BRANCHING PATTERNS OF THE TROPICAL HARDWOOD *Triplochiton scleroxylon* K. Schum, WITH SPECIAL REFERENCE TO THE SELECTION OF SUPERIOR CLONES AT AN EARLY AGE

BY

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FRONTISPIECE

Triplochiton scleroxylon K.schum.

(Aged about 40 years and girth at breast height about 1.5 metres).

DECLARATION

I hereby declare that this thesis has been composed by me and that the work of which it is a record is my own except where acknowledged to the contrary.

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D. O. LADIPO

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GLOSSARY

Apical dominance - The process whereby the shoot apex inhibits development of axillary buds on shoots formed in the current season.

Apical control - The process by which shoot apices maintain a control over the previous year's branches.

Abscission Index - Index (%) of the level of natural branch shedding.

Branch - Lateral shoot usually arising from an axillary bud.

Bud activity - The percentage of the axillary buds which are growing at any time following removal of the apex by decapitation.

Clone - A group of vegetatively propagated plants, originating from a single seedling, they are genetically identical.

Correlative Inhibition - The physiological process imposing apical dominance.

Cyclophysis - Effect of the age of source of cutting on the rooting or growth behaviour of vegetative propagules.

Decapitation - The removal of the apex of a plant.

Dominance reassertion - The phase following bud release; when bud activity is gradually being suppressed.

Hypostomatous - Distribution of stomata on only one side of a leaf.

Ortet - The original seedling source of clonal plants.

Progeny (half-sib) - Family of seedlings/clones originating from the same mother tree. (Source of pollen not known).

Progeny (full-sib) - Family of seedlings/clones originating from the same female and male plants.

Proleptic branch - Branch developed following the removal of correlative inhibition.

Ramet - The unit, (single representative) of a clone.

Sylleptic branch - Branches developed without a prior phase of correlative inhibition.

Topophysis - Effect of the original position of cutting on tree or ortet on its subsequent rooting or growth behaviour.

Tree form - Growth habit of a tree.

Tree Rose - Diagramatic representation of tree form.

ABSTRACT

Triplochiton scleroxylon K. schum., is a tropical tree, whose timber 'Obeche' until recently maintained an important position in West African forestry and in world timber trade. Heavy exploitation has resulted in its extensive reduction in the natural forest and an erosion of its natural genepool.

Studies of its form, branching and the physiological basis of its form development (apical dominance) were carried out on clonal materials in the tropical glasshouse in Edinburgh and in the nursery in Nigeria.

It was postulated that the form of the mature tree might be predicted from a study of apical dominance at a very early stage of growth. To measure apical dominance the plant apex was excised and the growth of lateral shoots was recorded. After trials in a range of conditions it was possible to specify standard conditions for the 'decapitation test' and hence, to measure the intensity of apical dominance of many clones.

Methods for assessing trees in plantations were initially developed using *Betula pubescens* a 7-year old planting of which happened to be available near Edinburgh. These methods were subsequently applied to 4-year old clonal plantings of *T. scleroxylon* in Nigeria. Substantial clonal variation was revealed in growth characteristics and particularly in branching habit. In addition, undesirable characteristics such as forking and multiple-stemming were found to be more frequent in some clones. The importance of such intra-specific variation was discussed in relation to selection for improvement.

Correlations between the results of the decapitation test and the field performance of the corresponding clones revealed a close relationship ($r \doteq +0.76$, $P \doteq 0.001$) between maximum bud activity in juvenile clones and branching habit at 4 years under narrow spacings. The importance of this relationship in the prediction of branching and yield in an improvement programme is stressed and fully discussed.

Further studies in *T. scleroxylon* showed that growth and apical dominance varied between two half-sib populations from dry (savannah) and wet (high forest) origins. In full-sib progenies (produced by controlled crosses at Edinburgh) appreciable variation was shown in the intensity of apical dominance and the occurrence of activity in cotyledonary nodes. The importance of the latter characteristic in selection within seedlings was stressed.

Some *T. scleroxylon* clones and progenies were shown to respond differently to site conditions, this being as a result of soil and rainfall distribution.

Substantial clonal variation was found in rates of photosynthesis, respiration, and the resistance components to CO_2 and H_2O. However, no relationship was evident between these parameters and clonal performances in the field.

CHAPTER 1

1. INTRODUCTION

1.1 State of the World's Tropical Moist Forests

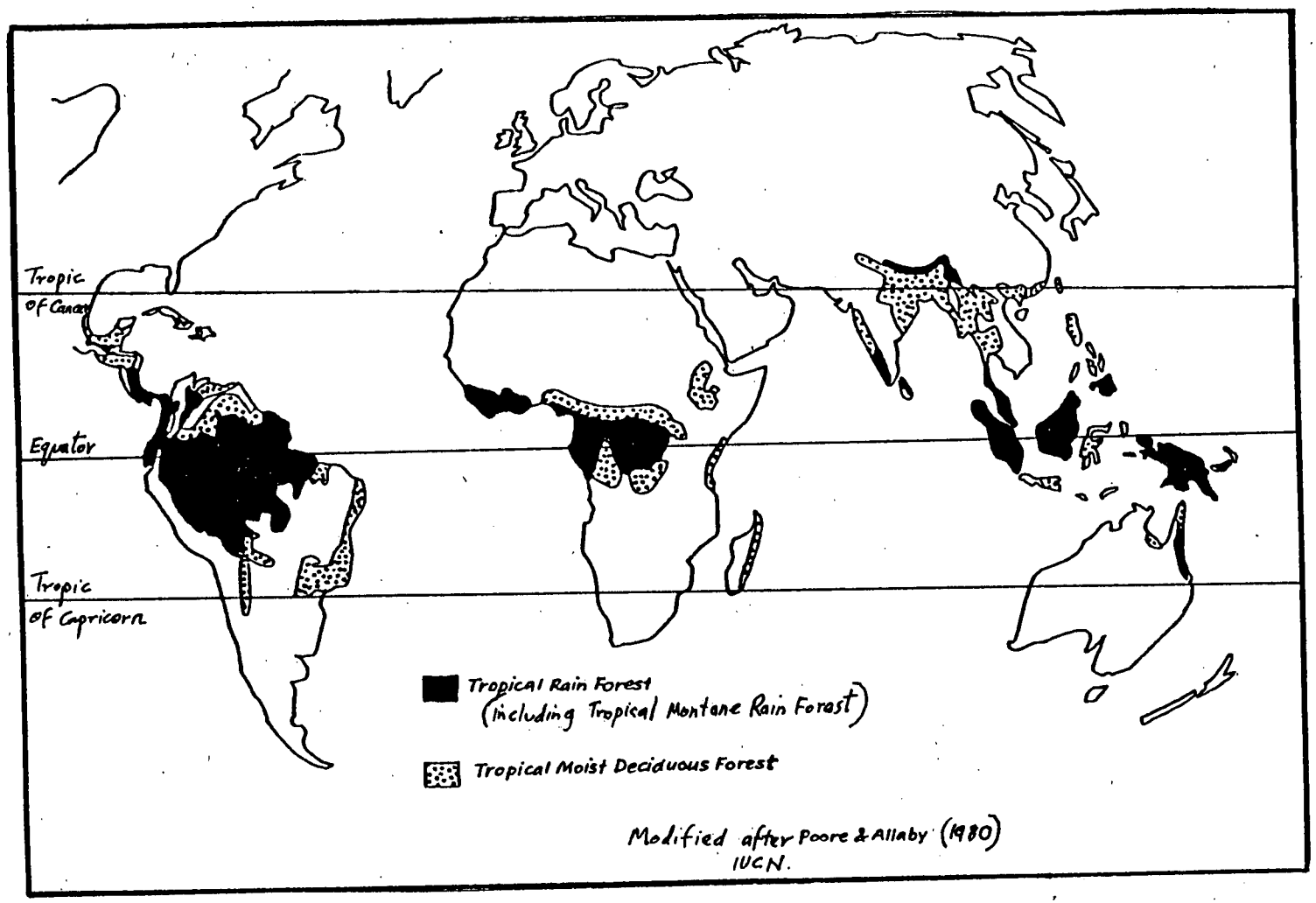
The world's tropical moist forests lie mostly between the tropics of cancer and capricorn (23.5 ^{o} North and South of the equator). They are comprised of two general forest types viz: the tropical rain forest and the tropical moist deciduous forest, and they extend into South America; the Central American Isthmus; South-East Asia, its islands; and East, West and Central Africa, (Fig. 1). They are probably the most complex and diverse terrestrial ecosystem known, and also contain the greatest concentration of species on earth.

In 1976, the area of the tropical moist forests was estimated at about 935 million hectares, which is about 71 % of the world's total area of closed tropical forest and 30 % of all the forests in the world (Grainger, 1980). As is well recognised, the tropical forests represent a considerable resource for timber and a wide range of other products; yet through exploitation and destruction, this is currently being eroded at a rate of about 50 hectares per minute (15 million hectares per annum). Although it is potentially a renewable resource, not enough re-afforestation is being done to halt, let alone reverse this situation (Persson, 1974; Spears, 1979; Myers, 1980). In addition to the destruction of the tropical ecosystem and some of the constituent species, this loss has important consequences, such as :

i) Global heat balance

The replacement of one vegetation type with another, particularly when on such an extensive scale may lead to changes in the energy and water balance of the landscape, which could lead to climatic change

Fig. 1



The Distribution of the worlds Moist Tropical Forests.

(Potter *et al*, 1975). This could happen as a result of differences in the characteristics of the vegetation in relation to albedo (forest absorbing much more solar energy than short vegetation), and in relation to inherent differences in the surface resistance to water vapour transfer. Whereas these characteristics are to some extent understood, their overall influence on regional and global climates is a more complex matter on which there is at present no consensus.

ii) CO_2 and oxygen balance

There has been much speculation as to the role of the world's forests in maintaining atmospheric equilibrium (Stewart 1978). The increase in CO_2 which has occured over the last two hundred years is largely attributable to the combustion of fossil fuels, although the picture is less clear when the role of the oceans as a CO_2-sink is considered. The role of the world's forests must be considered in relation to the activity of any substituted vegetation, which may differ substantially from that of forest. This subject is an area of active research at present, in which there is no general agreement.

and iii) Poor soils

Removal of forest cover exposes soils to erosion by water (Spears 1979), and to other deleterious effects such as leaching and laterization. In many cases the nutrient reserves of tropical forests are locked in the biomass while the soils remain relatively impoverished. Destruction of the forests leads to rapid release of nutrients, many of which are lost from the ecosystem.

Many of the points raised above, of course have important socio-economic consequences (Poore 1976) in addition to their effects on flora and fauna (Harrison, 1968).

In the West African moist tropical forests, which was one of world's major sources of tropical hardwoods, over half a century of trade, mainly with Europe, has seen its forests logged up to 4 times as much as the establishment of new plantations. A surprising feature of the planting history to date is that indigenous species have rarely been used (Grainger 1980).

Clearance for agriculture (shifting cultivation - Myers, 1980), mining, highway construction, the use of fire as a tool for hunting game and intensive logging have contributed to the rapid decline of forest lands. These, as well as selective tree felling have resulted in :

(i) Reduced floristic composition, as forests are degraded by preventing natural recovery.

(ii) Depletion of the natural genepool of important forest species, and

(iii) The permanent destruction of forests for roads etc.

FAO in (1979) reported an increase from 4.2 to 53.3 million m^{-3}, from 1950 to 1973 in timber export from tropical West Africa. As this trend continues, for example in Nigeria, (which still depends on the natural forests for almost all of its total production of timber), Bamgbala and Oguntala (1973) reported in Akure Forest Reserve, an area which lies in the heart of the moist tropical forest belt and which was earlier reported as highly productive (Richards 1939), a great fall in the frequency of ecnomic trees (18 trees per hectare) of the species: *Nesogordonia papaverifera, Sterculia rhinopetala, Celtis* spp, *Pterygota bequaertii, Mansonia altissima* and *Triplochiton scleroxylon*. This agrees with similar studies of the worlds tropical forests (Sommer 1976), and emphasises the need for strict conservation measures of natural forests, and the replacement of the exhausted ones with economically viable plantations from improved indigenous species,

(Jones 1975; Howland *et al*, 1978) rather than with unimproved stocks in compensatory plantations, which are known to be less economically viable. The need for this was further emphasised by Spears (1980) who reported that by 2025 AD the worlds timber demand will be 300 million m^3 $annum^{-1}$ which can be satisfied only by a 3-fold increase in current annual planting programmes. If this requirement is met, the pressure on the remaining natural forests will be considerably reduced.

The present study with *Triplochiton scleroxylon* is part of a programme to encourage the use of indigenous hardwoods in plantation forestry in the tropics, the work on *T. scleroxylon* being a model for the subsequent work on other indeginous species (Leakey *et al*, in press). It is envisaged that Nigerian forestry of the future will be based largely on such plantations which will be stocked with improved genotypes, probably in the form of clonal mixtures. Such a policy of planting should relieve pressure on the wild forest, which will remain as a natural genepool.

1.2 *Triplochiton scleroxylon* K. schum

1.2.1 Status

T. scleroxylon K.schum (Sterculiaceae) is an important forest species of West Africa. Its timber 'obeche' (African Whitewood) is a light hardwood with a specific gravity of 0.42 for mature trees (Omolodun, 1975), and generally has good mechanical and physical properties (Kinloch and Miller, 1949).

Uses of 'obeche' include: plywood (Okigbo 1964), interior joinery and panelling, utility furniture, boat building, match splints (Howland and Bowen 1977) and various other minor uses. As a result of its versatility of use, this species has been very

important commercially. In Nigeria, 'obeche' accounted for 22 % of the total timber exported in 1945, this rising to 60 % in 1970 (Howland and Bowen 1977), while in Ghana, it represented about 50 % of logs and 20 % of sawn timber exported in 1966 (Jones 1970). A similar situation exists in the Ivory Coast and Cameroon, the other main producers of this timber. Hall and Bada (1979) described this species as accounting for more of the timber volume extracted annually from West Africa, than any other single species.

1.2.2 Ecology and Distribution

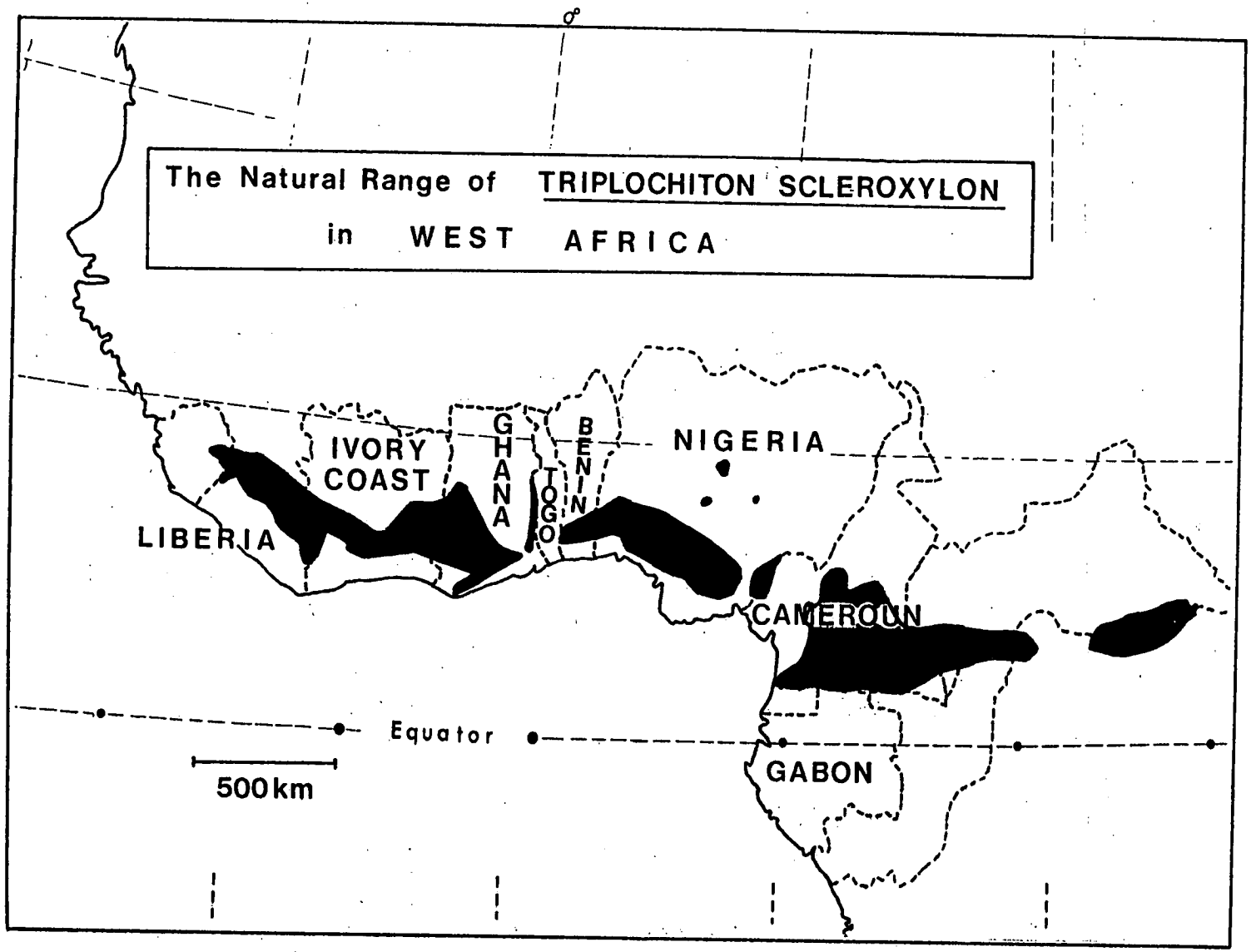
T. scleroxylon is an emergent tree of the moist tropical forests of West Africa (Taylor 1960), prefering areas with an annual rainfall of 1000 - 1400 mm, and being absent from wetter areas (3200 - 4000 mm) and on wet soils (Foster 1914, Kennedy 1936, Voorhoeve 1965).

Although Hall and Bada (1979) associated this species with the pre-cambrian rocks of the basement complex, over 35 % occur on younger soils in Nigeria, where apart from its distribution over the West African lowlands, it has also been reported at 800 metres altitude. Jones (1975) observed this species to be more plentiful in the Owo area in Nigeria, but eastwards in Nigeria after the River Niger, its distribution is reported to become sparse. Cousens (1946) attributed this to intensive human interference for agriculture and subsequent soil instability.

Within its range, 3 sections are recognised; the moist forest between (a) Sierra Leone to Togo, (b) Republic de Benin to Nigeria, and (c) from Cameroon to Zaire, separated by the Dahomey gap and the Cameroon highlands respectively. (Fig. 2).

At maturity, this relatively fast growing species attains 50 metres in height and a diameter of up to 2 metres (see Frontispiece),

Fig. 2


The Natural Range of TRIPLOCHITON SCLEROXYLON
in WEST AFRICA
LIBERIA
IVORY COAST
GHANA
TOGO
BENIN
NIGERIA
CAMEROUN
GABON
Equator
500km

with occasionally much larger specimens. The boles of large trees are usually buttressed, free of branches for a large percentage of their height due to self pruning. Now it is usually difficult to find sizeable and very well formed trees, as a result of, as earlier indicated, selective felling of good trees over the years. Undesirable characteristics commonly found include non-cylindrical boles which are often angular and heavily ridged or fluted (Jones 1969, 1970), multiple-stemmed trees, forked or with heavy (large diameter) branches, (Howland and Bowen 1977).

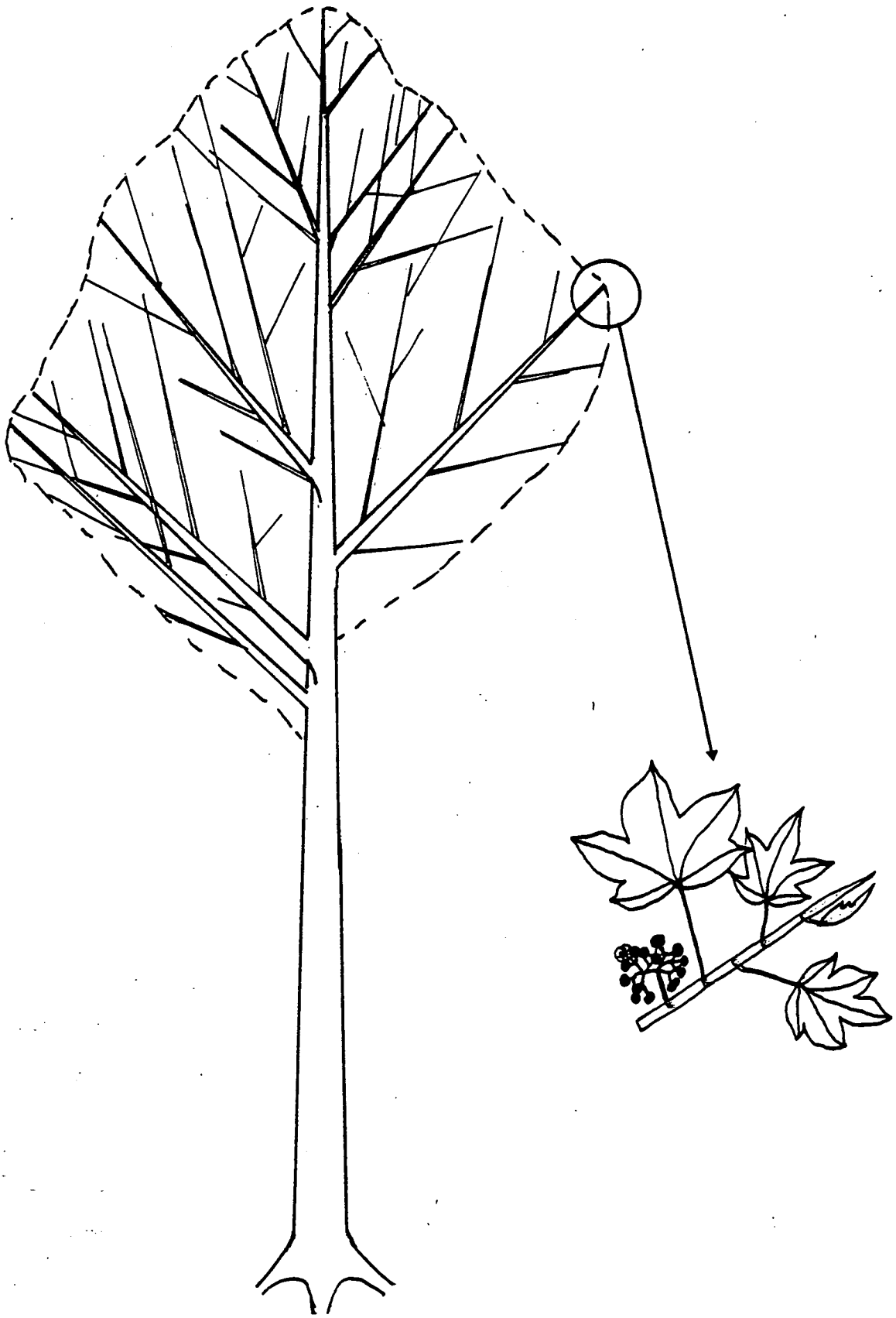
1.2.3 Branching habit of *T. scleroxylon*

The form of a tree, and hence its usefulness, is the result of its branching pattern, which is one of the most conspicuous features of woody plants (Pickett and Kempf, 1980). The branching habit of *T. scleroxylon* has been classified along with Ash (*Flaxinus* spp), Birch (*Betula* spp) and many other temperate trees, as following Rauh's model (Halle *et al*, 1978). Articulate and rythmic growth of the monopodial trunk leads to the development of a shoot system with branch tiers alternately arranged on it in indistinctive whorls, (Fig.3). Leaves (usually 5 to 7 lobed) are arranged radially on main stem and in a distichous pattern on its branches, and flowers borne by specialised short shoots, dichotomously branched, develop laterally from axillary buds, and lasting only the reproductive season or less, after which they are abscinded, thus not interfering with the growth of the shoot system. Jones (1969) reported a large variation in crown shapes in this species, varying between cylindrical to spherical. However in young trees, blunt cones are typical, although a wide variation exists.

1.2.4 The Plantation potential of *T. scleroxylon*

The rise in world demand for tropical hardwoods (Springle 1979)

Fig. 3



A diagram of the habit of a good sample of *T. scleroxylon* of about 15 years old, in closed cover, showing branching characteristics.

and the internal needs for building and fuel timbers cannot be met by the supplies from natural forests which are already severely depleted. It is clear therefore that there is an urgent need for the establishment of more forest plantations which are more productive than natural forests(Fig. 4 and Dyson, 1965; Johnson 1976; Odeyinde 1980). As indicated earlier, Spears (1980) estimates that planting rates need to be increased by 300 % to meet this challenge. *T. scleroxylon* like many other indigenous hardwoods throughout the Tropics has been rarely planted commercially because of lack of sufficient planting stock. For example at present, only 1 % of Nigeria's forest land is under man-made forest cover (Oseni 1980), and no commercial plantation of *T. scleroxylon* of appreciable size exists, although the potential of this species as a plantation crop has long been recognised (Unwin 1920; McGregor 1934; Lowe 1973; Ball 1975; Leakey *et al*, in press). Previous attempts at plantation establishment of *T. scleroxylon* have been of various types, such as :

(i) Enrichment planting by seedling transplant or seed broadcasting, after opening the canopy to provide light (Kennedy 1936).

