whytei* (>60 cm) have a balanced branching pattern, with conspicuously long branches emerging low down and shorter ones higher up. The branches are generally at an angle of between 60° and 70° with the vertical central axis of the tree (Fig. 13). The crown of young trees in open situations have a broad-based conical shape, while in crowded situations, the sideways expansion of the trees is restricted. The central axis ends in a growing tip at the apex of the tree. In older trees, the branching is no longer symmetrical around the central axis. Instead, the axis either ceases to grow or veers off to one side, while being balanced on the other side by equally heavy, spreading branches. This change in the pattern of growth gives old trees a sympodial appearance. At this stage in the life of the tree, the task of raising the height of the foliage canopy is shared among a number of equal, heavy branches, which spread outwards at an angle of 70° with the vertical. The wide crown may be multi-tiered, with branches emerging lower down the trunk supporting a secondary platform of foliage (Fig. 14). Lower branches often bear no foliage or break off, leaving a clear straight stem that may rise to a height of 20 meters. Trees which fit this description are common in old stands where they emerge above an understory of other forest trees. In these forests, trees 30 - 40m tall with a stem diameter of about 1m are the norm.

The above description contrasts with the tree architecture of *W. nodiflora*. The difference in the architecture of coppicing *W. nodiflora* and *W. whytei*, is immediately obvious, so I will discuss only the more subtle differences by which one can distinguish between single-stemmed *W. nodiflora* and *W. whytei*. Young single-stemmed *W. nodiflora* have many fine, short secondary branches which, in open situations, often extend low down the trunk. The many, short branches give the tree a dense, slender appearance. The fine branchlets near the base of a young tree are usually dead and brittle and can be snapped off easily. In thicker scrub, where the young trees have to reach up towards the light, secondary branches are produced much later. These saplings may have a lanky, bare stem 1.5m long. Larger trees (5m) generally still have a single vertical axis which is much thicker than any of the branches. The lower branches are only slightly longer than the branches higher up, giving the tree a slender, fastigiate appearance (Fig. 15 & 21).

Fig. 13. Young *W. whytei*, with long symetrical branches.

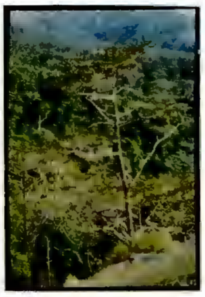


Fig. 14. Old *W. whytei*, with multi-tiered flat crown and asymetrical branching.

Fig. 15. Single-stemmed 19m tall *W. nodiflora* with long, narrow crown.

Fig. 16. Mildly damaged *W. nodiflora* with haphazard crown.

Fig. 17. Bark of young *W. whytei* with deep cracks.

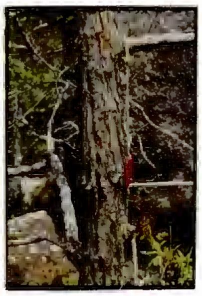


Fig. 18. Flaking bark of young single-stemmed *W. nodiflora*.

Fig. 19. Thick spongy bark of old *W. whytei*.

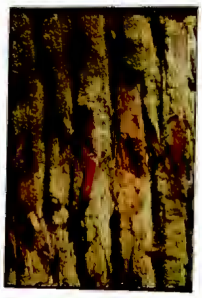


Fig. 20. Fibrous thin bark of old *W. nodiflora*.

While trees in entirely protected situations maintain their slender symmetry and slowly tapering, conical crowns, this is not always true for trees which are more exposed. These trees often have asymmetrical, rather haphazard crowns (Fig. 16). This asymmetry may be induced by minor damage caused by the heat waves of a passing fire. Because the damage is only superficial, the above ground parts survive and the tree need not coppice from below the ground. Typically, one or two low branches become unusually long. They curve upwards, become nearly vertical and similar in appearance to the original trunk. An intermediate degree of damage induces this phenotypic condition which is intermediate between the multi-stemmed coppicing phenotype and the single-stemmed phenotype.

Shape of the leaf sprays:

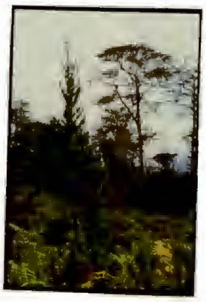
The leaf sprays of *W. whytei* and *W. nodiflora* seem to be miniature replicas of the adult trees. In *W. nodiflora* the leaf sprays, branches and the entire shrub all have a slowly tapering, narrow, conical outline. In contrast, the adult leaf sprays of *W. whytei* are dense, broad, blunt-ending clumps which are usually borne on the end of long, bare twigs.

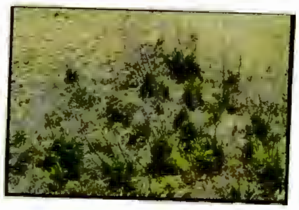
There is however almost as much variation in the shape of the leaf sprays as there is in the shape of the trees, and as with tree architecture, it is vital to consider the developmental stage of the leaf spray. Very young leaf sprays from the growing tips of branches of *W. whytei* are indistinguishable from the adult foliage of *W. nodiflora*. In both cases, the leaf sprays are sharp-pointed and conical in outline. The characteristic features of *W. whytei* leaf sprays are only expressed later in ontogeny, when the leaf spray takes on the shape of a dense, green pom-pom on the end of a bare brown twig.

In *W. nodiflora*, the difference between the mature and adult leaf sprays is much less profound than in *W. whytei*. The foliage bearing twigs do not become noticeably elongated as is the case in *W. whytei* (Fig. 9c), and leaf-bearing branchlets usually continue to emerge all the way down the leaf spray bearing twig, rather than only at its tip. This difference between the leaf sprays of *W. nodiflora* and *W. whytei* mirrors the

Fig. 22. Coppicing *W. nodiflora* on slopes of Mt. Inyangani.

Fig. 21. Fastigiate crown of *W. nodiflora* growing in fire-break near *W. whytei* forest.





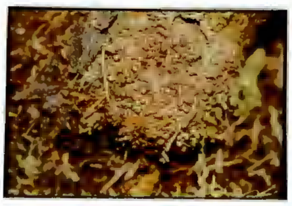


Fig. 24. Sixteen branches coppicing from a subterranean tuber of *W. nodiflora*.

Fig. 23. Green buds on the swollen base of *W. nodiflora*.

Fig. 25. Stages in the ontogeny of leaf sprays along the length of a growing branch of *W. whytei*.

difference in the branching patterns of the trees. In *W. nodiflora* the branches usually emerge all the way down the trunk, while in *W. whytei* the trunk may be bare to a height of 20m. However, just as *W. nodiflora* may, in forest situations have a fairly tall bare trunk, the leaf sprays may at times be borne on fairly long bare branches. It seems that *W. nodiflora* acquires these unusual features when the trees are growing slowly. More subtle differences between the species are still evident in these unusual specimens. Even when the leaf sprays of *W. nodiflora* are borne on the ends of bare twigs and do not have the typical sharp conical outline, they still differ from the leaf sprays of *W. whytei* in being less dense and compact, and usually longer than wide.

