

A REPORT ON THE INVASIVE STATUS OF *PINUS PATULA*
ON MOUNT MULANJE, MALAWI.

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ABSTRACT

Natural regeneration of the Mexican weeping pine *Pinus patula* on Mt. Mulanje was investigated and found to represent a serious threat to the natural vegetation, with the invasion already advanced on the north eastern plateaux. Various aspects of the biology of the pine are related to its success as an exotic invader on the mountain. Perhaps most important is the ability of the species to cope with fire, and the role of regular fires in enhancing the invasion. Urgent action is needed to halt the pine, if the Mulanje is to be maintained in a pristine state. To this end, fire-mediated eradication measures, based on work done in the western Cape, are recommended. A crude estimate of the costs of implementation of this programme is provided.

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1. INTRODUCTION

Like several of its relatives, the Mexican weeping pine *Pinus patula* is an important colonist and weed species, and it has become naturalised in various parts of Malawi where it has come to pose a considerable threat as an exotic invader. On Zomba Mountain, for example, nearly all the indigenous vegetation of the upper plateau has been supplanted by the pine, as have areas of the lower slopes (Chapman and White 1970; personal observation). The extent of invasion on Mt. Mulanje, the object of the present study, is not as advanced as that at Zomba, but it seems that it has the potential to be, if left unchecked, and a major aim of this report is to alert conservationists of the serious threat posed to Mt. Mulanje by *P. patula*.

The invasive potential of the pine has been noted previously. Wormald (1975) reported that there is prolific natural regeneration of this species in a range of countries where it has been introduced. These include South Africa (see also Macdonald and Jarman 1985), Malawi, Zimbabwe, Madagascar and New Zealand, while Richardson *et al.* (1990), on the basis of life history characteristics, ranked this species along with three other pine species that have proved to be particularly successful invaders in the Cape fynbos biome. Already, some work has been done to focus attention on the invasive threat posed by the pine on Mt. Mulanje (Edwards 1982; Sakai 1989*a,b*; Chapman 1990). However, efforts to control the invasion up to now appear to have been either lacking or unsuccessful, as its present extent seems to exceed that described earlier by Edwards (1982) and Sakai (1989*a*). If Mt. Mulanje is to be maintained in a pristine state then, as both these authors have recognised, the pine will need to be eradicated or at least brought under control, and there is ample incentive for this to be done.

At present, Mt. Mulanje is widely recognised for its outstanding natural beauty, and is one of Malawi's best-known tourist landmarks, attracting tourists from all over the world. Given the economic importance of tourism to Malawi, it is all too clear why Mt. Mulanje should be maintained in a pristine state. Apart from this economic argument, Mt. Mulanje also deserves protection because of its considerable biological value. The mountain supports a range of plant associations that fall into four main communities, namely *Brachystegia* woodland, afro-montane/

Widdringtonia forest, plateau/ afro-montane grassland, and high-altitude vegetation of the peaks and taller ridges (Chapman 1962). On the plateaux, most of the vegetation is of afro-montane affinity, and the mountain represents part of the afro-montane belt running from the Cape to Ethiopia. A number of endemics have been recorded here (Chapman and White 1970; Edwards 1982), and the majestic Mulanje cedar *Widdringtonia whytei*, has its northern distributional limit here. The cedar, the national tree of Malawi and one which is held in great esteem in that country, reaches its maximum size on Mt. Mulanje, as well as having its largest populations here. *P. patula*, however, poses a direct threat to the future of the Mulanje cedar: seedlings of both species recruit along forest margins following fire (Chapman 1962; Chapman and White 1970; Sakai 1989b), but the pine seedlings because they grow faster, invariably overtop cedar seedlings, and so competitively exclude the latter (Edwards 1982). Ironically, the pine was originally planted on Mt. Mulanje to act as a nurse species under which it was hoped cedar seedling recruitment would improve (Sakai 1989a).

The main goal of the present study was to obtain a better picture of the current status of the *P. patula* on Mt. Mulanje with an aim to developing a set of management principles. Although this work overlaps somewhat with that of Edwards (1982) and Sakai (1989a), the syntheses produced by these authors are very brief, and have become outdated. Despite not being highly quantitative, the current study does provide a survey map of the present distribution of pines on the mountain, which, ideally, will be used directly to locate pines in an eradication programme, but may also act as a baseline against which future data may be compared. In addition, an attempt is made to determine the age structure and reproductive status of the pine at various sites, as well as factors driving its dispersal. Finally, some management principles for controlling the pine are proposed and some very crude cost estimates for the implementation of these are provided.

2. STUDY AREA: THE MULANJE ENVIRONMENT

Occupying an area of some 500 km², and reaching over 3000 m a.s.l., Mt. Mulanje stands out as the most prominent landscape feature in south central Africa (Chapman 1962). Situated between 15°50'S and 16°05'S, it lies well within the tropics and so qualifies as a tropical highland. The geology and topography of Mt. Mulanje has been dealt with in some depth by Chapman (1962). Essentially, the massif consists of a series of plateaux and raised basins lying on intrusions of granite (late Jurassic), some 1000-2000 m above the surrounding lowlands of south east Malawi and western Mozambique. These are from west to east the Lichenya Plateau, the Chambe Basin, the Tuchila Shelf, the Ruo Basin, the Sombani Plateau, and the Madzeka Plateau (Fig. 1).

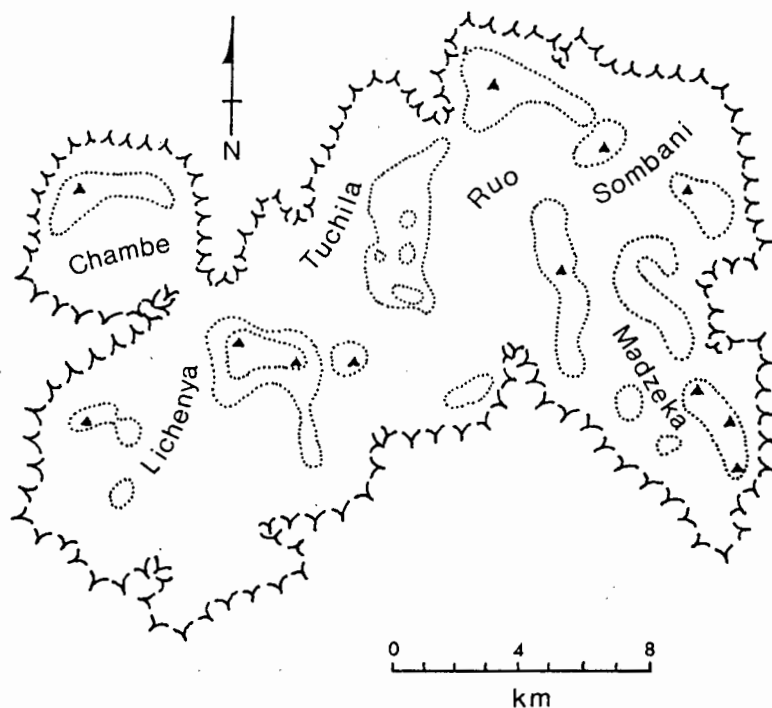


FIGURE 1. A schematic map of Mt. Mulanje showing the relative positions of the six major plateaux. The peripheral 'spike' pattern indicates the edge of the escarpment, while dotted lines and triangles demarcate high-altitude peaks and ridges.

Climatic conditions are fairly mild. The wet season falls between November and April, and is characterised by daily thunderstorms. The remainder of the year is, however, far from dry, as the south east trade winds periodically bring in moist air from the south east, bringing orographic cloud and precipitation known as 'chiperones' (Chapman 1962; Agnew and Stubbs 1972). Rainfall figures from different parts of the mountain are, however, variable, being highest and lowest in the south east (Lichenya, Ruo, Madzeka) and north west (Chambe, Tuchila, Sombani) sectors respectively (Chapman 1962). Even on the drier plateaux, however, rainfall is abundant, with the annual mean at Tuchila being around 2050mm (Chapman and White 1970). Temperature data are scarce. However, Chapman (1962) suggests that on the plateaux, maximum summer (January) shade temperatures are probably around 21°C, while minimum winter (July) temperatures are probably about -3°C. Frosts occur regularly during the colder months of the year (Chapman 1962; Chapman and White 1970). Wind data for Mt. Mulanje are also scarce. Agnew and Stubbs (1972) provide wind data for various weather stations in Malawi, although not for Mt. Mulanje itself. At these stations, wind patterns are variable, but easterly, south easterly and even north easterly directions seem to predominate at most stations.

Chapman and White (1970) examined a soil profile from the Chambe Basin on Mt. Mulanje and classified the soils here as humic ferrisols, finding that they contain a relatively high silt fraction, are very acidic (pH 4.2-4.9) and have a low cation exchange capacity. In many ways the soils on Mt. Mulanje are similar to those found in the fynbos region of the southern Cape. Soil depth seems to vary, and is probably greatest in ravines and the basins, and shallowest on peaks where sheets of granite lie near or at the surface.

The indigenous vegetation of Mt. Mulanje was briefly outlined in the introduction, and has been dealt with in detail by Chapman (1962) and Chapman and White (1970). It will not be discussed further here. It needs to be said, however, that vegetation dynamics seem to be strongly driven by fire, which seems to be a particularly important determinant of the success of cedar establishment (Chapman 1962; Chapman and White 1970; Sakai 1989b). In addition, I suspect fire may play an important role in maintaining the montane grasslands, preventing their replacement by scrub, and ultimately forest. Certainly, this suspicion is strongly

supported by the vast network on firebreaks that is maintained on the mountain, albeit in a seemingly random arrangement. Evidence of at least three recent fires was found during the present study, one of which was particularly extensive, having crept up the mountain from the tea plantations at Lujeri to the south, and having burnt large parts of the Ruo Basin, the Sombani Plateau, and the Madzeka Plateau. It is remarkably difficult to gain access to official fire history records, so that, effectively, this must be determined from the landscape itself.

Finally, two pine plantations stand on Mt. Mulanje, one at Chambe and the other at Sombani (Map 1). At present, these plantations are managed for softwood timber production (Edwards 1982), although Sombani plantation seems to be of limited commercial value. The current pine invasion on Mt. Mulanje has almost certainly originated from these plantations.

3. METHODS AND MATERIALS

3.1 Distribution of pines

A total area of about 9661 ha was surveyed during November/ December 1991 to determine the distribution pattern of pines on Mt. Mulanje (Map 1, Table 1). The survey area was largely restricted to the plateaux, because it is here that the pine invasion seems most extensive, and most threatening. Large parts of the Lichenya Plateau, the Tuchila Shelf, the Ruo Basin, the Sombani Plateau and the Madzeka Plateau were covered by the survey, although only a small part of the Chambe Plateau was surveyed, namely that part facing the main mountain massif (Map 1, Table 1).