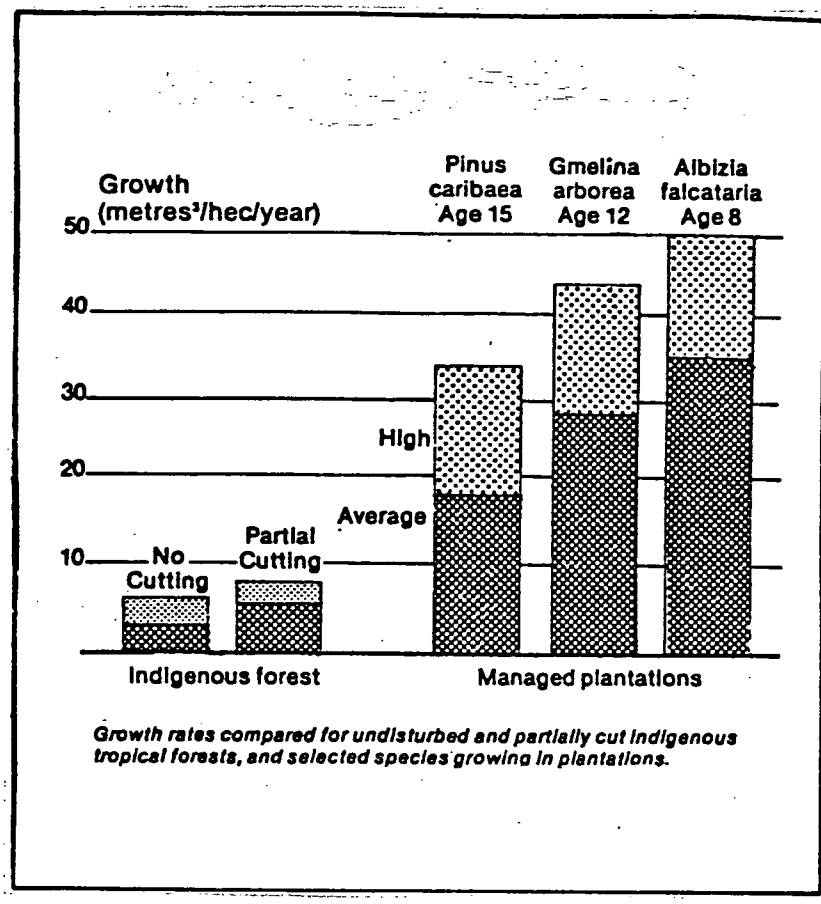
(ii) Taungya planting, where farmers clear forests and have responsibility for planting trees while intercropping for 3 years as the trees become established, (Kennedy, 1935).

(iii) Open plantations, in which trees alone are planted on cleared sites.

All three methods have been relatively successful, but have not been practiced on a large scale because of lack of sufficient seed samples.

The earliest plantations were established at Olokemeji Forest

Fig. 4



A comparison of forest productivity between indigenous (natural) and planted tropical forests. (Johnson 1976).

Reserve in 1915 (Unwin 1920), 1927 and 1933 (McGregor 1934). At Sapoba Forest Reserve in 1930 and 1933 (Kennedy 1933; McKay 1953), Ona Forest Reserve in 1948, Gambari Forest Reserve, which was the largest (13.5 ha) in 1951 and 1952, the Iduanwa stands planted in 1951, 1952 and 1954, Mamu Forest site, 1959, Omo Forest Reserve in 1961, and Ona Forest Reserve in 1963. Since 1969, experimental plantings have been made at Gambari, Sapoba, Ikom, Bende, Ore and Ibadan (Howland and Bowen 1977), as part of the West African Hardwood Improvement Project (WAHIP) of the Forestry Research Institute of Nigeria (FRIN).

1.3 The West African Hardwood Improvement Project

T. scleroxylon resources have been markedly reduced, as with other native hardwoods (Howland and Bowen 1977).

The realisation in 1970 that the quality and quantity of these species had been seriously eroded, prompted a proposal by the Nigerian Government to the U.K. Overseas Development Adminstration for a collaborative scheme for Research and Development of the indigenous hardwood species of West Africa. As a result, the West African Hardwood Improvement Project started at the Forestry Research Institute of Nigeria in 1971, and later in 1974, a sister project was established in Scotland at the Institute of Terrestrial Ecology near Edinburgh. The joint aims of these two projects were to conserve and improve the remaining resources of these West African hardwoods with particular emphasis at first on *T. scleroxylon*.

Early investigations included:

(i) The study of *T. scleroxylon* distribution and its phenology over West Africa and Nigeria in particular (Jones 1975).

(ii) Seed procurement (Odukwe and Ezunma 1975).

(iii) Viability, storage and germination studies of seeds (Olatoye 1968; Jones 1975; Bowen and Jones 1975).

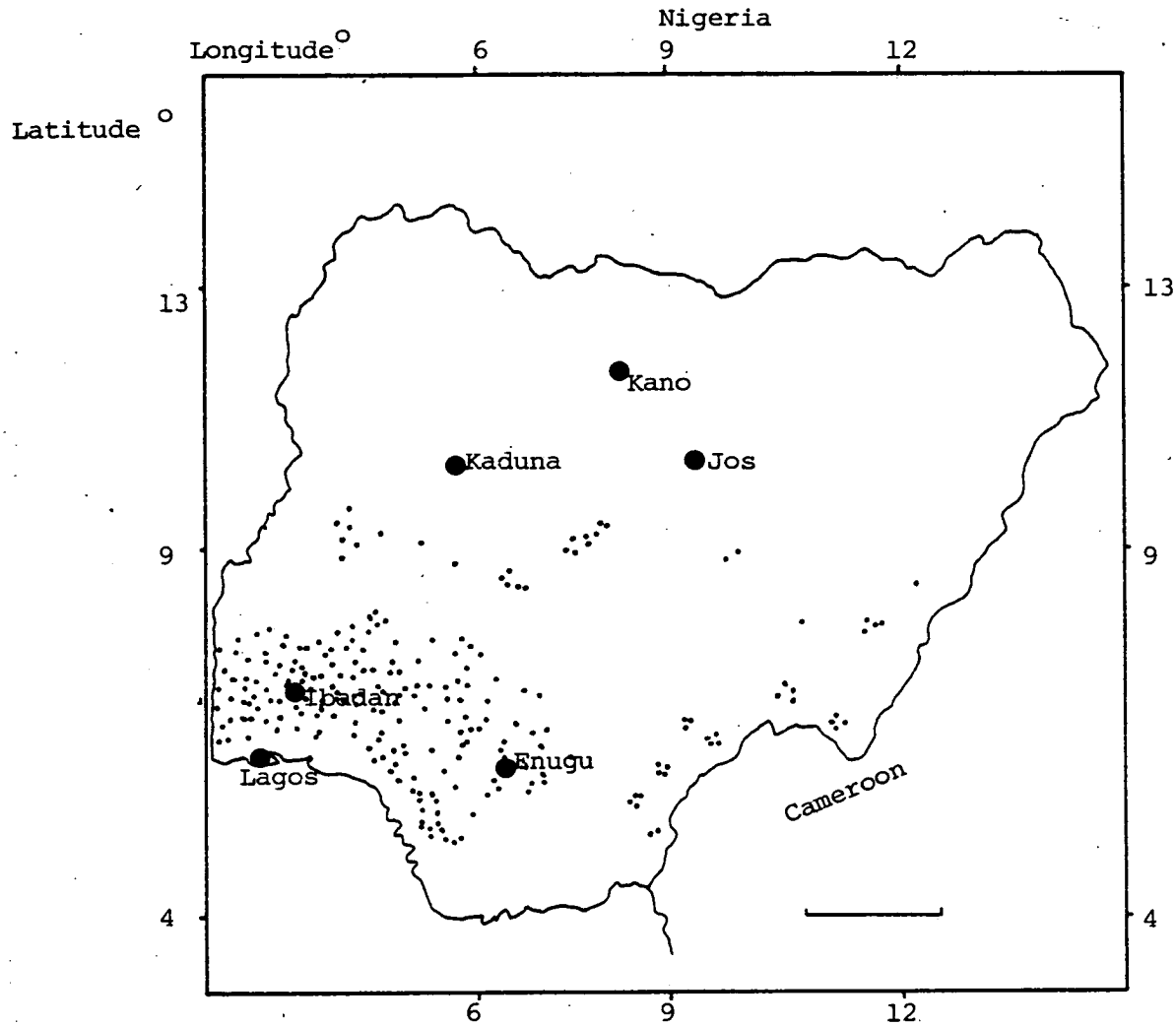
These were supplemented by studies of entomological and pathological problems, including seed boring by *Apion ghanaense* (Ashiru 1975), smut infestations of developing seeds by *Mycosyrinx nonveillei* (Odeyinde 1975) and

(iv) The development of a viable and economic method for vegetative propagation (Howland 1975, a, b, c, Leakey *et al*, 1975).

The use of vegetative propagation, which had earlier been thought to be very difficult (Okoro 1974), subsequently became the key to the project's successes, providing regular supplies of clonal planting stock. More recently, more fundamental studies of the factors influencing root initiation have been made (Leakey *et al*, in press) including the effects of manipulating stock plants to maximise the production of easily rooted cuttings. (Leakey, in press). With the development of methods for initiating roots on stem cuttings, over 250,000 plants have been propagated and planted in gene banks and field trials since 1975. These substantial plantings represent the diversity of this species over a major part of its natural range and more intensively within Nigeria. (Fig. 5).

In addition to providing ex-situ conservation stands of this species, these plantings provide excellent experimental material for preliminary determination of those characteristics of growth and form which contribute significantly to yield. It is, in large part, this determination which is the purpose of both the present thesis and the clonal plantations established in 1975 and 1976 (Howland and Bowen 1977). Other early results from these plantations indicate that there are as expected substantial differences within and between seed-

Fig. 5



Distribution of mother-plant sources of clonal materials in Experiments at Onigambari Field Station and other sites (1975-1979).

lots (Howland *et al*, 1978; Ladipo *et al*, in press). However no appreciable differences have been found between the growth of seedlings and cuttings (Howland and Bowen 1977; Ladipo, in press), and the latter also reported no long-term effect of topophysis, cyclophysis and harvest time on the field growth of *T. scleroxylon* cuttings.

Awareness over the last two decades has increased the need to develop lines of selected hardwoods for seed-orchards, research purposes, and general planting (Kormanic and Brown 1974). Vegetative propagation, in the form of budding and grafting (Ikekhuamen 1966; Britwum 1970; Howland 1975), as an additional approach to the tree improvement of *T. scleroxylon* has allowed candidate plus trees to be propagated successfully and established as seed orchards and materials for flowering experiments. So far, these, coupled with work in Edinburgh, have illustrated that the species is self-sterile, but that viable seeds can be produced by cross pollination (Howland and Bowen 1977; Leakey *et al*, 1981). Potentially important progress is also being made with precocious genotypes of juvenile *T. scleroxylon* in the determination of factors affecting floral initiation and general reproductive biology (Leakey *et al*, 1981).

The stage has therefore been reached where *T. scleroxylon* could be grown commercially as soon as superior clones can be identified and multiplied.

1.4 GENERAL AIMS

The aim of the work described in this thesis was to develop a new method for selecting superior clones on the basis of their branching habit, as early indications were that this might determine not only form but probably also yield (Ladipo *et al*, in press). The fundamental hypothesis under examination is whether the branching habit of trees in plantations can be predicted from a study of apical dominance in small potted plants.

This hypothesis is based on the finding that the tallest and most valuable trees in field experiments at Gambari - Nigeria have a particular branching habit, namely that they produce the fewest primary branches per unit of mainstem. Conversely, those clones with poor field performance have the greatest number of branches per unit of mainstem.

Branching processes in trees and plants generally are a function of apical dominance, and apical control, and it is probably significant that clones of *T. scleroxylon* have very considerable variation in apical dominance as expressed by their sprouting response following decapitation (Longman *et al*, 1979; Leakey and Longman, in Litt). The present study therefore further investigates the extent of genetic variation in *T. scleroxylon*, the environmental factors influencing its expression and attempts to relate apical dominance to branching habit. A detailed statement of the approach adopted is given at the end of the next chapter, following the review of subject matter considered to be relevant - namely : The nature of branching in trees, the role of apical dominance in branching and the current ideas concerning the mechanism of apical dominance and the effect of environment on branching and apical dominance.

CHAPTER 2

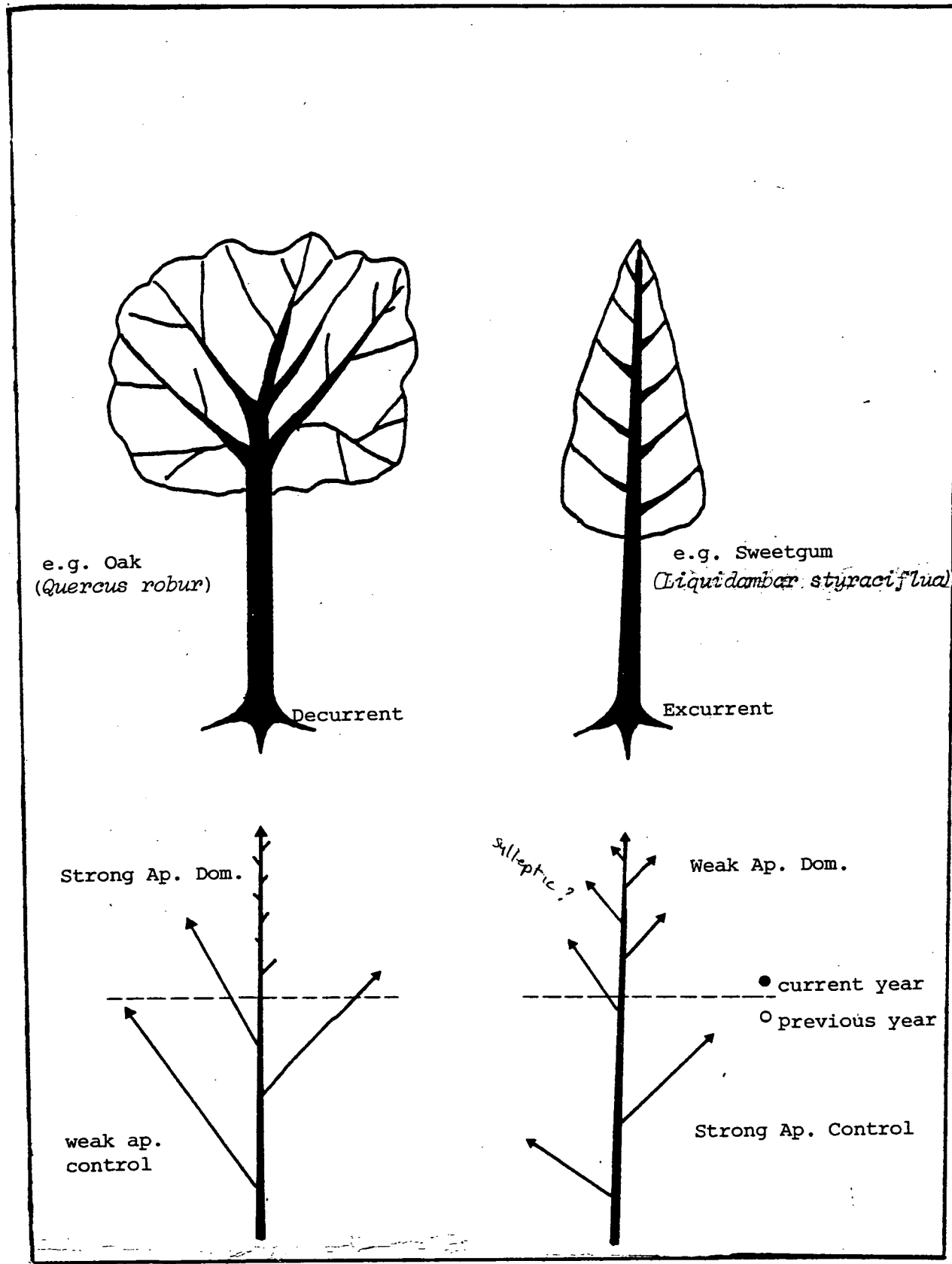
2.1 THE CONTROL OF BRANCHING IN TREES, AND THE THEORIES OF APICAL DOMINANCE

2.1 APICAL DOMINANCE: A review of Literature.

Plants grow in a co-ordinated manner, the growth of various tissues and organs being mutually correlated with each other. One such correlative association is the inhibition imposed by the terminal bud on axillary buds - this has been called 'correlative inhibition', and is the mechanism of apical dominance. The importance of this phenomenon in plants is easily illustrated by decapitation, which releases axillary buds from inhibition, allowing their growth. Subsequently it is usual for one lateral shoot to re-establish dominance over the others and in erect plants this is usually that from the uppermost node. Rather less attention has been paid to the study of apical dominance in perennial woody plants than in herbaceous species (Phillips 1969), because it is more complicated. However, Kozlowski (1964) has attempted to interpret the form of woody plants in terms of apical dominance; postulating that trees with decurrent branching either have weak or no apical dominance while trees with excurrent branching have strong apical dominance. Brown *et al*,(1967) subsequently refuted this and pointed out that in Oaks, hickories, and maples, inhibition and form was much more complex. He realised that the apical dominance as understood in herbaceous plants only occurred in shoots of the current growing season, and that this phenomenon appeared to be negatively correlated with what he termed 'apical control', the correlative effects of various shoots of the previous year's growth. Thus in Oak, Ash etc., there is strong apical dominance but weak apical control and so the crown is 'decurrent' (see Fig. 6). Conversely, where apical dominance is weak,'apical control' is strong and the crown is 'excurrent'.

A second factor of considerable importance in the determination

Fig. 6



The roles of apical dominance and apical control in the branching and crown development of some temperate hardwoods (*Quercus robur*, *Liquidambar styraciflua*).

of canopy structure and form in trees, is the type of the branch produced in the current season (sylleptic) and those produced the following season (Proleptic). In the majority of temperate trees, branching is proleptic but in tropical species, sylleptic branching is common. *T. scleroxylon* is basically a proleptic species, branches forming at the start of the growing season following their release from apical dominance by dormany of the terminal bud during the dry season. However, sylleptic branching can also occur.

2.2 Mechanism of Apical Dominance : Theories

Extensive literature exists on apical dominance in herbaceous plants and it is on this that physiologists have based their theories for this phenomena. (Guern and Usciati 1972; Phillips 1975). Since the early part of the century, 5 basic theories have been postulated, none of which have been completely accepted by all workers. However, a form of the Hormone Balance Theory, with auxins having some indirect effect on axillary bud initiation and other growth substances attracting nutrients (which do have important effects on correlative inhibition to the apex), have been most favoured.

A brief summary of the five theories is presented here as each contributes to the overall understanding of the phenomenon.

(i) Nutritive Theory

(ii) Direct auxin Inhibiting Theory

(iii) Indirect Auxin Inhibiting Theory

(iv) Nutrient Diversion Theory

(v) Hormone Balance Theory

2.3 The Nutritive Theory

This is the oldest theory, it being first proposed by Goebel (1900) who reported that the plant shoot apex inhibited axillary buds by

competing with them for a limited supply of nutrients. This was supported by the work of Loeb (1915; 1917 and 1918) on *Bryophyllum calcycinum*. Later, Dastal (1926) showed that the removal of leaf pairs from nodal segments of *Scrophularia nodosa* resulted in vigorous bud outgrowth. He therefore suggested that the leaf, by extracting nutrients and water from the stem, rendered them unavailable for bud outgrowth. In the 1930's this theory was superceded by others involving auxin inhibition, (see later) but more recently it has had a revival. In 1957, Gregory and Veale demonstrated that in *Linum usitatissimum* the degree of apical dominance depends on the nitrogen and carbohydrate supply of the plant and subsequently McIntyre (1964; 1965; 1968b; 1969; 1971b and 1972) similarly considered that competition for nutrients and water by the rhizome apex and axillary buds in *Agropyron repens* and other species is responsible for apical dominance.

2.4 The Direct Auxin Inhibition Theory

At about the same time the Nutritive Theory was receiving support, other workers were describing the diffusible nature of certain inhibitory substances in the stem tissues of plants. The best evidence arose from the work by Snow (1925) on *Phaseolus vulgaris*. He demonstrated that the diffusible inhibitory influence could pass across a water gap between adjacent stem tissues to suppress axillary bud outgrowth on a decapitated piece of stem. Snow (1937) further demonstrated with grafted *Phaseolus vulgaris*, that this inhibition was achieved with the presence of a diffusible substance from the growing apex. Subsequently Thimann and Skoog (1933; 1934) in decapitated *Vicia faba* demonstrated that agar blocks containing auxin could substitute for the shoot apex. This was later repeated in *Pisum sativum* (Thimann 1937).

Difficulties arose with this theory when Snow (1931) reported the involvement of acropetal movement of auxin which is generally considered to be basipetally translocated. Controversy also arose over the concentration of auxin necessary to substitute for the apex and its mode of action (Thimann and Skoog 1934; Thimann 1937; Libbert 1964; Hillman 1970). In particular, Sachs and Thimann (1964; 1967) and Panigrahi and Audus (1966) showed that auxin concentrations in the inhibited buds were sub-optimal rather than supra-optimal. They also demonstrated that cytokinin could initiate bud growth although continued growth was only possible when Indole-Acetic Acid (IAA) was added. These, with the results of Sêbanek (1966a; 1967) showed that when low concentrations of auxin were applied to the cut stumps of decapitated plants, lateral bud outgrowth was promoted while only high concentrations inhibited it. Thus it became clear that auxin *per se* could not be the inhibitor.

2.5 Indirect Auxin Inhibition Theory

As a result of his data in opposition to the Direct Auxin Inhibition Theory, Snow (1937) established the theory of indirect auxin inhibition; where he suggested that auxin as it passes through the stem stimulates in it, a secondary inhibiting influence which can travel in a non-polar way. Various workers have tried to establish the identify of this inhibitor; Fletcher and Zalik (1964, 1965) suggested that in *Phaseolus vulgaris*, red light converts IAA to Indol-3yl-aldehyde, while Arney and Mitchell (1969) working with *P. satiurm* suggested that abscisic acid (ABA) might be this substance. This suggestion has also been taken up by Ingersoll and Smith (1971) who demonstrated that it is readily transported acropetally. Tucker and Mansfield (1972, 1973) working with *Xanthium straumarium* extracted ABA from buds under strong apical dominance following irradiation

with far-red light treatments. Similar effects have also been reported for tomato (Tucker 1976), but this is not yet generally confirmed by other workers. Indeed, no evidence of this mechanism was found in, for example, rhizomes of *Agropyron repens* (Leakey, 1975), and the occurrence of ABA in these correlatively inhibited buds may be a result of the irradiation treatments.

2.6 The Nutrient Diversion Theory

Having accepted that Direct Inhibition by auxin was unlikely and that inhibition by a secondary substance was also dubious, several workers tried to amalgamate the auxin theories with the role of nutrients and formulated the Nutrient Diversion Theory. Until recently, this has been about the most popular explanation for apical dominance in plants, and arose from the suggestion by Went (1936) that nutrients are attracted to locations of highest auxin concentration. Nakamura (1964), Hussain and Link (1967 and Wakhloo (1970) working with *Pisum satiurm* and *Solanum sisymbrifolium* showed that the patterns of P^{32} translocation was closely related to growth of lateral buds following decapitation, and their release from inhibition. This is also supported by the work of Moreland (1934) with *Phaseolus vulgaris* in which he noted within 48 hours of removing the stem apex, that the vascular supply to the buds had been strengthened. The notion that differentiation of vascular system is important has also been supported to some extent by Sorokin and Thimann (1964), Sachs and Thimann (1967 and Sachs (1969, 1970), but differences in their results as regards the presence of vascular connection between buds and stem, may be attributed to genetic differences in plant species, although it can also be seen as contrary evidence. For example, in *Coleus* and Soyabean, the vascular bundles are differentiated even before apical dominance is broken by decapitation (Clowes 1960; Alli and Fletcher 1970). Evidence contrary

to the Nutrient Diversion Theory came from Goodwin and Cansfield (1967) who found that correlatively inhibited, non-dormant, lateral buds in potato tubers were not induced to grow by direct introduction of nutrient solution containing Cytokinin, auxin and gibberellin to the inhibited buds, although the same solution did support the growth of similar but isolated buds. Similarly, Panigrahi and Audus (1966) found that applying Uracil-2-^{14}C to the Cotyledons of *Vicia faba* seedlings did not affect the distribution of radio-activity in the decapitated or IAA-treated stems. They thus concluded that diversion of nutrients towards the bud apices played no significant part in correlative inhibition. Further evidence against the theory came from the findings that in *Populus robusta* (Davies and Wareing 1965) and in *P. sativum* (Sebanek 1966a; 1967) high concentration of IAA inhibited the growth of axillary buds not by attracting nutrients but rather by some 'toxic effect'.

2.7 The Hormone Balance Theory

The first indication that other plant regulators (e.g. Cytokinin) might be involved in apical dominance resulted from the findings that, when cultured on cytokinin-rich medium, tobacco tissue exhibited weak apical dominance (Skoog and Miller 1957). This was then supported by the demonstration that the inhibiting action of auxin can be antagonised by ethylene in Pea (Wickson and Thimann 1958). Other growth regulators known to influence apical dominance are abscisic acid (White and Mansfield 1977; Sêbanek 1973) Ethylene, (Hillman and Yeang 1979; Yeang and Hillman 1981) and Gibberellin (Ruddard and Pharis 1966; Pharis, *et. al.* 1970), with some interactions, as between auxin and gibberellin (Scot *et al*, 1967; Phillips 1969; 1971; Sebanek 1972) and Gibberellin with Cytokinin (Sebanek and Obhlidalova 1975).

The Hormone Balance Tehory arose from studies by Shein and Jackson (1971; 1972) and Jackson and Field (1972) following applications of Gibberellic acid (GA_3), Kinetin and IAA under different conditions and the observation that altering any of the combinations had different effects which indicated a wide range of interracting influences partly endogenous and partly environmental. Field and Jackson (1974) further substantiated their theory with evidence from 2, 3, 5 - Triodobenzoic acid (TIBA), GA_3 and Kinetin applications to decapitated and un-decapitated *Phaseolus vulgaris*. The theory is further supported by Tomaszewski (1970) who demonstrated a synergistic effect of GA_3 on IAA in maintaining apical dominance in *Pinus sylvestris*.

From the above review, it is clear that the controversy over the mechanism of the phenomena of apical dominance is far from being over. Its overall role in the habit, branching or form of plants is however generally accepted.

2.8 Effects of Environmental Factors in Apical Dominance

In recent years, a wide range of environmental factors have been found to affect apical dominance in a considerable number of species. The following factors have been considered :-

(i) Light intensity, quality and photoperiod.