Leaves:

The shape and length of the leaves and their angle with the central axis determines the outline of the leaf bearing branchlet. At a distance of 1cm from the branchlet tip, the leaves of *W. whytei* and *W. nodiflora* are of equal length (Fig. 9a). However, the leaves of *W. whytei* are at an angle to the leaf bearing branchlet and the tips of the leaves usually stand free from the central axis. This gives the leaf bearing branchlets a rough, serrated appearance. In *W. nodiflora*, the leaf tips are closely appressed to their axis, giving the leaf bearing branchlet a smooth appearance. While the leaves of *W. nodiflora* are very occasionally free standing, those of *W. whytei* are never closely appressed to the leaf axis.

The leaves of specimens from Mount Inyangani and the Soutpansberg have convex abaxial surfaces, bulging out slightly in the centre, while the tips curve inwards. This gives the leaf bearing branchlets a wavy outline. This feature distinguishes these specimens from the trees on Mulanje in which the leaf bearing branchlets have straight sides. According to Stapf (1933), the leaf bearing branchlets of *W. cupressoides* (Syn. *W. nodiflora*) from the Cape are straight sided, while those of the Widdringtonias in the Drakensberg are wavy.

The twigs which bear the leaf sprays in both *W. nodiflora* and *W. whytei* have leaves which arise directly from them. These leaves are quite different to the leaves born on the ultimate branchlets. In *W. nodiflora* the leaves are lanceolate and acuminate with a acute, slightly spreading or appressed blade. The leaves retain their green colour for a considerable distance down the stem (up to 20cm from the tips of growing branches) before turning yellow and eventually brown. The leaves continue to lengthen even after they have lost their green colour and may attain a length of 3cm. In *W. nodiflora* the leaves turn from green to yellow before they are about 6mm in length.

In *W. whytei* the leaves on the leaf bearing branches are green for only a short distance from the tip of the leaf spray before turning brown and woody. The leaves turn from green to yellow when they are less than about 4mm in length (Fig. 9b). In *W. whytei* the stems of the leaf spray bearing twigs are rough with the remains of the lignified leaves. In *W. nodiflora* the leaves on the long branches do not become as woody as is *W. whytei* and are more sparsely arranged.

W. whytei generally has dark green leaves, while *W. nodiflora* has light green leaves. There is, however, a considerable amount of overlap.

Bark:

A regression analysis of bark thickness at breast height on stem diameter at the same height, shows that there is a strong linear relationship between these two variables. The slope of the regression line for *W. whytei* is more than twice as steep as for *W. nodiflora*, indicating that the bark of *W. whytei* is much thicker than that of *W. nodiflora* at a given stem diameter.

When dealing with bark descriptions, the compounding effects of environment and ontogeny are again a vital consideration. The bark of a 3m tall *W. whytei* sapling may be only 1mm thick, smooth and uncracked. However, bark thickness initially increases very rapidly with increasing diameter (a non-linear regression analysis may have been more appropriate), and trees 10cm across have bark that is 5 to 10mm thick. At this stage, the bark is already slightly spongy, and will cushion a blow with a hard object.

The bark begins to split along longitudinal cracks to compensate for the increase in tree diameter (Fig. 17). Trees greater than 20cm in diameter have bark more than 10mm thick. This thick, spongy bark is a striking feature of large *W. whytei* (Fig.19).

The environment influences both the colour and thickness of the bark of *W. whytei*. Inside moist, dark forests, the spongy bark matrix contains a lot of water. This prevents the outer layers of bark from drying out and pealing off. Under these conditions, the increment in tree circumference splits the bark into high triangular ridges separated by deep fissures (e.g. specimen ABN1 has bark 180mm thick at the base and 47mm thick at b.h.). In exposed conditions, the outer layers of bark become dry and flake off. Instead of triangular ridges, the bark is raised into flat strips. Horizontal cracks appear which divide the strips of bark into rectangular blocks. Below the outer surface, the bark of all *W. whytei* is a deep red-brown colour. The outer layer of bark on trees inside forests is red-brown like the deeper layers. However, the dry outer bark of exposed *W. whytei* is often grey-brown rather than red-brown.

The bark of *W. nodiflora* also starts off smooth and uncracked, but soon starts to flake off in small papery strips (Fig. 18). The bark of a 2m tall tree may already be flaking. Unlike *W. whytei* in which the bark flakes off in thick strips, the flakes of *W. nodiflora* bark are thin and fibrous. The bark never becomes spongy like that of *W. whytei*, and even that of the largest *W. nodiflora* is tough, dense and fibrous (Fig. 20). This individual was 45cm in diameter at breast height, and had bark 14mm thick. In contrast, *W. whytei* of the same size has bark which is about 25mm thick (Fig. 11 & 12). The bark is generally of a lighter colour than that of *W. whytei* and never absorbs water to the extent that *W. whytei* does. The colour of the outer bark ranges from brown to pink-brown to grey, while the inner bark is red-brown or orange-brown.

Female cones:

The female cones of *W. whytei* and *W. nodiflora* can be distinguished from each other, and be used to distinguish the species, if a number of cone features are considered simultaneously. *W. nodiflora* produces cones at an early age. Single stemmed coning individual my be less than 2m tall, while coppicing shoots cone even earlier. In contrast, the smallest cone bearing *W. whytei* which I came across was 5m tall. The four cones were borne at the apex of the tree among adult foliage, while the rest of the tree had juvenile foliage. Chapman (1961; 1992) mentions that precocious coning is a feature of the *dwarf form* of the Mulanje cedar.

On young trees and coppicing shoots of *W. nodiflora* the cones are borne directly off the main stem on short peduncles. These clusters of cones may consist of up to 48 cones, but usually number around 8 (Fig. 6b). On larger coppicing shoots or single stemmed trees, the cones tend to be borne on 2nd, 3rd, or 4th order branches. These branches are less sturdy, and the cluster tend to contain fewer cones (about 4). In *W. whytei* the number of cones per cluster is much less variable (Fig. 6b). Two is the most frequent number, and clusters containing more than 8 cones were found in only one instance. The cones are most frequently borne just proximal to one of the dense, broad leaf sprays.

In *W. nodiflora*, the cones remain closed for up to four or five years (Fig. 6a). This is particularly obvious when the cones are borne as sequential sets along the central axis of the tree. It seems that in *W. whytei* the female cones seldom remain closed for more than one year. When branches have young green cones at their tips, the cones further down the branch (which were probably formed the year before) are often open.

