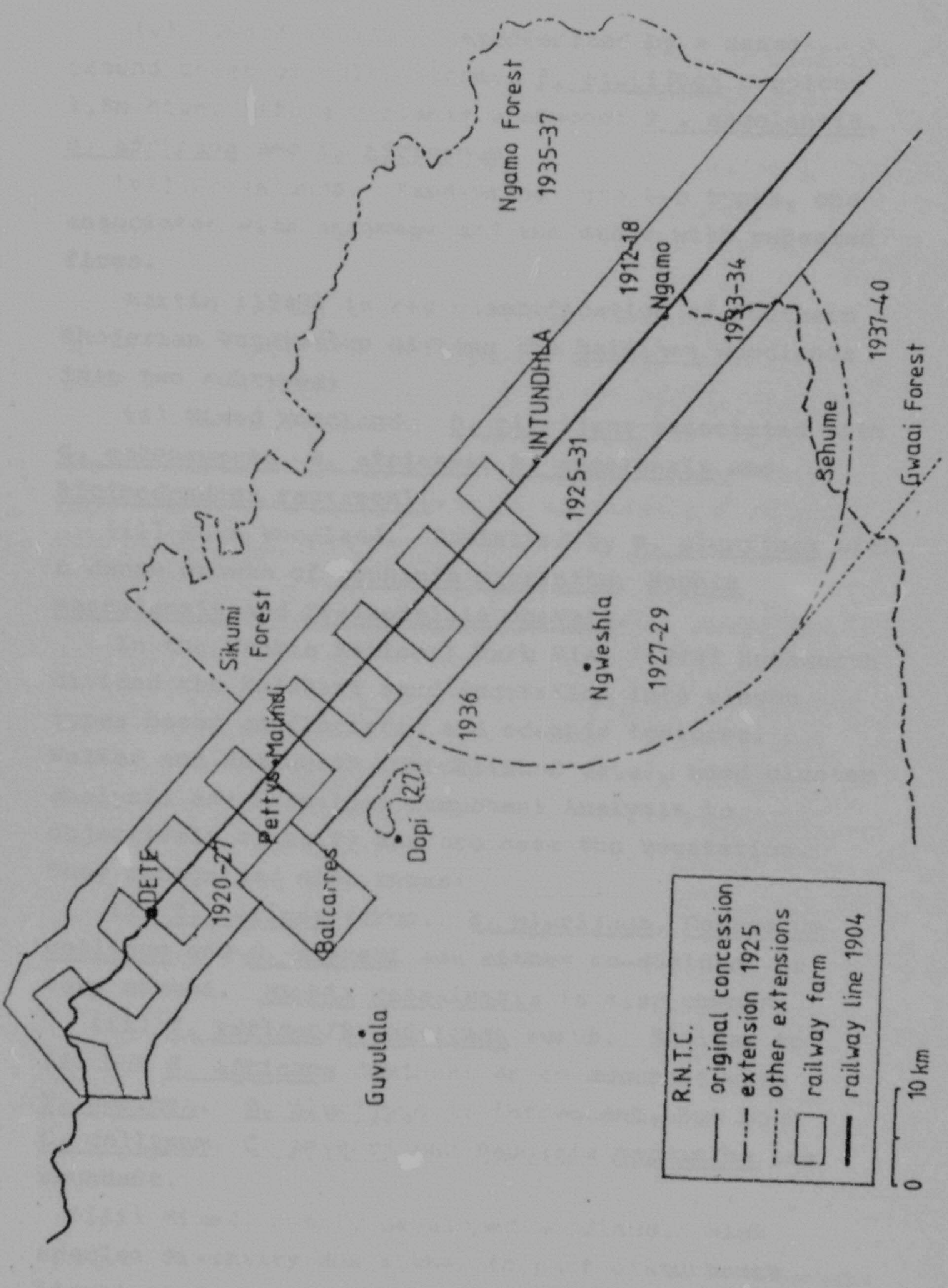

Fig. 3.1. Map of Forestry concessions in Hwange National Park and adjacent areas. By kind permission of the Forestry Commission.

(v) 'Dwarf Teak'. Characterised by a dense ground cover of multi-stemmed B. plurijuga coppice, 1,5m high, with a variable overwood: P . angolensis, B. africana and E. africanum.

(vi) Grasslands. Subdivided into two types, one associated with drainage and the other with repeated fires.