(ii) Temperature

(iii) Relative humidity and water stress

(iv) Inorganic Nutrients

(v) Gravity, and

(vi) Carbon dioxide.

2.8.1 Light intensity, quality and photoperiod

It is frequently reported that low light intensity enhances apical dominance. (Gregory and Veale 1957); Thimann, *et al* (1971); Shein

and Jackson 1971; McIntyre 1973; Field and Jackson 1974) presumably through its effects on carbohydrate status. By contrast, light quality effects seem to be specific phytochrome responses for example in *Xanthium strumarium* (Tucker and Mansfield 1972), *Apropyron repens* (Leakey *et al* 1978) and in tomato (Tucker 1979) where far-red light increased apical dominance substantially. In several instances, light effects such as these have interacted with hormone applications (Tucker and Mansfield 1972), and this often interacting with warm temperatures. Gregory and Veale (1957) also demonstrated in flax that apical dominance with restricted nitrogen supply was independent of light intensity, showing that photoassimilate availability is of less importance than inorganic nutrient supply. Piringer and Cathey (1960) reported that apical dominance in Petunia plants is stronger under long days while it is weaker under short days. This unexpected conclusion may be due to experimental procedures, and the interaction between photoperiod and temperature.

2.8.2 Temperature

High temperatures (28 ^{o}C) have been found to lessen apical dominance in *Eucalyptus obliqua* seedlings (Blake 1976), this agreeing with earlier work with Engelman spruce (Hellmers *et al* 1970), and more recent work in *Agropyron repens* (Leakey *et al* 1978).

2.8.3 Relative humidity and Water Stress

McIntyre (1971) working with *Agropyron repens* suggested that the supply of water could be a limiting factor to axillary bud growth, so enhancing apical dominance. Further experiments with *Phaseolus vulgaris* and *Pisum sativum* (McIntyre 1971; 1973) confirmed this and indicated that water stress could be a particularly significant factor. This

assumption agrees with the earlier findings of Remy (1968) with the same species. More conclusive evidence has been reported in *Coffee arabica* in which water supply limited axillary bud development, this effect however being more on floral initiation (Mes, 1957). By contrast, high humidity has been reported to weaken apical dominance in *Chrysanthemum* (Keppeler, 1968), *Phaseolus vulgaris* (McIntyre 1973) and *Agropyron repens* (McIntyre 1981).

2.8.4 Inorganic Nutrients

This is about the best substantiated of all environmental factors affecting apical dominance. As mentioned above, Nitrogen can stimulate the growth of axillary buds and weaken apical dominance. This has been demonstrated for flax (Gregory and Veale 1957) and *Agropyron repens* (McIntyre 1964; 1969; 1972), while Leakey *et al* (1978) working with this same species explained his findings in terms of competition for nutrients between shoots, and the antagonistic effects of nitrogen on an auxin-mediated inhibition by the dominant shoot.

In addition to Nitrogen effects. Gardner (1942) has reported tillering in wheat under calcium and phosphorous deficiency, while Nakamura (1965) showed suppressed branching (high apical dominance) in pea seedlings under calcium and magnesium deficiency. In *Bidens pilosus*, Kramer *et al* (1980) demonstrated that immediately after decapitation, K^+ is accumulated in stem tissue around nodes. They proposed that potassium accumulation is a primary factor in bud activation and the subsequent decrease in apical dominance. Boron deficiency has also recently been demonstrated to be involved in apical dominance of *Cola nitida* and *Hevea brasiliensis* where growth of the apical bud is arrested and axillary buds of young seedlings develop, thus decreasing apical dominance (Shorrocks 1975).

2.8.5 Gravity

Together with the nutrient effects described above, the influence of gravity on apical dominance is probably one of the best known environmental effects on correlative inhibition, particularly in trees. Orientation of shoots away from the vertical, or arching them, weakens apical dominance. These effects perhaps being best known in fruit trees (Wareing and Nasr 1958; 1961; Smith and Wareing 1964a, b; 1966). They postulated that nutrients are diverted to the highest upwardly directed meristem and the proximity of laterals to the root, appearing to give an advantage. This supports the views of Loeb (1917) who emphasised the importance of a root factor. Despite the predominance of studies in temperate tree species, a few tropical trees have been found to respond similarly. Damptey (1964) and Longman (1978) investigated this factor in *Terminalia ivorensis*, *Manihot esculentus* and other tropical species, and reported substantial effects in the position of dominant axillary buds in the horizontally placed plants. This supports the findings of Wareing and Nasr (1958) and Longman (1968).

2.8.6 Carbon dioxide

Finally, conflicting reports have been made regarding the effects of CO_2 on apical dominance. In one study, high CO_2 concentrations were reported to weaken apical dominance in *Pisum sativum*, (Anderson 1976), while in another study, raising concentrations from 0.035 % to 0.10 % by volume enhanced apical dominance. This however was only at the earlier growth stages (Hellners and Strain, 1980). The differences in results could however be attributed to varietal differences in the test species.

2.9 THE PRESENT STUDY

The general aim of the work described in this thesis has been described at the end of the previous chapter. The stages in the investigation are outlined on Fig. 7. The programme of work combines glasshouse studies with field observations of branching and form in Nigeria. Critical to the success of the study is the assessment of the strength of apical dominance, using the decapitation test and the correlation between the results of this test and the performance of trees in plantations in Nigeria. These aspects and the relationship between this work and the existing West African Hardwood Improvement Project (WAHIP) and the Tropical Project at Bush Estate near Edinburgh, form the bulk of the thesis.

The contents of this thesis are listed on pages i - viii. It is divided into 5 sections for convenience. The organisation of the experimental and observational parts of the work, according to chapter, is outlined below.

Chapter 4 describes preliminary studies of *Betula pubescens*, which was used to establish assessment standards for work with the main test-species of this work, *T. scleroxylon*. The problem of assessor-bias was also fully considered.

Chapter 5 describes glasshouse experiments aimed at studying the various environmental factors which may affect the subsequent screening of clones for their levels of apical dominance. Environmental factors studied included : plant physiological states, aerial environmental and edaphic environmental factors.

Chapter 6 describes the performance of clones in plantation in Nigeria after 4 years. Assessments in this study were based on experience accrued following the work on *B. pubescens* already mentioned.

Chapter 7 further describes field performances of clones, with emphasis on branch characteristics and the effects of these on crown shape.

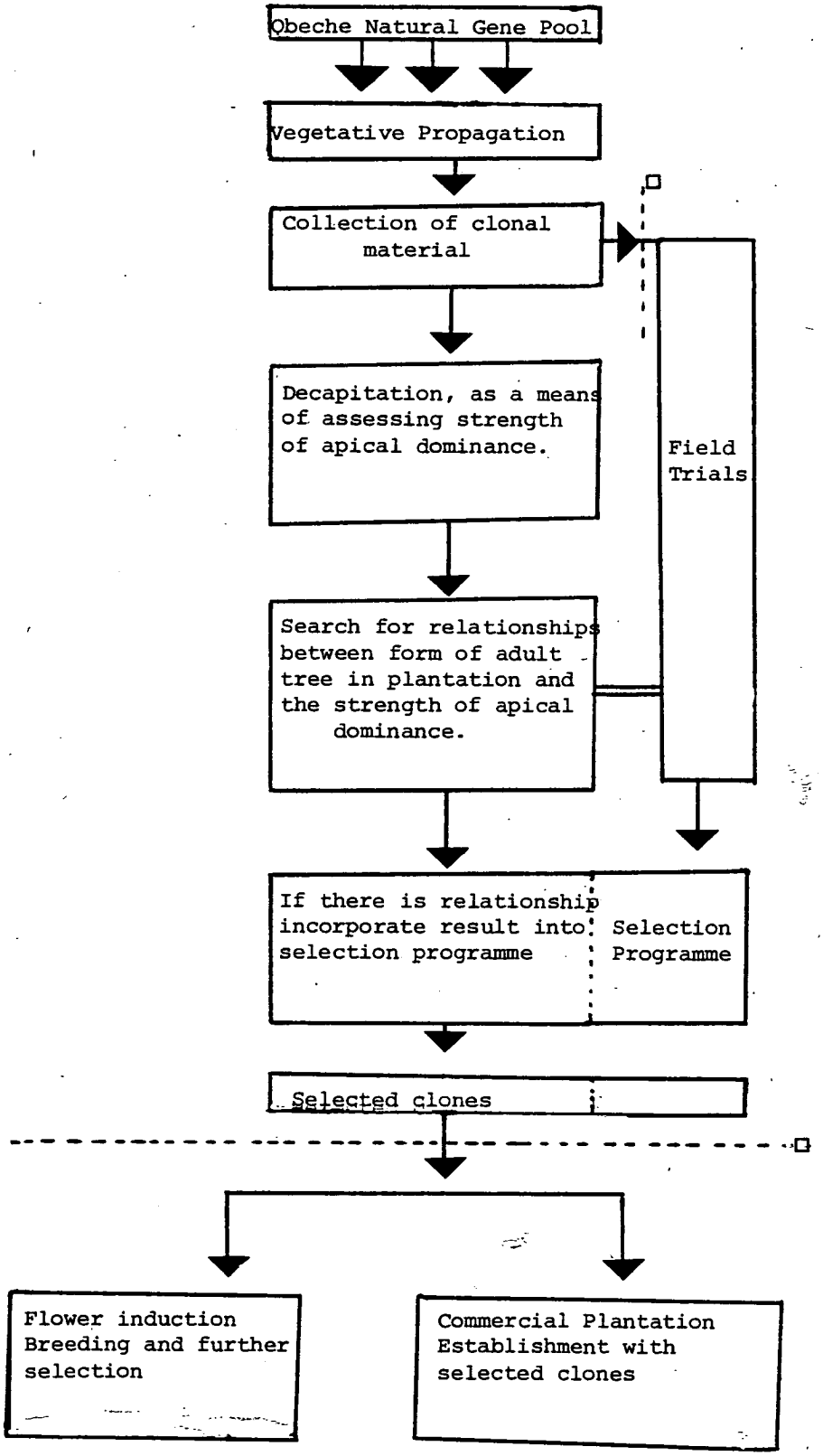


Fig. 7 Flow diagram of the phases in the selection of *T. scleroxylon* for commercial clonal plantations.

Chapter 8 describes the development of a 'predictive test' for branching habit. It includes the screening of clones by decapitation, under standard environmental conditions based on the findings in Chapter 5. It further reports the relationship between the assessed field parameters and their relationships to the results of the glasshouse screens earlier reported. The implications of this are fully discussed.

Chapter 9 describes subsidiary studies in other aspects of genetic variation in *T. scleroxylon*. It reports seedling variation in response to decapitation of half sib and full sib progenies (populations), their growth and juvenile characteristics.

Chapter 10 reports the effect of environment (site) on the growth of some clones from 4 progenies.

Chapter 11 describes the effect of clone upon photosynthesis, respiration, transpiration and resistances to CO_2 and H_2O. variation between the clones and relationship to their field performances are reported.

In Chapter 12, the results of this thesis are summarised and discussed generally with particular reference to the West African Hardwood Improvement Project.

CHAPTER 3

3. MATERIALS AND METHODS

3.1. Materials - Origin of clones and their culture

Extensive collections of *T. scleroxylon* seed had already been made over the natural range in West Africa and especially within Nigeria (See Chapter 1). Plants derived from some of these collections were utilized in the experiments reported in this thesis. They included :

(i) Clonal material established in Edinburgh in June, 1978 and January 1979 from ortets (source of cutting) originating from Nigeria. These clones were part of the 1975 experimental field plantings, and form the bulk of the materials used in this work (Table 1).

(ii) Clones with known characteristics established in 1971 in Edinburgh from seeds and seedling ortets originating from Nigeria (Table 2).

(iii) Clones established in Nigeria and used for nursery experiments at the Forestry Research Institute of Nigeria (FRIN) in 1979 and 1980 (Table 3).

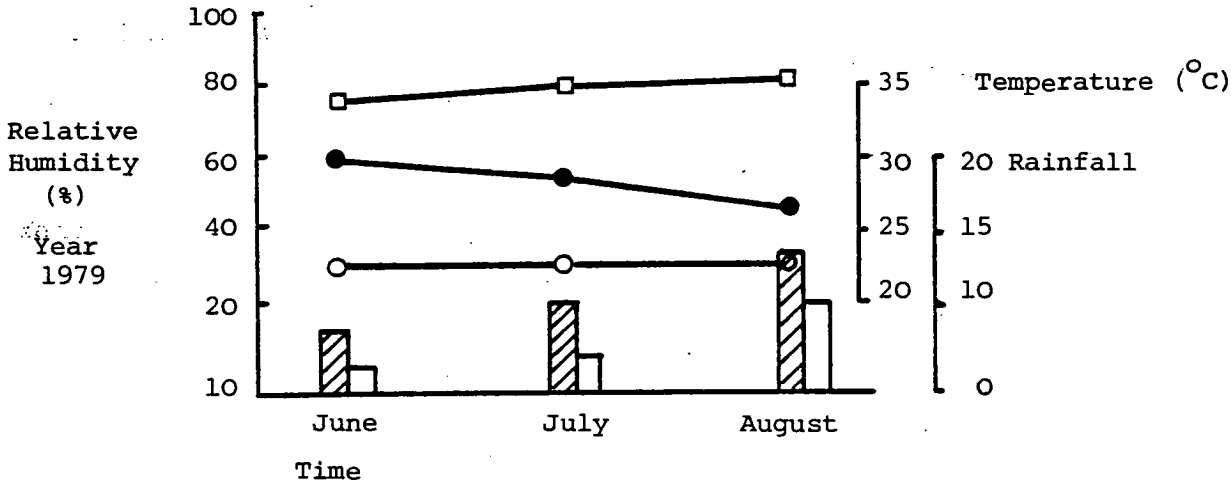
As will be seen in Chapter 9, seedlings were later used to study populations of *T. scleroxylon*. The origins of these, and their culture will be reported in the appropriate places.

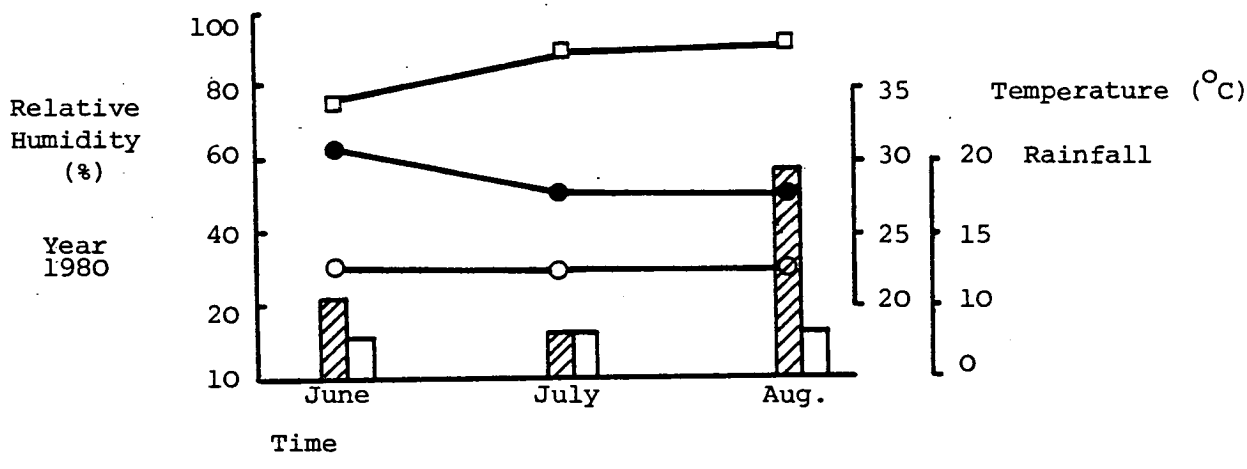
3.2 Environments

3.2.1 Nursery Environment in Nigeria (FRIN)

Experimental work at the FRIN nursery was done between June and August of 1979 and 1980. The environmental conditions of these months, in the respective years are presented graphically in Figure 8a. Day

Fig. 8a





Mean monthly values of temperature (● = Max : o = Min), rainfall (solid bars = mm : open bars = rain days) and relative humidity (□ % RH) at FRIN between June and August, 1979 and 1980.

Table 1 : FRIN clones utilized in Scottish experiments : all originate from Nigeria.

Source No.	Clone No.	Nigerian Location	Latitude	Longitude	Rainfall Zone mmy^{-1}	Expt. Site
137	137/9	Olokemeji	7°.21 N	3°.32 E	1300-1500	ITE
139	139/6 139/9	Olokemeji	7°.26 N	3°.32 E	1300-1500	ITE
144	144/1 144/4 144/7 144/5 144/9	Igbo-ora	7°.27	5°.37	1300-1500	ITE
161	161/3 161/5	Owo	7°.02	5°.43	1300-1500	FRIN
166	166/1 166/5 166/3	Azukala	7°.02	6°.27	1300-1500	ITE
175	175/1 175/8 175/5 175/9 175/6 175/7	Igbado	6°.49	4°.52	1500-2000	ITE
177	177/10	Ilugun	7°.21	3°.39	1300-1500	ITE
224	224/3 224/7	Ede Tree I	7°.42	4°.26	1300-1500	FRIN
225	225/8	Ede Tree II	7°.42	4°.26	1300-1500	FRIN
255	255/2 255/6	Ibarapa	7°.23	3°.20	1300-1500	FRIN
261	261/4	Iyamyong Tree II	5°.58	8°.21	2000-2500	FRIN ITE
335	335/2 335/7	Nkalagu Junction	6°.30	7°.45	1500-2000	FRIN
501	501/2	Igbo-ora	7°.27	5°.37	1300-1500	FRIN
505	505/2	Ikere	7°.38	5°.12	1500-2000	FRIN
506	506/14	Near Ayangba	7°.40 N	7°.02	1300-1500	ITE
514	514/11	Ibadan	7°.17	3°.30	1500-2000	FRIN

Table 2 : ITE clones utilized in Scottish experiments : all originate from Nigeria.

Clone No.	Nigerian Location	Latitude	Longitude	Rainfall mm yv^{-1}	Expt. Site
8045	Mile 19 Iwo Rd.	7^{o}.38 N	4^{o}.11 E	1500-2000	ITE
8046	Igbo-ora	7^{o}.27 N	5^{o}.37 E	1300-1500	ITE
8047	Igbo-ora	7^{o}.27 N	5^{o}.37 E	1300-1500	ITE
8048	Gbitigbiti	8^{o}.30 N	3^{o}.26 E	1300-1500	ITE
8049	Igbo-ora	7^{o}.27 N	5^{o}.37 E	1300-1500	ITE
8050	Iwo Rd.	7^{o}.38 N	4^{o}.11 E	1500-2000	ITE
8051	Gbitigbiti	8^{o}.30 N	3^{o}.26 E	1300-1500	ITE
8052	Igbo-ora	7^{o}.27 N	5^{o}.37 E	1300-1500	ITE
8053	Iwo Rd.	7^{o}.38 N	4^{o}.37 E	1300-1500	ITE
8054	Igbo-ora	7^{o}.27 N	5^{o}.37 E	1300-1500	ITE
8055	Iwo Rd.	7^{o}.38 N	4^{o}.11 E	1500-2000	ITE
8038	Ilugun	7^{o}.21 N	3^{o}.39 E	1300-1500	ITE

Table 3 : FRIN clones utilized in Nigerian experiments; originating from West African countries - Nigeria, Cameroon, Ghana, Liberia.

Clone No.	West-African Location	Latitude	Longitude	Expt. Site
238/6	Ibadan-Ilugun Rd. Tree No.2 Nigeria	7°.43 N	3°.48 E	FRIN
342/7	Apurere Ml.18 Ondo-Akure Rd. Nigeria	7°.12 N	4°.58E	FRIN
368/5	Tazzi (Abakaliki Rd.)	6°.10 N	7°.50 E	FRIN
368/6	Tazzi (Abakaliki Rd.)	6°.10 N	7°.50 E	FRIN
368/19	Tazzi (Abakaliki Rd.)	6°.10 N	7°.50 E	FRIN
392/9	Igbo-ora Nigeria	7°.27 N	5°.37 E	FRIN
404/10	Minkama Cameroon	4°.04 N	11°.35 E	FRIN
404/18	Minkama Cameroon	4°.04 N	11°.35 E	FRIN
404/1	Minkama Cameroon	4°.04 N	11°.35 E	FRIN
410/12	Biatcholla Cameroon	4°.27 N	11°.28 E	FRIN
410/20	Biatcholla Cameroon	4°.27 N	11°.28 E	FRIN
410/3	Biatcholla Cameroon	4°.27 N	11°.28 E	FRIN
424/16	Asuso,Ghana	6°.00 N	1°.00 W	FRIN
431/9	Gregheu Liberia	6°.45 N	6°.50 W	FRIN
431/10	Gregheu Liberia	6°.45 N	6°.50 W	FRIN

Continued/..

Table 3 (Continued)

Clone No.	West-African Location	Latitude	Longitude	Expt. Site
431/20	Gregheu Liberia	6°.45 N	6°.50 W	FRIN
432/11	Boguoine Liberia	6°.05 N	4°.55 W	FRIN
432/2	Boguoine Liberia	6°.05 N	4°.55 W	FRIN
436/8	Laseguie Liberia	6°.12 N	4°.20 W	FRIN
436/11	Laseguie Liberia	6°.12 N	4°.20 W	FRIN
436/18	Laseguie Liberia	6°.12 N	4°.20 W	FRIN
445/1	Tappita Liberia	6°.20 N	9°.00 W	FRIN

length was 13 hours and natural light intensity peaked aroung 2000 μE m^{-2} s^{-1} at midday. Further, during this period, which was the rainy season, the relative humidity was constantly high (>80 %), frequently approaching the point of saturation after rains or at night and the temperature was around 28° to 30° C, typical of this area of Nigeria.

3.2.2 Gambari Experimental Site - Nigeria

This is a long-established experimental site situated near Ibadan in Oyo State. It is within the moist deciduous forest zone, where rainfall is usually above 1500 mm y^{-1}, falling mainly between May and September. It lies on latitude 7°.07 N and longtitude 3°.45 E. Figure 8b shows the climate of this site from 1975, when experiments involving *T. scleroxylon* were planted, to 1979 when assessments presented here were made. The soils are typically variable as in most tropical forest sites (Onweluzo *et al* , 1976) shallow, and moderately fertile (Howland *et al*, 1978), and range from yellow-red to brownish loamy type, overlying crystalline acid rocks of the basement complex. Topography is gently undulating plain with a maximum height above sea level of less than 190 metres.

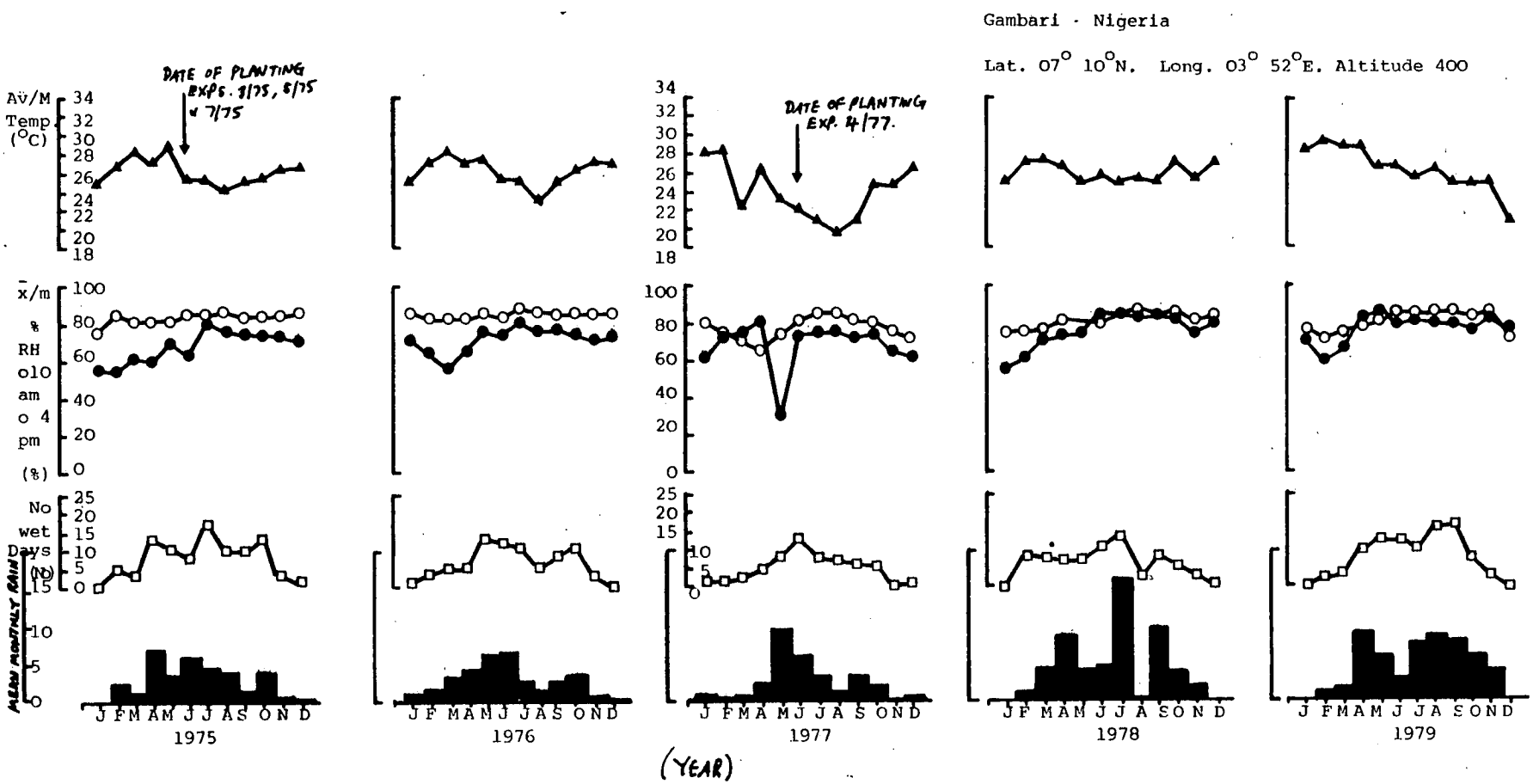
3.2.3 Tropical Glasshouses in Edinburgh

The tropical glasshouses at ITE have automatically controlled environments which are more or less constant throughout the year, although light intensities are lower in winter, when temperatures are slightly lower.