Figures 6d and 6e show that cone length and width are fairly good character for distinguishing *W. nodiflora* and *W. whytei* since the area of overlap in the distribution functions is small. Cone width is not an informative character in cones with a length of between 13.5mm and 16mm. However, cones narrower than 13mm are very likely to belong to *W. whytei*, while those wider than 16mm almost certainly belong to *W. nodiflora*.

In both *W. whytei* and *W. nodiflora* one occasionally comes across cones which have three, five or six valves instead of the usual four. These freak cones are rare, and thus are not of much value as characters in taxonomy.

The cone valves of *Widdringtonia* are of two types. The one set of opposite valves is wide and they meet at the apex of the cone along a broad margin. The two narrow valves usually do not meet at the apex. Each of the four cone valves bears a pointed cusp. The cusp is the anatomical apex of the valve, the point where the fibres of the cone converge. The position of the cusp marks the point at which the ovuliferous scale and the bract scale have become fused (C.J. Humphries pers. com.). It is hard to imagine that these cusps can serve a protective function, which suggests that the reason for its presence is historical rather than ecological. On the broad valves, the cusps are closer to the apex of the cone than on the narrow valves. In *W. nodiflora* the cusps on the broad valves are usually directed upwards and project beyond the central apex of the cone. Those on the narrow valves are usually directed downwards and do not project beyond the central apex. In *W. whytei*, the cusps on both the broad and narrow valves are usually directed downwards, and only in unusual circumstances do the cusps of the broad valves project beyond the apex of the cone.

Cone texture is a property often referred to in *Widdringtonia* taxonomy (Stapf 1933; Marsh 1966). I found that there was great variation in the relative roughness or smoothness of cones of both species within the study area. *W. nodiflora* (Syn. *W. cupressoides* (L.) Endl. *sensu* Stapf 1933) from the Cape generally has smooth cone valves, which are rarely slightly and irregularly tubercled (Stapf 1933). I found specimens of *W. nodiflora* on Mulanje, Soutpansberg and Inyangani with heavily warted cone surfaces. In some cases, the tubercles and warts entirely obscure the cusps. The range of variation in the cone texture of *W. nodiflora* entirely overlaps with that in *W. whytei* so cone texture is not a useful character for identifying the species.

W. nodiflora has more seeds per cone than *W. whytei*, and the number per cone is also more variable (Fig 6c). *W. whytei* most often has 5 mature seeds per cone, while in *W. nodiflora* they usually number between 8 and 18. There is, however, a complete overlap in the distribution functions for the two species, so the number of seeds per cone can only give an indication as to the possible identity of the species. The smaller cones of *W. whytei* cannot contain the same number of large seeds as the cones of *W. nodiflora*. However, it seems that the number of ovules initially produced is the same in the two species. *W. whytei* is forced to abort those ovules which are located towards the outside of the cone. These aborted ovules, which look like tiny black flakes, can be found in most *W. whytei* cones. The fact that these ovules are initially produced in *W. whytei*, but then aborted, suggests that the reduced cone size is a derived feature.

In all outcrossing plants the number of ovules greatly exceeds the number of seeds which are produced. Progeny improvement through ovule abortion on the basis of paternity and ecological bet hedging are the most popular hypotheses to explain this phenomenon (Charlesworth 1989; Marshall 1991). However, in the case of *W. whytei* the probability of seed abortion is dependant on the position of the seed in the cone, so seed paternity can play no role. Seed abortion seems to occur as a predictable step during cone ontogeny, so the ecological hypothesis is also not relevant in this case. Allometric constraints seem to be the only determining factor.

Seeds:

The distribution functions for seed width and length in *W. whytei* and *W. nodiflora* are slightly shifted relative to each other (Fig. 7a & 7b). Thus, while mean seed size and width in *W. nodiflora* is greater than in *W. whytei*, there is a great deal of overlap and this diminishes the value of this character for taxonomy.

The median ratio of seed length to width is greater in *W. nodiflora* than in *W. whytei* (Fig. 7c). Figure 8 shows that *W. nodiflora* from the Soutpansberg have unusual seed dimension. These cedars have long, narrow seeds which are slightly bent. The bend is in the same plane as the bend in a boomerang. The unusual seed dimension of the Soutpansberg populations probably played an important role in determining their distinctness in the phenetic analysis (Fig. 5).

The fraction of seeds that germinated and the number of days to germination were not much different in *W. whytei* and *W. nodiflora*. In both cases, the radicles emerged after about 21 days.

Seedlings:

The number of cotyledonary leaves is a fairly good character for the identification of seedlings, and one that foresters and ecologists may find particularly useful. In Stapf's (1933) synopsis of the genus *Widdringtonia*, he states that all the members of the genus have two cotyledonary leaves. However, it is unusual for the seedlings of *W. whytei* to have two cotyledonary leaves. The seedlings descended from one maternal plant usually all have three cotyledonary leaves, however, a varying fraction of these seedlings may have two or four cotyledonary leaves (Fig. 10a). *W. nodiflora* seedlings usually have two cotyledonary leaves, though seedlings with three cotyledonary leaves are quite common among the descendants of Mulanje specimens. The fact that *W. nodiflora* produce seedlings with three cotyledonary leaves only on Mulanje, seemed to suggest that it was hybridizing with *W. whytei*. I thought that the three-leafed seedlings among the descendants of *W. nodiflora* might have been fathered by *W. whytei*. The absence of adult hybrids, could be accounted for if the hybrid seedlings were competitively inferior. However, two and three-leafed *W. nodiflora* seedlings seemed to grow equally well under controlled conditions. In addition, when the seedlings started to produce true leaves the foliage of both 2 and 3-leafed *W. nodiflora* seedlings was strikingly different from that of *W. whytei*.

The main difference between the young juvenile foliage of the two species lies in the width of the leaves. On 7 month old seedlings, the leaves of *W. whytei* are narrower than 0.9mm and those of *W. nodiflora* are broader than 1mm (Fig. 26).

Fig. 26 The 7 month old seedlings of *W. nodiflora* (the 8 on the left) have broad, glaucus green leaves compared to the narrow, light green leaves of the seedlings *W. whytei* (the 5 on the right).