Martin (1940) in his classification of Southern Rhodesian Vegetation divides the Baikiaea woodlands into two subtypes:

(i) Mixed Woodland. B. plurijuga associated with G. coleosperma, B. africana, P. angolensis and Ricinodendron rautanenii.

(ii) Pure Woodland. Dominated by B. plurijuga with a dense growth of Bauhinia macrantha, Baphia massaiensis and Freisodelsia obovata.

In the Wankie National Park Plan (1974) Rushworth divided the Kalahari sand vegetation into eleven types based on floristic and edaphic features. Walker and Rushworth (unpublished data), used cluster analysis and Principal Component Analysis to objectively classify and ordinate the vegetation. They recognised nine types:

(i) T. sericea scrub. B. plurijuga, Combretum collinum and C. zeyheri are either co-dominant or very common. Baphia massaiensis is also common.

(ii) T. sericea/B. africana scrub. Similar to (i) but B. africana dominant or co-dominant with T. sericea. B. plurijuga is infrequent, but both C. collinum, C. zeyheri and Bauhinia macrantha are abundant.

(iii) Mixed, poorly developed woodland. High species diversity due either to part disturbance (logging), or a slight increase in the impermeability of the soil, caused by an increase in clay content or the presence of a hard layer of sand. Major species include Baikiaea plurijuga, Burkea africana,

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E. africanum, T. sericea and Brachystegia spiciformis with occasional Acacia erioloba and Lonchocarpus nelsii.

Baphia massaiensis, C. collinum, C. zeyheri, C. celastroides, C. apiculatum, Dichrostachys cinerea and Lannea discolor are found in the shrub layer.

(iv) Mixed, well developed woodland, dominated by B. plurijuga and G. coleosperma with lesser amounts of E. africanum, B. africana and T. sericea.

(v) Sparsely wooded, open vegetation. The presence of a calcrete layer and increase in clay content causes the soils to be seasonally flooded. Combretum hereroense is the main tree. Typical pan vegetation.

(vi) Colophospermum mopane woodland. Found in areas where the clay content is up to 35% - often in the B horizon. This type is found in the troughs between the ridges in the south west of the Park.

(vii) Mature Baikiaea woodland. Well developed undisturbed woodland on deep sands. The woodland has a closed canopy dominated by B. plurijuga. It is divided into two groups according to the percentage coarse and fine sand:

A. >10-40% coarse sand supports almost pure B. plurijuga in the tree layer, with B. massaiensis and Croton pseudopulchellus as the major shrubs.

B. <10% coarse sand has a few other tree species, especially L. nelsii, with Croton gratissimus as an addition to the shrub layer.

(viii) Mixed mature woodland. Occurs on soils which are very compacted or have a higher % clay than (vii). Dominants are L. nelsii, B. plurijuga and A. erioloba with a wide variety of species in the understorey. A. erioloba dominates when this vegetation fringes drainage lines.

(ix) Terminalia prunioides/Acacia tortilis woodland. A more extreme variation of (viii) on very hard soils. Commiphora africana and C. pyracanthioides are found in the shrub layer.

3.2.3 Succession

Henkel (1931) considered the 'umgusu' (Baikiaea) type to be the north west equivalent of the 'msasa' (Brachystegia) the pure type occupying a restricted area because of the invasion of the miombo components. He suggested the following changes. The 'muhatja' (Parinari) type was dominant at one time on the Kalahari Sands. This was displaced by the umgusu type, originating in north west Central Africa. In turn this umgusu type is being displaced by species entering from the east: msasa and mfuti (Brachystegia boehmii).

3.2.3.1 Edaphic Influences

Miller (1938) commented on the influences affecting the Mukusi Forests of Bechuanaland. He found Burkea africana growing in regions where the sand was too shallow for B. plurijuga. B. africana was occasionally found in association with B. plurijuga, for like T. sericea, it is a colonizer of badly burnt forest. Where it occupied large areas in pure stands or associated with P. angolensis, it was on partially denuded lines of drainage. There was heavy grass cover in the Burkea areas, and both B. africana and P. angolensis are fire resistant. The soils were found to be more compacted, dark grey and more acid than mukusi soils. Tinley (1976, 1982) emphasised the role of pan horizons in controlling the soil hydrology and therefore the type of vegetation. He defined two classes of pan horizons for the Kalahari Sands in the Western Caprivi:

(a) An indurated/cemented type e.g. calcrete, ferricrete.