To assist with the design of experimental layouts, and to ensure that plants would be exposed to as uniform an environment as possible, detailed records were made of temperature variation within the house used for experiments with potted plants.

Fig. 8b

Mean monthly values of rainfall(solid bars), raindays (▣), relative humidity (o = 10 a.m.: ● = 4 p.m.) and temperature (▲) of Gambari Forest Reserve Experimental Site, near Ibadan. ↓ = date of planting.



To reduce heat losses, the glasshouses were lined with a layer of polythene enclosing 8 cm air space between it and the outer glass shell. Heating was provided by electrical 16 kw fan heaters with polythene ducting to help even heat distribution. Air movement was maintained by paddle fans drawing warm air from the roof and blowing it down to the floor. Supplementary gas heaters at both ends of the glasshouse provided standby heating in the event of an electrical failure.

3.2.4 Temperature

Forty thermistor temperature probes (20 per recorder) placed at 25 cm distance from each other were connected to a Grant miniature temperature recorder (Model D) and set on the automatic mode. Temperature was thus monitored continuously all over the glasshouse. This revealed (Fig. 9), a central area of uniform temperature 28 ^{o} ± 2 ^{o}C which could be used for experimental purposes. Night temperature was slightly lower at 26 ^{o}C ± 2 ^{o}C, this drop being attributable to the unusual severity of the winter of 1978/79.

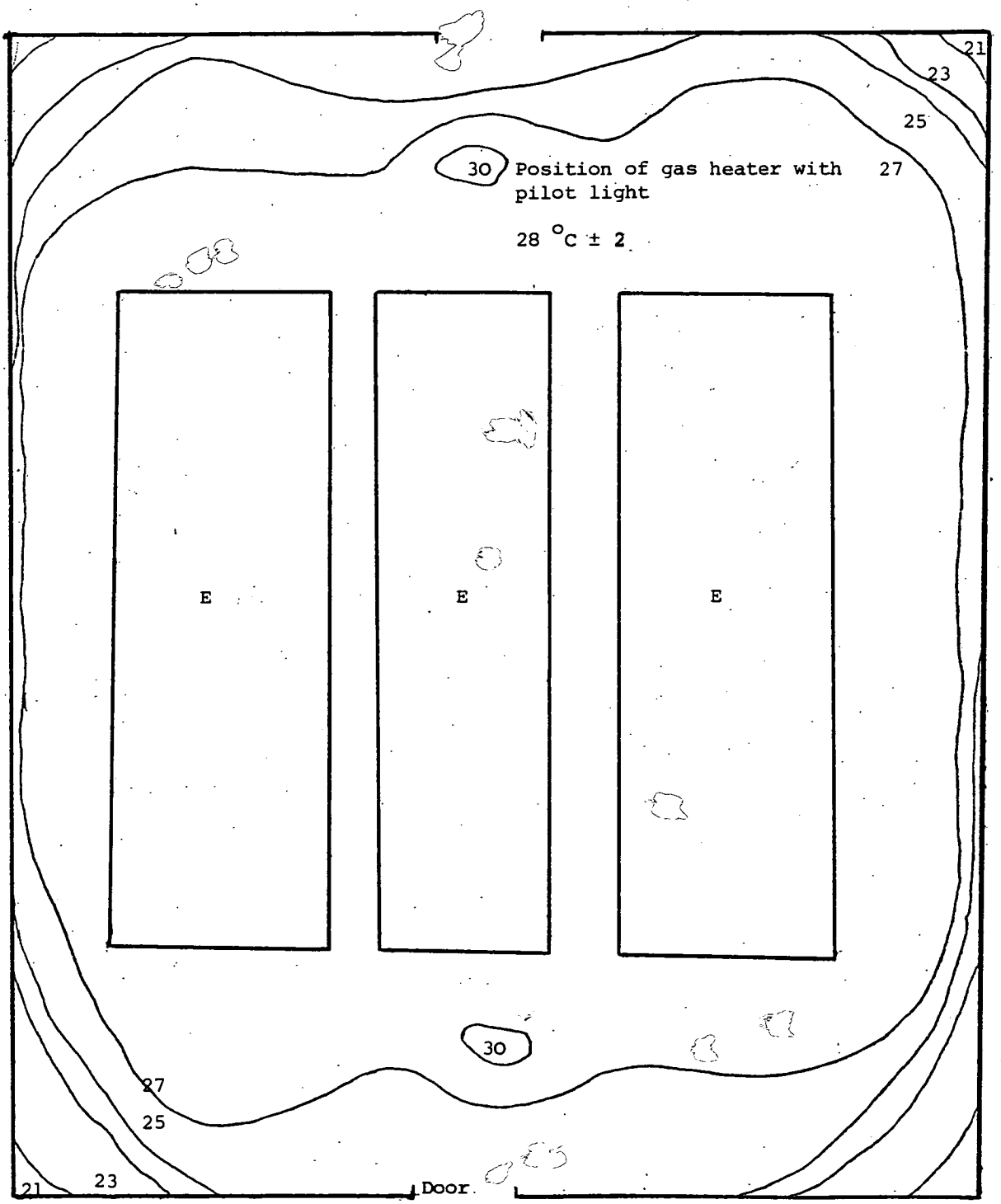
3.2.5 Light

Of all controllable variables, light creates the biggest problem. To provide adequate control, four rows of 9 mercury vapour lamps (White MB F (R)/u) each of 400 Watts run along the glasshouse to provide a uniform intensity of light over the experimental plants. Light was measured at various points with a Lambda quantum sensor, and at plant level, photosynthetically active radiation (PhAR) was 650 µE m^{-2} s^{-1}, and at 30 cm from the light source, it was 1500 µE m^{-2} s^{-1}. Photoperiod was controlled by means of a time clock at 19.5 hours.

3.2.6 Relative Humidity

The level of relative humidity (%) was related to the glasshouse management, particularly the watering regime, but there was fairly

Fig. 9



E - Experimental sites

Isotherms showing the distribution of temperature (°C) in the glasshouse from the 6th to 16th January, 1979.

consistent variation within the experimental areas of the glasshouse, during the span of 2 year experimentation. A continuous sprinkler hose runs on the floor of the house to provide moisture, thus preventing drastic falls in relative humidity. A mean value of 70 % is typical before watering which is at about 10 a.m. after which it often rises to 90 % for about 4 hours. At the nominal temperature of 28 ^{o}C this corresponds to a saturation vapour pressure deficit of 11 to 4 mb, an absolute humidity of 26 to 34 mb, and a dew point of 22 to 26 ^{o}C.

3.2.7 Air-exchange

Finally adequate ventilation and fresh air exchange is allowed by the roof-fitted electroflora autovent and the side-wall-fitted breeza fans which only operate in hot weather. Although carbon dioxide levels was not under control, it was assumed that the intermittent ventilation, and the ceiling fan ensured adequate air mixing and CO_2, comparable to its atmospheric level.

The standardization of the above climatic parameters in this automatically-controlled glasshouse provided relatively uniform conditions for all experimental plants and were optimal for the growth of *T. scleroxylon*.

3.2.8 A comparison between environments at ITE glasshouses and FRIN Nursery

Evans (1963) discussed the biological and technical limitations involved in artifical simulation of natural conditions. Between the two sites described earlier, it was apparent that :-

(i) Light intensity is lower in ITE glasshouses than at Mid-day at FRIN nursery where other experiments were performed. (650 $\mu E\ m^{-2}\ s^{-1}$ - 2000 $\mu E\ m^{-2}\ s^{-1}$). However the light at FRIN was far from steady as

overcast cloud reduced light intensity several times in a day, and on some rainy days did not exceed 1500 μE m^{-2} s^{-1}.

(ii) The diurnal fluctuations of temperature were 2 °C in the glasshouse and 5 °C or more in the nursery at FRIN.

(iii) Relative humidity at ITE was usually lower by 10 - 20 % than would be expected in Ibadan during the rainy season. However, in general, these environmental differences are small enough to be negligible, while the uniformity of the glasshouses provided an environment which increases the comparability of experiments, as compared with those done in the open in Nigeria, which are open to seasonal and diurnal fluctuation.

3.3 Cultural Methods

3.3.1 Vegetative Propagation (ITE)

Apart from seedling ortets, raised from seed in Edinburgh (ITE), clonal ortets were transported by air from Nigeria in wet sawdust and adequately protected from frost. They were potted into 5" pots on arrival and allowed to recover from the physiological stress of the journey on the 'weaning' bench. After one month, when plants were in full vegetative growth, single-node leafy cuttings were taken using the methods described by Leakey *et al* (1975; in press and illustrated in Plate 1) and treated with 0.1 % NAA + 0.1 % IBA in industrial methylated spirit. The leaf on each cutting was trimmed to an area of about 50 cm^2 before cuttings were set on heated propagation beds at a bed temperature of 30 °C and an air temperature of 20 °C. Mist was controlled by an electronic leaf. Rooting success exceeding 75 % was obtained, and further cuttings were taken from original ortets as necessary. Rooted cuttings were potted into John Innes potting compost and set to wean for

two weeks. Unbranched plants c 600 mm tall were subsequently used as experimental material. Plants were given 1 % 'Solufeed' fertiliser, containing NPK in the ratio of 1:1:2 during watering, using a continuous dilution controller (Keylutor Mk III).

3.3.2 Potting Compost ITE

The standard potting compost is made up with 7:3:1, peat:sand: loam with 4.2 g kg^{-1} 'Enmag', 2.6 g kg^{-1} John Innes Base and 0.3 g kg^{-1} trace elements. pH was maintained at 5.0.

3.3.3 Vegetative Propagation (FRIN)

Single-node leafy cuttings were prepared as above but they were then set in sterilized washed river sand in propagation tents at high humidity (see Fig.10) as developed by Howland (1975a). Auxins were not used to aid rooting, and here, rather than being fixed, temperature of the medium followed the ambient pattern, viz. 25 - 30 ^{o}C and pH was 7.5. Plant treatment after rooting were similar at ITE and FRIN except that at FRIN all plants were subsequently give 1 % 'Welgro' fertilizer fortnightly, during watering.

3.3.4 Potting Compost (FRIN)

The standard potting compost at FRIN is 5:3:2 forest top soil, horse manure, gravel, with 13.5 g kg^{-2} ICI fertilizer (N.P.K.15.15.15) Fatokun (1977).

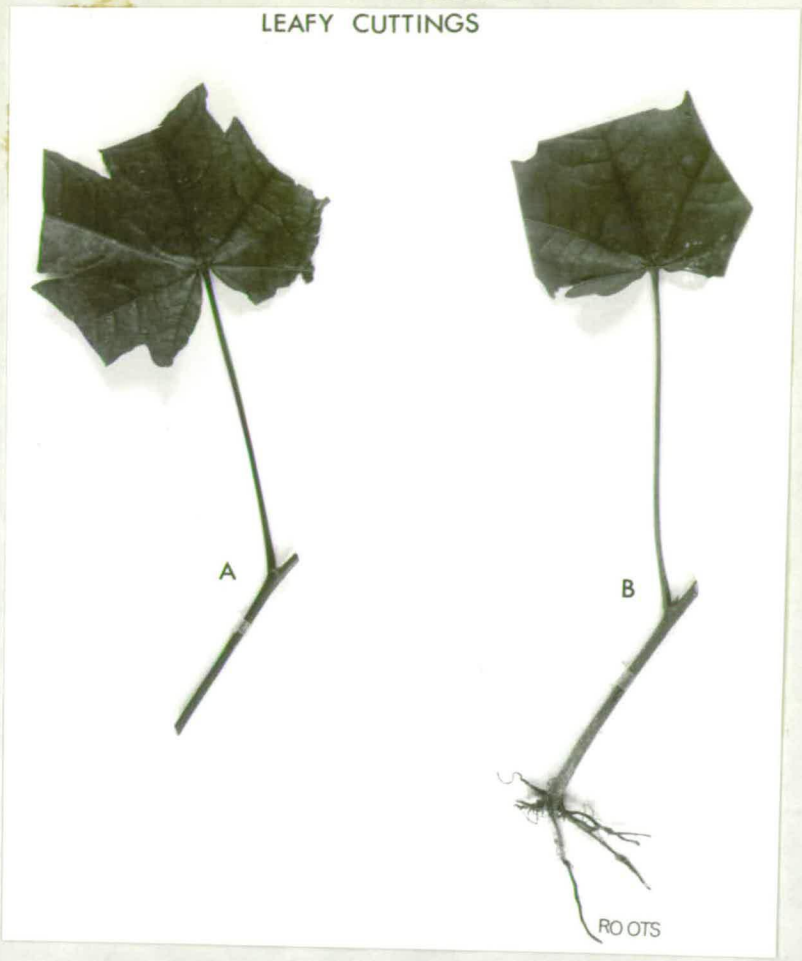
PLATE 1

i. A freshly cut unrooted (A) and rooted (B) single node leafy cutting of *T. scleroxylon*.

ii. Single node, auxin-treated leafy cuttings of *T. scleroxylon* set in a heated mist propagation bench at ITE.

Plate 1

LEAFY CUTTINGS



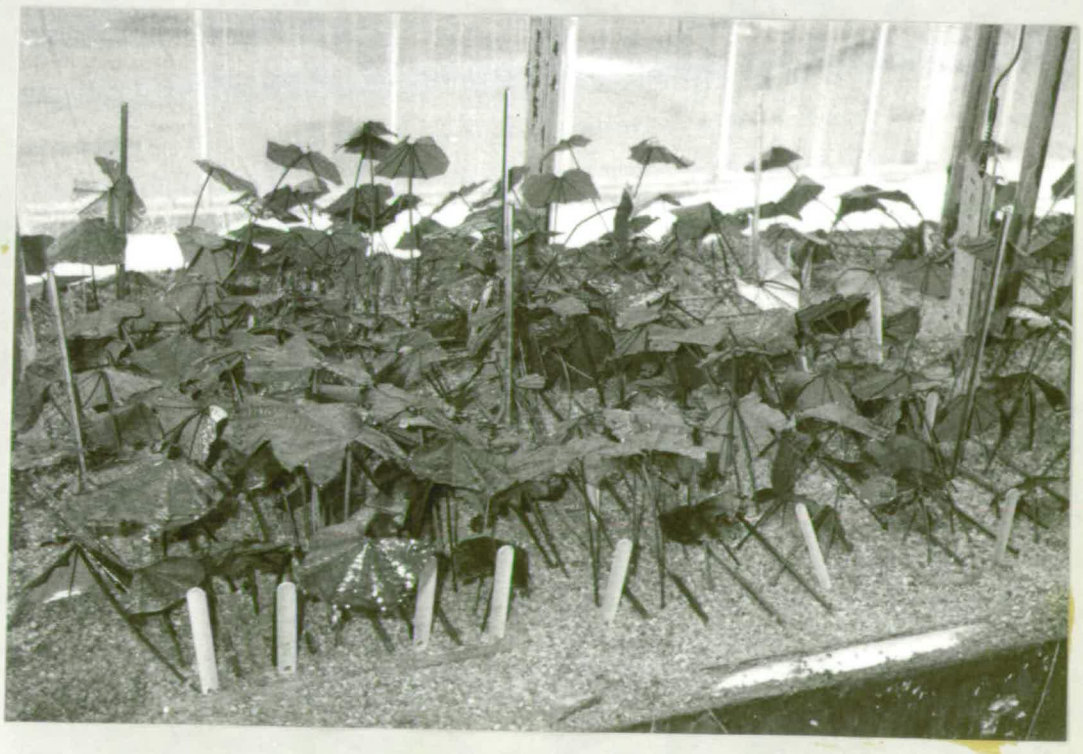
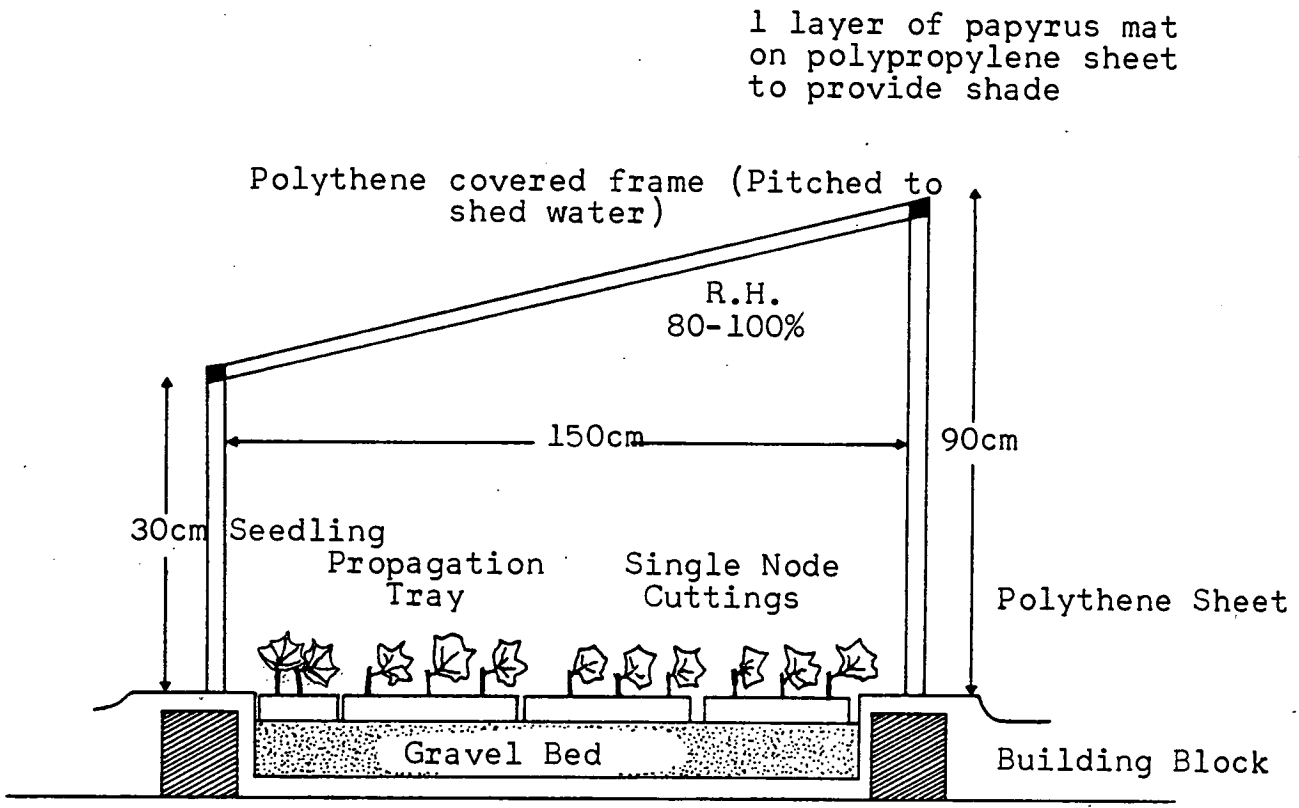


Fig. 10



HIGH HUMIDITY PROPAGATOR
(after Howland 1975)

High humidity propagation tents, where single node leafy cuttings of *T. scleroxylon* are rooted without auxin application at FRIN.

SECTION 1

PRELIMINARY STUDIES

Before beginning field work on *Triplochiton* in Nigeria, techniques of assessment were tried out on *Betula pubescens* growing near Edinburgh.

CHAPTER 4

4. EVALUATION OF TREE FORM

4.1. Preliminary Studies of *Betula pubescens*

4.1.2 Introduction

A prerequisite of any tree improvement programme is the study of genotypic variation within the chosen species. Genotypic variation is revealed when materials from diverse provenances are grown together in a standard plantation, so that comparisons can be made between individuals of equal age, growing in the same environment. In a large scale programme, such as that for *Triplochiton scleroxylon* in Nigeria, the measurements to be made in this way may be numerous and expensive. In designing a programme of measurements, it is desirable to make only a few recordings from each tree, for reasons of economy. Many people would argue that for certain characters, a subjective assessment is preferable. The complexity of the form of wild trees may defy rigorous description, and so some subjectivity may be a necessary expedient, objective assessment being too time consuming for certain characters. On the other hand, a subjective assessment, especially where several observers are involved may be entirely spurious, because assessors have different standards or understanding of important attributes. Furthermore, there have been few published attempts to evaluate the type of measurements that might be made in this context.

The work described in this chapter was an attempt to investigate the practical problems involved in the measurement and description of tree forms and to develop expertise at field assessment. It was carried out prior to visiting Nigeria to assess *T. scleroxylon*. The species chosen for this preliminary investigation was *Betula pubescens*

Erhrh., a temperate broadleaved tree. There were two reasons for studying this species:

(i) Its branching patterns and form are fairly similar to that of *T. scleroxylon*, and

(ii) A collection of material of this species was available in a small plantation at the Institute of Terrestrial Ecology (Farfield plots).

A feature of the work described is the use of several observers, enabling observer error to be evaluated.

4.1.3 Brief review of Provenance variation in forest trees

Intraspecific variation in tree species has been studied by many authors, especially in temperate gymmosperms, such as *Pinus contorta*, (Burley 1966a, b,; Burley *et al*, 1967; Lamb, 1970; Pollard 1973) and *Picea sitchensis* (Cannell 1974). In broad leaf species, more attention has been paid to multipurpose trees capable of rapid growth such as *Populus* spp. Ying and Bagley (1976), in an investigation of genetic diversity in morphological, phenological and growth characters of *Populus deltoides* provenances from Eastern United States found that height and diameter growth were influenced by provenance at seven years of growth, with height increasing from Northern to Southern provenances. Southern provenances had the greatest diameter at breast height (dbh) while dense crowns with numerous small, short branches were characteristic of Northern and Western provenances; and Eastern sources tended to have a spreading crown with long large branches. Agreeing with the work of Farmer (1970) they further reported that data of leaf flush and anthesis differed significantly between provenances (Ying and Bagley 1976).

In yellow birch (*Betula alleghaniensis*) an important hardwood of

the Lake States, (Northern United States and Eastern Canada), Clausen (1967) reported natural variation in catkin and fruit characteristics in 9 provenances. He concluded that the Illinois and Michigan provenances have the largest rachis length and mean fruit size. This work is supported by the report of Dancik and Barnes (1972) who also found variation in Catkin and fruit size, even between individual trees in the same provenances. Further, Clausen (1967) studied height growth in 25 provenances and reported that the West Virginia and lower Michigan provences were growing almost twice as fast as the Nova Scotia provenance which was the poorest. He identified also that the northern provenances stopped growing earlier than the southern ones, this agreeing with the earlier work of Wang and Perry (1958) with *Betula papyrifera* (Paper birch).

Furthermore, Clausen and Garrett (1969) working at Rhinelander (U.S.A.) tested 21 provenances of yellow birch and reported highly significant height differences between the best and poorest provenances after 1 year; the Nova Scotia provenance being taller than the New Brunswick provenance.

In a within-provenance study of the same species, Clausen (1972, 1980) reported that certain provenances were much more variable in height growth than the others, diameter growth however was less variable between provenances although it was also variable within the provenances studied.

On the age at flowering, seed production and seed yield, in this same species, Clausen (1976) reported significant differences between provenances. He found that trees of the northern origin began to flower and bear seed at an earlier age (6 years) than those of the southern origin (7-8 years). He later reported also, that the presence

of flowers or fruits depended more on crown size than on tree height or diameter (Clausen 1979) while total seed yield depended much on geographic origin or provenance (Clausen 1980).

4.1.4 The Status of *Betula pubescens*

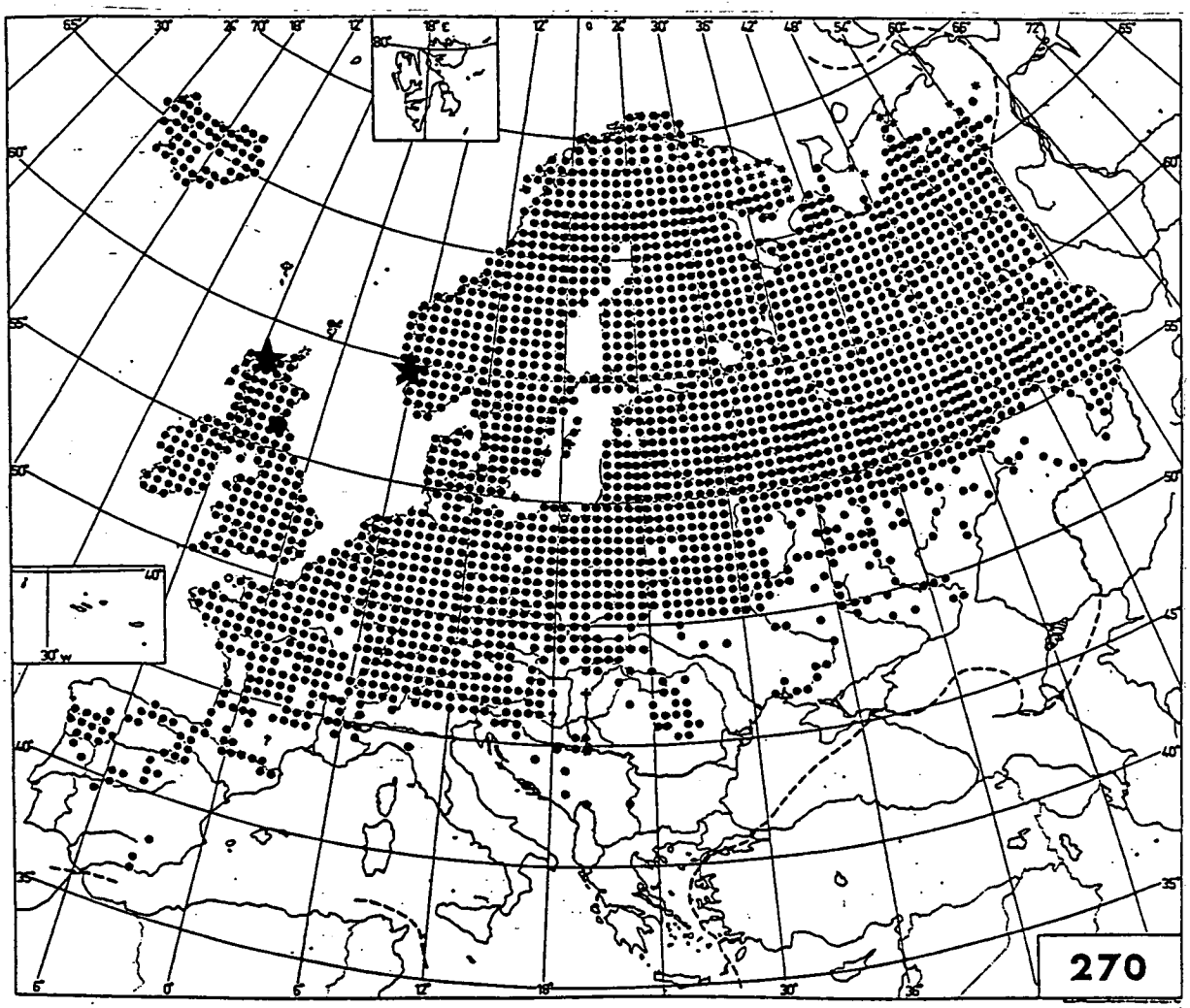
The work reported is firstly on provenance differences and secondly on the study of variation within provenances, in growth, form and behaviour of young trees and coppice growth in the field, of *Betula pubescens* Erhrh. (White birch).