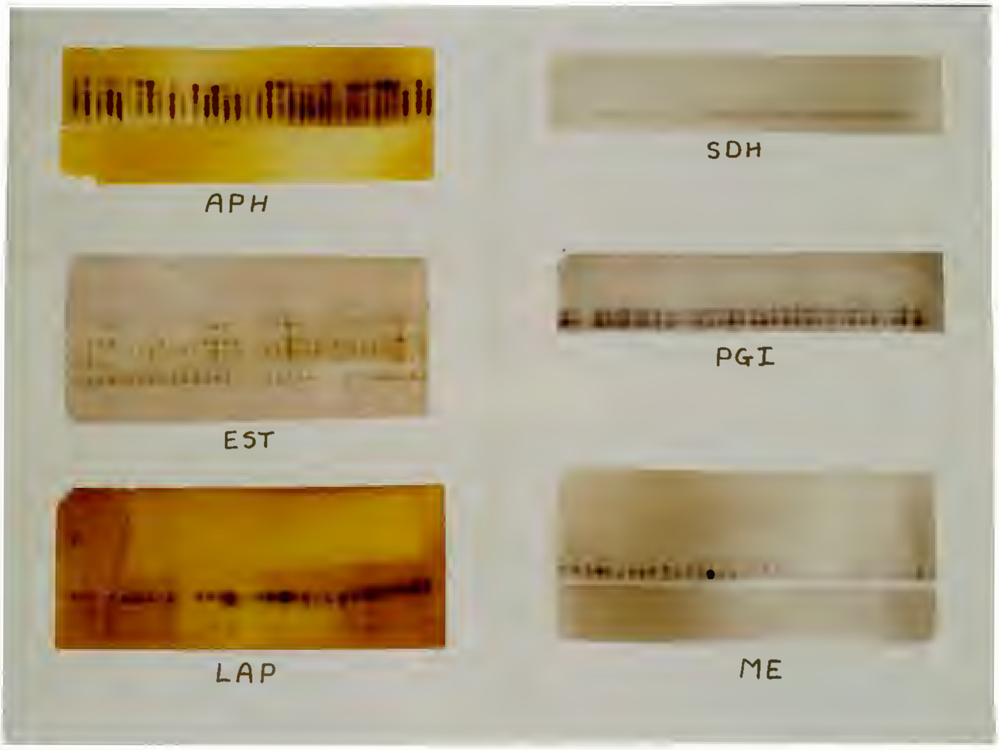


Fig. 27. Starch gels showing allozyme diversity in six enzymes: alcohol dehydrogenase, esterase, leucine aminopeptidase, shikimic acid dehydrogenase, phosphoglucose isomerase and malic enzyme.

Cotyledonary leaf length and width are not informative characters. As with the seeds, the "packing factor" is again important. Figures 10b and 10c show that the length and width of the cotyledonary leaves is dependant on the number of leaves. The size of the seed constrains the amount of leaf material that can be packed in, so the more leaves there are, the shorter and narrower they have to be. Leaf size characters contain no additional information since the size of the leaf is so dependent on the number of leaves.

Persistence of juvenile foliage:

The extent of juvenile foliage is a further useful means of distinguishing between young individuals of *W. whytei* and *W. nodiflora*. *W. whytei* seems to retain its needle shaped juvenile leaves for longer than *W. nodiflora*. Four meter tall *W. whytei* frequently have only juvenile foliage. Bigger trees of about 6 meters may still have juvenile foliage on the lower branches. The smallest *W. whytei* which I have seen with adult foliage was 3m tall.

W. nodiflora seems to change to adult foliage at a much earlier stage. On single stemmed trees about 2 m tall, the only trace of juvenile foliage is a skirt of dry branchlets near the base of the sapling. This skirt may extend 80cm up the trunk, suggesting that the tree switched to adult foliage at this stage. Coppicing branches of *W. nodiflora* bear juvenile foliage. The coppicing branches soon switch to adult foliage, but the remains of the juvenile leaves often remain attached to the lower part of the stem.

This difference between *W. whytei* and *W. nodiflora* was most noticeable in an area of tall *Phillipia* (now *Erica*) scrub on the Tuchila shelf (Mulanje) that had not been burnt for a number of years. A coppicing shoot that emerged from the trunk of a 5m tall single-stemmed *W. nodiflora*, was the only sign of juvenile foliage on the tree. A 6m tall *W. whytei* within sight of the *W. nodiflora* had only juvenile foliage.

Chapman (1961) describes a *scaly form* of *W. whytei*, which differs from the *typical form* only in having scale-like foliage in the juvenile state. Bond (per. com.) has observed that *W. nodiflora* in the Cape may coppice young branches which bear adult foliage directly, without passing through a juvenile foliage stage. He suggests that this is the case only in older individuals. Bond's observation suggests that Chapman's (1961) *scaly form* of *W. whytei* may be a twig of an old *W. nodiflora* which is coppicing from a hidden subterranean tuber.

Discussion of electrophoretic results

It was difficult to find diagnostic morphological characters for the two species because they are morphologically so similarity. On the other hand, I could not find diagnostic loci or alleles because there is so much variation within each species, that differences between species become obscured.

Janet Thomas (unpublished research) has also failed to find allozymatic autapomorphies for *W. cederberensis* and *W. schwartzii*. It seems that allozymes are too sensitive to genetic drift, to be used for species level studies in this genus (Hamrick 1987). Chloroplast DNA sequencing may be a more appropriate molecular technique.

Kananji (1990) attempted to determine the exact area of origin of the Widdringtonias in the Zomba plantation on the basis of their allozymatic affinities with populations on Mulanje. Kananji found that the genotype frequencies for material collected both on Mt. Mulanje and in the plantations deviated significantly from Hardy-Weinberg expectations at most loci. The departures were the result of a deficiency of heterozygotes. Kananji suggested that this deficiency resulted either from the removal of heterozygotes through biased harvesting, or from the inclusion of more than one distinct breeding group within the "populations" which were sampled. It seems likely that the distinct breeding groups to which Kananji is referring are in fact the two species *W. whytei* and *W. nodiflora* both of which are present throughout the areas which were included in his study.

The use of phenetics in subgeneric taxonomy

In systematics, there is currently an almost complete swing away from phenetic methodology, towards the "new" alternative, cladistics. Cladistic methodology emphasizes the importance of shared derived features. Organism which share a derived feature are grouped together. This produces nested groupings which can be displayed as a branching diagram, or cladogram. Organisms which share a unique organ or structure, are very likely to have shared a common ancestor in which this organ was present. Thus, cladograms can, with reasonable certainty, be interpreted as phylogenies, and in this respect, cladistic classifications tell a true story about the relationship between organisms.

The emphasis in phenetics, on the other hand, is on overall similarity. Organisms which look similar are clustered together. Nested clusters of similar organisms can be displayed as a branching diagram, or phenogram (Sneath and Sokal 1977). In contrast with cladograms, phenograms can usually not be interpreted as phylogenies. This is because similarity may often not be the direct result of shared ancestry. Convergent evolution in distantly related taxa, is an often cited example. Through convergence, distantly related organisms can come to look very similar, while closely related organisms often look very dissimilar as a result of rapid differentiation.