TABLE 1. Estimated areas surveyed on each of the six plateaux.

| Plateau | Area surveyed (ha) | Percentage of total survey area |
|----------|--------------------|---------------------------------|
| Lichenya | 2344.0 | 24.3 |
| Chambe | 261.8 | 2.7 |
| Tuchila | 2023.2 | 20.9 |
| Ruo | 2669.2 | 27.6 |
| Sombani | 1656.0 | 17.1 |
| Madzeka | 707.0 | 7.3 |
| Total | 9661.2 | 100 |

The method used to plot and estimate pine tree density was fairly crude. The survey was performed on foot, with binoculars being used to scan the vegetation for pines. Fortunately, pine trees have a rather characteristic appearance so that they are relatively easy to discern. Pine-infested areas with fairly uniform spacing of trees were treated as unitary 'density blocks'. Each density block was then assigned a particular density ranking, on the basis of the estimated mean inter-tree distance (Table 2), and this was converted into a trees-per-unit-area density value, using the

TABLE 2. Tree density ranking as used in the present study. Refer to Appendix 1 for details.

| Density rank | Inter-tree distance (m) | Number of trees per ha. |
|--------------|-------------------------|-------------------------|
| 1 | > 100 | - |
| 2 | 50-100 | 4 |
| 3 | 25-50 | 9 |
| 4 | 10-25 | 25 |
| 5 | 5-10 | 121 |
| 6 | <5 | 441 |

method outlined in Appendix 1. Density blocks were marked off on a 1:50 000 scale topographical map (Malawi Dept. of Surveys, Sheet no. 1535D3), and their pine densities noted. Where pine trees were sparsely distributed (i.e. >100m between trees) or very isolated, trees were mapped individually.

The total area invaded by the pine, as well as the areas occupied by different densities of pine trees on the various plateaux, were calculated from the completed map. Cut-outs representing invaded areas were weighed, and their weights converted into areas by a conversion sum that incorporated the weight of a known area of the same paper.

The same method was employed to calculate the total area covered by the survey, as well as the areas surveyed on each plateau. Given the area occupied by each density block, it was possible to produce a crude estimate of the numbers of pine trees occurring within the different density blocks. This permitted calculation of the approximate number of trees occurring in each density rank on each plateau.

The vegetation type associated with each density block or individual tree marked off on the map during the survey was also noted. This was done in order to test whether certain vegetation types are more susceptible to pine invasions than others. Testing was performed using chi-square analysis (goodness-of-fit test), with two vegetation categories eventually being recognised: (i) forest, including both *Widdringtonia* and other afro-montane forest, and (ii) grassland and scrub, comprising the vegetational continuum between pure grassland and fairly tall scrub, as well as the high altitude vegetation of the peaks and ridges (separation of these different vegetation types is very difficult, and may be unjustified). The test was set up to determine whether the distribution of individuals (determined from the density block data) in the two

vegetation types differed significantly from expected values, based on the relative abundance of the two vegetation types in the survey area.

3.2 Age structure

Time constraints necessitated a rapid, easy measure of tree age. Three measures were used: tree height, stem circumference at shoulder height, and the number of whorls of branches on the main stem. These measures are problematic, as they may not accurately represent tree age and, further, their translation into time units (e.g. years) is difficult. Despite these shortcomings, the use of these measures was necessitated because they are quick, and because of a lack of alternatives. Although the number of wood rings is usually a better measure of tree age, even this is problematic in the tropics, where growth seasons may be year-round. To test the reliability of whorls, height and circumference as age measures, I tested the correlation between each of these against the others, using data from trees at all the test sites, but excluding the smallest seedlings and some damaged individuals.

Age structure, as indicated by height, circumference and whorls was examined at six sites, L1, L2 and L3 on the Lichenya Plateau, and T1, T2 and T3 on the Tuchila Shelf (Map 1), although not all these variables were considered at every site. Site descriptions, and sample methods are provided in Table 3. Age structure at the various sites was determined by producing frequency histograms of whorls, height and/or circumference. Trees at L3 and T2 were of particular interest in that they appeared to be the offspring of a single parent in each case, as evidenced by the presence at each site of a single burnt tree-stump (Table 3). Inclement weather prevented extensive age structure sampling at Sombani. However, a seventh site, S1 (Map 1, Table 3), adjacent to the Sombani plantation, was examined, because it demonstrated some interesting features about the behaviour of the invading pine.

TABLE 3. Description of sites and sampling methods used in collection of age structure and reproductive data. Refer to Map 1 for site locations.

| Site | Plot dimensions and type | Site description | Parameters measured* |
|------|--|--|------------------------|
| L1 | Rectangular plot, 250m x 300m. | South west facing slope. Shrubby grassland. Shrubby component up to 4m high. Pines widely spaced (50-100m apart) except for a single dense cluster surrounding a burnt stump. | Ht, Wh, Circ, Fst, Con |
| L2 | Circular plot, radius 10m. | Level area, near CCAP hut. Ground rather bare, as if disturbed. 17 burnt pine stumps in plot, each with 9-10 growth rings, probably dead parents. | Ht, Wh |
| L3 | Transect, length 100m, width 2m. Placed along density gradient of pine trees, starting at parent stump. Distances of trees from dead parent noted. This was also done for 14 trees standing outside the transect, but which were further from the parent than those inside the transect (i.e. to determine the maximum length of the seedling shadow). | South East facing valley. Moist grassland. Dense pine stand (trees mostly < 5m apart), 100+ m long, 50m wide. Long axis of stand runs east to west. Trees all similar size. Density of trees gradually decreases from east to west side of stand. Single burnt stump at east end, almost certainly the dead parent of all the (live) trees in the stand (i.e. stand is a 'seedling shadow'). | Circ, Fst, Con, Par |

* Parameters measured; Ht, tree height; Wh, number of whorls; Circ, stem circumference; Fst, position of lowest cone; Con, reproductive (cone) status.

TABLE 3. Continued

| Site | Plot dimensions and type | Site description | Parameters measured* |
|------|---|---|------------------------|
| T1 | Irregular plot, probably about 30m x 50m. | West facing slope. Grassland with some scrub, but fairly open. Pine trees recently felled, densely packed (5-10m between trees). | Ht, Wh, Circ, Fst, Con |
| T2 | Irregular plot/transect. All pines in stand examined, but not the 2 isolated individuals. | West facing slope. Grassland with some scrub. Pines in very dense stand, about 50+ m long and 20m wide. Long axis running north west to south east. Tree density gradient along this axis, decreasing from the south east. Single burnt stump at south east end of stand, almost certainly dead parent of all trees in the stand. 'Seedling shadow' as at L3. Two individual trees 70-80m north west of parent. | |
| T3 | Rectangular plot, 30m x 80m. | North West facing slope. Grassland-shrub community. Pine trees fairly dense (10-25m between trees). | Ht, Wh, Circ, Fst, Con |

* Parameters measured; Ht, tree height; Wh, number of whorls; Circ, stem circumference; Fst, position of lowest cone; Con, reproductive (cone) status.

TABLE 3. Continued

| Site | Plot dimensions and type | Site description | Parameters measured* |
|------|------------------------------|--|--|
| S1 | Rectangular plot, 50m x 30m. | Very recently burnt area, adjacent to the Sombani plantation. Apparently three cohorts of plants in present: (i) three very large trees, two of which been killed by the fire, and the third scorched, (ii) a stand of smaller trees, which had survived the fire lightly scorched, and (iii) a large number of tiny seedlings standing below the three large trees, that had presumably recruited following the fire. | Different variables noted for the different cohorts: (i) Wh, Ht, Circ, Fst, Con (ii) Circ, Fst, Con (iii) Wh, Con |

* Parameters measured; Ht, tree height; Wh, number of whorls; Circ, stem circumference; Fst, position of lowest cone; Con, reproductive (cone) status.

3.3. Reproductive status

An important consideration in an investigation of this type is the current reproductive status of invaders, as this indicates the immediate potential for further invasion. In pines this is indicated by the state of maturity of the female cones as these are the sources of new seeds. In this study, trees were classified into six reproductive classes (Table 4) on the basis of the maturity of their cones. Data on the cone status of individuals were collected at six sites (L1, L3, T1, T2, T3 and S1). For those trees which possessed cones (i.e. class 1 and above) it was also noted at which whorl the lowest cones were situated (whorls counted as shown in Appendix 2).

TABLE 4. Reproductive classes of trees as considered in the current study, as defined by features of the most mature cones.

| | |
|----------|--|
| Class 0. | No cones on tree. |
| Class 1. | Cones very small (up to about 3 cm in length), non-woody. |
| Class 2. | Cones small (up to about 5 cm in length), tending to woodiness, but green. |
| Class 3. | Cones larger, reaching mature size, woody, but still green. |
| Class 4. | Cones mature, large, woody, brown in colour. |
| Class 5. | Cones open (often associated with burnt/ scorched trees). |

3.4 Dispersal data

Seed dispersal in *P. patula* is wind driven, with the seed being a samara. Seed wing loading index (mass of seed/ area of seed) and seed mass give an indication of the distances that seeds may be dispersed by wind, and both were considered by Richardson *et al.* (1990) to be important determinants of the invasive success of pine species. This study provides values for seed wing loading index and seed mass for *P. patula*, obtained from a set of 95 seeds taken from 10 cones from various trees. Only larger seeds were selected, because the smaller seeds almost certainly were not viable. The mass of each seed was measured on a mettler balance, precise to 0.0001 g, while wing loading indices were obtained by passing paper cut outs representative of the seed areas through a leaf area meter, precise to 0.01 cm².

Richardson *et al.* (1990) provide a list of wing loading indices and seed masses for a series of pine species that are very useful for comparison.

Seed characters provide insight into the potential dispersal capacity of pines. Actual dispersal distances of pines are, however, best gained from looking at the patterns of seedling dispersal downwind of a seed source (i.e. seedling shadows). On Mt. Mulanje it is difficult to locate seed sources with any certainty because over the years reproductive trees have been felled here and there, so that these seed sources are now difficult or impossible to locate. However, the pine stands at sites L3 and T2 formed distinct seedling shadows, each having a single identifiable parent tree which had been burnt and killed. At these two sites, the patterns of seedling distribution along a transect from the burnt parent along the long axis of the seedling shadow was investigated, by producing histograms plotting the density of trees with distance from their 'parent'. Changes in mean circumference and reproductive state of trees with distance from the parents were also examined. This was done by calculating the mean tree circumference, and the proportion of trees with mature cones (proportion of class 4 individuals), of trees standing within successive, adjacent areas of 2m x 2m (L3) and 2m x 3m (T2) along the 2m-wide transects.

4. RESULTS

4.1 Distribution of pines

The distribution of pines in the survey area is indicated in Map 1. Of the six plateaux surveyed, pines occurred on all but Madzeka, although they had almost reached the boundary of that basin. Quite apparent was the extremely high level of pine infestation in the north eastern sector of the mountain, particularly on the Sombani Plateau and the upper Ruo Basin. Tables 5 and 6 list, respectively, estimated figures for the areas occupied by pines at different densities on the different plateaux, and the numbers of individual pines occurring in these areas. Individuals or small clusters of individuals (<20) that were fairly isolated (i.e. density rank 1) did not occupy clearly defined invasion areas (density blocks), and so have been omitted from Table 5; however, they have been incorporated into Table 6. These data clearly indicate the concentration of the pine invasion in the Ruo and Sombani areas. The latter plateau had both the greatest proportion of its area invaded (15.1%) as well as the greatest estimated number of invaders for any of the plateaux, and appeared to be the most heavily invaded. Although the absolute area occupied by invaders in the Ruo basin was greater than that at Sombani, this represents a smaller proportion of its total area. Interestingly, the much higher levels of invasion in Ruo and Sombani relative to the other plateaux, arose primarily because these areas seemed to have greater areas of dense invasion (i.e. density ranks 3, 4, 5 and 6). On the other plateaux, with the exception of Madzeka which had no pines, the pine was thinly distributed, being mainly represented either by isolated/ scattered individuals or small, dense clusters of individuals, each probably being the offspring of a single founder tree. Over the entire survey area (9661 ha), roughly 610.1 ha (6.3%) was estimated to be invaded by pines, excluding those in density rank 1, while the total number of invasive pines was roughly estimated at just over 36 000. The data provided in Tables 5 and 6 remain very crude, and may well be slight over-estimates. Nevertheless, the general patterns they show are of interest, and seem representative of the real situation on Mt. Mulanje.