It is a native tree, abundant in Northern Britain, most of Europe and Northern Asia (Figure 11) where it is a fast-growing early colonizer of poor soils. Few studies exist on this species unlike *Betula alleghaniensis* (Yellow birch) of America and Canada on which most of the earlier literature review was based. However, extensive variation in leaf shape has been reported by Gardiner and Pearce (1978), variation in form by Brown and Tulley (1971), in photosynthesis by Thomas and Kenworth (1980). In an earlier study on the provenances, Last (1976, 1977) reported substantial differences in growth characteristics and emphasised the effect of latitude, daylength, and altitude of origin. *B. pubescens* has not been artificially selected or improved to any great extent in Britain (Mason and Pelham 1976); only in Finland, where Birch is an important forest tree, have appreciable selection and breeding been done. Its uses there include plywood manufacture and as a possible alternative energy source. Selection of *B. pubescens* for derelict or unfavourable sites has now been started in Scotland (Last 1975).

4.1.5 Problems of Assessor bias in subjective morphological assessments

There is general agreement that well formed trees are highly desirable; for example, straightness in sawlogs is favoured (Bannister 1979). For assessing large numbers of trees, subjective methods are

Fig. 11



(Map adapted from Jaakko and Juna (1976)

Showing sources of provenances (Norway and Scotland), the general distribution of *Betula pubescens* over Europe and the experimental site in Scotland.

used in many parts of the world, which depend on rapid visual evaluations. This, as already mentioned earlier, is bound to vary from assessor to assessor. With this in mind, Andrew and Wright (1976) in a manual of Methods on Sepcies and Provenance Research, extensively discussed the timing, methods, and recommended traits for assessment at each stage of tree development; such as (1) nursery stage, when vigour and survival are important traits, and (2) Field stages, when height, diameter (dbh), crown characteristics and stem form are important parameters. For example they recommended for stem form assessment, an artificial class interval scale such as 0 - 6. This method was applied in the subjective assessment of crookedness in *Pinus radiata* stems (Bannister 1979) and gave inconsistencies in the scoring of 5 individual observers resulting in erratic changes in the mean values.

This work with *Betula pubescens* was designed to investigate assessor bias between 4 experienced assessors and to ascertain the importance of developing a unified set of rules for field work.

4.2 Materials and Methods

In 1971, seed of *Betula pubescens* was collected from approximately the same latitude, but different altitudes: Haukelifjell, in Norway at an altitude of 960 m and Inverpolly, Scotland at 45 m above sea level ($58^{\circ}.48$ N - $4^{\circ}.17$ W and $59^{\circ}.4$ N - $7^{\circ}.17$ E respectively), nearly $\frac{1}{4}^{\circ}$ apart. The seedlings from these were planted out at the Institute of Terrestiral Ecology - Farfield experimental site near Bush Estate (Fig. 11 and Plate 2) at 1 metre espacement. Assessments were made in 1979, seven years after planting, when of 110 trees originally planted 105 survived, 2 trees of Scottish and 3 of Norwegian origins having died.

Plate 3

Showing variation in growth between plants of two provenances of *B. pubescens* at Farfield Field Station.

Height, branching, its components, and other associated parameters were measured in the winter months and flowering, bud-break, and coppice growth were assessed later throughout the summer and autumn of 1979.

To demonstrate the problems involved in subjective assessments in the field, 4 observers (A, B, C, and D) assessed morphological characters such as forking, multistemming and stem form. Observers began at different parts of the experiment and worked independently. Each set of data were analysed and compared, and if necessary new definitions were developed and tested. A 'committee' assessment was finally done to assess the amount of "error" for each assessor.

4.2.1 Rationale for choice of characters

One approach to the study of intraspecific variation would be to measure as many characteristics as possible. This approach is favoured by the modern school of numerical taxonomy. The rationale of this approach is that choice of a number of characters implies sampling of a large proportion of the total genetic make-up of the individual (Sneath and Sokal 1973). This approach is largely rejected by classical taxonomists, who choose 'conservative' characteristics; that is, ones which are not sensitive to environmental changes and therefore can be said to be a 'reliable' guide to taxonomic affinity. Another approach, used extensively by breeders of food crops, is to measure only those characters, like economic yield, flavour and disease resistance, that are of immediate practical concern. None of these approaches seem wholely useful in tree breeding.

The taxonomic approaches, at best reveal taxonomic affinities, which may be of interest to the tree breeder, but only of marginal practical value in improving the species. The conventional approach

of plant breeding is a more relevant one, though the longevity of tree crops precludes the use of final yield as a convenient character. Much more useful would be some combination of characters which are predictors of yield, or contributors to yield or good stem form, which may be recorded at a relatively early stage in the development of the crop. This approach was used in the present study, bearing in mind that the *T. scleroxylon* crop would have to be evaluated at an age of 4 years. It is hoped that by this age useful trees will be beginning to show desired characteristics and generally exhibiting their genetic potentials.

The following assessment procedures were developed after some modifications for the work :

(a) Height of plant was measured with an extendable measuring rod from ground level to tip of the leading shoot. The use of a measuring tape, where a ladder was needed to reach the tree top was both inaccurate, difficult and dangerous.

(b) Total branches present included dead ones but not the abscinded ones. This was to show current crown structures and the number of branches per metre to show intensity of branching.

(c) Stem form or straightness, an important attribute of bole quality, was assessed as recommended by Andrew and Wright (1976) using a subjective score of straightness, in which the average score was 5, O for very straight and lO for very crooked or leaning stems.

(d) Multiple stems were defined as erect shoots half the height of the original stem, originating within the first lO cm above ground level. At an earlier stage in the work, the angles and proportion of sizes between the multiple stem and main stem were not considered important. These were later refinements considered.

(e) Height to the lowest living branch was taken as an indicator of

the tendency to self-prune, and so produce a good clean stem, which can readily be utilized.

(f) Diameter of the stem was taken at 10 cm from the ground, and at 1.3 metres (breast height) on tall trees, using a pair of precision calipers or a girth tape. Points of measurements were marked with paint as standards.

(g) Branching characteristics are numerous and variable, and may be genotypic or phenotypic. Common traits in *Betula* were :

(a) Forking : two co-dominant shoots which are almost equal in diameter, the diameter of one shoot had to be more than half the other to be considered a fork, and caused deflection from the mainstem axis to make a V-shape; the positioning (upper, mid, lower) was also specified, and the fork was also scored for symmetry i.e. on a score of 0 - 5. A low score implied that the limbs were unequal - a feature sometimes considered as 'attempted forking'. (An attempted fork may probably be overcome or dominated in the next growing season).

In the early stages of the work, the deflection from the mainstem axis when forking occurs was not recognised. This attribute, and multistemming, were the main parameters used for assessing observer bias in later assessments.

(b) Heavy branching: normally, proleptic branches make considerable diameter growth to qualify as a heavy branch, the branch diameter should equal or exceed 25 % of the main stem diameter. The annual occurrence of heavy branching, and forking were also recorded.

Other attributes, such as stem rot, presence or absence of adventitious shoots, decapitation or loss of apex from the leading shoot, presence of sylleptic shoots on current year

growth, stem basal sweep and angles of branches were also noted.

(h) Finally scoring of each tree relative to its neighbours was done on scale 1-10 for vigour and 1-5 for form. This enabled the removal of the effects of small-scale heterogeneity at the site. Flowering between the provenances was also assessed on a scale of 0-10 for the proportion of buds in flower. This was also done for flushing in the spring.

A diagramatic summation of 6 parameters (form, fork, height, branch per meter, stem number and heavy branch number) were used to construct a polygonal 'Tree rose' of representative trees within each of the provenances.

4.2.2 Determination of Dry Matter

100 trees, 50 from each provenance, were later cut down after the above measurements had been made, and 12 contrasting individuals were chosen for detailed assessment in the laboratory. Detailed measurements included the number, length and diameter of primary, secondary, and tertiary branches, forks, and the height of attachment on the main stem of these. After this, branches were cut off and placed in separate marked paper bags and put in the oven set to 98 ^{o}C for 4 days. On the first day, oven vents were opened to allow moisture to escape. Weights were recorded when no further loss in weight occurred.

4.3 Results

4.3.1 Assessor bias

There was substantial variation between observers in both the 1st and 2nd assessments of forking, with Observer A making 44 % more,

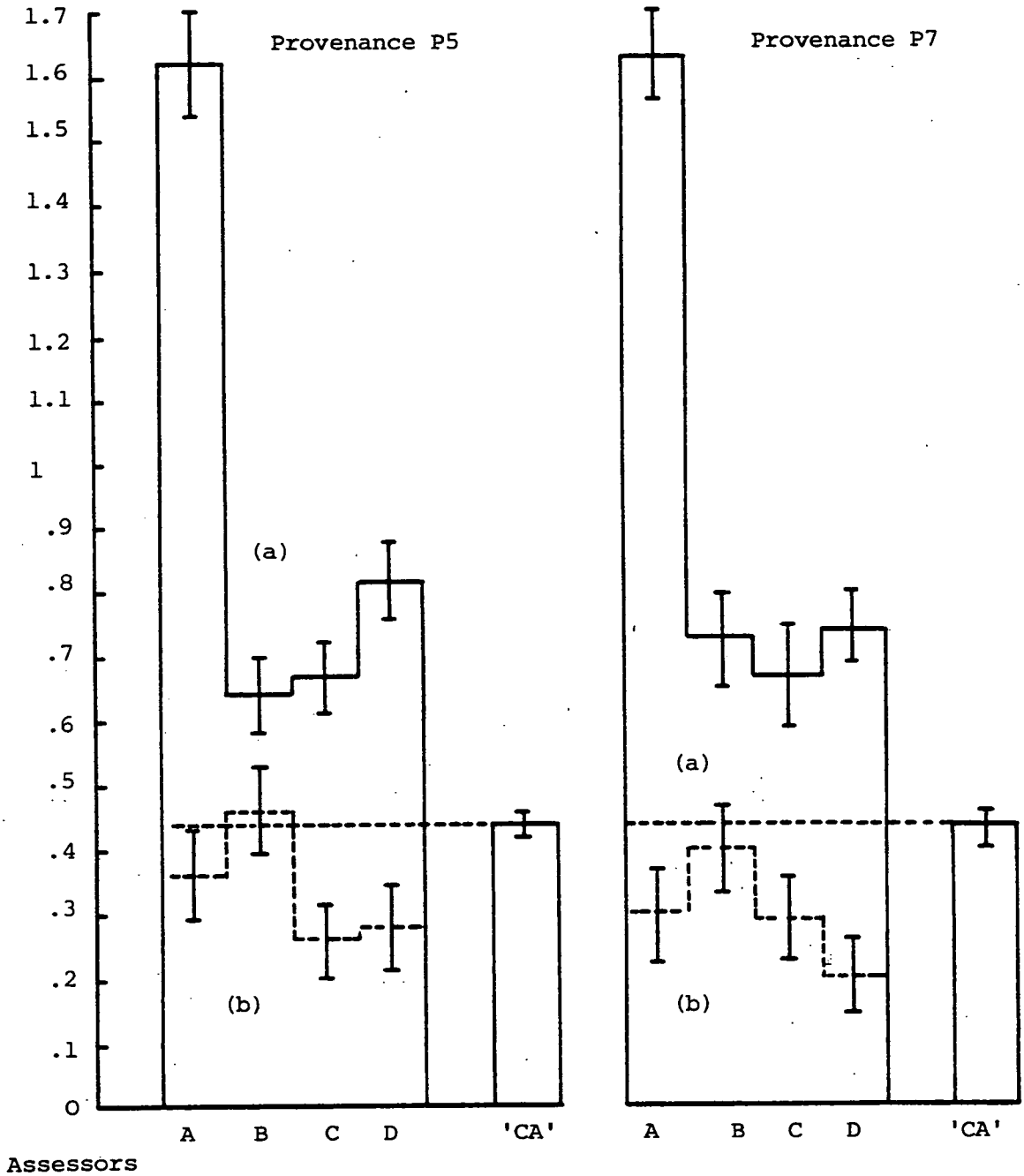
over the 3 other observers and 27 % more than the committee assessment ('CA') in the 1st assessment (Fig.12). Substantial differences were also apparent in the variance values between assessments and between observation made by each of the observers (Table 4) at the two assessments, this being improved on the second assessments.

Table 4 : Variations between assessors in fork assessment at 2 different assessments in *B. pubescens* at Farfield.

Observer	Prov.	No.Trees	Mean (forks per tree)		Variance	
			1st Assmt.	2nd Assmt.	1st Assmt.	2nd Assmt.
A	P5	50	1.60	0.36	2.44	0.27
	P7	50	1.63	0.30	1.80	0.29
	Mean		1.61	0.33	4.24	0.56
B	P5	50	0.64	0.46	0.27	0.33
	P7	50	0.73	0.40	0.36	0.24
	Mean		0.69	0.43	0.63	0.57
C	P5	50	0.67	0.26	0.50	0.19
	P7	50	0.66	0.28	0.42	0.20
	Mean		0.67	0.27	0.92	0.39
D	P5	50	0.82	0.28	0.60	0.24
	P7	50	0.74	0.20	0.55	0.20
	Mean		0.78	0.24	1.15	0.44
'CA'	P5	50	-	0.44	-	0.33
	P7	50	-	0.42	-	0.36
	Mean		-	0.43	-	0.69

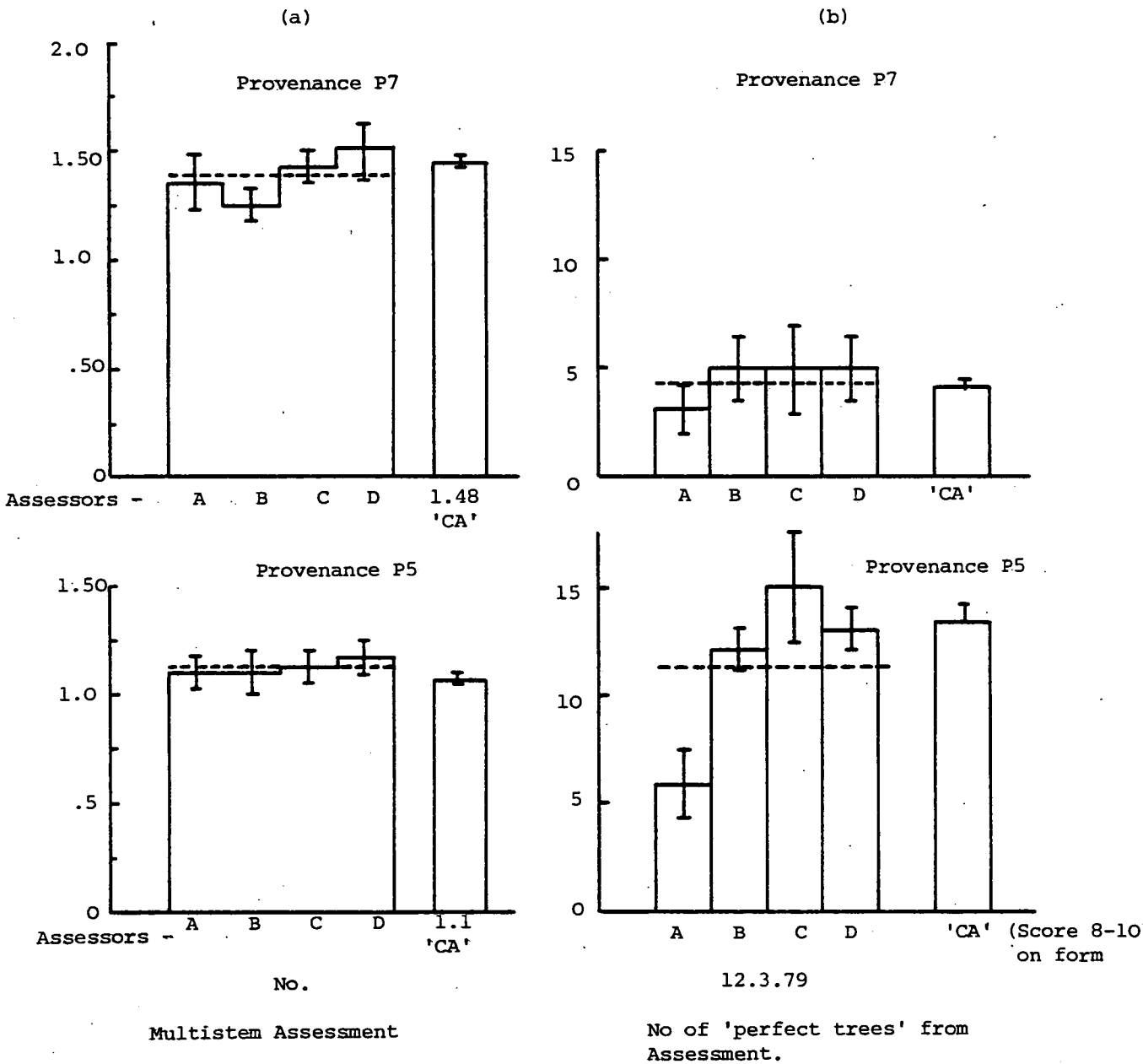
Where assessments were made once, viz: Multistem and perfect tree number scores (Fig. 13), no substantial differences existed between observers in multistem number and even when compared to the committee

Fig. 12



Histograms showing effect of assessor bias in fork assessment in 2 provenances of *B. pubescens* after 7 years growth in field. (Assessors A, B, C & D. (a) first assessment (b) second assessment, 'CA' Committee assessment after 2nd assessment)
Vertical lines denote Standard Error (±SE).

Fig. 13



Histograms showing effects of assessor bias in assessment of multisteming (a) and the total number of perfect trees (b) in 2 provenances of *B. pubescens* after 7 years growth in field. (Assessors A, B, C & D).
Vertical line denote standard error (±SE).

assessment. However, in the assessment of form, Assessor A differed significantly, giving a mean value 20 % lower for Provenance 7 and about 40 % lower in Provenance 5, compared to the other assessors.

4.3.2 Comparison of Provenance

Trees of the Scottish provenance (P5) were twice as tall as the Norwegian provenance (P7), the latter having 25 % more multistems, while the former had 46 % greater stem diameter at 1.30 m on main stem (Table 5a).

There were also substantial differences in branch characteristics between the provenances, with P5 producing 41 % more branches than P7, both in the heavy branch category and in the light branch category (Table 5b).

The variation in flowering between these provenances was also substantial (Table 6) with P5 scoring 5.7 while P7 had an average score of 0.25. This is a highly significant difference between these seed lots, and it is worth noticing that P7 produced only male flowers while P5 produced both male and female.

In flushing, (Fig. 14), P5 started producing new leaves in the spring, 3 weeks earlier than P7 and continued at a significantly faster rate. By October, observations in the field revealed that while P5 still bore leaves, P7 had shed its leaves.

4.3.3 Comparison of individual trees within each provenance

Large variations exist between individual trees in the diagramatic representations presented on Fig. 15. Here a summary diagram of the parameters: stem form, forking, plant height, stem number, branch diameter >10 mm and branches per meter of mainstem height allows a comparison between provenances and also comparison with hypothetical

Table 5(a) : Provenance differences in height, diameter, multiple stem production and form in *B. pubescens* 7 years after growing in field at ITE, Farfield.

	Provenance P5		Provenance P7	
	Mean	± SE	Mean	± SE
Height (cm)	323.0	7.0	186.0	4.1
Stem diameter at 10 cm	4.8	0.1	3.2	0.1
Stem diameter at 1.30 m	2.6	0.09	1.2	0.07
Stem number	1.1	0.03	1.5	0.06
Score of stem form straightness (0-5)	2.7	0.20	2.5	0.20
Score of mean tree form-subjective	6.2	0.27	5.08	0.27

Table 5(b) : Provenance differences in branching characteristics of *B. pubescens* after 7 years growth in field at ITE, Farfield.

	Provenance P5		Provenance P7	
	Mean	± SE	Mean	± SE
$\bar{X}$ Total Br. No.	42.1	1.18	25.0	1.2
$\bar{X}$ Total Br. No. above 1.3 m	17.34	1.07	0.46	0.37
$\bar{X}$ Total Br. Below 1.3 m to .30	24.02	.50	23.74	0.63
B. No. with Dia. 10mm - 5 mm (Lower tree)	13.26	.91	8.61	0.67
B. No. with Dia. 10 mm - 5 mm (Upper tree)	11.96	1.26	1.63	0.33
Primary Br. No. with Dia. >10 mm top	.82	0.19	0.06	0.03
Primary Br. No. with Dia. >10mm Lower	1.14	0.24	0.31	0.07
Primary Br. No. with Dia. >5mm Top	11.14	1.07	1.57	0.3
Primary Br. No. with Dia. > 5mm Lower	12.12	0.67	8.3	0.6
Primary Br. No. with Dia. > 5mm (upper & lower)	16.7	1.47	14.6	1.2

Fig. 14 The relationship between various environmental parameters and flushing of trees of 2 provenances of Birch (*Betula pubescens* Erhrh) at Farfield.

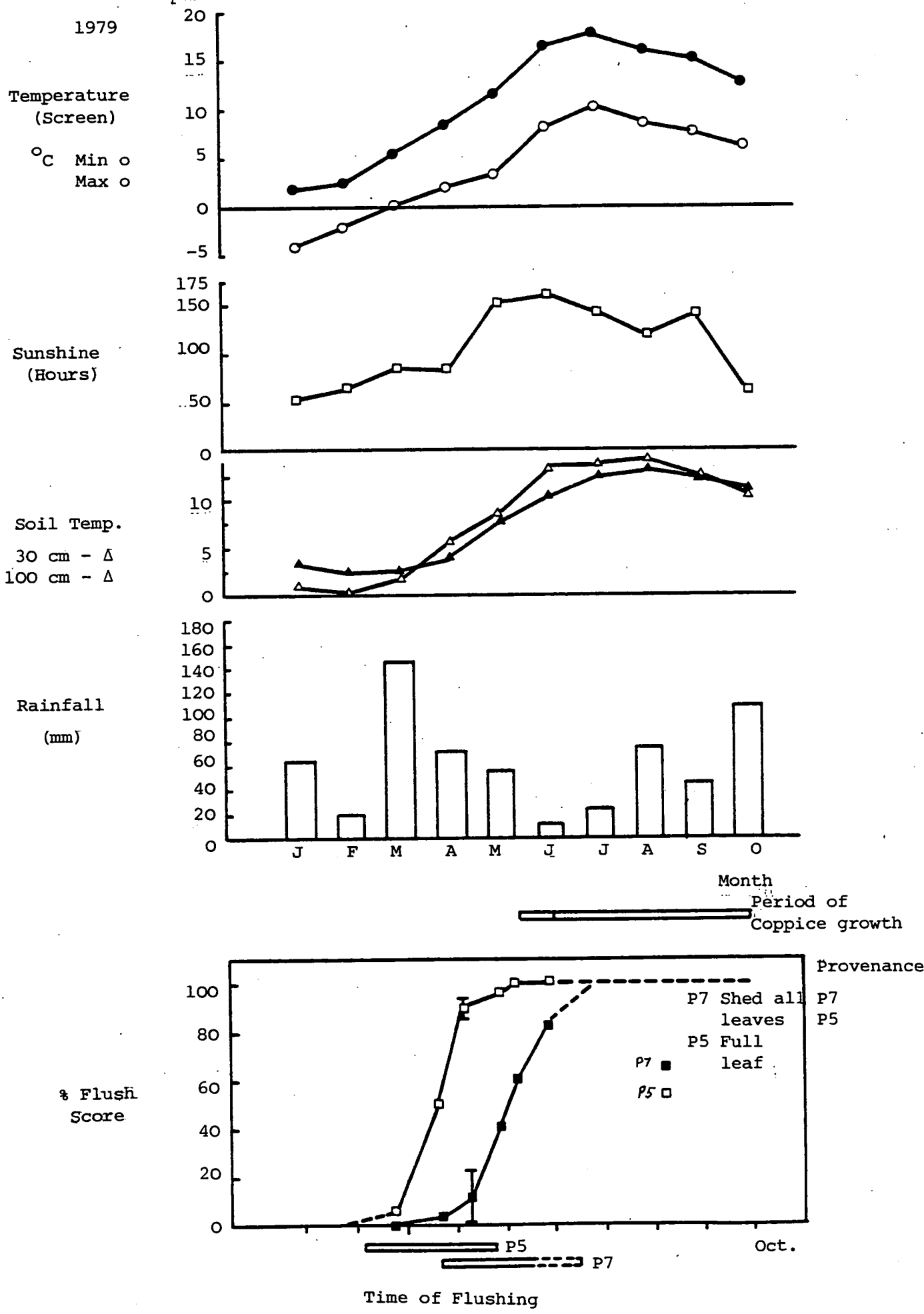


Table 6 : Variation in flowering of two provenances (P5, P7) of *Betula pubescens* Erhrh. 7 years after planting at 1 metre spacing at ITE, Farfield.
(Scored on scale 0 - 10 for the proportion of buds in flower), HLFB = height to lowest flower bud).
(Means of 50 plants per provenance)

	Flowering			
Provenance	$\bar{X}$	SE ±		
P5	3.0	0.47	♂	(78)
Inverpolly	2.7	0.37	♀	(77)
Alt. 46 m	78.4	.065	H.E.F.B.	
P7	.025	.021	♂	
Haukelifjell	0	0	♀	
Alt. 960 m	.05	.035	H.L.F.B. cm	

Fig. 15a

Polygonal graphs (Rose diagrams) of tree form in two provenances of *Betula pubescens*. Axes are always as defined in Fig. 15b(i).