While convergent evolution can result in "false" similarity between taxa, convergence to similar habitats through a plastic response can result in "false" similarity between individuals. The phenetic analysis reveals that the most distinct subgroup within the *W. nodiflora* group contains 19 individuals from four widely separated populations (MCY, MCZ, MLY and MNX)(Fig. 5). Unlike most other *W. nodiflora*, these trees all grow in fire protected habitats and are single stemmed. It is obvious that the similarity between the individuals in this tight cluster is the results of similar habitats, not similar genes.

Appendix 1 contains two lists of attributes which defined the two groups *W. nodiflora* and *W. whytei*. It is often necessary to consider a number of the attributes of an individual before it can be assigned to a group. I detected these groups in the field and found that a phenetical analysis confirmed my subjective groupings. My subjectively delineated groups and the groups revealed in the phenetic analysis were defined on the basis of overall similarity between the member of a group, and dissimilarity between members of different groups. Although the groups were not defined on this basis, the individuals in the *W. nodiflora* group do share a derived feature, the ability to coppice. The individuals which share the ability to coppice are very likely to shared a ancestor from which they all inherited the ability. In other words, *W. nodiflora* (as defined in Appendix 1) is monophyletic. It is not as easy to find an autapomorphy for *W. whytei* (as defined in Apendix 1). The reduction in cone size is perhaps the best candidate.

Evolutionary relationship between *W. whytei* and *W. nodiflora*

In most of the histograms depicted in figures 6 to 10 there is considerable overlap between the distribution functions of *W. nodiflora* and *W. whytei*. In many cases, the normal distribution curve for the one species is only slightly shifted relative to the other species. Thus, most of the differences between *W. whytei* and *W. nodiflora* are quantitative rather than qualitative, and involve only slight shifts in the size of organs. Generally, the normal distributions depicted in these figures have fairly wide bases, indicating that there is considerable variation on which directional selection can act. This is particularly true in *W. nodiflora*.

The different leaf spray shapes and tree architectures seem at first to be profound qualitative differences between the two species. However, these large differences in morphology can be largely the result of small differences in the relative rate of development of various organs. I have mentioned that young leaf sprays from the growing tips of *W. whytei* are indistinguishable from the adult foliage of *W. nodiflora*. Like the adult branches of *W. nodiflora*, the branch tips of *W. whytei* are fastigiate, with short internodes, and leaf bearing branchlets which emerge all the way down the leaf-spray bearing twigs. The large leaves on the leaf-spray bearing twigs are green for a considerable distance down the length of the twig before turning brown and woody. Further down the branch, the leaf-sprays gradually acquire the adult features which distinguish the foliage of *W. whytei* from *W. nodiflora* (Fig. 25). The adult leaf sprays of *W. whytei* are borne on the ends of bare branches. They are broad, dense and blunt ending and the internodes of the leaf bearing branches are long. The large leaves on the leaf-spray bearing twigs are green for only a short distance down the twig before becoming brown and woody.

A phenetic analysis which considered only foliage characters confirmed these observations. Foliage from branch-tips of *W. whytei* was grouped with adult foliage from *W. nodiflora* rather than with adult foliage from *W. whytei*.

Relative to *W. whytei*, the branches of *W. nodiflora* become fertile while still in an early stage of ontogeny. It is unfortunately beyond the scope of this study to determine whether this is an ancestral or derived condition, as this question can only be answered if the other two species in the genus are considered. However, the fact that *W. nodiflora* is able to produce foliage similar to that of *W. whytei* when the growth rate of its branches are slowed down (as happens in old, or shaded trees), suggests that the timing of sex expression in *W. nodiflora* represents the derived condition.

The premature acquisition of primary sexual characteristics in otherwise juvenile animals has been termed paedogenesis (Gould 1977). In plants, unlike animals there is a frequent redevelopment of organs, so the constituent parts of one organism are of various ages. For example, *W. nodiflora* may regularly coppice young branches from an ancient subterranean tuber. Thus, assigning the term "paedogenesis" to coppicing branches which have juvenile vegetative characteristics (relative to *W. whytei*), but bare cones, requires a slight alteration of the definition of the term.

The differences in the relative rate of organ development in *W. nodiflora* and *W. whytei* appear to be of adaptive significance. *W. nodiflora* initially puts a much greater investment into cone production that *W. whytei*. It would not make ecological "sense" for *W. nodiflora* to produce "expensive" above-ground structures, if these are sure to be destroyed within a few years by the next fire which sweeps through its fire-prone habitat. Fires are much less frequent in the deep moist valleys where *W. whytei* occurs. In this habitat, competition from other trees is the main threat, so trees that allocate resources to vertical growth will be at a competitive advantage.

Ecology

The ability to coppice distinguishes *W. nodiflora* from the other three *Widdringtonia* species. Ecologically, this is a very significant difference.

Grime (1977) proposed an ecological classification which divides all plants into 3 categories: ruderals, competitors, and stress tolerators. I would classify *W. whytei* as a competitor because its architecture suggests that competition for light has been an important factor in its evolution. On the other hand, its ability to coppice means that *W. nodiflora* can exploit an entirely different ecological strategy. I would classify it as a stress tolerator because of its ability to tolerate fairly frequent fires. Thus, what is probably a relatively small genetic difference has resulted in a profound ecological difference.

The ability to coppice enables *W. nodiflora* to survive in fire-prone habitats which are out of bounds for other species of *Widdringtonia*. Nowhere is this more evident than on Mulanje: *W. whytei* is restricted to deep fire protected valleys where it is a member of the Afromontane forests (White 1983); *W. nodiflora* usually occurs in the fire-prone ericaceous scrub and grassland which surround the forests (Fig. 21).

Chapman (1961) and Venkatesh (1989) give entirely different descriptions of the same species from two different habitats. Chapman (1961) describes *W. nodiflora* (the *dwarf form* of *W. whytei*) as "a multiple stemmed shrub which may attain 5m in height." Venkatesh's narrow crowned variants are single-stemmed trees 30m tall (Venkatesh 1987). This incredible phenotypic plasticity allows *W. nodiflora* to exploit a wide range of habitats. In fire protected forest edges (and plantations), where it may occasionally grow side by side with *W. whytei*, it adopts a growth form which allows it to compete for light. By virtue of its ability to coppice, it is also able to survive in fire-prone habitats, where it is a multistemmed shrub which coppices from a large underground tuber. In these fire-prone habitats, the relative resource allocation to above-ground woody structures is much less that in fire protected habitats.

In addition to its ability to coppice, *W. nodiflora* has several other adaptations which enable it to survive frequent fires. The premature production of cones has already been discussed. This feature, coupled with the long seed retention times (Fig. 6a) mean that a substantial supply of canopy stored seeds is accumulated within a short space of time. The large number of cones per cluster (Fig. 6b) and seeds per cone (Fig. 6c) will further hasten the process. The seeds survive the destructive fires inside the large cones (Fig. 6d & 6e). The cones open and release their winged seeds when the branches are killed by fire. Fire synchronized seed release means that the seeds have the maximum amount of time available to become established before the next fire. The black colouration of the seeds will hide them from the eyes of birds in the charred landscape.