TABLE 5. Estimated areas occupied by different densities of the patula pine on the six plateaux surveyed. Density ranks as outlined in Table 2. Figures in hectares. Figures in parentheses indicate percentages of the total area surveyed on the corresponding plateau.

| Density rank | Lichenya | Chambe | Tuchila | Plateau Ruo | Sombani | Madzeka | Total |
|----------------------------|------------------|-----------------|------------------|------------------|------------------|----------------|---------------------|
| 0+1 | 2334.0 (99.5) | 244.3 (93.3) | 1827.8 (99.9) | 2339.3 (87.8) | 1405.6 (84.9) | 707.0 (100) | 9051.2 (93.7) |
| 2 | 0 (0) | 9.1 (3.5) | 0 (0) | 53.3 (2.0) | 10.1 (0.6) | 0 (0) | 72.5 (0.8) |
| 3 | 6.1 (0.3) | 0 (0) | 0 (0) | 149.7 (5.6) | 38.7 (2.3) | 0 (0) | 194.5 (2.0) |
| 4 | 0 (0) | 8.3 (3.2) | 0 (0) | 63.4 (2.4) | 94.7 (5.7) | 0 (0) | 166.4 (1.7) |
| 5 | 1.1 (0) | 0 (0) | 1.1 (0.1) | 52.4 (2.0) | 96.4 (5.8) | 0 (0) | 151.0 (1.6) |
| 6 | 2.8 (0.1) | 0 (0) | 1.1 (0.1) | 11.2 (0.4) | 10.6 (0.6) | 0 (0) | 25.8 (0.3) |
| 2-6 ¹ | 10.1 (0.4) | 17.5 (6.7) | 2.28 (0.1) | 329.9 (12.4) | 250.4 (15.1) | 0 (0) | 610.1 (6.3) |
| Total ² area | 2344.0 | 261.8 | 2023.2 | 2669.3 | 1656.1 | 707.0 | 9661.3 ³ |

1. Summation of areas occupied by density ranks 2, 3, 4, 5 and 6.

2. Represents total area of corresponding plateau covered by survey.

3. Represents total survey area.

TABLE 6. Estimated numbers of pine trees occurring in each density rank on the six plateaux surveyed. Density ranks as outlined in Table 2. Figures in parentheses indicate percentages of the total number of pines on the corresponding plateau.

| Density rank | Lichenya | Chambe | Tuchila | Plateau Ruo | Sombani | Madzeka | Totals |
|-------------------------------|----------------|---------------|---------------|----------------|-----------------|----------|--------------------|
| 1 | 66 (4.4) | 10 (3.9) | 62 (8.8) | 70 (0.5) | 70 (0.4) | 0 (0) | 278 (0.8) |
| 2 | 0 (0) | 36 (14.3) | 0 (0) | 213 (1.5) | 40 (0.2) | 0 (0) | 290 (0.8) |
| 3 | 55 (3.6) | 0 (0) | 0 (0) | 1347 (9.3) | 348 (1.8) | 0 (0) | 1750 (4.8) |
| 4 | 0 (0) | 209 (81.8) | 0 (0) | 1584 (10.9) | 2367 (12.3) | 0 (0) | 4159 (11.5) |
| 5 | 138 (9.1) | 0 (0) | 138 (19.6) | 6335 (43.7) | 11661 (60.8) | 0 (0) | 18272 (50.6) |
| 6 | 1255 (82.9) | 0 (0) | 502 (71.5) | 4936 (34.1) | 4685 (24.4) | 0 (0) | 11378 (31.5) |
| Total ¹ numbers | 1513 | 255 | 702 | 14486 | 19171 | 0 | 36127 ² |

1. Estimated total numbers of pines in surveyed part of each plateau.
2. Estimated total number of pines in entire survey area.

TABLE 7. Estimated number of pine individuals occurring in grassland and forest vegetation within each density ranking. Figures in parentheses represent percentages of the total number of trees in each density category.

| Density ranking | Grassland | Forest |
|-----------------|--------------|-----------|
| 1 | 266 (95.7) | 12 (4.3) |
| 2 | 289 (100) | 0 (0) |
| 3 | 1750 (100) | 0 (0) |
| 4 | 3951 (95.0) | 209 (0) |
| 5 | 18272 (100) | 0 (0) |
| 6 | 11378 (100) | 0 (0) |
| Total | 35906 (99.4) | 221 (0.6) |

Table 7 presents the estimated numbers of individuals observed in the two broad vegetation types on Mt. Mulanje: forest and grassland. The total number of individuals in forest was significantly lower than what would be expected if ease of invasion in the two vegetation types was equal, given that these different vegetation types occupy different proportions of the survey area (Table 8) (X^2 goodness-of-fit test: $X^2=3408.43$, $df=1$, $P<0.0005$). Further, although not statistically tested, there was a noticeable absence of pines from firebreaks, with only three individuals being recorded in that habitat. Also, pines seemed to be absent from the higher altitudes, and particularly the granite domes, except on Namasile, the peak that lies directly west of the Sombani plantation.

TABLE 8. Estimated area occupied by four vegetation types in the survey area.

| Vegetation type | Area occupied (ha) | Percentage of total survey area |
|------------------------------|--------------------|---------------------------------|
| Cedar forest | 628.0 | 6.5 |
| Non-cedar forest | 299.5 | 3.1 |
| Grassland/ scrub | 8685.5 | 89.9 |
| Pine plantation ¹ | 48.3 | 0.5 |

1. Excludes areas in which pines have arisen because of natural regeneration (i.e. areas of invasion).

4.2 Age structure

Numbers of whorls, stem circumference and tree height are all problematic as measures of tree age. However, correlation analysis suggests that these variables are strongly related in a positive linear fashion (Table 9), for which the most obvious explanation is that they are all related to tree age. A particularly strong correlation ($r^2=0.8321$, d.f.=82, $P<0.0005$) was found between tree height and whorl number, a relationship with the equation: $Wh = 2.55 \times Ht + 3.14$.

TABLE 9. Correlation coefficients of the relationships between the various age measures, as determined using linear regression analysis.

| Relationship | r. | d.f. | P. |
|--------------|--------|------|---------|
| Ht vs Wh | 0.9122 | 82 | <0.0005 |
| Ht vs Circ | 0.8362 | 34 | <0.0005 |
| Wh vs Circ | 0.4946 | 105 | <0.0005 |

The mean, minimum and maximum values for the three age measures at the different sampling sites are provided in Table 10, while data from the three Lichenya sites (L1, L2, L3) and the three Tuchila sites (T1, T2, T3) were pooled and used to generate the frequency histograms in Figs. 2, 3 and 4. These data were pooled because frequency histograms of these variables done individually for each of these sites were very similar, indicating that the pines at these sites had a similar age structure. In all cases, there was no evidence of more than one cohort of trees being present, with histograms most commonly being normal to slightly skewed to the right. All evidence suggests that the trees at these sites were relatively young: stem circumference, for example, had a maximum value of 45 cm, while trees within the Sombani plantation had circumferences far greater than this, as did the dead stumps of the 'parent' trees at L3 and T2. The age structure pattern at the Lichenya and Tuchila sites, however, was representative of the age structure of pines on the majority of Mt. Mulanje, with the possible exception of some stands closer to the plantations themselves. The site at Sombani (S1), for example, had a

TABLE 10. Some statistics for parameters measured at the seven sampling sites. The first datum is the mean value, the second the range (i.e. minimum-maximum), and the third the sample size.

| Parameter | L1 | L2 | L3 | Site T1 | T2 | T3 | L1-T3 ¹ | S1 | Mat ² |
|--|-------------------------|-----------------------|-------------------------|------------------------|-----------------------|-----------------------|------------------------|-----------------------|-----------------------|
| Height (m) | 3.90 1.9-6 (22) | 2.01 0.3-4 (48) | - | - | - | 4.48 1-5.8 (13) | 2.90 0.3-6 (83) | - | - |
| Number of whorls | 13.38 7-23 (26) | 8.13 3-11 (48) | - | 13.53 7-22 (19) | 12.06 7-33 (52) | 14.23 3-20 (13) | 11.44 3-33 (158) | 3.16 0-25 (630) | 15.2 7-23 (25) |
| Stem circumference (cm) | 13.29 2.5-39 (26) | - | 16.41 1-35.5 (50) | 27.00 13-45 (15) | 15.89 3-45 (52) | 22.81 0-41 (13) | 17.27 0-45 (156) | - | 24.54 6-45 (78) |
| Cone maturity (Table 4) | 1.42 0-4 (26) | - | 2.42 0-4 (50) | 1.79 0-4 (19) | 2.08 0-4 (52) | 1.69 0-4 (13) | 2.01 0-4 (160) | 0.24 0-5 (629) | |
| Position of lowest cone (whorl no) | 9.35 5-15 (17) | - | 7.38 4-16 (50) | 9.06 4-14 (16) | 8.08 6-11 (39) | 7.92 5-12 (12) | 8.19 4-16 (116) | 6.21 1-14 (61) | |

1. Pooled data from six sites: L1, L2, L3, T1, T2 and T3.

2. Pooled whorl number and circumference data from living trees with mature cones (Class 4) from all seven sites

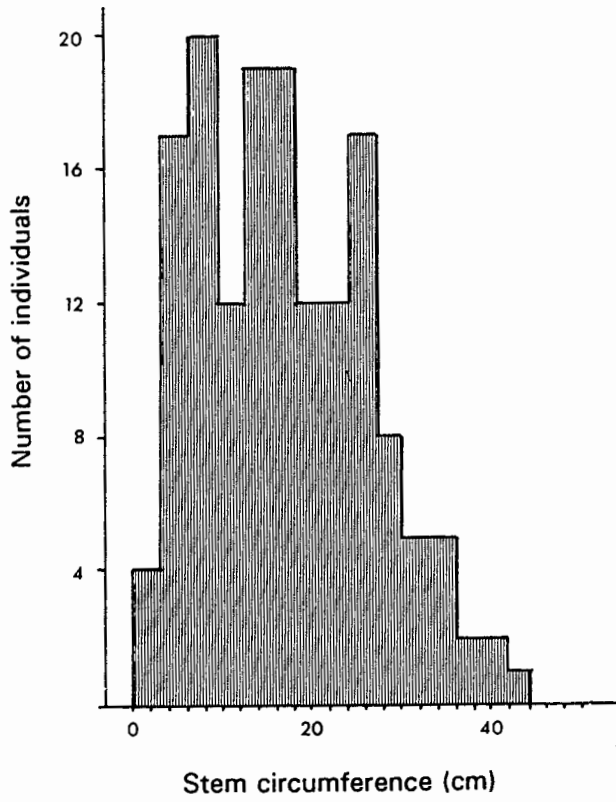


FIGURE 2. Distribution of stem circumferences of trees at L1, L3, T1, T2 and T3. (n=156)