(b) A compact sand or clay type formed in duplex sands (the former type) or from illuviated humic gleys (the latter).

The pan horizons may be undulating, inclined or horizontal and of varying thickness according to their genesis. The distribution of these impermeable horizons does not necessarily follow the present day surface undulations. The distance of the horizon from the surface can play a fundamental part in the soil moisture balance, affecting the amount of saturation possible and the degree of water loss. This controls the spatial separation of plants and ratio of grasses to woody species (Walter, 1971). Where there are gley layers or fine compacted sands the vegetation becomes noticeably denser than that on the surrounding deep horizonless sands. Examples are the Acacia erioloba woodland patches in the Central Kalahari and the Baikiaea thicket in Caprivi (Tinley, 1976).

Walker and Rushworth's ordination results showed two major gradients affecting the vegetation: succession and edaphic. The successional gradient accounted for 19% of the variance, with stages moving through open mixed scrub to mixed woodland, to stands of pure B. plurijuga. No comment was made as to the role of animals in the succession.

The edaphic gradient (13% of the variance) was based on the proportion of sand, silt and clay in the soil. Because of the distinct boundaries of the soil types, the gradient was not continuous. Examples of the two extremes of soil type (and vegetation) can be seen growing in close proximity in the dune areas (Fig. 3.2). The gradient was from deep, coarse, grained sands through sands with an increasing clay content and the presence of a hard layer, to the extreme of almost pure clay found in the troughs and depressions.

Fig. 3.2. *Baikiaea plurijuga* and *Colophospermum mopane* growing in close proximity, indicating the abrupt soil changes in the dunes. Basha Pan, Hwange National Park.

3.2.3.2 Biotic Influences: Fire and Animals

Early travellers in Matabeleland commented on the fires which ravaged the areas during the dry months. Sim's report (1911) on forestry to the B.S.A. Company stated 'a large percentage of the trees have been damaged by fires which almost annually go through them'. Kelly-Edwards'annual report in 1925 listed the following causes of fires in the Kalahari Sand Forests:

(i) Superstition and traditional practices of the local people, e.g. burning to appease rain gods and to provide grazing.

(ii) Hunters were very careless, and two culprits Lundin and Herbst used to boast about how many fires they started in the Ngamo area.

(iii) Sparks from the trains on the Victoria Falls line.

(iv) Farmers burnt to improve grazing and had no fire control measures.

(v) Lightning strikes during dry electric storms.

Boughey (1963) presented two hypothetical successional schemes for Kalahari Sand vegetation in Wankie, showing the main trends from (1) Teak (Baikiaea) Woodland and (2) Mixed Savanna Woodland both ending in a fire climax grass savanna (see Fig. 3.3). He considered elephant and fire damage the two major ecological factors operating in the system. He also thought that most of the vegetation was composed of secondary communities which 'were much more suitable for game occupation'. Each secondary community was associated with a particular game species.

In his report on the vegetation of the Shesheke District in Zambia, Fanshawe (1965) describes a series of stages in the degradation of Baikiaea forest through the action of fire:

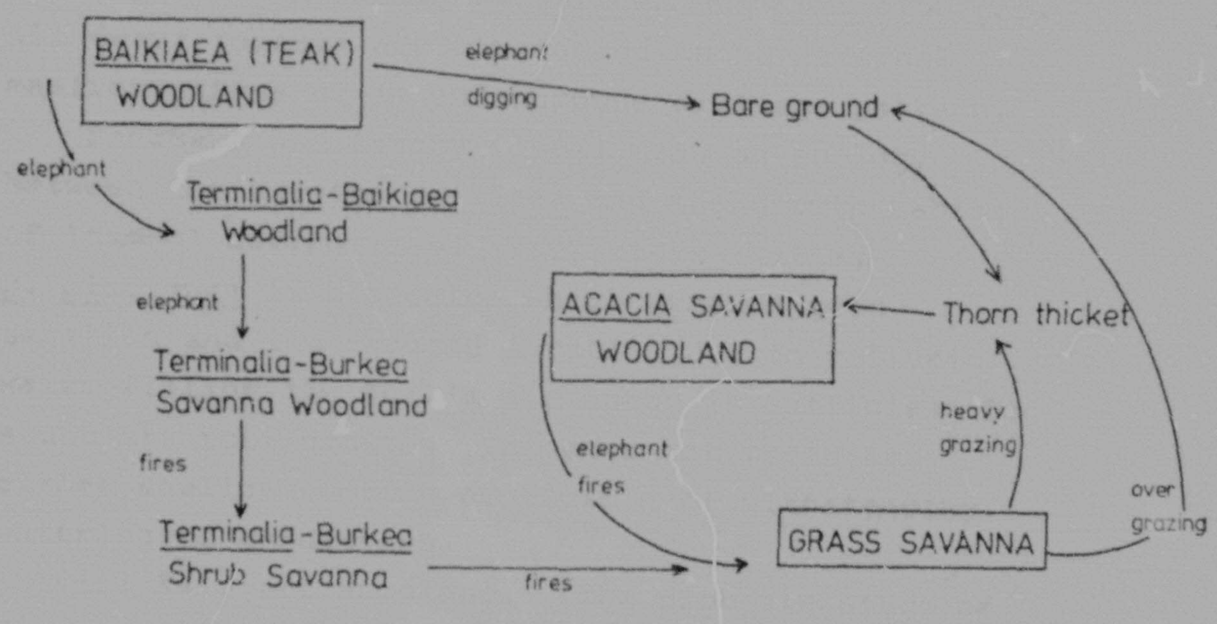

Fig. 3.3. Boughey's (1963) hypothesis for the derivation of various secondary communities from *Baikiaea* woodland.

(i) *Baikiaea* Forest. A closed canopy of approximately 18m tall *B. plurijuga*. The understorey is a *Baphia* - *Bauhinia* - *Combretum* - *Dalbergia* complex. *Acacia fleckii* and *A. ataxacantha* invade the fire holes and *Baphia massaiensis*, *Bauhinia macrantha* and *Croton pseudopulchellus* tend to dominate with further fire degradation. *Baikiaea* forest has a variant termed 'dwarf' *Baikiaea*, which is literally *Baikiaea* forest compressed to 1,5m height. Occasional emergents grow up to 3m - mostly *T. sericea* and *Combretum spp*. All dwarf forests are considered to be external manifestations of an underground drainage pattern.

Fanshawe and Savory (1964) draw an analogy between the stunted *Baikiaea* and the growth habits of 'dambo' suffrutices. They state that as *B. plurijuga* is a species which demands good aeration and the reduced aeration due to telluric water filling the soil's air space is sufficient to stunt its root growth. The emergent trees are either shallow rooting or capable of withstanding waterlogged conditions.

(ii) Kalahari Woodland. (The probable stage of Hwange Kalahari Sand vegetation). There has been a decrease in *B. plurijuga* (fire sensitive) and an invasion of fire hardy species.

(a) *Burkea* - *Guibourtia* - *Erythrophleum* woodland, with or without *Baikiaea*. *P. angolensis*, *R. rautanenii* and *Dialium englerum* can be locally common.

(b) *Burkea* and *Erythrophleum* dominate. Very open woodland, around 6m high. *P. angolensis* can replace *E. africanum*. Shrubs are *Combretum spp*. *Ochna pulchra*, *Diplorhynchus condylocarpon*, *B. massaiensis*, *B. macrantha* and *Grewia spp*. *Baikiaea* and *Guibourtia* are lost being fire sensitive.

(c) Burkea - Diplorynchus Scrub. 1,5m to 3m high. Open with subshrubs of Brackenridgea arenaria, O. pulchra and Annona stenophylla.

(d) Suffrutex Savanna. The final regression stage. Suffrutices are interspersed with perennial grasses and bulbous herbs. Lannea edulis, Pygmaeothamnus zeyheri, Ochna sp. are examples. The interesting point about Fanshawe's proposed succession is that it ends in a suffrutex savanna and not a grassland, as Boughey suggested.

Miller (1938) suggested that areas in Botswana (Bechuanaland) where B. plurijuga and T. sericea occurred together were probably the result of fire damage to the original Baikiaea forest. With its more prolific seeding and wider range of dispersal, T. sericea would take advantage of the cleared ground. It would eventually disappear in the secondary succession as it has a more light demanding habit.