W. whytei is at the same time vulnerable to fire damage and dependant upon fire. The seedlings of *W. whytei* are light demanding. I have seen seedlings of this species only in open shrub near the edges of forests. In the old forests where there is a overstory of giant wide crowned *W. whytei*, there are no small cedars at all. Gaps in the forest are filled by other tree species. This suggests that *W. whytei* is a forest pioneer.

In the Lichenya Valley I have seen the very slow growing seedlings and saplings of various ages, growing up through the fynbos-like scrub. Like other gymnosperms, they probably start growing quite rapidly once they are a few feet tall and have accumulated a substantial supply of tracheids. If a fire sweeps through the scrub before the seedlings are a couple of meters tall, it is sure to kill them. Larger trees seem able to survive mild fires, which are fueled by grass and low shrubs, by virtue of their unusually thick bark (Fig. 12 & 19). Large *W. whytei* frequently have blackened bark on the lower 2m of trunk.

Once a thicket has been established, birds, carrying the seeds of other Afromontane (White 1983) tree species, will be attracted. These trees form the understory in forests which have *W. whytei* as the overstory. It is a paradox that despite its extreme vulnerability to fire, *W. whytei* is dependent on fire to enter the successional process. In "overmature" forests which might be 500 years old (Chapman 1992), the cedar super-canopy consists largely of moribund trees and lichen draped skeletons. The cedars are unable to recruit in the shade of the forest. Only if there is a fire sufficiently fierce to destroy the broad-leafed trees, can *W. whytei* enter the succession. According to Chapman (1992) this process explains how, in otherwise uniform stands of old cedars, some trees may be much older than their neighbours. These would, by virtue of their thick bark, have survived an all-but consuming fire to reseed the area (Chapman 1992).

This story of forest succession finds additional support from dendrochronological studies. Recurrent fire scars are found deep in the wood of trees with a diameter of 60cm, suggesting that large trees are able to survive infrequent, mild fires (Chapman 1992).

The absence of *W. whytei* from the forested gorges of the Ruo valley, demonstrates the importance of occasional fierce fires. These gorges are very moist, and it is probable that the long-term exclusion of fire has in turn excluded *W. whytei*. The trees which are present in the gorge probably have seedlings which are not as light demanding as those of *W. whytei*. These trees are able to perpetuate themselves indefinitely through the colonization of treefall gaps.

The same successional process can be observed on small scale in the forest margin. Seedlings become established as trees if the inter-fire period is long enough for them to acquire a protective bark. The forests thus expand into the surrounding plateau grassland under favourable conditions. Frequent fire would however constantly knock the advancing forest back.

Exploitation and Conservation

It is now just over 100 years since the exploitation of *W. whytei* started on Mulanje. The timber is durable and fragrant, much like that of the true cedars (*Cedras spp.*), and has been used extensively in construction, for furniture and paneling and as roofing shingles. Pit-sawing, and the headloading of timber down thousands of feet by paths often narrow and tortuous, call for skill and stamina. The Mulanje sawyers and timber carriers are indefatigable. Their operations have gradually extended to every part of the Mulanje massif (Chapman 1992).

The early foresters had some success in re-planting cut-over Cedar stands. Later, plans for an extensive re-afforestation programme were not realized. Today this potentially sustainable resource faces extinction (Chapman 1992).

The importance which is attached to the "Mulanje Cedar" was demonstrated in June 1984, when His Excellency the Life President of Malawi declared Mulanje Cedar to be the National Tree of Malawi. This status heightens its priority for conservation.

In 1991 a "Committee for the Integrated Conservation and Management of Mulanje Mountain" was constituted. Objectives are "to formulate and implement broad spectrum conservation measures in which plants, animals, water and other resources will be integrated on a sustainable utilization basis." Situated as the mountain is, entirely surrounded by villages or cultivation largely bereft of trees, or by tea estates, this is a formidable undertaking. According to Chapman (1992), the involvement of an international conservation organization is a "sine qua non".

This study affects conservation and forestry efforts in a number of ways. Species are the currency of conservation. For this reason, systematics can play a determining role in the assessment of priorities for conservation. *Widdringtonia cupressoides* (L.) Endl., the "Mulanje Cedar", is considered to be widespread (Palgrave 1977) and not threatened (Hall *et al.* 1980). The results of this study suggest to the contrary that the "Mulanje Cedar" (*W. whytei*) is a localized endemic which should be classified as "vulnerable" in accordance with the IUCN's conservation categories (Hall *et al.* 1980). As a "vulnerable localized species," the "Mulanje Cedar" is likely to attract more attention from international conservation organizations; certainly more than "the large form of *W. cupressoides.*"

Sakai (1989) calculated the total area of cedar forest (*W. whytei* as diagnosed in this study) to be 1462ha (5.64 sq. miles). He found that young stands account for 2% of the total, i.e. 300ha. Healthy, well stocked forests of older trees are virtually non-existent and almost throughout, decrepit or dead stands severely damaged by fire and exploitation predominate. It is not surprising that cedar has become a prestige wood with a high scarcity value. One large tree might fetch a price of R5777 (Chapman 1992).

Afforestation with cedar began in 1907, when the first trees were planted on Zomba Plateau, about 60km north of Mulanje. However, seeds were collected without the knowledge that there are two species of *Widdringtonia* on Mulanje. The two species which are currently being grown together in compartment 34C can easily be distinguished on the basis of the diagnoses given in Appendix 1.

Venkatesh (1987) noticed the differences between the two species in the plantation, and described them as "wide" and "narrow-crowned" variants of *W. nodiflora* Powrie. Venkatesh's finding were followed up by Chapola (1990) who found that the narrow and wide-crowned "variants" from the Zomba plantation differ significantly in their wood properties. Narrow-crowned trees yield less dense wood, with a shorter fibre length, making the wood unsuitable for construction work.

Anyone who has spent a few weeks collecting *Widdringtonia* cones on Mulanje, will know that collecting cones from the coppicing, shrubby cedars (*W. nodiflora*), is considerably easier than scaling the bare, 20m tall trunks of the wide crowned cedars (*W. whytei*). In fact, I sure that no seed at all would have been collected from *W. whytei* if these trees were not being felled at the time when plantations were being established.

It seems that in later plantings the proportion of *W. nodiflora* seed which was used was even higher. Chapman (1992) describes a plantation at the Ntchisi Forest Reserve, 60km north of Lilongwe which was planted in 1951. Thirty years after the trees were planted, Chapman had difficulty in finding any "typical" trees. "With few exceptions they were short (4m compared with 10m for the others) crooked and much branched. From the swollen bases of some trees there grew numerous short shoots with juvenile foliage, otherwise they had only scale leaves."