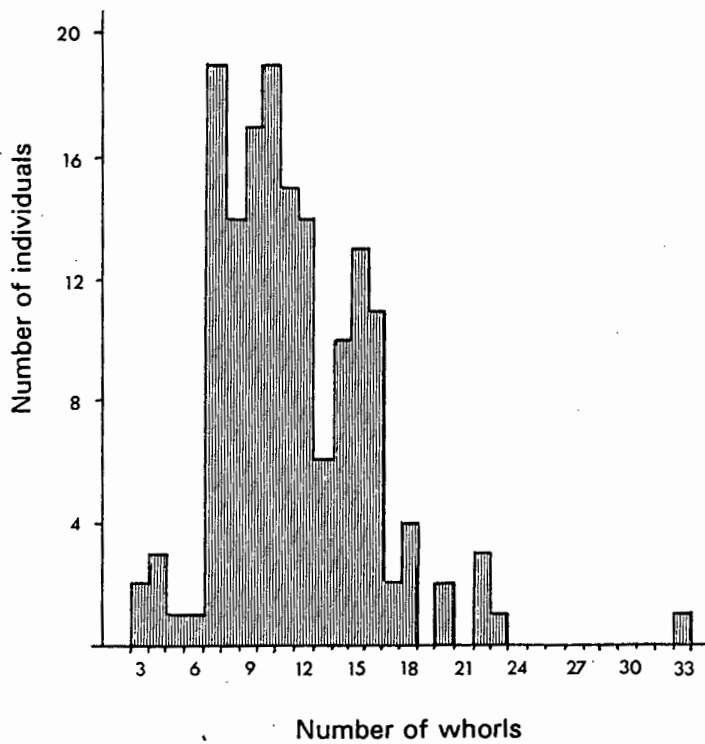


FIGURE 3. Distribution of the numbers of whorls possessed by trees at L1, L2, T1, T2 and T3. (n=158)

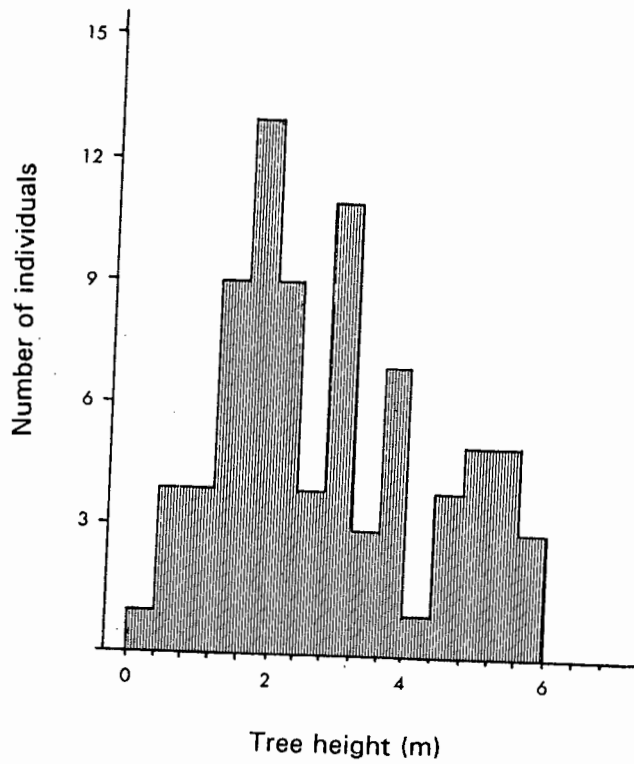


FIGURE 4. Distribution of the heights of trees at L1, L2 and T3. (n=83)

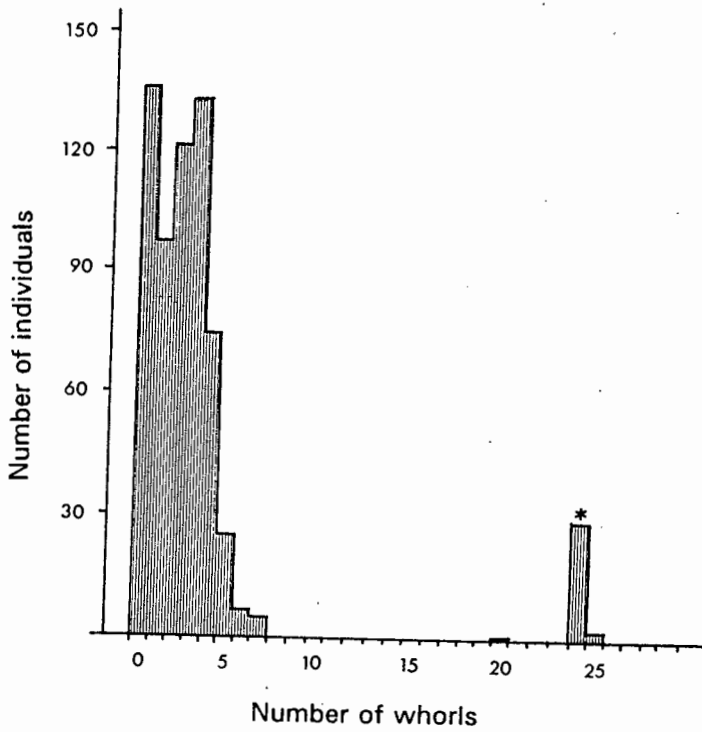


FIGURE 5. Distribution of the numbers of whorls possessed by trees at S1. Asterisk marks a group of 29 trees for which whorl number was calculated from measured height data. (n=630)

very different age structure. A frequency distribution of the whorl number for trees at this site is presented in Fig. 5. For twenty nine of the trees at this site the number of whorls was not counted directly, but was calculated from height measures using the equation for the regression between tree height and whorl number. Fig. 5 indicates the existence at S1 of at least two distinct cohorts: one, whose members had 0-7 whorls, and a second, smaller cohort, whose members had 20-25 whorls. In fact, stem circumference data suggest that the latter cohort probably comprised two cohorts, one of about 29 living individuals (circ. 7-41 cm), and one of three individuals, two of which had been burnt and killed in a recent fire (circ. 84-105 cm).

4.3 Reproductive status

The cone status of living individuals at all seven sampling sites is indicated in Fig. 6 and Table 10. Individuals with mature cones (Class 4 individuals) occurred at all

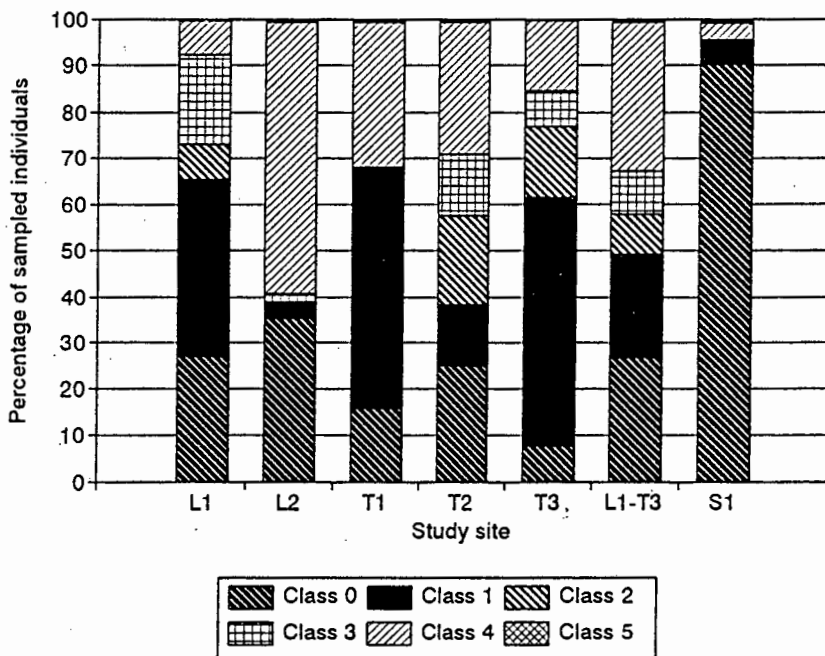


FIGURE 6. Percentages of trees in different reproductive classes at each of the seven study sites. Sample sizes as indicated in Table 10.

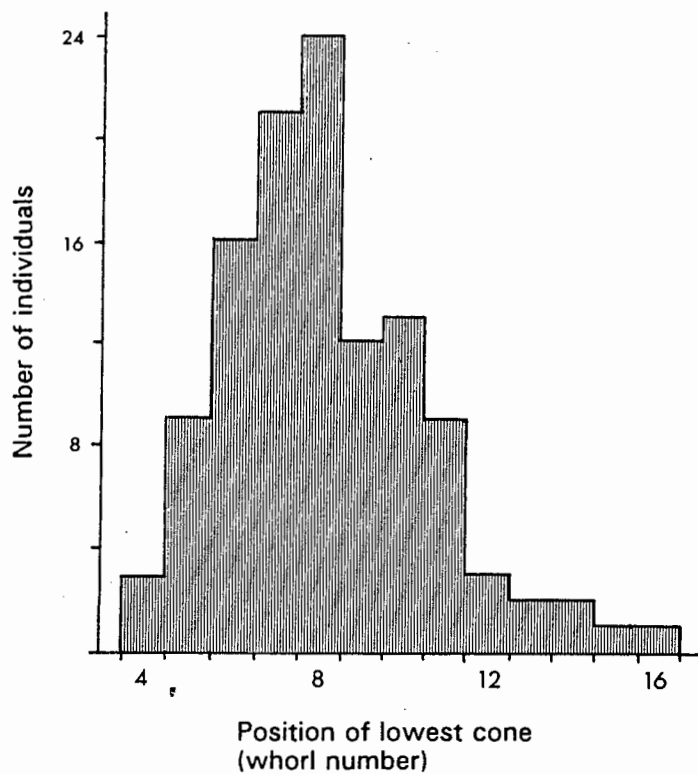


FIGURE 7. Distribution of the position of the first cone on trees at the Lichenya and Tuchila sites. (n=116)

sites, although in different proportions. The relatively small proportion of individuals with mature cones at S1 may be attributed to the presence here of a very large number of very small seedlings. Dead individuals have been omitted from Fig. 6, and include single trees at L3 and T1, and two trees at S1.

The position of the lowest cones on pine trees was also determined for cone-bearing trees at six sites (L1, L2, T1, T2, T3, S1). Means, minima and maxima are presented in Table 10. In addition, individual site data, excluding those from S1, were pooled to produce the frequency histogram shown in Fig. 7. For these five sites the mean position of the first cone is at about the eighth whorl, while the minimum position is at the fourth whorl. Interestingly, the cohort of small seedlings at S1 had a lower first-cone mean (about the fourth whorl) and minimum (the first whorl), suggesting that trees have the potential to produce cones very early, but that the earliest cones are usually aborted.