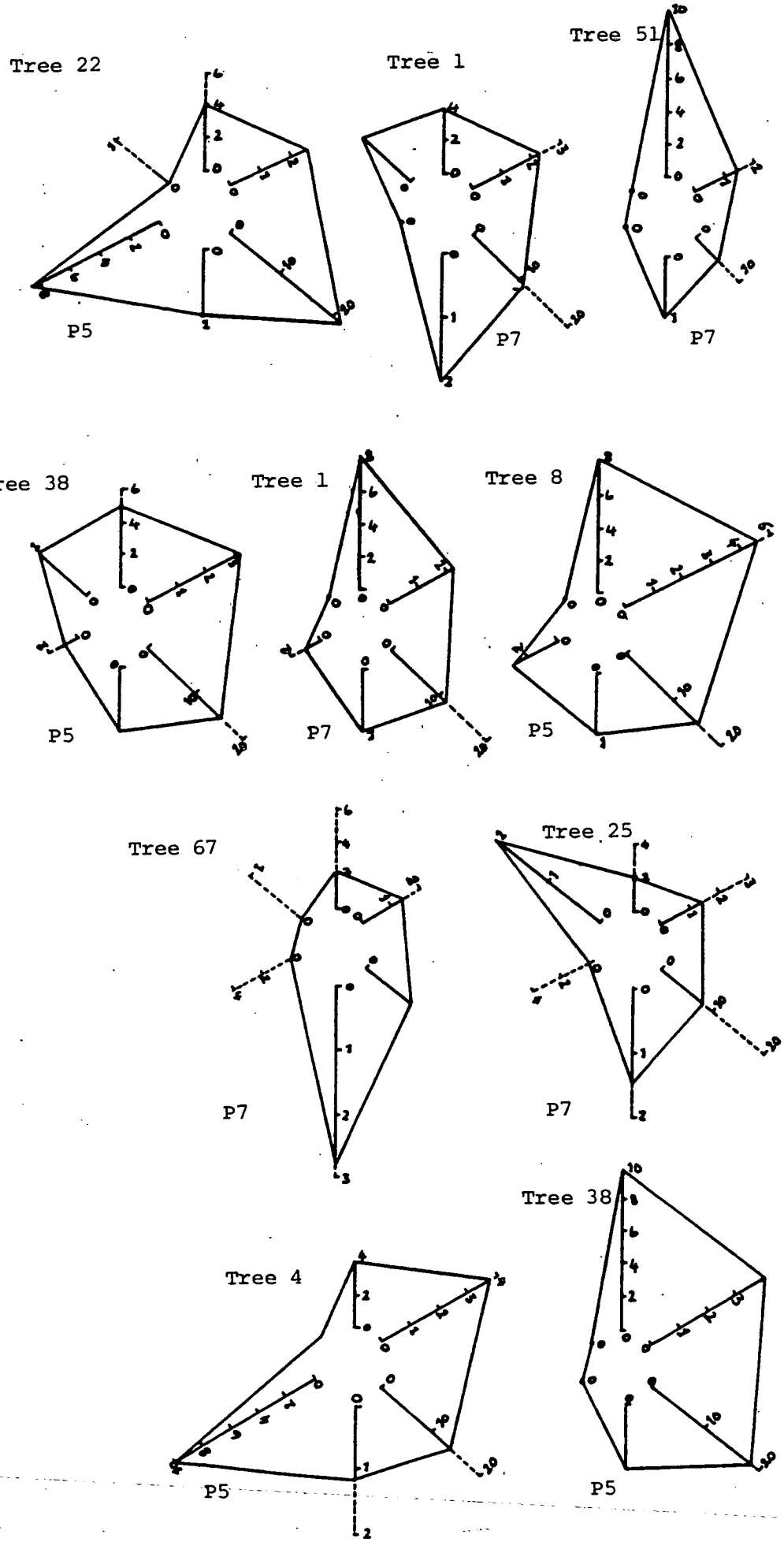
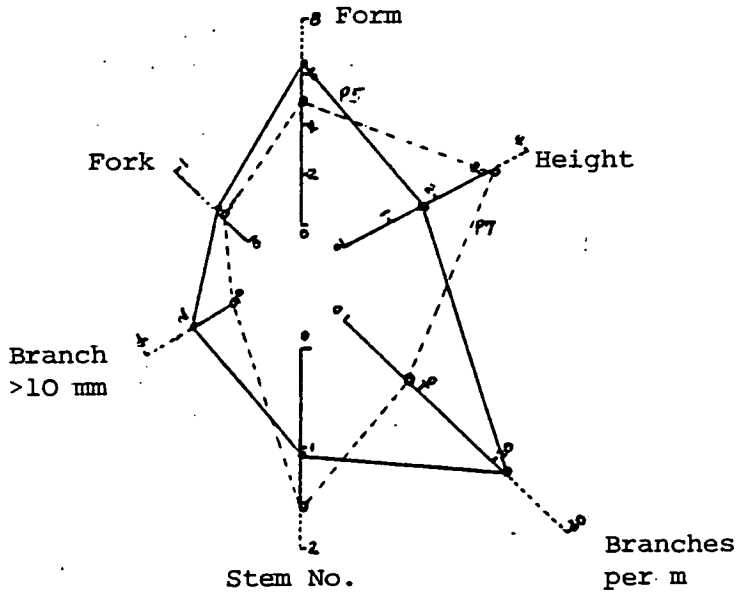


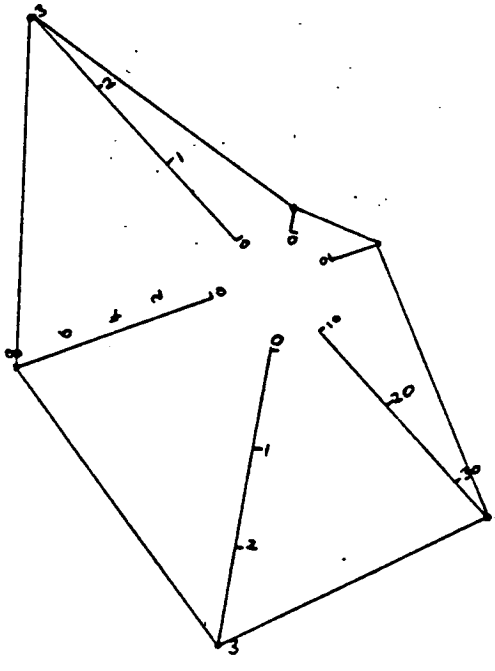
Fig. 15b

Mean tree form for provenances oP7 and oP5. Means of 50 trees per provenance.

(i)

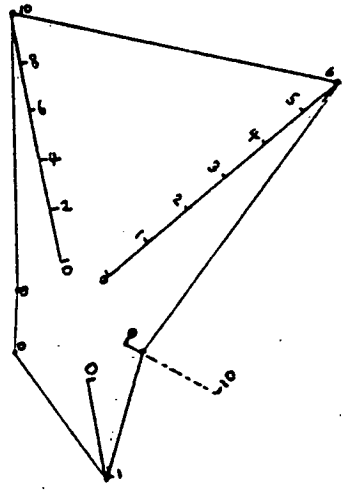


(ii)



Hypothetical 'Worst possible' Tree

(iii)



Hypothetical 'best possible' tree

forms for 'very good' and 'very bad' trees (Fig. 15a).

In the dry matter produced by 12 contrasting branching trees within these provenances there are substantial differences in all parameters investigated (Fig. 16). From provenance 5 (Scottish) trees 8 and 56 produced most stem dry matter, much exceeding the average of 936.8 g while tree 55 produced most in the other provenance (P7 Norwegian), this greatly exceeding the average of 148.4 g from trees in Provenance 7. The same order exists in Primary branch dry matter, but in P5, tree number 22 joins with high dry matter producers, a situation reflected throughout other parameters (secondary branches, and tertiary branches).

4.3.4 Coppice growth

There was substantial variation in coppice growth from the same 12 individual trees studied. As in the trees before they were cut down, there was more height growth in Provenance P5 (Scottish) than P7 (Norwegian), with Coppices 8, 56, and 22 being taller (1200 - 1400 mm) than others in P5 and Coppices 55, and 51 substantially taller (600 - 900 mm) than 31, 67 and 25 in P7 (Fig. 17a).

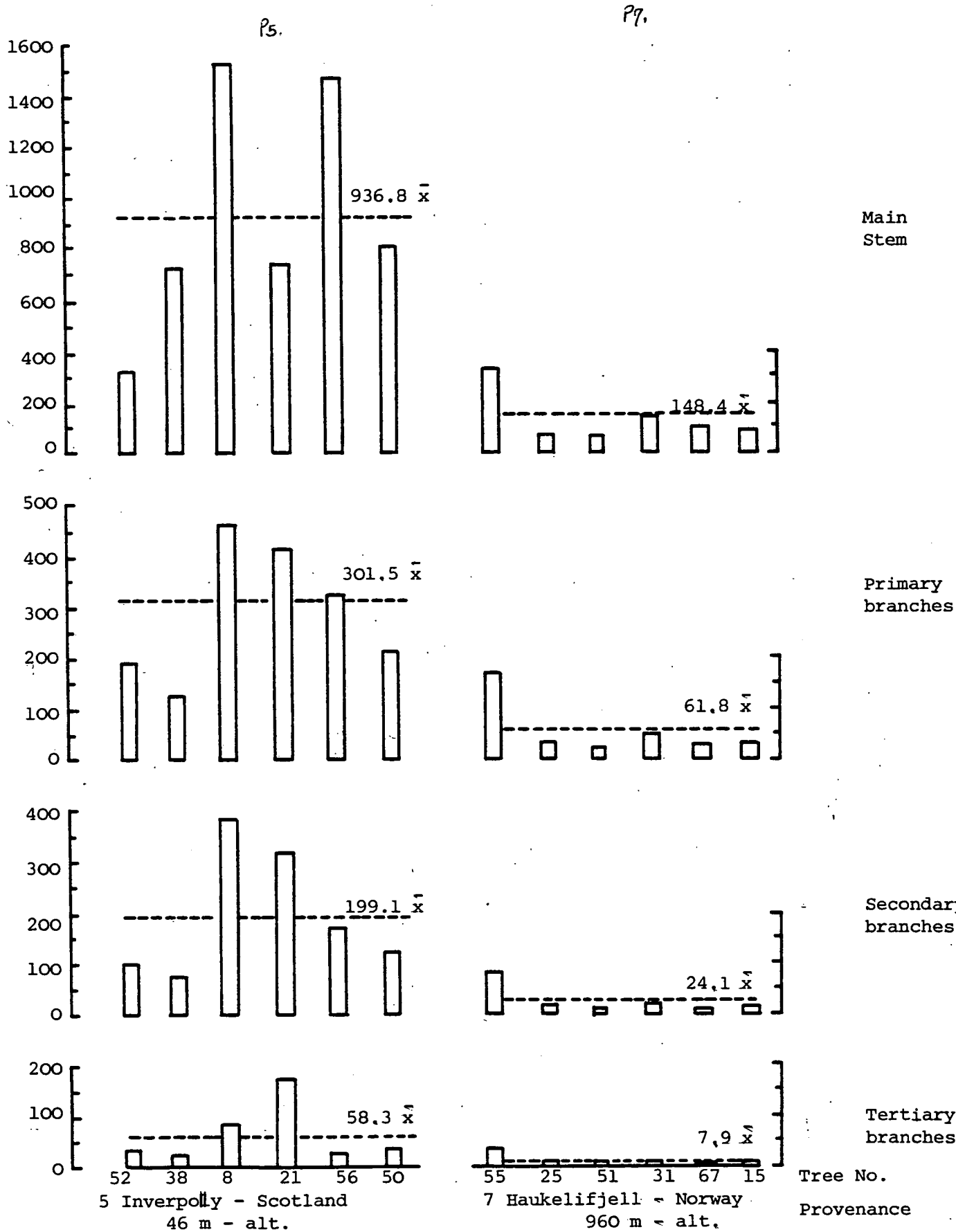
In branch production, there is substantially more primary and secondary branches in P5 than in P7 (Fig. 17bi,ii). Coppices from trees 56, 50, 22 and 8 produced more primary and secondary branches in P5 than those from trees 52, and 38, which produced least. Furthermore, in P7 coppice from tree number 51 produced greatest primary branches although not substantially different from those of other trees.

4.4 Discussion

4.4.1 Observer bias

The differences shown between observers (observer bias effect) in the subjective assessments of the parameters reported above clearly

Fig. 16



Variation within and between provenances of *Betula pubescens* in dry matter production and its distribution after 7 years growth in the field (Farfield-Scotland) Spacing = 1 m.

Fig. 17(a)

(Summer 1979)

Variation within and between two provenances of *Betula pubescens* in height growth of coppice shoots, from the individual original trees. (Numbers on figure indicate original tree number from each provenance).

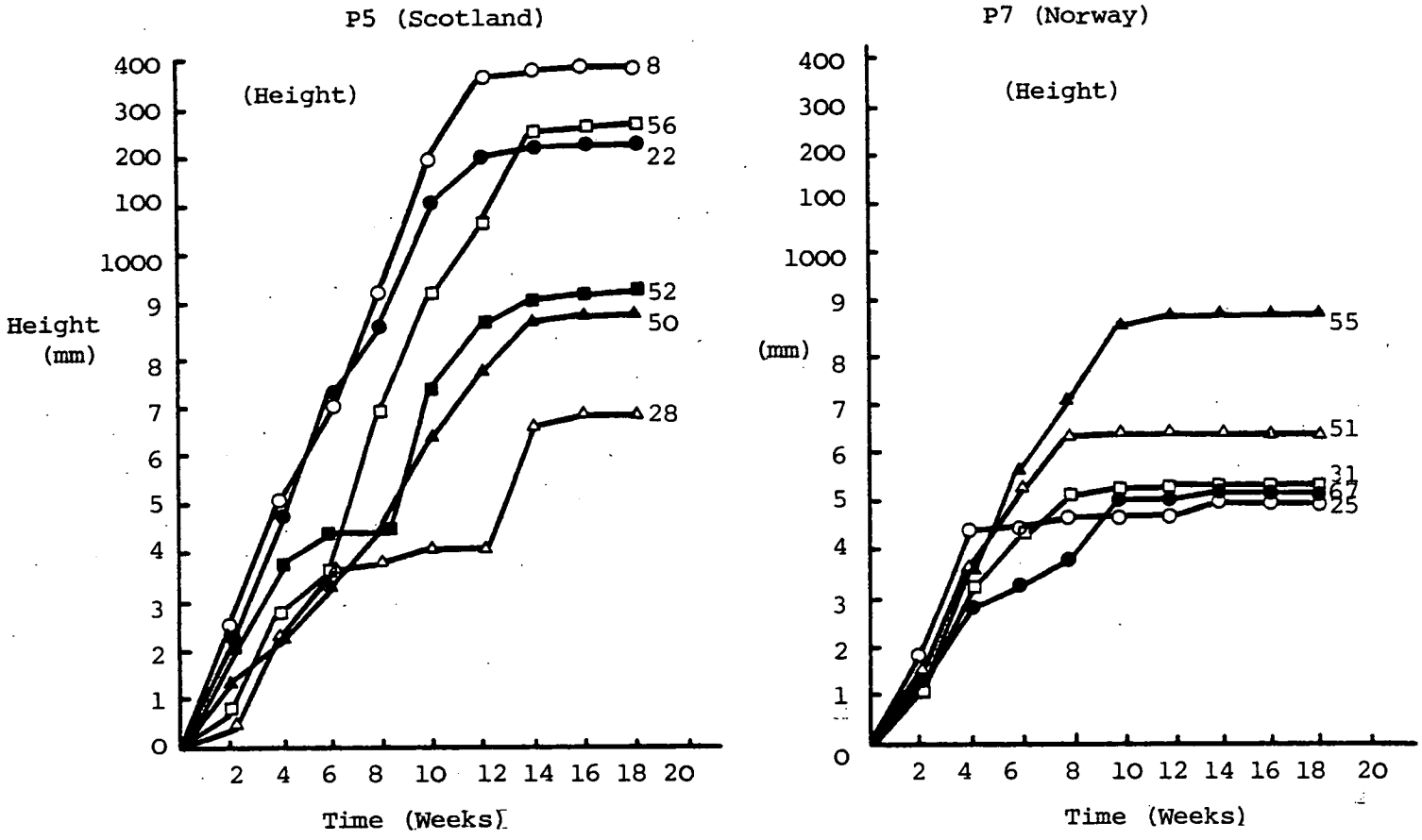
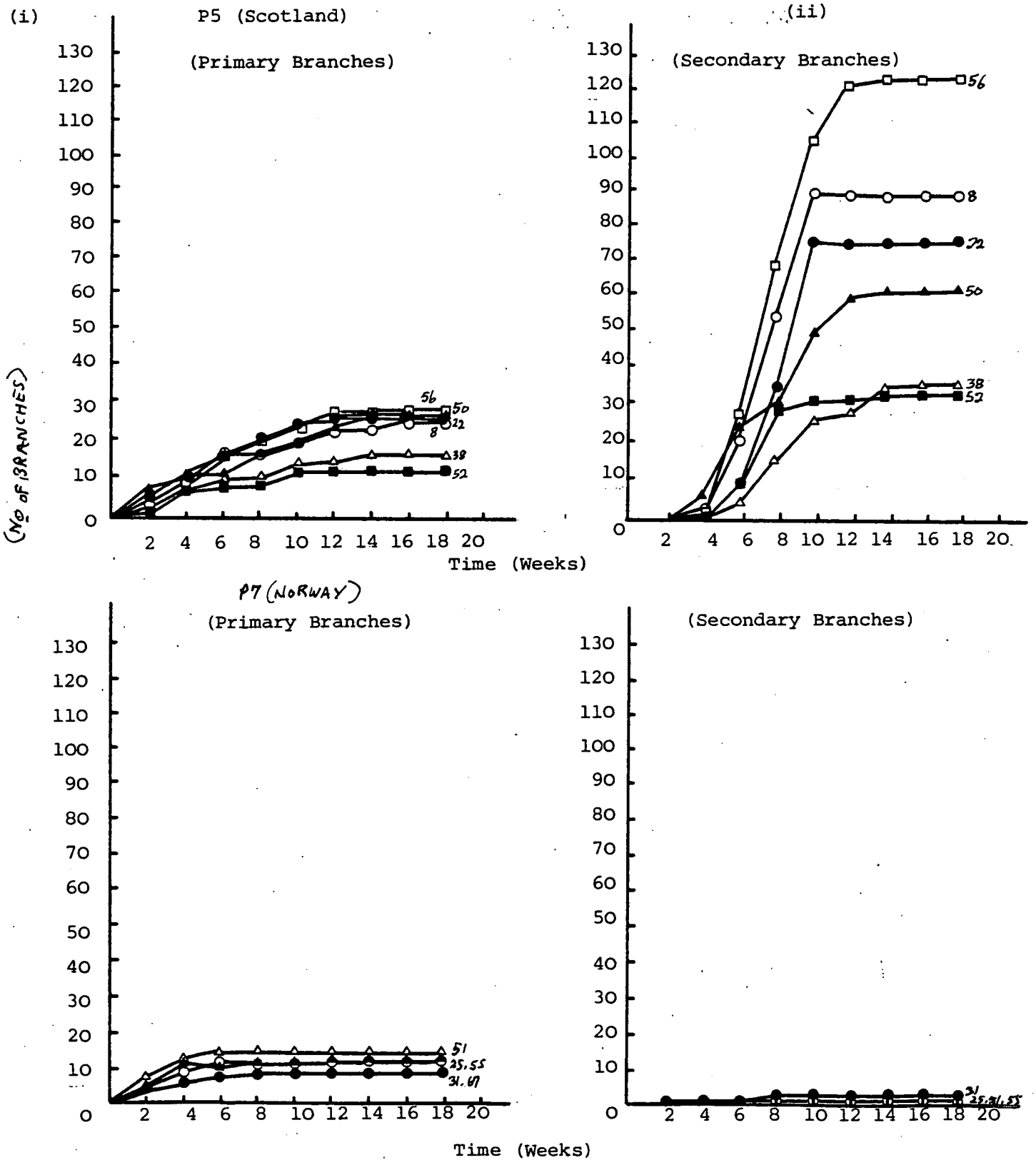


Fig. 17(b)

Variation within and between two provenances of *Betula pubescens* in branching characteristics of coppice shoots from individual original trees. (Numbers on figure indicate original tree number from each provenance).



demonstrated that when adequate rules are not available, observers may provide misleading data. This agrees with the findings of Bannister (1979) who with *P. radiata* demonstrated substantial assessor bias in the assessment of stem crookedness. It was also clear from this study that if the definitions of particular characteristics were not clearly and very strictly defined, different assessors scored trees very differently. Discussion between assessors often showed major differences in the observations of detail, in the understanding of criteria affecting tree form, and in their assessment of the importance of different characteristics. The formation of an agreed 'committee decision' was sometimes quite difficult; for example, in the assessment of a fork as opposed to a heavy branch. The identification of the mainbranch from the co-dominating fork branch was difficult when in some cases deflection on main stem was not easily visible.

However, subjective assessment is likely to be used in forestry for a long time hence, and indeed is practicable, when adequate guidances are given such as :

(a) Parameters to be assessed need to be perfectly identified and listed.

(b) Assessors selected need to be experienced in tree biology work and physically fit so as not to suffer from observer fatigue.

(c) Suitable assessment sheets need to be drawn up.

(d) Parameters should be assessed one at a time for all trees, guided by a universally-accepted and documented set of rules. This will ensure that local and international studies are comparable in quality and standard.

4.4.2 Within and between provenance growth differences

The differences between the provenances under study which are separated by only about ½° latitude, can presumably be attributed mostly to selection forces differing according to the altitude difference between the two origins (Inverpolly-Scotland, 46 m and Haukelifjell - Norway, 960 m). This was suggested also by Last (1976, 1977), who emphasised the associated changes in climate (temperature changing -0.5 °c per 100 m altitude) and soil. As might be expected from other provenance studies of widely distributed genera like *Betula*, e.g.*Betula alleghaniensis* from different latitudes (Clausen 1980), the growth characteristics most affected by altitude of origin were, height, branching and stem diameter growth, this agrees with the findings of Ying and Bagley (1976) in *Populus deltoides* provenances, where substantial differences between provenances from 7 sources were recorded in height, branching and stem diameter over 7 years; with the Mississippi provenance being least, and the Missouri provenance best in these parameters. In explaining this difference, it is also likely that soils at the different altitudes differ, this being supported by the works of Mason and Pelham (1976) in *Betula pubescens* and *B. verrucosa*, where genotypic variation in nutrient uptake of different populations was reported. Last (1977) on the other hand, earlier attributed differences in growth between these provenances i.e. (P7 - Norwegian) to less growing time; an adaptation to minimise risks of frost damage in its native habitat. This is substantiated by the observations in this study (Fig. 14) in the differences in flushing and the early leaf drop in Provenance 7 (Norwegian). This agrees with Sharik (1970) who reported in yellow birch provenances that growth initiation and cessation took place earliest in high-elevation populations in Vermont and New Hampshire

and latest in low-elevation populations in South-western North Carolina and South-Western Virginia in U.S.A., infering that temperature changes with altitude at their origins was involved.

This type of variation is similar to that found in latitudinal variation in a wide range of species such as in *Prosopis* spp. (Leakey, and Last 1980). The inter-provenance variation in flowering reported earlier, is like that in Yellow birch: Clausen (1976, 1979 and 1980) reported early flowering in provenances of the northern origin. He also reported the occurrence of bisexuality in some provenances in their early stages of flowering, being effects of origin, which in the case of the provenances under study, probably reflects differences in temperature as a result of the altitude of origin.

The individual trees making up the provenances in this study were themselves highly variable as one might expect in an outbreeding species. It was the assessment of this variability which probably accounted for most of the assessor bias earlier discussed. However, having arrived at firm definitions of the characteristics which best illustrate the differences between individual trees within populations, the object of this study was primarily to try and select those individuals which have the greatest potential for commercial forestry and secondarily to observe ways in which individual trees differ. With this in mind, it was interesting to observe substantial variation between individual trees in their dry matter production, (Fig.16), where trees 8, 56 (P5) and tree 55 (P7 produced most stem dry matter. Trees 38 and 50 which produced less primary branch dry matter are likewise good candidates in selection for improvement of this species. This finding agrees with that of Clausen (1973) who reported in *Betula alleghaniensis* substantial provenance variation in dry matter production between 5 sources in mean stem and branch mean dry weight

at 2 years. It was also clear from the present study that while it is relatively easy to see visual differences between individual trees, it was relatively difficult to quantify these and present them graphically in such a way that trees with particular attributes, and more importantly, those with many desirable characters were clearly visible.