The Forestry Department of Malawi has over the years made available cedar seed for trials in various countries. In Africa these have included Zambia (the north-east), Tanzania, Kenya, Uganda, Cameroon (Bamenda Highlands), Nigeria (Mambilla Plateau) and South Africa (Soutpansberg Forestry Area). Elsewhere, seed has been supplied to Australia (Victoria), New Zealand (Fielding in the North Island), California, Canary Islands, Costa Rica, Hong Kong, St. Helena and the United Kingdom (mild western seaboard) (Chapman 1992). Little appears to be known about these trials.

I visited one of the trials in the Soutpansberg where seed of the "Mulanje Cedar" had been planted. It was obvious that all the cedars in this compartment had been raised from *W. nodiflora* (as diagnosed in this study) seed collected on Mulanje. On the basis of these trials, it was, not surprisingly, decided that the "Mulanje cedar" is not a suitable species for silviculture in the Soutpansberg (Van der Merwe pers. com.). Ironically, *W. nodiflora* is common in the mountains surrounding the plantation.

Appendix 1

Species diagnoses

These diagnoses differ significantly from earlier descriptions. The emphasis is on characters by which *W. whytei* can be distinguished from *W. nodiflora*. The diagnosis of *W. nodiflora* is based only on material from the Soutpansberg, Zimbabwe and Malawi and can not serve as a description for *W. nodiflora* throughout its range. However, I have seen *W. nodiflora* from the South of its range, and have found that the diagnosis given here covers most of the variation in the species. Principle differences are: smaller seed wings in specimens from the Drakensberg; and smaller cusps which may not extend beyond the cone apex in specimens from the Cape. This diagnosis does not include reference to properties which are common to all the members of *Widdringtonia*.

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W. whytei **Rengle**

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W. whytei Rengle in Trans. Linn. ser. 2, Bot. iv. 60-69, figs. 6-11 (1894); Masters, Journ. Linn. Soc. Bot. 37: 270 (1905).
Typical form of W. *whytei* Chapman, Kirkia 1: 141 (1961).
W. cupressoides (L.) Endl., Marsh in Flora of Southern Africa 1 (1966), p.p.
W. nodiflora (L.) Powrie in S.Afr.J.Bot. 38(4): 301-304 (1972), p.p.

Crown shape: Single stemmed, does not have the ability to coppice; crown of young trees is a broad-based cone, branches symmetrical around the axis, with the lower branches conspicuously long and spreading outwards at an angle of 70; in older trees the branching is no longer symmetrical around the central axis, the axis either ceases to grow or veers off to one side while being balanced on the other side by equally heavy, spreading branches, the wide, often flat, canopy is supported by a number of equal, heavy branches; crown may be multi-teared, with branches emerging lower down the trunk supporting secondary platforms of foliage; lower branches often bear no foliage or break off, leaving a clear straight stem that may rise to a height of 20 meters; 79 year old trees are 32m tall under ideal conditions. **Leaf spray shape:** mature leaf-sprays dense, broad, blunt-ending clumps, pom-pom-like, borne on the end of long, bare twigs; young leaf sprays near growing tip of branch fastigiate; leaf bearing branchlets have long internodes, typically 12-20mm. **Foliage:** foliage green to dark-green; juvenile leaves acicular about 10-15mm; switches to adult foliage at a height of 3-6m; adult foliage 10mm from tip of branchlets about 1.2-2.7mm, scale-like decussate, blade at a slight angle to the branchlet, never tightly appressed to branchlet, leaf tips may curve outwards; outline of leaf bearing branchlets serrate; leaves on leaf-spray-bearing twigs lanceolate, acute to acuminate, with a long, straight-sided adenate base and a shorter free portion, usually become brown and woody a short distance (10cm) from branch tip, but this distance may be greater on rapidly growing branches, visible on bare branches as closely packed, sometimes overlapping, dark-brown scales, may be more sparse on rapidly growing branches. **Bark:** at a height of 1.4m above ground about 1mm thick for trees <5cm in diameter (at 1.4m above ground), 5-10mm at 10cm, 7-17mm at 20cm, 12-30mm at 30cm, 20-45mm at 50cm, about 60mm at 1m, smooth and uncracked initially, becoming slightly spongy on trees 10cm in diameter, and cracked longitudinally, deeply fissured on larger trees, will cushion a blow with a clenched fist; grey-brown to red-brown outside, red-brown inside. **Female cones:** bears cones when >4m tall; cones usually 2 in a cluster occasionally up to 8, 9-16mm wide usually 10-12mm, 9-18mm long, usually 11-15, ratio of length to width 1-1.3; cusps on the two wide cone valves usually reflexed, directed towards base of cone, never projecting beyond central apex of cone; cusps on narrow valves reflexed and directed downwards, never projecting beyond cone apex; cone valves smooth to warty. **Seeds:** 2-32 mature seeds per cone, usually 7-18; seeds towards outside of cone often aborted, minute; mature seeds 5.5-10.5mm long (including wing), usually 6.5-8.5, 2.5-5.5mm wide, usually 3-4. **Seedlings:** cotyledonary leaves 3, rarely 2 or 4 **[include widths for each?]**; after 7 months, about 7cm tall, foliage light green, extend about half-way or further down seedling, leaves usually 0.5-0.8mm wide, 15-20mm long, stem red-brown; seedling greater than 10cm do not have axiliary buds.

W. nodiflora (L.) Powrie

W. nodiflora (L.) Powrie in S.Afr.J.Bot. 38(4): 301-304 (1972), p.p.
Narrow-crowned variants of W. nodiflora, Venkatesh, Silvae Genetica 36: 5-6 (1987).
W. cupressoides (L.) Endl., Marsh in Flora of Southern Africa 1 (1966), p.p.; Stapf in Flora Capensis (1933).
W. mahoni, Masters in Journ. Linn. Soc. Bot. 37, (1905).
W. dracomontana Stapf in Kew Bull. 206 (1918). (but needs to be checked)
W. stipitata Stapf in Flora Capensis 5 sec 2 (1933).
Scaly form, dwarf form and *glaucous form* of *W. whytei,* Chapman, Kirkia 1: 141 (1961).
Dwarf variety of *W. whytei*, Palgrave, Trees of Central Africa (1957).