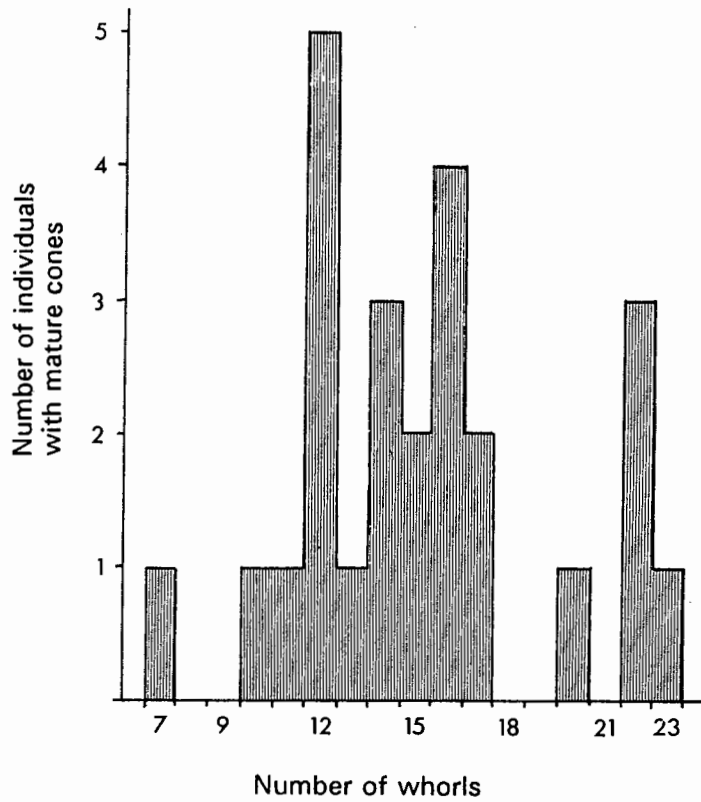


FIGURE 8. Distribution of the numbers of whorls possessed by trees with mature cones (Class 4) from all seven sample sites. (n=25)

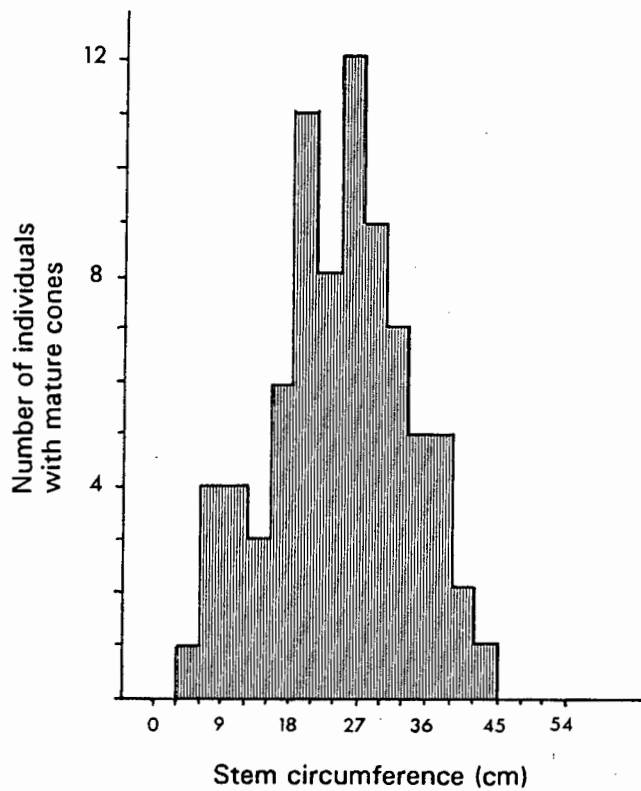


FIGURE 9. Distribution of stem circumferences for trees with mature cones (Class 4) from all seven sampling sites. (n=78)

Whorl number and circumference frequency histograms for the set of all living individuals with mature cones from all seven sites are presented in Figs. 8 and 9, with means and minima listed in Table 10. These data indicate at what stage trees first become reproductively mature. The mean and minimum numbers of whorls on such trees were, respectively, 15.2 and 7. These values translate into mean and minimum heights of 4.91 m and 1.75 m respectively (using the equation of the regression between whorl number and tree height).

4.4 Dispersal data

For the sample of 95 seeds measured, wing loading index was calculated at $9.69 \pm 3.43 \text{ mg} \cdot 100\text{mm}^{-2}$ (mean \pm standard deviation), a value that represents perhaps a maximum for this species since the seeds sampled here had above-average masses. Seed masses were found to have a value of $4.899 \pm 1.647 \text{ mg}$.

Seedling shadows originating from single 'parent' trees (killed in fire) were observed at sites L3 and T2. At both sites the density of individual trees dropped off

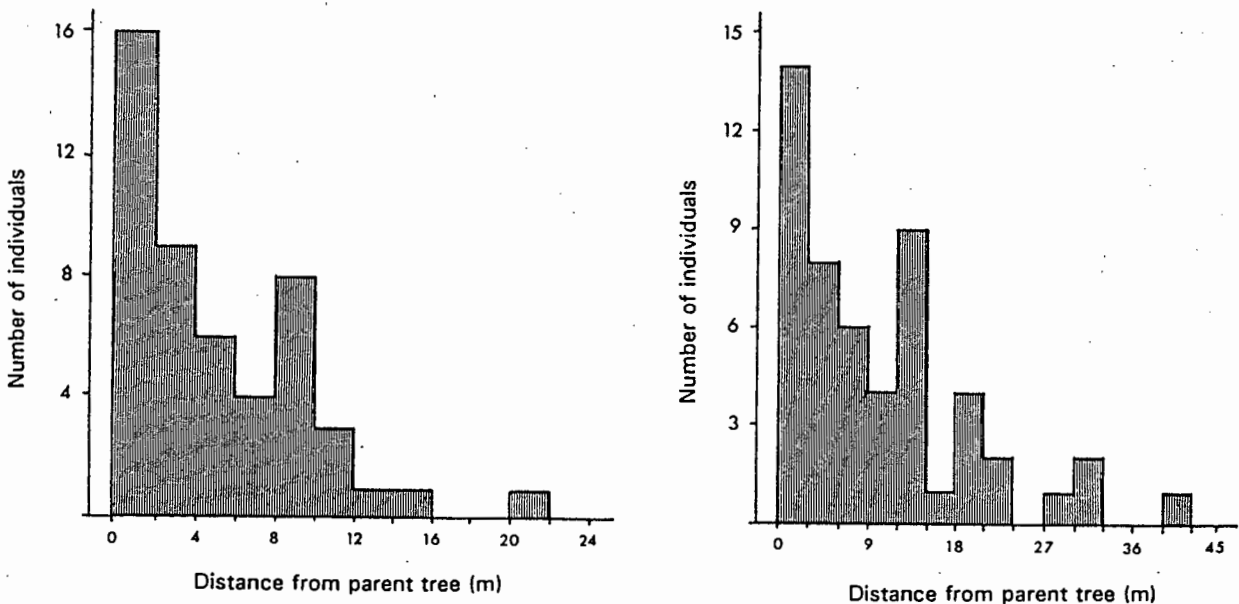


FIGURE 10. Distribution of saplings along two transects, each following a seedling shadow originating from single (dead) parent tree, at (a) L3 and (b) T2.

with distance from the parent tree, giving rise to leptokurtic distributions (Fig. 10a,b). However, the furthest-dispersed individuals are not indicated in these graphs, because they stood outside the sample transect. At L3 individuals were recorded up to 49.1 m from the 'parent' tree, while at T2, the maximum recorded distance was about 80 m. In addition, it is possible that other trees even further away belonged to the same seedling shadow, but this is difficult to verify without genetic or other evidence.

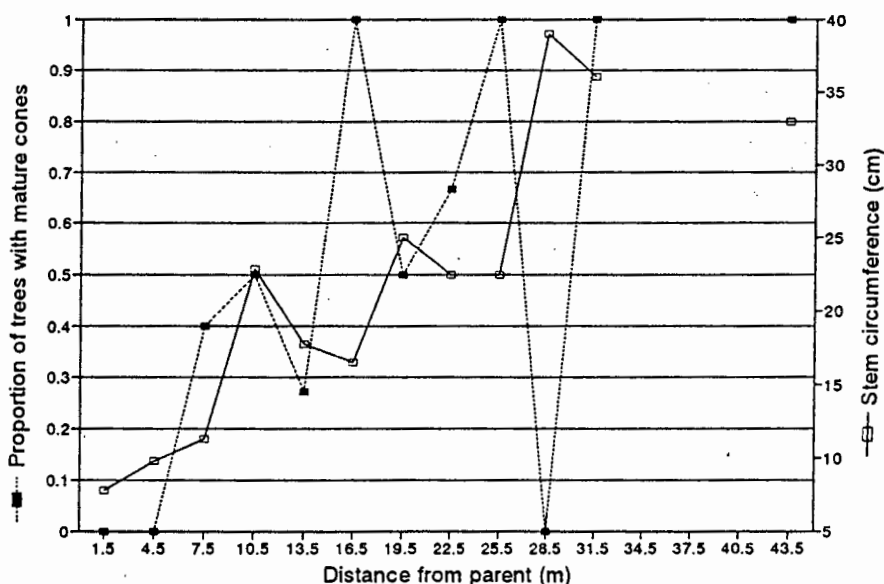


FIGURE 11. Patterns in mean stem circumference and proportion of individuals with mature cones of trees along a seedling shadow originating from a single parent tree at T2. Each point represents trees occurring within a two meter interval along a two meter wide sample transect.

An interesting pattern emerging from the T2 data was the tendency for trees to have increased stem circumference and for a greater proportion of trees to have mature cones at greater distances from the parent tree (Fig. 11), where tree densities were lower. Both of these trends were tested for significance using, respectively, regression analysis and Spearman rank testing, and both proved to be significant ($r^2=0.7567$, $df=11$, $P<0.0005$ and $r_s=0.638$, $df=12$, $P<0.05$, respectively). Although, this pattern was not repeated at L3, there was a significant linear correlation between stem circumference and cone maturity at that site ($r^2=0.6089$, $df=8$, $P<0.0005$). Similar results were obtained when the circumferences and

reproductive status of individual trees were correlated against distance from parent, although the trends were not as strong or as clear.

5. DISCUSSION

5.1 Why has the pine invaded so successfully?

Kruger *et al.* (1986) identified three barriers that need to be overcome by invaders if they are to establish in a new environment: a geographic barrier, a habitat barrier, and a biotic barrier. The geographic barrier entails the problems of reaching the new environment, and are overcome by natural or man-mediated dispersal. The habitat barrier is the barrier posed by the physical conditions of the new environment to which, for successful establishment, the plant must be able to adapt. The biotic barrier includes those biotic forces such as competition and predation which may retard or prevent the establishment of the alien.

In considering why an invader species has been successful, it is useful to think in terms of these barriers, and here, I consider the magnitude of each of these barriers as faced by *P. patula* on Mt. Mulanje, and then discuss some of the features of the pine which has allowed it to overcome these obstacles.

5.1.1 The introduction of the pine

P. patula was introduced to Mt. Mulanje in 1946, at which time it was intended for use as a nurse plant to promote recruitment of the Mulanje cedar *Widdringtonia whytei* (Edwards 1982; Sakai 1989a). Apparently, however, this intention seems never to have been realised and the pine, with its superior competitive ability, now represents more of a threat to the cedar than a help (Sakai 1989a). Presently, two officially recognised plantations stand on the mountain at Chambe and Sombani, although extensive natural regeneration has occurred outside these.

5.1.2 Habitat factors

A major factor determining the success of an invader species is its ability to cope with the physical conditions of its target environment. The physical environment of Mt. Mulanje almost perfectly matches the habitat of *P. patula* in its natural distribution range in Mexico, so that the habitat barrier faced by this species on Mt. Mulanje must be negligible. Wormald (1975) reports that in Mexico, the species occurs on warm and cool temperate volcanic peaks (18°N-24°N) mainly in the altitudinal range 1850-2750 m. Rainfall here is high (1000-1500 mm p.a.), and occurs mainly during the summer, with the drier winter season being short, and ameliorated by mists. These climatic conditions are almost identical to those on Mt. Mulanje (see section 2.1). Soil conditions on Mt. Mulanje also suit the pine. In its home range the species grows on sandy to loamy, porous soils of good depth (Wormald 1975). While soil fertility does not seem to be very important for the pine, high soil moisture, low soil pH, and deep soils are, and these conditions also seem to be satisfied on Mt. Mulanje. The pine's requirement for greater rooting depth may explain why it is largely absent from the high-altitude granite domes on Mt. Mulanje, as the soils here are shallow. In general, on Mt. Mulanje, the pine seems to prefer the conditions of the flatter plateau and basins, and it is here that the invasions are most extensive. They may, however, occur in crevices when their roots can penetrate these.