In Fig. 15a and b, where 'tree rose' diagrams are presented it is clearly practicable to identify the general quality between these provenances. Furthermore decisions also have to be made as to whether certain undesirable characteristics are of genetic origin or whether they are responses to chance damage, like the predation of leading shoots by birds, insect pests or frost damage. To try and develop a greater understanding of the processes leading to, for example forking, and branching, selected trees were felled and the coppice regrowth studied to observe the genotype re-expression in singled coppice shoots. The variation between the coppices from the individual trees studied showed similar variability and ranking to that of the original trees (see Fig. 17a and b), this agreeing with the findings of Clausen (1972) with Yellow birch progenies.

Finally the knowledge gained from this study was of considerable value in deciding how subsequently to assess the clonal experiments of *T. scleroxylon* in Nigeria, which form an important part of this thesis.

4.5

THE DECAPITATION TEST

The concept of the decapitation test as a measure of apical dominance in *T. scleroxylon* was first tested by Leakey and Longman (ODA Annual Report 1976; and paper in press). The present study develops this concept and investigates the possibility of establishing a predictive test for branching.

Leakey and Longman found that following decapitation many axillary buds start active growth (the exact proportion varying between clones) and that subsequently one shoot, normally the top one re-establishes dominance. Thus it is possible to identify 2 Phases :-

(i) The sprouting phase, which usually reaches its peak 3 - 4 weeks after decapitation, and

(ii) the phase of dominance re-establishment (Fig. 18).

It is postulated that the mechanism for dominance imposed by the new lateral shoots is probably the same as that of the original shoot apex and the environmental and endogenous influences are the same.

Thus plants with weak apical dominance could be expected to release many lateral shoots following decapitation.

Fig. 18

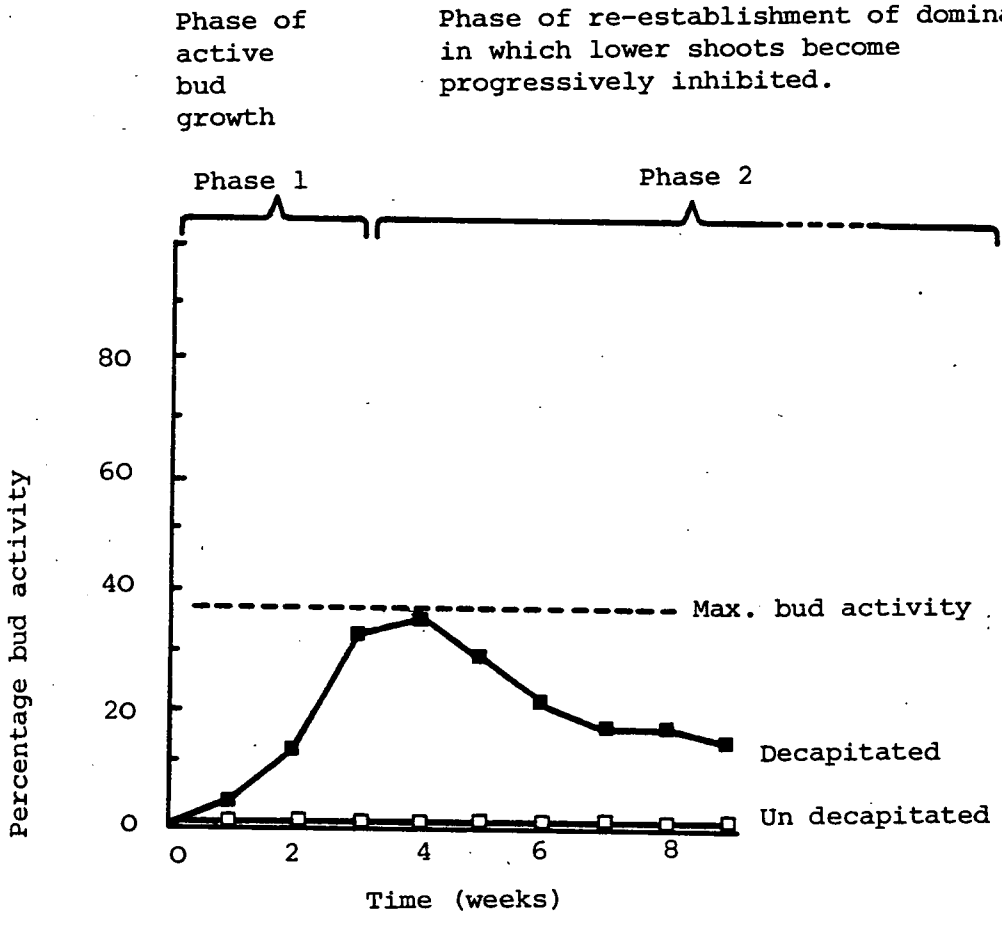


Diagram showing a typical response to decapitation in which inactive axillary buds first sprout and then subsequently become re-inhibited.

SECTION 2

THE DECAPITATION TEST : A MEASURE OF APICAL DOMINANCE

To measure the strength of apical dominance in different clones, the plant apex was removed, subsequent bud activity followed different patterns in different clones, and from these patterns were made inferences about apical dominance.

However, before clonal differences could be investigated it was necessary to examine effects of the environment, so that subsequent tests could be suitably standardized, hence revealing clonal variation.

CHAPTER 5

FACTORS AFFECTING APICAL DOMINANCE IN DECAPITATED PLANTS

5.1 General Introduction

To remove correlative inhibition, different workers have used various methods, including physical restriction of apical growth (Mulder, 1941; Leong *et al*, 1976) by covering of the apical bud, chemical, nutritional, or environmental treatments (Phillips, 1975), and the surgical removal of the apical bud or shoot(decapitation), which Snow (1925) first practiced and whose effect, Thimann and Skoog (1933, 1934) demonstrated could be reimposed by the application of auxin to the decapitated stump.

Hillman and Yeang (1979) considered decapitation to be the most effective and simplest method of removal of correlative inhibition. This view is opposed by Tucker and Mansfield (1972)and Tucker (1974) who prefer light treatments, as opposed to decapitation, in which the manipulation of the spectral balance in the red/far-red region (through its effects on phytochrome) was said to alter the endogenous hormonal balance within the plant, hence influencing axillary bud inhibition. As this light effect, and Tucker and Mansfield's measurements of ABA levels designed to support the above claim (Tucker and Mansfield 1972), have not been confirmed, their findings may have been an artefact of their technique.

Thus, in this thesis, the surgical removal of the top 2 nodes (decapitation) was used in the study of 'apical dominance' in the monopodial, unbranched and juvenile cuttings of *T. scleroxylon*.

As discussed in Chapter 2, numerous factors are known to influence apical dominance. Although many aspects are poorly understood, the factors involved may be broadly classified as either plant factors (Phillips 1971; Hartung and Funfer 1981) or environmental (a) aerial,

(b) edaphic, (McIntyre 1971a,b; 1973; Tucker and Mansfield, 1973). In this type of investigation, inadequate attention has often been given to the conditions under which experimental plants are grown (Shein and Jackson 1971), the micro-environments around the plant buds (Cutter and Chiu, 1975) or season (White 1976), all of which may have led to difficulties in experimental interpretation.

The experiments presented here investigate the effects of various factors on apical dominance, in order to identify the conditions required to reveal the greatest genetic variation and so establish standardized conditions for the screening of large numbers of different clones.

5.2 PHYSIOLOGICAL STATE OF PLANTS

The physiological state of plants is likely to substantially affect growth and most plant processes. In this part of the work, the effects of defoliation and plant size are examined in decapitated plants of a range of *T. scleroxylon* clones, to assess the effects of these physiological or plant factors on axillary bud activity; a measure of apical dominance.

5.2.1 Effect of Defoliation on Axillary bud activity in Decapitated Plants

5.2.2 Introduction

Young expanding leaves are known to contribute to the inhibitory effects of apical buds [redacted]. This has been attributed to the effects of their endogenous auxins (Snow 1929; Thimann and Skoog, 1934) [redacted] while Dostal (1926) [redacted] related this to the assimilatory effects of the lamina. Champagnat (1955) on the other hand, in his experiments with Lilac (*Syringa vulgaris*) concluded that the complex system of older leaves along the stem in woody species, rather than the young expanding ones contribute more to the inhibitory effects of the apical buds. Opposing this view, Güvern and Varder (1977)

concluded that the character of the inhibitory effect varies according to developmental stage, and the point at which the leaves are inserted on the stem and that younger leaves affect apical dominance more than older ones.

5.2.3 Materials and Methods

The effects of various amounts of defoliation on 'apical dominance' of juvenile clonal cuttings of *T. scleroxylon* was investigated in FRIN (Nigeria) from July to September 1979. 32 plants of each of 5 clones (392/9, 404/1, 410/20, 431/9 and 431/20) were chosen, whose culture and origins had earlier been described in Chapter 3.

Their heights varied between 45 to 55 cm, and had an average of 14 nodes, with 8 - 10 fully expanded leaves.

To test the effect of different types of defoliation, 8 ramets of each clone were allocated to 4 treatment levels, viz: complete defoliation, and partial defoliation in which, 2, 4 or 6 leaves were retained. They were then allocated randomly into 4 blocks of 32 plants.

5.2.4 Assessment of bud activity

All axillary buds and lateral shoots were examined weekly following decapitation and shoots were considered to be actively growing if their length increased >2 mm week^{-1} (Leakey and Longman, in press).

5.2.5 Data analysis

Bud activity was calculated, as the proportion of all axillary buds sprouting, and the standard error (±SE) of the means were calculated according to the formula of Bailey (1959), p 24.

$$SE = \sqrt{\frac{(\frac{x}{n})\ (1-\frac{x}{n})}{n}}$$

where x is the number of buds active at a time, and n is the total number of buds.

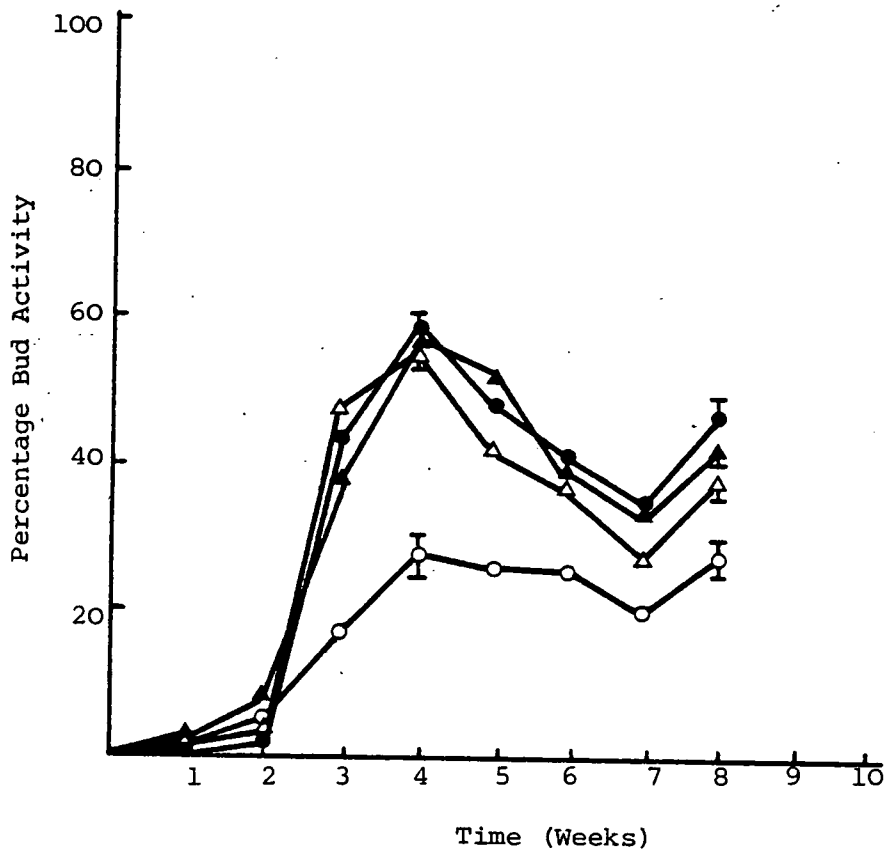
5.2.6 Results

Different degrees of partial defoliation produced essentially identical responses, but total defoliation resulted in a much lower percentage bud activity (Fig. 19). Plants with 4 and 6 leaves displayed the highest bud activity at most assessments, with no mortality, unlike in the total defoliation where 20 % of plants died. Clones differed considerably in their response to different degrees of defoliation (Fig. 20). The effect of complete defoliation treatment in clone 404/1 was only overcome after the 5th week, it took clone 410/20,7 weeks, while clones 431/9 and 431/20 never recovered. Clone 392/9, on the other hand, was completely insensitive to the number of leaves retained, thus differing in this respect from other clones.

5.2.7 Discussion

The presence or absence of leaves had important effects on the ability of buds to sprout following decapitation, a result confirming the observations of Leakey and Longman (1976; in press) who also found that bud activity was lower in fully defoliated plants than in those partially defoliated. Correlative effects of leaves have also been reported by Guven and Varder (1977) in *Phaseolus vulgaris*, who emphasised the importance of the position of leaves, and concluded that leaves contributed endogenous auxins for correlative bud inhibition, thus agreeing with the report of Thimann and Skoog (1934). The plant mortality in the total defoliation treatment and the lower overall bud activity may be purely an effect of the reduction in available assimilate. A consideration of the variation between clones

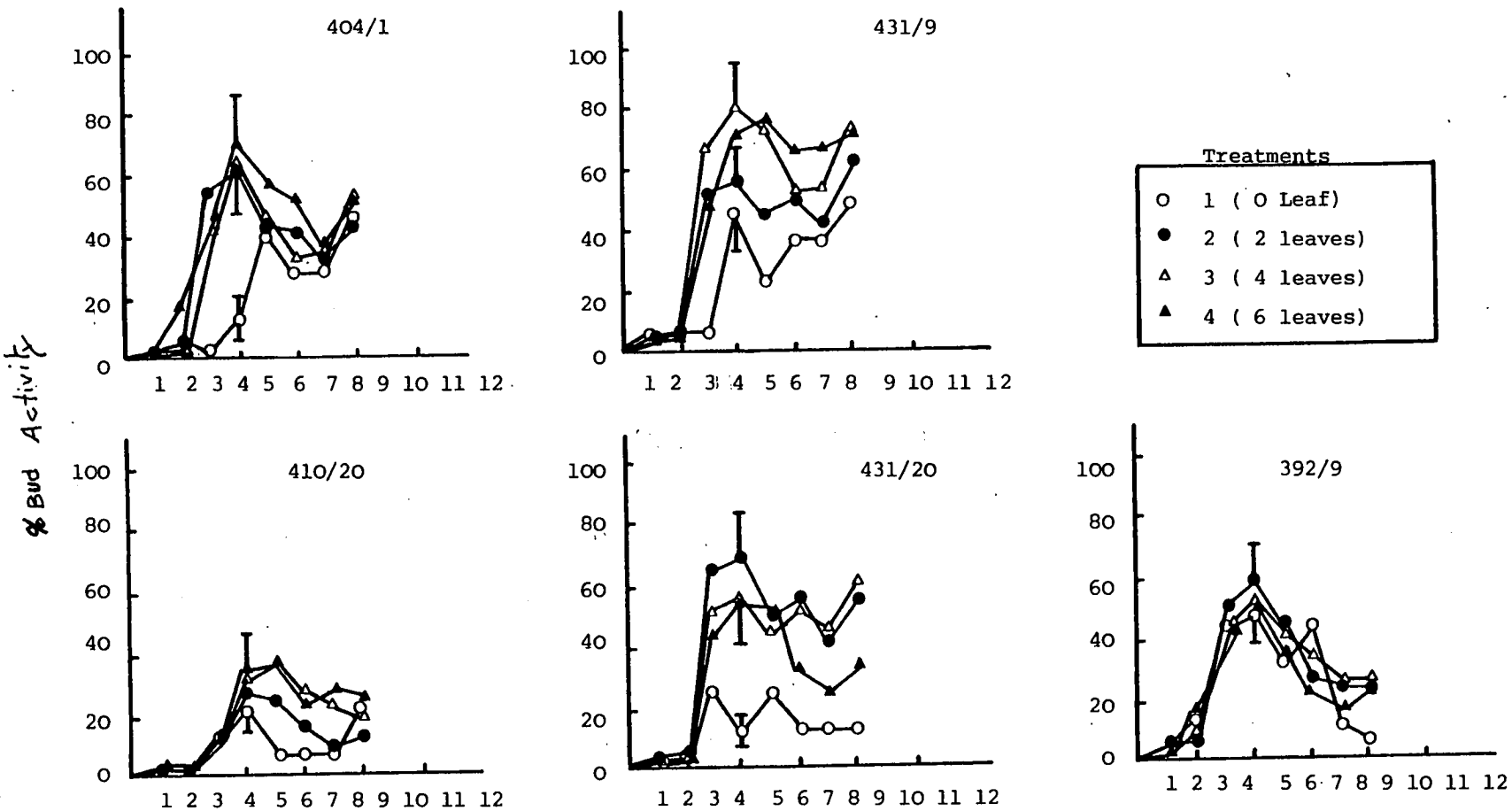
Fig. 19



Effect of the number of leaves retained on bud activity of decapitated plants of *T. scleroxylon*.

(O - No leaves, Δ - 2 leaves, ● - 4 leaves, ▲ - 6 leaves.
Mean values of 8 x 5 plants per treatment are presented with the corresponding standard error for weeks 4 and 8.)

Fig. 20



Variation in bud activity, between decapitated clones of *T. scleroxylon* subjected to various amounts of defoliation (O - No. Leaf, O - 2 leaves, Δ - 4 leaves, Δ - 6 leaves left) Mean values of 8* ramets per clone are presented.

* 6 for No leaves

suggests that some of the variation in response to defoliation may be due to the levels of stored assimilates (clone 392/9 is almost unaffected by total as opposed to partial defoliation, and so, presumably, possesses a large carbohydrate reserve). Although the effects are not statistically significant, there is a progressive trend of enhanced bud activity with increasing leaf number. Although not tested here there has also been a suggestion that more than 6 leaves may have deleterious effects on bud activity (Leakey and Longman in press), for in three of these clones, bud activity peaked when only 2 or 4 leaves were retained. This is consistent with the suggestions of Champagnat (1955) in Lilac that older leaves may have some influence on the correlative inhibition of buds. As clones differ in their response to defoliation, some appearing to be much more tolerant, as indicated by the time taken for some clones to recover, this may perhaps reflect the fact that subsequent production or activity of leaf area differs between clones.

The data suggests that if decapitation is to be used as a method of assessing the genetic variation in the 'strength' of apical dominance in *T. scleroxylon* clones, about 4 leaves should be retained, so maximising the response. Leafless plants should not be used, as this seems to impose severe constraints on subsequent bud activity.

5.3 Effects of plant height and point of decapitation on axillary bud activity.

5.3.1 Introduction

Although Phillips (1975) suggested that all vegetative buds on a plant possess essentially equal developmental potential, Cutler and Chiu (1975) demonstrated that lateral buds along the stem of intact plants respond differently to different factors which break apical

dominance; thus indicating some endogenous hormonal gradients in the shoot and possible differences in relation to tissue age and state of the buds. This is probably also the case in decapitated plants, but the experiments of Kulasegaram and Janakiram (1970) with tea (*Camellia sinensis*) suggested that although the effect of node position was significant in the early stages, it did not conform to any definite pattern, and the differences disappeared as the plants grew older.

The present study investigates the effect of plant height and the age or position of *T. scleroxylon* buds on the activity of axillary buds following decapitation at ITE in Scotland.

5.3.2 Materials and Methods

24 plants of clone 144/9 were chosen; 16 of them were 110 cm tall whilst the remaining 8 were only 65 cm tall; they had 23 and 15 nodes respectively and 4 leaves were retained on each of them. All plants had been grown under similar conditions, the differences in height reflecting only their time of propagation.

Of the tall plants, 8 were left at their full height while the remaining 8 were cut down to 13 nodes to bring them to about the same height as the small plants, thus having at their tip unlike the other 2 batches, nodes slightly older.

Thus experimental treatments included:

(i) Tall plants (T)

(ii) Short plants (S)

(iii) Tall plants cut short (T/S)

On 12-11-79, the same day that plants were selected, decapitation was done by the removal of 2 uppermost nodes for treatments T and S while treatment T/S was decapitated by the removal of 10 nodes. The treated plants were now randomly allocated into 3 blocks and short plants were stood on large inverted pots to bring all plants to the

same height and to prevent shading between them. Assessment was made of bud activity (>2 mm week^{-1}) at weekly intervals, as well as the mean shoot and leaf production at the end of the experiment (15-1-80).

5.3.3 Results

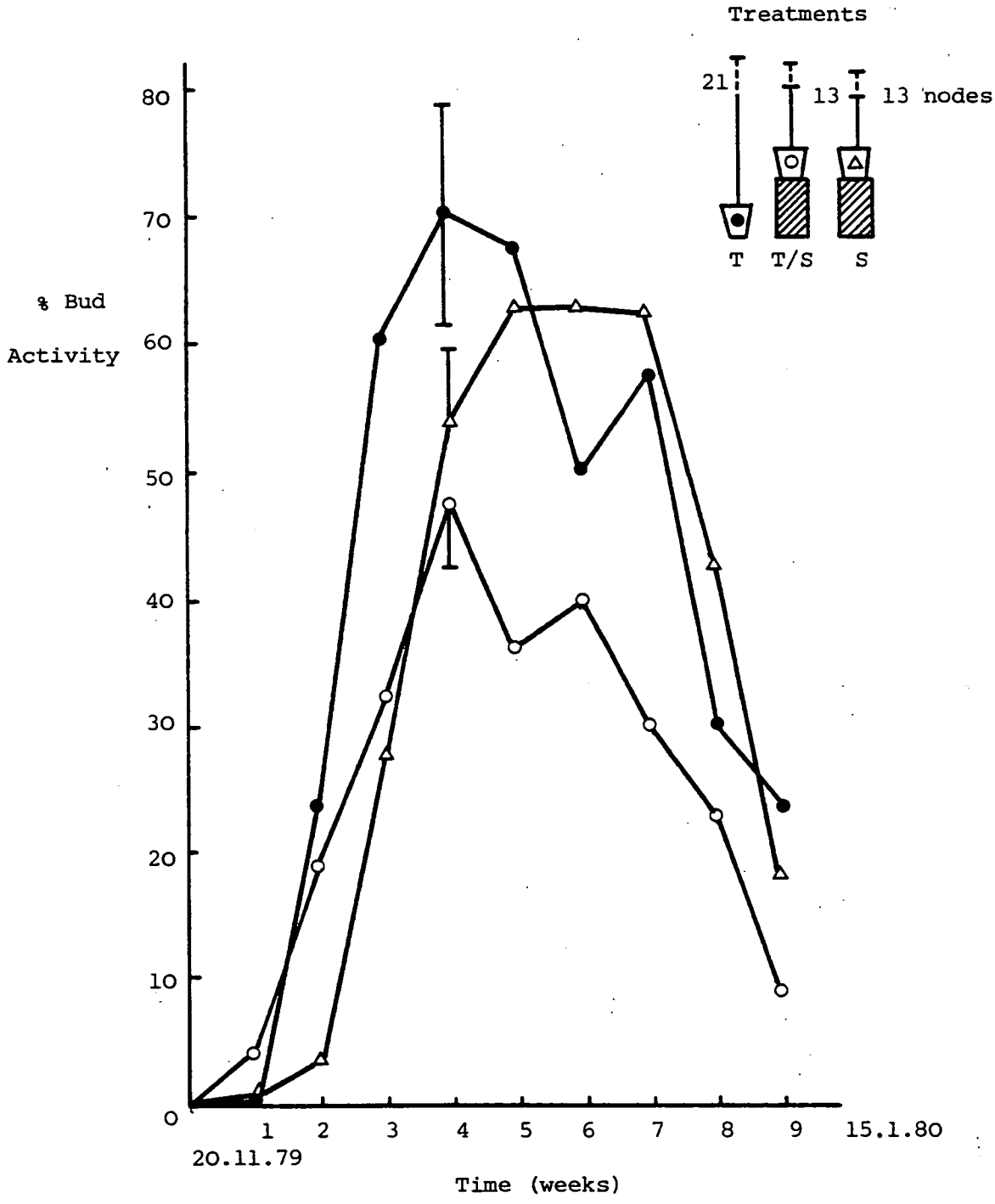
Bud activity following decapitation was greater in the plants from which only the top 2 nodes had been removed (T,S) than those which were cut down shorter (T/S), the greaterst response (after 3 weeks) being in those which were tallest(Fig.21). There was, however, a general similarity in the rate and pattern of increase in the early bud outgrowth and in the reassertion of dominance. There were also statistically significant differences between all treatments, tall plants producing the longest shoots when top decapitated but shortest when severely cut back (Fig. 22). There was however no significant difference in the mean number of leaves produced by plants under all treatments (28 ± 2.3, 30 ± 4.1 and 34 ± 7.3 respectively).

5.3.4 Discussion

The overall pattern of bud outgrwoth is similar in all treatments and also to that recorded in other species, with a release phase, and a re-establishment of dominance phase. In *T. scleroxylon* and as confirmed by the plants in the present study, after the first phase, basal buds are first inhibited and gradually, the upper ones are affected until only a few remain active. Leakey *et al*, (1978) suggested that apical buds in *Agropyron repens* multinode fragments normally have a competitive advantage over basal buds for rhizome carbohydrate reserves, and hence the dominant shoot is usually one of the apical nodes. The same applies in *T. scleroxylon*.