Mitchell (1961) attempted to relate the effects of fire and animals on the vegetation, giving a somewhat controversial explanation as to the disappearance of the Teak forests in Zambia. He felt that the drastic reduction in game numbers by modern hunting methods was responsible for the increased fire hazard and therefore the destruction of the forests. While this may have applied to Zambia, Hwange never contained as much game as it does at present, so Mitchell's hypothesis is untenable.

3.2.3.3 Climatic Influence: Frost

Process of Frost Formation

Law (1969) states that although frost can be caused by advection and evaporation, radiation was the most important source of frost in this country. The amount of water vapour in the air, wind, cloud cover and land surface have a marked effect on the degree of frosting. Radiation frost is more frequent in the drier western parts of Zimbabwe which are in close proximity to the Botswana 'Dry Air'.

Severe Frosts

A severe 'black' frost occurs when a critical minimum is reached (usually taken as $\leqslant -6,5^{\circ}C$ or $20,0^{\circ}F$), when the cell protoplasm is fatally injured by (a) precipitation of proteins or (b) formation of intercellular ice which draws water out of the protoplasm or (c) disruption of cell organelles by the formation of ice crystals in the protoplasm (Daubenmire, 1967). The degree of frost injury depends on the duration of the minimum temperatures, the suddenness of change, the plant's physiological condition and adaptational characteristics e.g. waxy bloom, hairs.

Frost Hardiness

A temporary adaptation giving a plant a measure of immunity is called frost hardening. The process is complex and not well understood. In many plants it is closely tied to the effects of photoperiod and dormancy. This primary induction is followed by a requirement for growth or survival at reduced temperatures (Bidwell, 1979). Several inter-related physiological changes take place:

(a) The protoplasm develops low structural viscosity and is able to better accommodate deformation.

(b) The free water content decreases and soluble proteins and sugars increase. Both changes are pronounced in aerial organs. The importance of abundant carbohydrate is shown by the fact that defoliation renders a plant more susceptible to cold injury (Daubenmire, 1967).

Rushworth (1978) is the only author to consider frost a major modifier of vegetation composition in the scrub areas. He lists the pioneers Acacia fleckii, Terminalia sericea and Ochna pulchra as frost hardy, while Baikiaea plurijuga, Pterocarpus angolensis, and Combretum zeyheri shrubs are easily damaged by severe frosts. Frost has a similar effect to fire, killing stems up to 3m tall. This results in stem coppicing or the production of many even-sized stems from a single root stock. He draws attention to the fact that frost can have a moulding effect on scrub, altering both composition and physiognomy.

CHAPTER 4. VEGETATION PHYSIOGNOMY, GROWTH AND MORTALITY

4.1 INTRODUCTION

Since the life cycles of many plants are very complex it is necessary to simplify some aspects in order to deduce the general principles. In analysing and modelling complex systems the choice of relevant variables is crucial (Solbrig, 1980). Three approaches can be identified based on the principal variable studied: energetic, genetic and demographic. The last approach is based on the changes over time in numbers of individuals in a population. Its apparent simplicity is complicated by the fact that plants have variable and indeterminate growth (plasticity) which often invalidates life table data based on age. The second problem is that of vegetative reproduction. Clone forming or coppicing species create a dilemma as to the definition of an individual, and compound the determination of a life span for a plant (Abrahamson, 1980). Also, in coppiced vegetation, the age of the above ground regrowth may not be the age of the underground structures (Harper, 1977).

The ability to regenerate from underground structures is common in African, Australian and South American savannas which have evolved under the selective pressures of extensive fires and periodic droughts. Many _Eucalyptus sp_. are capable of producing ligno-tubers which are specialised structures that develop under annual recurring drought and frequent burning. Other species of eucalyptus produce rhizomes which form networks of underground stems, giving rise to dense clonal patches of even aged aerial stems (Lacey, _et. al._, 1982). These clumps of regenerating stems closely resemble those of the local _Guibourtia coleosperma_, _Baikiaea plurijuga_, _Diplorhynchus condylocarpon_ and

Pseudolachnostylis maprouneifolia. Cryptophytic or 'subterranean' trees and specialised woody structures known as xylopodia are also found in the Brazilian 'cerrado' (Coutinho, 1982). The former are well adapted to frequent burning with most of the woody component being protected underground.

Most of the work on plant demography has been concerned with genetically distinct plants (genets) and concentrated on temperate or boreal trees that can be successfully aged using growth rings (White, 1980). In tropical and sub-tropical systems the classic approach using life table data is often inappropriate since most sub-tropical and tropical trees do not accumulate clearly decipherable annual increments (Tomlinson and Craighead, 1972). A possible exception are palm trees (Sarukhan, 1980).