Another feature of the Mulanje environment is the regular occurrence of fire in the plateau grasslands (see section 2.1). *P. patula* has a number of preadaptations that allow it not only to cope with fire but even to utilise fire to promote its spread on the mountain. These include the possession of serotinous cones and a short juvenile period (period necessary for attainment of reproductive maturity), and are discussed in greater depth in section 5.1.4.

5.1.3 Biotic factors

The biotic barriers faced by a plant invader may include resource competition by other plants, and predation by herbivores. In environments where resource

competition is intense, invaders may frequently be excluded because of a lack of niche space. Various workers have recognised that under these circumstances, disturbance may play an important role in 'opening up' a community to invasion (Geldenhuys *et al.* 1986; Kruger *et al.* 1986; Richardson and Cowling 1992; Richardson *et al.* 1992). Disturbance, whether this be natural or man induced, may cause normal community function to be disturbed so that openings appear for invaders to become established.

The important role of regular fires, a natural disturbance regime, in producing so called 'invasion windows' in the southern Cape fynbos biome has been intensively investigated by a number of workers (Kruger *et al.* 1986; Richardson and Cowling 1992; Richardson *et al.* 1992). The extensive invasion of that biome by a range of fire-adapted woody aliens, including three species of serotinous pines, *Pinus radiata*, *P. pinaster* and *P. halepensis*, has been greatly facilitated by the occurrence of regular fires.

The regular occurrence of fire on the plateau grasslands of Mt. Mulanje may, therefore, be of great significance in breaking down biotic barriers and promoting the invasion by *P. patula*. Surprisingly, the pine has only had moderate invasive success in South African grasslands and savannas where fires are also regular (Macdonald and Jarman 1985; Henderson and Wells 1986). Here, the invasion by the pine seems to be restricted to areas that are physically disturbed, such as fence-lines and road-cuttings, and areas that are protected from fire. Richardson (1990) and Richardson and Cowling (1992) attempted to explain the relatively low levels of invasion in these areas by invoking the predominance here of vigorous, fast-growing C₄ grasses which are able to outcompete invader seedlings in the post-fire environment. However, *P. patula* has had great success on Mt. Mulanje in spite of the presence of a range of C₄ grasses, including *Themeda triandra*, as well as species of *Eragrostis* and *Festuca* (Chapman 1962), suggesting that this explanation is inadequate here. An alternative explanation for the relative non-success of *P. patula* in South African grasslands is that fire here are too frequent for it to cope with. This is not really a problem on Mt. Mulanje where current management practices seem to be aimed at reducing fire frequencies. A more frequent fire regime in the grasslands might well help to reduce the success of the pine.

In the present study it was found that pines were significantly over-represented in the grasslands relative to the forests. The relatively higher frequency of fires in grassland goes some of the way to explain this pattern. Another factor, however, is the nature of the vegetation itself. Due to the low stature of the grassland vegetation, some pine recruitment may occur here even in the absence of fire. In contrast, forests generally have a closed dense canopy under which recruitment of pine seedlings is virtually impossible, so that pine invasion is almost exclusively restricted to places where openings have been created by fire or physical disturbances, or where the forest margin has been damaged (Edwards 1982; Geldenhuys 1986). Significantly, of the estimated 221 pine individuals noted in forest vegetation in the current study, all but about 10 were growing in situations that showed signs of recent fire, while the remainder stood at the forest margin. Finally, a third factor promoting enhanced pine invasion in grassland concerns seed dispersal. Dispersal of *P. patula* seed is by wind, and may be severely limited in tall, forest vegetation where wind currents may be greatly reduced. In open grassland, even with a sparse shrub cover, wind dispersed pine seeds may travel far, so that invasion is greatly facilitated.

The role of predation of pines in relation to their invasive success has received relatively little study. On Zomba Mountain, however, Happold and Happold (1987) found that the numbers of rodents (species and individuals) in plantations of *P. patula* were lower than in adjacent indigenous vegetation, suggesting perhaps that these animals avoid the pines. On the other hand, Wormald (1975) lists numerous pests of the pine, suggesting that it has a great number of potential herbivores, and seed predators. Without more empirical data specific to Mt. Mulanje it is difficult to assess the effects of herbivory or seed predation on the pine invasion here, although, judging from the success of the pine, it seems to be minimal.

5.1.4 Invasive characteristics of the *Pinus patula*

Richardson *et al.* (1990) examined the relative invasive success of pine species, and found that the three most successful pinaceous fynbos invaders, *Pinus radiata*, *P. pinaster* and *P. halepensis*, shared a range of attributes which, they and other workers (Kruger *et al.* 1986; Richardson and Cowling 1992; Richardson *et al.* 1992) have suggested, makes them particularly successful invaders of the fire-prone fynbos vegetation. These characters include: cone serotiny, intermediate-short juvenile period, low seed crop variability, large seed crop, low fire tolerance, small seed size, low seed wing loading. Interestingly, they grouped *P. patula* with these species, suggesting that it too possesses characteristics which enhance its invasive success in vegetation experiencing periodic fire events. Some of these are discussed here.

(a) **Cone serotiny.** Wormald (1975) reports that the cones of *P. patula* are serotinous, noting that they open readily with heat. Thus seed release in this species will be concentrated into post-fire periods, when the cones are burned and dry out. In this way *P. patula* is able to flood the post-fire environment with its seeds, improving its establishment at a time when the competitors are relatively sparse, and nutrients relatively abundant. Age structure approximations, using whorl number, stem circumference or height, at six of the sampling sites (L1-3, T1-3) did not produce clear patterns in which different age groups formed distinct cohorts (each relating to a single post-fire recruitment event). The main reason for this is, I suggest, that at these sites there was only one age group (cohort) of relatively young trees present, older age groups having been killed by fire and/ or felling. This is certainly true for sites L3 and T2, where individuals were in each case the offspring of a single parent. Another factor that may obscure any patterns present is the relative crudeness of the age measures used. At S1, however, a clear cohort pattern was observed (Fig. 5), with at least two cohorts, and probably three, being clearly evident. The mass of tiny pine seedlings on this plot, concentrated chiefly below 2-3 large trees that had been burnt in a recent fire strongly suggests that recruitment in the pine is massive following fire.

The data presented above, and the serotinous nature of *P. patula* cones, do not preclude the possibility of inter-fire seed release from older cones, a trait which might be advantageous during inter-fire periods. In addition to natural seed release mechanisms, felling of trees also causes cone opening and seed release. Current measures to 'control' the pine involve haphazard and inconsistent felling of pines, and this may be enhancing inter-fire recruitment by the pine.

(b) Juvenile period. Richardson *et al.* (1990) reported the juvenile periods of the three fynbos-invading pines, *P. radiata*, *P. pinaster* and *P. halepensis*, as 8, 6, and 12 years respectively. *P. patula* has a comparable juvenile period, with the first viable seed being set in about the fifth year, and cone production usually being heavy by the eighth or tenth year (Wormald 1975). Apparently, female flowers are common by the third year.

In the current investigation it was found that the female flower production starts very early, with young cones being found even on the first whorl of seedlings at S1, which were almost certainly less than 2 years old. However, visual observation suggests that the first female cones produced are probably aborted early on in most cases. On older trees at the Lichenya and Tuchila sampling sites, the mean position of the lowest cone was at the eighth whorl, with the fourth whorl being the minimum (Table 10, Fig. 7). All evidence suggests, however, that reproductive maturity in *P. patula* is attained early on, with mature-coned (Class 4) trees having as few as seven whorls and a mean of only 15.2 whorls, and having stem circumferences as low as 6 cm (Table 10, Figs. 8,9). This, a short juvenile period, is an important feature that allows the pine to persist in an environment that burns regularly. So long as inter-fire intervals are greater than about 8-10 years, new pines will be able to recruit following fires and build up new crop of canopy stored seed before the next fire.

(c) Seed mass and wing loading. The seeds of *P. patula* are samaras, whose inherent dispersability depends on two factors: (i) seed mass, and (ii) the area of the wing in relation to the mass of the seed (seed wing loading index). For the highly invasive *P. radiata*, *P. pinaster* and *P. halepensis*, values for these parameters range between 24.4 and 56.8 mg (seed mass) and 14.2 and 26.8 mg.mm⁻²

(Richardson *et al.* 1990). In this investigation the corresponding values for *P. patula* were found to be around 5 mg and 10 mg.mm⁻² respectively, suggesting that the seeds of that species have the capacity to disperse even further than those of these other species, given suitable wind conditions. Such distances may be great, with Richardson and Brown (1986) noting dispersal distances of over 3 km for *P. radiata* in Cape fynbos. Seedling shadows of *P. patula* were observed at two sites on Mt. Mulanje (L3 and T2), in the current study. Maximum dispersal distances recorded here were 49.1 m and 80 m respectively. However, these data undoubtedly severely underestimate the absolute maximum dispersal distance of the pine on Mt. Mulanje. As mentioned earlier, wind data for Mt. Mulanje are scarce. However, in many parts of Malawi winds may be fairly strong (up to 15 knots) (Agnew and Stubbs 1972). Although directions are variable, easterly winds dominate (Agnew and Stubbs 1972). Thus east to west seed movement may be expected to predominate, suggesting that the extensive pine invasions in the Sombani and Ruo areas has resulted from the dispersal of seeds from the Sombani plantation to the east.

(d) Fire tolerance. The fire tolerance of *P. patula* seems to be rather variable, depending on the age of trees as well as the intensity of fires. Young trees have a thin, reddish bark (Wormald 1975), that presumably makes them more susceptible to fire than adult trees with their much thicker bark. General observation on Mt. Mulanje suggests, however, that even young trees may be fairly tolerant of fires, as long as these are not too hot, as may often be the case in grasslands, where fuel loads are low. A large number of young trees in the Ruo and Sombani areas survived a fire that swept through this area in August 1990, one year before the present survey. Only the lower branches of these trees had been scorched. On the margins of the Sombani plantation the reverse was observed: here, a number of large trees had been killed in another fire, which presumably had been very hot.

5.2 Current status of the pine on Mt. Mulanje, and its potential threat.

5.2.1 Current state of the pine invasion

The present distribution of invasive pines on Mt. Mulanje (Map 1, Tables 5,6) is rather alarming when the high invasive potential of the pine is taken into consideration. Even if the figures presented in Tables 5 and 6 are over-estimates, as I suspect, the pine problem remains serious.

The extent of the pine invasion has not, seemingly, changed much since 1989 when Sakai (1989a) published his report. At that time, he tried to implement programme for the eradication of the pine, which, although it may have started successfully, presumably faltered subsequently. Perhaps the main result of that programme is that the older trees have been felled, so that today very few large pine trees occur outside the plantations. The vast majority of invading pines seem to be relatively young, with the age structure of trees on most of the mountain being fairly similar to that in the Lichenya and Tuchila sample plots. In these plots trees had relatively low numbers of whorls, low heights and small stem circumferences. Although the precise relationship of these parameters to tree age remain unclear, Wormald (1975) reported that at the age of about 30 years, trees have a stem circumference of between 78.5 cm and 141.4 cm, while older trees have even greater circumferences, and reach heights up to 50m. Mean and maximum circumference and height values at the Lichenya and Tuchila sample sites were substantially lower than this suggesting that even the oldest trees here were very young (Table 10, Figs. 2-4). Sakai (1989a) reports that the formation of the 'unbroken green carpet' of pines that occupies parts of the Sombani Plateau followed a fire in 1985, in which large amounts of seed from scorched cones were scattered through the area. With the exception of a few isolated individuals, and the trees within or adjacent to the plantations, the Mulanje pines all seem to be of a relatively young age, most being less than ten years old. Despite their young age, a proportion of the pines are reproductively mature (Fig. 6) so that they constitute an immediate seed source for further invasion.