Crown shape: usually multistemmed, with stems arising as coppicing shoots from a subterranean lignified tuber, single stemmed only in habitats protected from fire; crown of young trees, and young coppicing shoots, narrow and conical, the many short branches give the tree a dense fastigiate appearance; in open situations the branches extend far down the trunk, but start higher up in when the surrounding vegetation is denser, large single-stemmed trees have long narrow crowns consisting of many thin, equal length branches, single stemmed trees that have suffered mild damage may have a haphazard crown when one or a few branches become unusually long, curve upwards and become nearly vertical and similar to the main trunk; single-stemmed 79 year old trees are 31m tall. **Leaf spray shape:** fastigiate, leaf-bearing branchlets usually extending down the entire length of the branches from which they arise, on slow-growing branches leaf sprays may occasionally be borne on the ends of bare branches and be blunt ending, however, usually still differ from leaf clumps of *W. whytei* in being longer than wide and diffuse rather than dense; leaf bearing branchlets with short internodes, typically 8mm. **Foliage:** green to light green; juvenile leaves acicular about 9-23mm; usually switches to adult foliage at a height of 80cm, may retain juvenile foliage for longer in shaded conditions; adult foliage 1cm from tip 2.1-2.7mm, scale-like decussate, blade closely appressed to branchlet, very occasionally free standing, at a slight angle to branchlet, leaf tips may curve inwards; outline of leaf bearing branchlets straight or wavy, very occasionally serrate; leaves on leaf-spray-bearing branches lanceolate, acute to acuminate, with a long, straight-sided adenate base and a shorter free portion, may remain green for a distance of up to 40cm from the tips of growing branches visible on bare branches as sparse brown scales. **Bark:** about 1mm for trees <5cm in diameter, <4mm at 10cm, <7mm at 20cm, <9mm at 30cm, about 15mm at 50cm, initially smooth and uncracked but cracked and flaking when 1.5mm thick, cracks often spiral slightly around trunk; even when 15mm thick, still dense and fibrous rather than spongy; pink-grey to brown-grey outside, red-brown inside. **Female cones:** single-stemmed saplings may bear female cones when <2mm tall; cones usually about 8 per cluster; ranges from 1-48; mature cones 13-29mm wide usually 17-23mm, 14-24mm long usually 17-22, ratio of length to width 0.9-1.1; cusps on the two wide cone valves projecting upwards, extending beyond central apex of cone, occasionally subapical, but not reflexed; cusps on narrow valves directed downwards, not projecting beyond cone apex, very occasionally directed upwards and extending beyond apex; smooth to grotesquely warty with cusps entirely obscured. **Seeds:** mature seeds 2-14 per cone usually 3-8; 6-12mm long, usually 8-10.5, 3-8mm wide, usually 4-5.6. **Seedlings:** cotyledonary leaves 2, on Mulanje sometimes 3; after 7 months, about 7cm tall, foliage dull green to glaucous green with a blue tinge, extend about half-way or further down seedling, leaves usually 1-1.6mm wide, 15-20mm long, stem red-brown; seedling greater than 10cm often have axiliary buds in the axils of older leaves.

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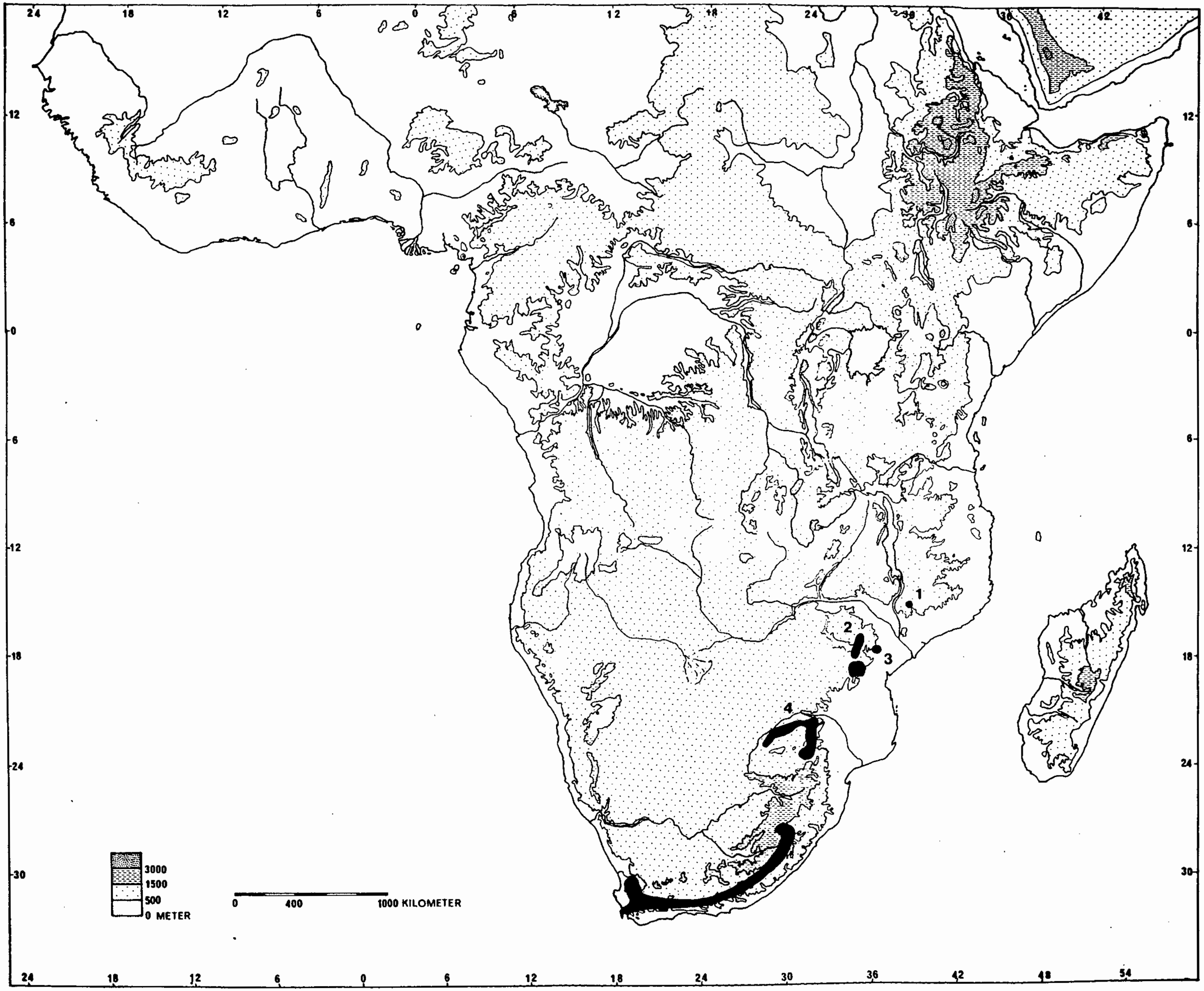

Fig. 1. The distribution of the genus *Widdringtonia* Endl. Material was examined from Mulanje (1)(Malawi), Inyanga (2)(Zimbabwe), Mt. Gorongosa (3)(Mozambique) and the Soutpansberg (4)(South Africa).