Age and size are often poorly correlated, and a population of trees may develop towards a characteristic size structure irrespective of its age structure (Harper, 1977). For this reason age is often a poor predictor of reproductive activity, especially in dense mono-specific stands (Sarukhan, 1980). White (1980) stressed the degree to which numbers and size are inter-twined in plant population biology. de Liocourt (undated in Harper, 1977) found that the quotients between numbers of trees in successive diameter classes remained essentially constant over the range of diameters found in any large forests.

Population distributions measured at one point in time only show the structure of survivors: past births minus past deaths. It is impossible to determine how much mortality has occurred in the past history of the population and a number of assumptions have to be made about past recruitment and mortality. The interpretation of forest structure usually looks forward to what it is becoming i.e. towards some equilibrium state or climax. Harper (1977) suggested that a historical interpretation is more realistic and can give valuable insights into successional events.

The objectives of this chapter were to:

(a) establish the size structures of populations of the six species: Baikiaea plurijuga, Guibourtia coleosperma, Burkea africana, Erythrophleum africanum, Terminalia sericea and Ochna pulchra in examples of the two main physiognomic types of vegetation - woodland and scrub.

(b) Obtain estimates of the growth rate and mortality of each species. A detailed long term monitoring of growth and mortality rates was not possible in the time available for this study.

4.2 METHODS

4.2.1 Vegetation Size Structure and Composition

Stands of vegetation were located at random in previously selected vegetation types. Stands were 50 x 50m in scrub and 100 x 100m in woodland, areas that were considered by Walker and Rushworth (1974, unpubl.) to be the most suitable sample size. In dense vegetation the 100 x 100m stand was subdivided into four 50 x 50m plots. The vegetation was sampled in areas known to have been disturbed by logging (see Section 3.2.1), and in an area too remote for any large scale human disturbance (see Figs. 3.1 and 4.1). Three woodland and two scrub areas were measured (see Table 4.1 and Fig. 3.1 for detail). In each stand the above ground circumference, measured just above the buttress swelling, and the underground circumference, measured just below the swelling (Fig. 4.2), were recorded for each individual of

Fig. 4.1. Dry season Baikiaea plurijuga woodland near Mitswiri Pan, Hwange National Park. The mature undisturbed woodland was one of the main study sites.

TABLE 4.1. Stands Sampled for Vegetation Structure, Composition and Damage Assessments

Stand	Location	Community	Size (m)
Mitswiri 2	±4km S of Mitswiri Pan	*Baikiaea* Forest	100 x 100
Umtchibi	±6km N o Umtchibi Camp	Disturbed *Baikiaea* Woodland	100 x 100
Dopi	2km NE of Dopi Pan	Disturbed *Baikiaea* Woodland	100 x 100
Sinanga	1km S of Sinanga Pan	Mixed species scrub	50 x 50
Shakwanki	±1,5km E of Shakwanki Seep	*Terminalia* scrub	50 x 50

the six selected species. Below ground circumferences were included as this overcomes the problem of finding a uniform method for comparing large trees and coppiced shrubs. A coppice may have an extensive underground stock and only a few small aerial stems. When a coppiced plant was encountered, three representative stems were measured. After measuring, each plant was marked with chalk to prevent duplications. A list of other woody plants, forbs and grasses was drawn up, together with notes on soil colour and texture. Modifications were made to an existing computer programme (Walker, 1976) to analyse the data.

4.2.2 Growth Rates

Circumference changes were monitored for all six species. Trees were selected for a healthy uniform appearance from a wide range of life stages and size classes. On each tree one end of a length of 1,5cm wide, weather resistant, non-stretch tape was nailed into the trunk. Tapes were positioned 20-50cm above the ground. Allowance for growth was made by cutting the tape approximately 10cm greater than the trunk's circumference. The tape was drawn tight and a small scalpel cut made to mark the original circumference (see Fig. 4.3). The changes in circumference were recorded by again tightening the tape, making another mark, and using calipers to measure the difference. With seedlings and small stems that would be damaged by nails, a line of enamel paint was used as a marker for the position of re-measurement. Circumference changes were recorded mid rains and mid dry season for two years.

Additional information on growth rate, germination and seedling survivorship was made