Richardson and Brown (1986) investigated the patterns of invasion of *P. radiata* in mountain fynbos, and noted that the process comprises two phases: (i) Initially, a

number of primary colonists establish from seed that has been blown from plantations, often at great distances from these seed sources due to the high dispersability of the seed. (ii) These primary colonists now act as foci for further colonisation, and give rise to dense stands of trees outside the plantations, which ultimately may coalesce to form a dense, continuous cover of trees. Judging from the age structure and distribution of pine trees on Mt. Mulanje, the invasion there has reached its second phase in many areas. In the Sombani and Ruo areas, where the invasion is most advanced, it is well into its second phase. On Lichenya and Tuchila, the second phase has started in various places, as evidenced by the presence of dense, single-cohort stands, originating from primary colonists that have been felled or burned and now remain only as dead stumps.

5.2.2 Sources of invasion

The fact that most of the older invading pines on Mt. Mulanje have been felled or burned means that it is now difficult to identify the sources of the invasion. The heavy infestation of the Sombani and Ruo areas, however, has almost certainly originated from seeds blown from the Sombani plantation. This is corroborated by a number of factors, including (i) a density gradient of pines running from the plantation in the east to the Tuchila Shelf in the west, and (ii) the predominance of easterly wind directions in the region. The absence of high densities of pines in the area immediately adjacent to the plantation may be attributed to the presence here of much unsuitable habitat, including a steep granite cliff (eastern face of Namasile peak), and a series of broad firebreaks. The latter were presumably intended to contain the pines in the plantation, although without apparent success. A factor that has probably exacerbated the distribution of pines in these areas is the successful establishment of high densities of pines on the peak called Namasile that overlooks both Ruo and Sombani. The elevated nature of these trees means that their seeds may be dispersed even more widely than normal, thus greatly hastening the spread of the invasion.

The plantation at Chambe seems to be less important as a source of invaders than that at Sombani. Apparently, some invasion of the forests at the periphery of the plateau does occur, but this appears to be largely limited to forest margins, gaps and

fire-damaged areas (Sakai 1989a; C.A. Pauw, pers. comm.). Fortunately, the main Mt. Mulanje massif seems to have suffered relatively little invasion from the Chambe plantation, and that area of the main massif lying directly to the west of the Chambe Plateau is relatively sparsely invaded (Map 1). This situation may be attributed to two main factors: (i) The predominance of easterly winds in the region favours east to west seed dispersal, while Chambe lies to the west of the main massif. (ii) Chambe is separated from the main massif by two wide, forested gorges that behave as an invasion barrier, which if it is to be successfully traversed, requires seeds to be transported across in one, big 'jump', and this seems to be difficult. Between these two gorges, there is, however, a small neck that joins Chambe to the rest of Mt. Mulanje. A recent fire on this 'bridge' has allowed a small, dense stand of pine trees to become established in the forest margin vegetation there. This has created a hole in the invasion barrier which, I believe, represents a serious threat as an invader source.

Other invaders occurring on some parts of Mt. Mulanje have undoubtedly come from sources other than the two plantations. Those occurring in the southern parts of Lichenya have almost certainly come from pines that had been planted there, but which have now been felled. The same may be true for some trees on the Tuchila Shelf and the Ruo Basin, but this is more speculative.

5.2.3 The threat of the invasion.

The current state of the invasion on the plateaux of Mt. Mulanje is fairly advanced, with stands of small trees in many areas (especially the Ruo and Sombani areas) being fairly dense to very dense. The fact that many of these trees already possess mature cones suggests that the immediate potential for further invasion is great. A recent (August 1990) fire that swept over large parts of the Ruo, Sombani and Madzeka areas scorched several of these trees, resulting in cone opening and seed release, and opened large areas to further invasion via these seeds. These areas include the eastern side of the Ruo basin, the south western part of Sombani, and the north western side of Madzeka.

The consequences of a dense and extensive pine invasion on Mt. Mulanje are potentially wide-ranging, and in the long-term could be very costly, given Mt.

Mulanje's value as a tourist venue. Perhaps of greatest concern is the irreversible damage that may be inflicted on the local flora and fauna. In the Cape fynbos it has been found that high densities of pines invariably result in serious losses of plant species, a decrease in vegetation cover, and changes in plant community composition and structure (Breytenbach 1986; Macdonald and Richardson 1986; Van Wilgen and Richardson 1986a; Van Wilgen *et al.* 1992). These effects may, in turn, result in faunal changes, and changes in overall ecosystem function (Breytenbach 1986; Macdonald and Richardson 1986). In addition, a range of other negative effects, including increased soil erosion, changes in the fire regime (hotter fires), and reduced catchment water flow, have been associated with pine invasions (Macdonald and Richardson 1986; Versveld and Van Wilgen 1986; Van Wilgen *et al.* 1992).

Although the invasion of *P. patula* on Mt. Mulanje is not yet extensive enough for these effects to be operating at a significant scale, if the pine is allowed to continue its spread on Mt. Mulanje as at present, then it ultimately will. In certain parts of the Sombani Plateau, however, the situation seems to be near critical. Thus, urgent management is required to bring the pine under control and to eradicate it from those areas where it poses a serious threat.

5.3 Control of the pine

5.3.1 Areas for eradication

Sakai (1989a) noted that the only satisfactory solution to the problem of the pine is its total eradication, including plantations, from Mt. Mulanje. Economic considerations, however, make this a difficult proposition, both because eradication programmes are expensive and because one of the plantations is actively used for the production of softwood timber.

The costs of control need, however, to be weighed against the long term costs, both economic and aesthetic, of allowing the invasion to continue its spread.

A minimum solution would require the eradication of at least all the trees standing outside the plantations. In addition, I believe, the Sombani plantation, because of its

major role as a source of invasive propagules should also be removed. Because of its isolated position, this plantation seems to be of limited commercial value, and seems to be utilised by private sawyers only (H.N. Manyunso [Patrol officer, Cedar section, Forestry, Fort Lister], pers. comm.). Its removal would not, therefore represent a major commercial loss. The Chambe plantation, however, seems to be of greater importance, and is heavily exploited for timber.

Given the relatively low threat posed by Chambe plantation as a source of invaders, its removal is not imperative. However, if the plantation is retained, then it is essential that those parts of Chambe facing the main Mt. Mulanje massif, as well as the small bridge of land connecting it to the rest of the mountain should be kept clear of pines, and carefully monitored so that pines are not able to cross the gap here.

5.3.2 Method of eradication

The Mulanje environment shares several features with that of the Cape region, including vegetational and edaphic similarities, as well as a pattern of regular fire events. For this reason, I propose, it is legitimate to apply procedures for controlling aliens on Mt. Mulanje, that have been developed in the Cape fynbos. Moreover, some of these methods have been aimed specifically at serotinous pine invaders, which makes them ideal tools for dealing with *P. patula*.

A method that has been used with great success in the Cape is the fell-and-burn procedure (Kluge and Richardson 1983): (i) Adult and semi-adult trees are felled, following which their cones dry out, and release the seed, some of which is lost to predators and pathogens, and some of which germinates. (ii) 9-12 months later, a fire is sent through the recently felled area, killing all/ most of the newly-germinated seedlings present. (iii) A follow up operation is carried out, in which the vegetation is regularly monitored and any surviving seedlings are killed.

This eradication procedure, though fairly expensive, has seen rapid removal of serotinous aliens in large parts of the fynbos (Macdonald and Richardson 1986; Van Wilgen *et al.* 1992), and would probably be most effective on Mt. Mulanje. Edwards (1982) advocated a similar procedure for Mt. Mulanje, but his

recommendations were ostensibly never implemented. Edwards, however, recommended a period of 12-24 months before burning. Since it takes about five years for *P. patula* to develop its first mature cones, any period up to about four or five years is acceptable. However, some benefits of burning sooner are (i) that the fuel load is minimised (thus preventing hot, destructive fires), and (ii) that the seedlings are smaller and, therefore, killed more easily.

Monitoring of the vegetation following the initial felling and burning procedures, is of paramount importance if the elimination of the invader is to be permanent. In addition, the eradication needs to be thorough: even isolated individuals should not be ignored. Observations at the L3, T2 and S1 sites show that even single tree may give rise to entire pine stands. Moreover, at T2 it was found that pines along a gradient of decreasing tree density, showed increased levels of cone maturity and increased mean stem circumference (Fig. 11), a pattern almost certainly due to competition. These data suggest that isolated individuals may frequently be the most successful individuals, being able to grow larger and produce more offspring in the absence of competing trees.

Other possible eradication procedures, besides the fell-and-burn method, do exist (see Van Wilgen *et al.* 1992), but these are often less efficient. They include:

- (i) Felling only. For success, this method must be thoroughly executed, both in time and in space. A felling programme seems to be in operation on Mt. Mulanje at present (evidence of recent felling at various places), but this has been sporadic and inconsistent, and, as a result, highly ineffective.
- (ii) Burn-and-fell. This method, recommended by Sakai (1989a), involves the stimulation of seed release and germination through fire, followed by felling of the resulting seedlings. One of its problems is that dead, standing trees (from the initial burn) make subsequent eradication of seedlings difficult. Another is that the initial burn may not kill all the adults/ semi-adults present, because these may be fire-tolerant, and because fires may be patchy.
- (iii) Burning only. For success, this technique requires the vegetation to be burnt two or more times in close succession. Besides the inefficiency of fires at killing the pine, a serious problem with this procedure is the potentially damaging effect of closely successive fires on the indigenous vegetation.

(iv) Biological control. This method would require more research to identify a suitable control agent, a costly process, both in terms of money and time. Despite a host of potential control agents (see Wormald 1975), biological control is also problematic because of the commercial importance of *P. patula* in Malawi.

In terms of overall cost and efficiency, I believe the fell-and-burn technique, presents the best solution for the eradication of *P. patula* from large parts of Mt. Mulanje. Moreover, the method is relatively benevolent to the indigenous vegetation. However, Richardson and Van Wilgen (1986b), have pointed out that felled trees, when burnt, may produce large amounts of heat that penetrate the soil beneath them, damaging rootstocks and subterranean storage organs. This damage depends on the intensity of the fire, and needs to be minimised by managers. Fire intensity is strongly dependent on the fuel load at the time of burning. It is therefore urgent that an eradication programme be implemented as soon as possible, before pine infested areas become even more densely invaded, thereby raising fuel loads beyond current levels.

5.3.3 Costs of eradication

Here, I present a crude estimated budget for the eradication of the pine by the fell-and-burn method.

The current study estimates that around 36 000 young pine trees need to be eradicated on Mt. Mulanje (excluding those outside the study area and in the Sombani plantation). Assuming, a single worker armed with a hand-saw or an axe is able to fell about 20 trees in a day, and is paid a daily wage of K16, this translates into a total felling cost of just under K30 000 (1806 man-days). For various reasons I believe this figure is an over-estimate: (i) the estimated number of invaders is possibly a slight over-estimate, (ii) in many areas, pines are so small and densely packed that a good worker should be able to fell up to 150 plants in a day, and (iii) a daily wage of K15 is relatively high, compared with the earnings of porters and wood-runners in the area, and considering the levels of unemployment in the area (Agnew and Stubbs 1972). In addition, the use of mechanical equipment such as

chain-saws may greatly increase the number of trees a man can fell in a day, thus reducing the overall number of man-days needed, although this may create a range of other problems.

In addition to the basic felling operation other costs will need to be considered, including the cost of destroying the Sombani plantation, the cost of a controlled burn to follow the felling operation, the costs of monitoring the vegetation after the burn, and general administration costs. The total cost of the eradication programme may therefore amount to more than K50 000. This expense needs to be balanced against the longer term value of the mountain as a source of tourist income, and as a natural area of considerable scientific and aesthetic value.

If the implementation of a full eradication programme is deemed economically impossible, then it will be necessary to identify priority areas for clearing, as it is better to clear fewer areas thoroughly, than to cover more area less thoroughly.

5.4 Suggestions for further research

Given the widespread planting of *P. patula* as a timber crop, particularly in Africa, as well as the invasive potential of this species, there is scope for further work to be done on this species. This work should aim specifically to identify/ refine measures to control this alien if and when it becomes a pest, as it has on Mt. Mulanje. A detailed understanding of the interaction between the pine and fire is the most obvious gap in our knowledge. Questions that require more thorough answers than are presently available include:

- How is fire survival of trees related to their age, and to fire intensity, and to what extent is this a function of bark development?
- To what extent is seed release in *Pinus patula* triggered by fire?
- How successfully does the pine recruit in the absence of fire, particularly in grasslands?

These questions, and others, are of importance for the practical management of the pine, and although in some cases tentative data are available, thorough answers are not. In most cases the questions being addressed are complex, and their answers influenced by a range of factors.

6. CONCLUSION

The pine invasion on Mt. Mulanje is clearly serious, and if the mountain is to be maintained in its present state, then the pine will need to be brought under control and eliminated, as soon as possible. The cost of eradication may be considerable, but the costs of no eradication may, ultimately, be even greater. Delaying the implementation of a full eradication programme only causes the pine problem to increase, so that, correspondingly, the costs of control also rise. There is thus an urgent need for control measures.

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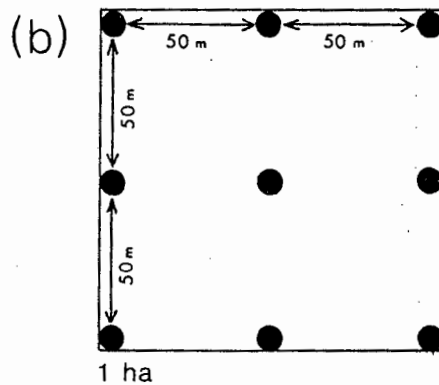
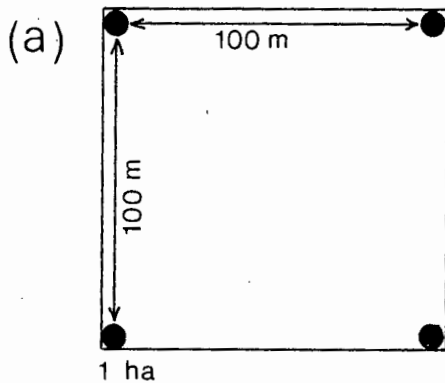
APPENDIX 1. Tree density conversion procedures.

During sampling, pine tree densities were recorded as estimated average inter-tree densities, as this was the easiest and fastest method, and the only workable method given the severe time constraints. In order to convert these into more conventional trees-per-unit-area values, the following procedure was applied.

The procedure assumes that trees were arranged in a regular, square matrix, viz:

+ + +
+ + +
+ + +

Thus, an inter-tree distance of 100 m produces a value of 4 trees per hectare (below, a), while an inter-tree distance of 50 m produces a value of 9 trees per hectare (below, b).



Continuing this method, the following table is obtained.

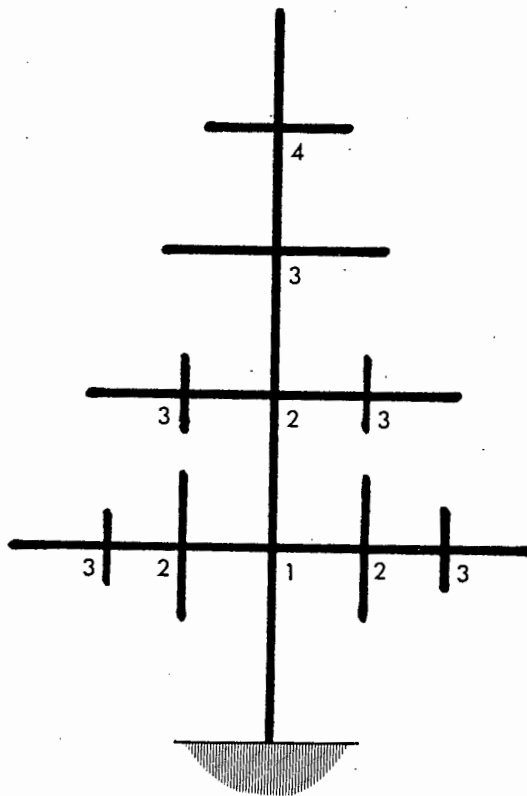
| Inter-tree distance (m) | No. of trees per ha. |
|-------------------------|----------------------|
| 100 | 4 |
| 50 | 9 |
| 25 | 25 |
| 10 | 121 |
| 5 | 441 |

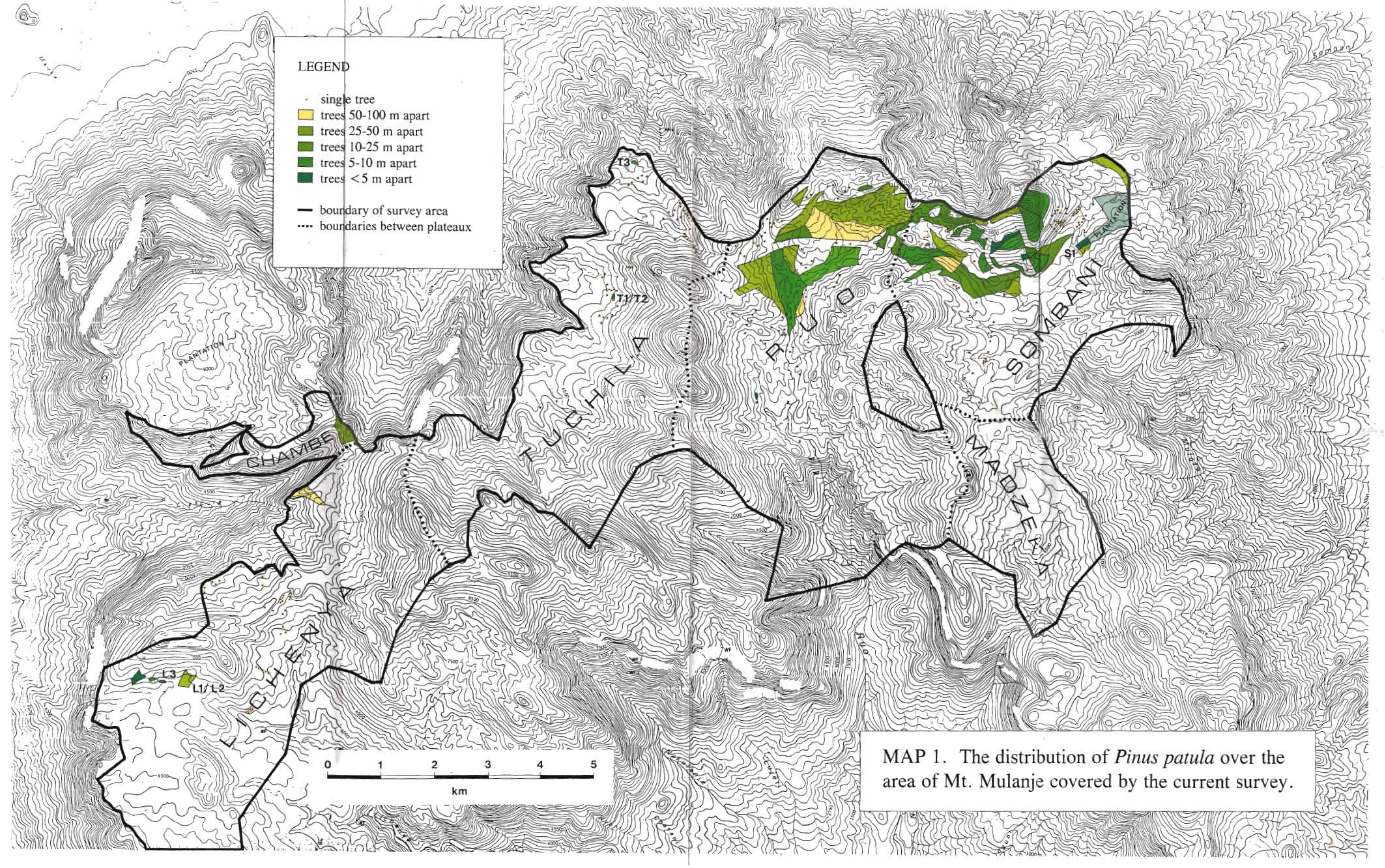
Although this method of conversion is crude and its assumptions somewhat unrealistic, the crudeness of the initial sampling procedure did not warrant the application of a more accurate conversion procedure. This crude methodology may, admittedly, lead to inaccuracies in absolute density values. However, patterns in relative tree density between one part of the survey area and another remain fully valid.

Each of the density rankings used in the initial sampling procedure is associated with a range/ interval of inter-tree distances (e.g. density ranking 2 = 50-100 m between trees). However, the conversion procedure required that each ranking be associated with a single inter-tree distance value. Because initial sampling probably overestimated actual tree densities, it was decided to consider only the maximum inter-tree distance associated with each density ranking (e.g. density ranking 2 = 100 m between trees; Table 2), to partially correct for this.

APPENDIX 2. Whorl counting procedure.

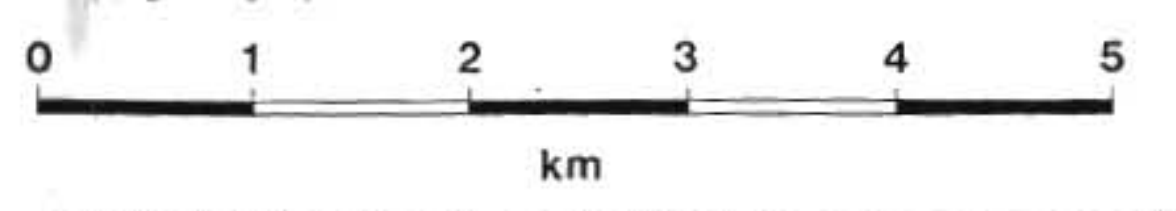
Whorls on pine trees were counted as depicted in the diagram below, starting at the base of the tree and moving upwards and outwards. Thus, cones situated at any of the whorls marked with a '2' would be regarded to be positioned at the second whorl. This counting procedure most accurately reflects the growth pattern of pines, in which new growth takes the form of whorl addition at the apices.





LEGEND

- single tree
- trees 50-100 m apart
- trees 25-50 m apart
- trees 10-25 m apart
- trees 5-10 m apart
- trees <5 m apart
- boundary of survey area
- ⋯ boundaries between plateaux



MAP 1. The distribution of *Pinus patula* over the area of Mt. Mulanje covered by the current survey.