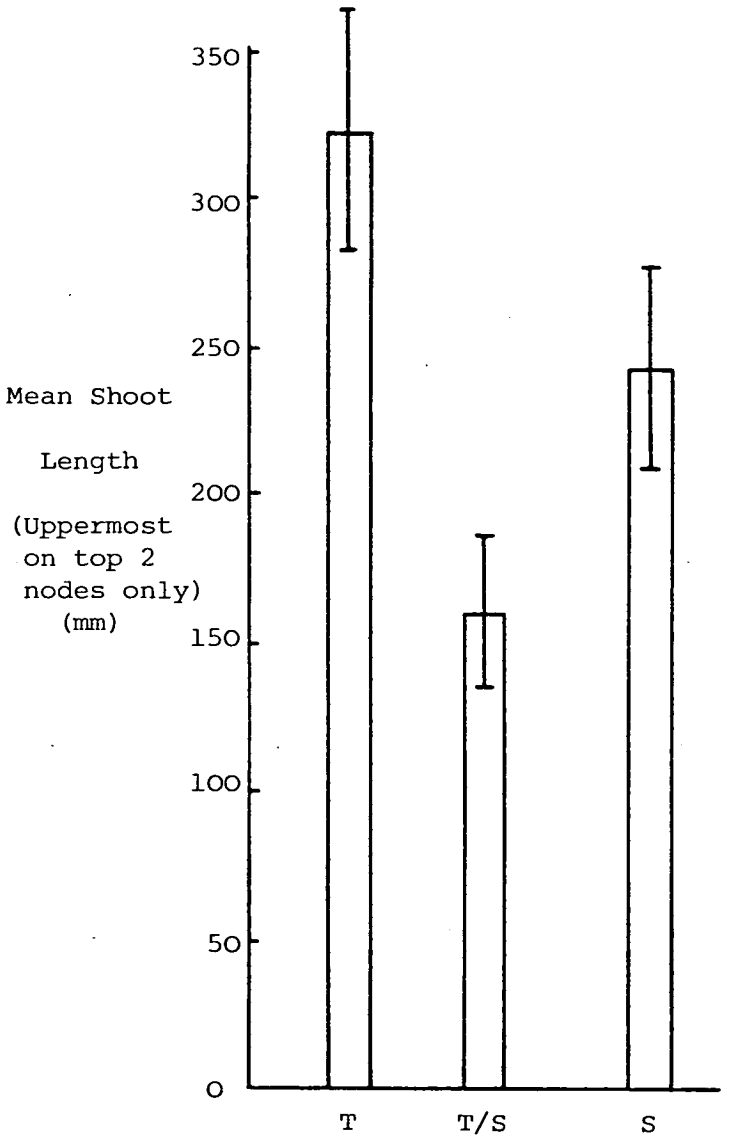
Recently, Leakey and Longman (1979, in press) demonstrated that after single 1,10,20 or 25 node decapitation of 30 node *T. scleroxylon*

Fig. 21



Effect on plant height and the number of nodes removed on bud ongrowth of decapitated plants of *Triplochiton scleroxylon* clone 144/9. (means of 8 plants with standard error for Week 4

Fig. 22.



Effect of plant height and the number of nodes removed on the growth of the top 2 lateral shoots from decapitated plants of clone 144/9 (Vertical lines = ±SE, T = Tall plants, T/S = Tall plants cut short, and S = Short plants).

plants, the greatest mean number of branches was in the 29 node plants rather than in the 10 node ones, although percentage axillary buds sprouting was similar in all plants regardless of their height after decapitation or number of nodes removed. They also showed that mean shoot length was greatest in plants of medium height rather than in the tall ones. The results presented here agree with those of Leakey and Longman (1979, in press), in that 2 node decapitated plants (T and S) also produced the greatest bud outgrowth in this experiment; but disagrees with them as regards shoot production, as in the present work, the 2 node decapitated plants produced greatest mean shoot (although only the first top two axillary buds were considered). The reasons for this disparity may be as already suggested in their work :- that limits to shoot growth was probably being imposed by pot size, and shading, which was prevented in this test by raising short plants to an equal level with the tall ones. The possibility of the involvement of stored reserves in the behaviour of the tall but cut short plants (T/S) may also be important, as the younger shoot in the top of the short and tall (S, T) 2 node decapitated plants may also have younger and more photosynthetically active leaves. Furthermore, these results indicate that age of the buds may exert an important influence on the hormonal relations of the system, thus agreeing with the conclusions of Cutter and Chiu (1975).

The practical conclusions from this experiment are that plants respond to decapitation in a matter not affected by how tall they are, thus when screening clones for genetic traits, attempts to standardize the plants by clipping them to the same height should be avoided, instead prefering plants of the same size as cutting them down reduces their potential for bud activity and this will mask the genetic variation in apical dominance.

5.4 EFFECTS OF AERIAL ENVIRONMENTS ON APICAL DOMINANCE

The effect of aerial environment on the regulation of apical dominance has received much attention recently. Variables chosen for study have included irradiance (McIntyre, 1973), Carbon dioxide concentration (Anderson 1976; Hellmers and Strain 1980), temperature (Leakey *et al*, 1978a), relative humidity (McIntyre 1981), gravity (Nasr and Wareing 1958; Longman 1968) and light quality (Tucker 1976; Leakey *et al*, 1978b).

The influences of these factors on the phenomenon of apical dominance are likely to be mediated through the influences on both the hormonal balance (Field and Jackson 1974), and the nutritional status of the plant (Phillips 1969).

In this part of the work, the effects of some factors of the aerial environment on lateral bud activity following the decapitation of *T. scleroxylon* plants are considered. They include :

(i) The effects of shading,

(ii) Humidity,

(iii) Temperature, and

(iv) Day length.

5.4.1 Effects of shade on bud activity of decapitated plants

5.4.2 Introduction

Although extensive work exist on the effect of shading on the growth of plants (Njoku 1960; Loach 1969; Okali 1972), its effects on apical dominance have not received much attention. However, correlative inhibition of buds is generally thought to be enhanced in shade, perhaps by lowering the levels of photoassimilates and increasing auxin levels (Phillips 1969; 1975). This has been demonstrated in *Linum ussitatissimum* (Gregory and Veale 1957), and in *Phaseolus vulgaris*,

Shein and Jackson 1972; Field and Jackson 1975). This effect is thought to result from light effects on the different hormone balances occurring at different positions in the plants. However the physiological basis of this, is still not clearly understood. The work reported here investigates the effect of full natural light versus shade on the axillary bud activity of decapitated plants at FRIN (Nigeria).

5.4.3 Materials and Methods

18 plants each of 5 clones (368/16, 368/19, 436/8, 436/11, 436/18) were selected, choosing individuals of nearly equal height. Dayling was reduced by screens of 1 layer fibre glass roof sheet and 1 layer of palm fronds from *Elaeis guineensis*, placed on a frame of a 5 m high and 3 m wide plant shed (such a shade is presumed to act as a neutral filter). The shed was further covered on the East-West sides with local papyrus mats to reduce lateral light inside this area, and providing a light intensity of 200 $\mu E\ m^{-2}\ s^{-1}$ which usually occurred according to time of day and weather. Actual intensities were often rather low owing to a seasonal effect, this period being the rainy season and often overcast.

Air temperatures varied between 25 - 30 ^{o}C in the open and were only about 3 ^{o}C less in the shade.

9 plants per clone were randomly allocated to each treatment and decapitated at about 60 cm high, (18 nodes) and with an average of 5 leaves on each plant.

Assessments of lateral bud length were made at weekly intervals for 8 weeks. All experimental plants were spaced out to minimise between-plant shading, and surrounded with two guard rows of similarly sized decapitated plants.

5.4.4 Results

Bud activity was considerably greater when plants were in the open than under shade (Fig. 23), there was no statistically significant difference in the initial responses of different clones to decapitation.

Clones 436/11 and 436/18 were however faster than the other clones in reasserting dominance, irrespective of light climate (Fig. 24).

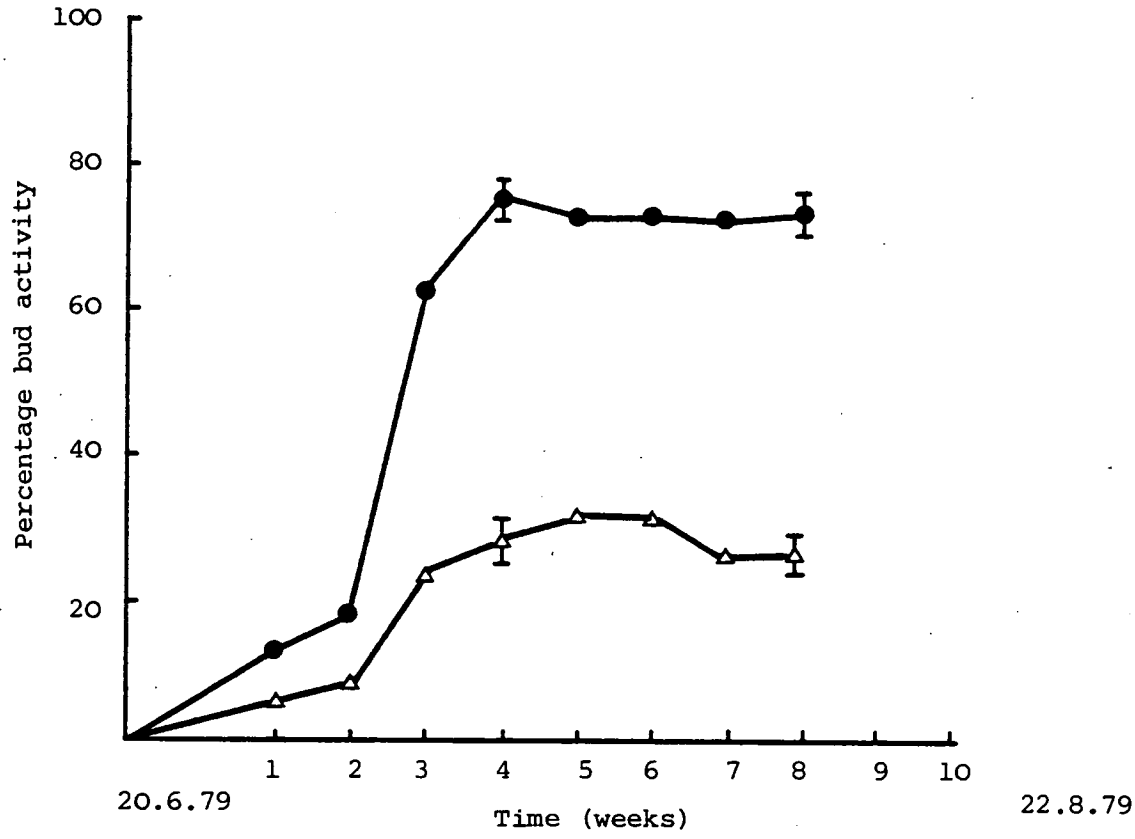
Plants in full light produced longer lateral shoots than those in the shade, mean shoot length from the top 3 nodes and the number of leaves both being three times greater. Under both light environments, clone 436/11 produced the shortest shoots and clone 368/19 the least number of leaves (see tables 7a,b). The relationship between shoot length and number of leaves was not significant at both treatments ($r = +0.25$ - shade and $r = \pm 0.20$ for full light).

Table 7(a) :

	Mean shot length of top 3 lateral shoots (mm)	
Clone	Shade	Full light
368/16	101.8 (15.4)	265.2 (7.8)
368/19	95.0 (7.3)	275.4 (14.3)
436/8	128.7 (13.4)	260.8 (22.3)
436/11	48.4 (4.1)	174.2 (21.0)
436/18	71.8 (12.0)	212.0 (16.2)
Mean	89.1 (13.6)	237.5 (19.2)

Effect of light intensity on mean shoot length in decapitated *T. scleroxylon* plants (means of 9 plants per clone with standard Error ± in parentheses.

Fig. 23

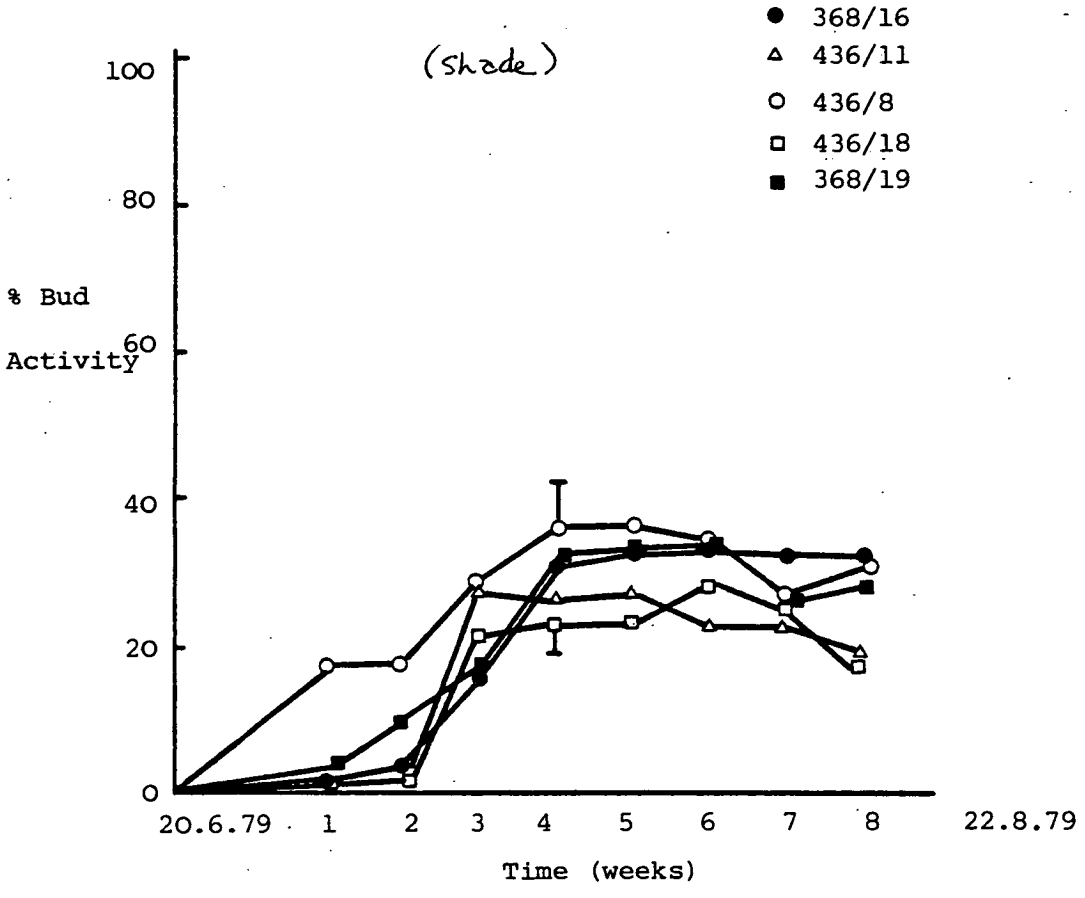


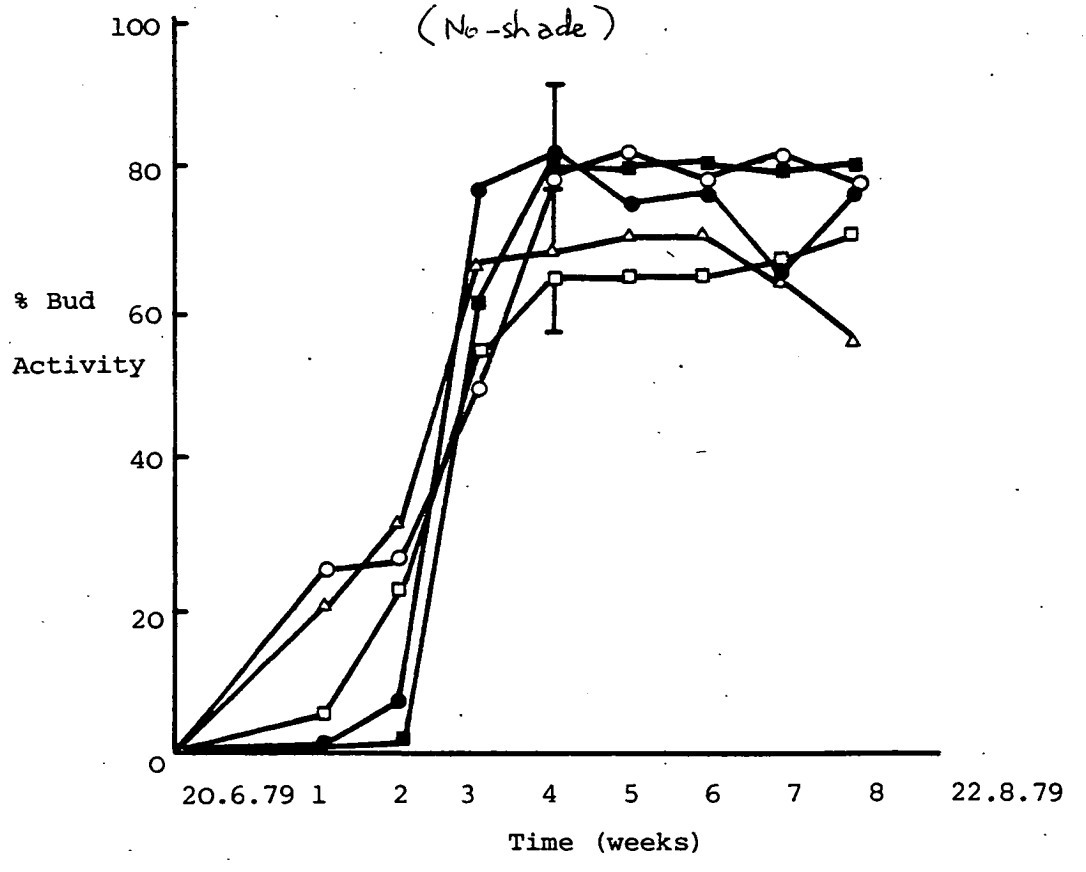
Effects of shade (200 μE m^{-2} s^{-1}) and full light (2000 μE m^{-2} s^{-1}) on bud activity of decapitated *T. scleroxylon* plants.

(Mean of 5 clones x 9 plants per treatment. ● = Full light, Δ = Shade and vertical lines for weeks 4 and 8 denote ±SE).

Fig. 24

Effects of light intensity (shade - 20 % and full light 100 %) on bud activity of decapitated *T. scleroxylon* in FRIN Nursery - Nigeria.





Means of 9 plants per clone. (Vertical bar is Standard Error for Week 4)

Table 7(b) :

Clone	Mean number of leaves produced by final assessment	
	Shade	Full Light
368/16	9.0 (0.7)	30.8 (1.6)
368/19	6.0 (0.5)	24.0 (1.8)
436/8	12.5 (0.7)	42.1 (1.8)
436/11	10.4 (0.6)	28.2 (2.6)
436/18	8.4 (0.9)	28.2 (2.0)
Mean	9.3 (1.1)	30.7 (3.1)

Means of 9 plants per clone with standard error ± in parentheses.

5.4.5 Discussion

The decrease in bud activity when shaded, interpreted as an increase in apical dominance, agrees with the findings of Jackson and Field (1972) and Field and Jackson (1975) with *Phaseolus vulgaris* and Gregory and Veale (1957) with *Linum ussitatisimum*, and can probably be explained in terms of increased competition for carbohydrates, and possible changes in the production of various plant hormones as demonstrated by Shein and Jackson (1972), McIntyre (1973) and Phillips (1975). The similarity between individual clones in bud activity however suggests a genetic similarity between them in responses to decapitation and thus presumably in apical dominance.

The lack of a re-establishment phase in this experiment however, as in others done in Ibadan, suggests that the occurrence of this phenomena in Ibadan and not in Edinburgh has nothing to do with differences in light environment, but probably in the potting media. Furthermore, the reaction of *T. scleroxylon* to shading in terms of

shoot length is not unexpected as it is known to be an early colonizer of forest sites and a high light demander; a requirement typical of other pioneer trees of the natural West African forest (Okali 1972). On the other hand, reaction to natural shade may not be the same as reaction to neutral shade. The shade of forest canopies is rich in those parts of the spectrum which leaves transmit : in particular the far-red component is enriched relative to the red. Such spectral shifts are known to be detected by phytochrome and other pigment systems and may elicit hormone - controlled growth reactions (Smith 1981). These differences may be responsible for the lack of better shoot growth (longer internodes) in the shade treatment relative to the full light, and the lack of relationship between shoot and leaves produced at the two treatments.

Practically useful inferences that can be drawn from this test include the possibility that the method of shading or the shade itself has been too dense for a light demander like *Triplochiton* and the fact that tests of this nature probably should be done in average rather than in full light,perhaps something similar to that in ITE glasshouses. This aspect however needs further investigation.

5.5 Effects of humidity on bud activity of decapitated plants

5.5.1 Introduction

As well as having a direct effect on water loss, ambient humidity is known in many cases to be a significant controlling variable of stomatal conductance, thence photosynthesis and the various parameters of plant growth. Its role in the tropical forest has not yet been fully elucidated, though appreciable literature now exist on tropical grasses and herbs. Most authors have stressed its importance in relation to changes in botanical composition that

occur along gradients of moisture, e.g. with vegetation in the tropics (Longman and Jênik 1974).

Very few workers have studied the effect of this factor on the apical dominance of plants and only in *Pisum sativum* (Remy 1968; McIntyre 1971), and *Agropyron repens* (mcIntyre 1979) has it been demonstrated that humidity is important in correlative inhibition.

The present work investigates the effects of humidity on the sprouting of decapitated *T. scleroxylon* plants, as part of the other experiments, to assist in selecting standard test conditions in future.

5.5.2 Materials and Methods

16 plants, ranging between 50 and 60 cm tall each of 7 clones (238/6, 342/7, 368/5, 404/10, 404/18, 424/16 and 431/10) with four leaves were chosen, repotted into 9" diameter pots and allowed to recover for 3 days prior to decapitation. Experimental areas at FRIN were also prepared at the same time and also left to equilibrate. The high humidity (100 %) treatment was provided with a Defensor mk II humidifier in an enclosed polythene tent enclosed in an asbestos-roofed wire enclosure which provided shade and allowed good control of temperature, and adequate ventilation.

Supplementary light was provided by 6 fluorescent tubes hanging low enough to provide comparable light intensity with the low humidity treatment area which was otherwise the ambient environment, in the roofed wire enclosure about 50 m away from the high humidity tent.

Humidity levels and temperature were investigated at these two sites with a Cassella thermohygrograph at an air temperature of

30 °C, the maximum humidity occurring at watering.

Environmental conditions of both experimental areas are as given in Table 8.

Table 8 : Probable vapour pressure and Vpd, calculated from temperature and relative humidity data using the equation.

Treatment	Temp. °C	Rel. Hum %	Vapour Pressure (mb)	Leaf-air deficit (mb)
High	28	95 - 100	36.1 - 37.8	0 - 1.7
Low	30	40 - 70	17.1 - 29.9	25.3 - 12.5

Plants were randomised in two blocks in both areas with each clone replicated four times per block.

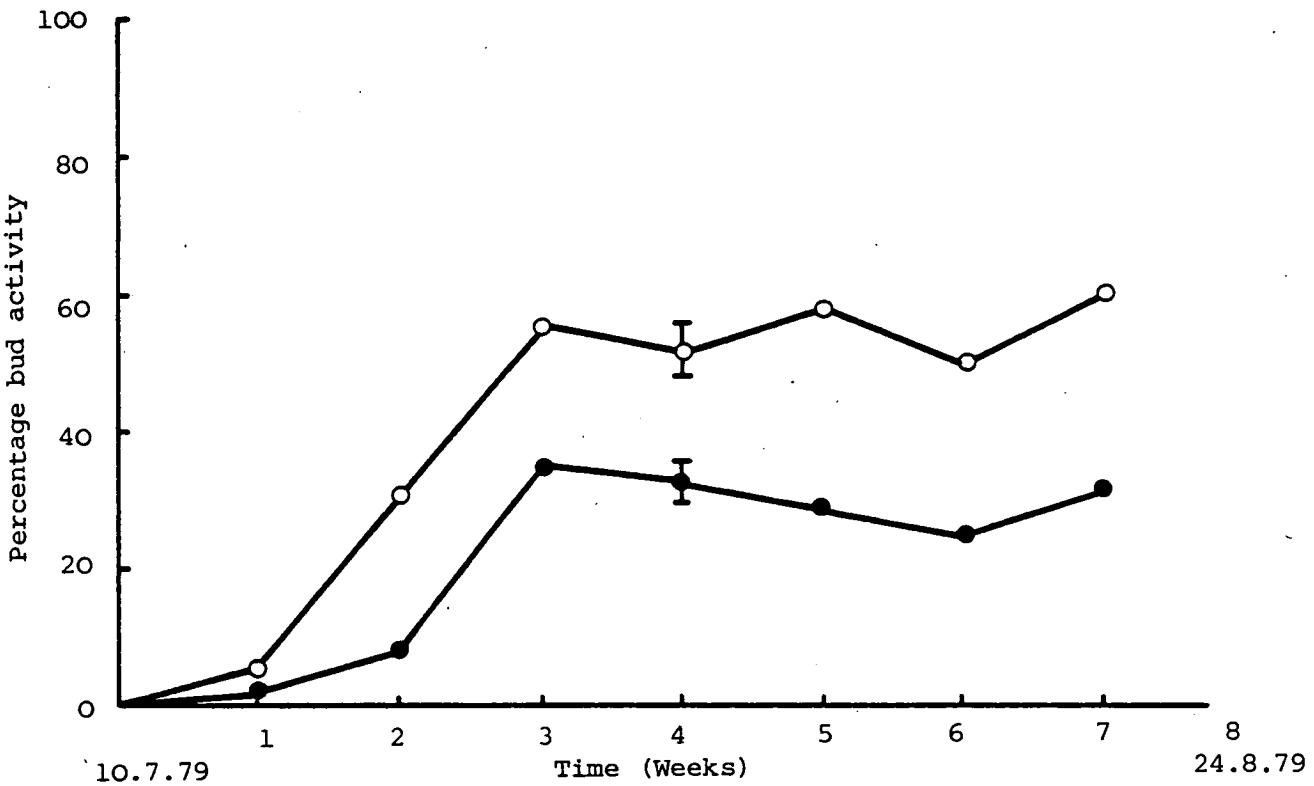
Assessment of lateral shoot length were made weekly and on the final day, the total number of leaves produced by each plant and the mean lengths of the three uppermost lateral shoots were also assessed.

5.5.3 Results

High humidity significantly increased bud activity following decapitation (Fig. 25) and also increased the mean length of the top 3 lateral shoots and the number of leaves produced (Tables 9a and 9b).

There was considerable variation between clones in bud activity under both humidities this being greatest at high humidity, where

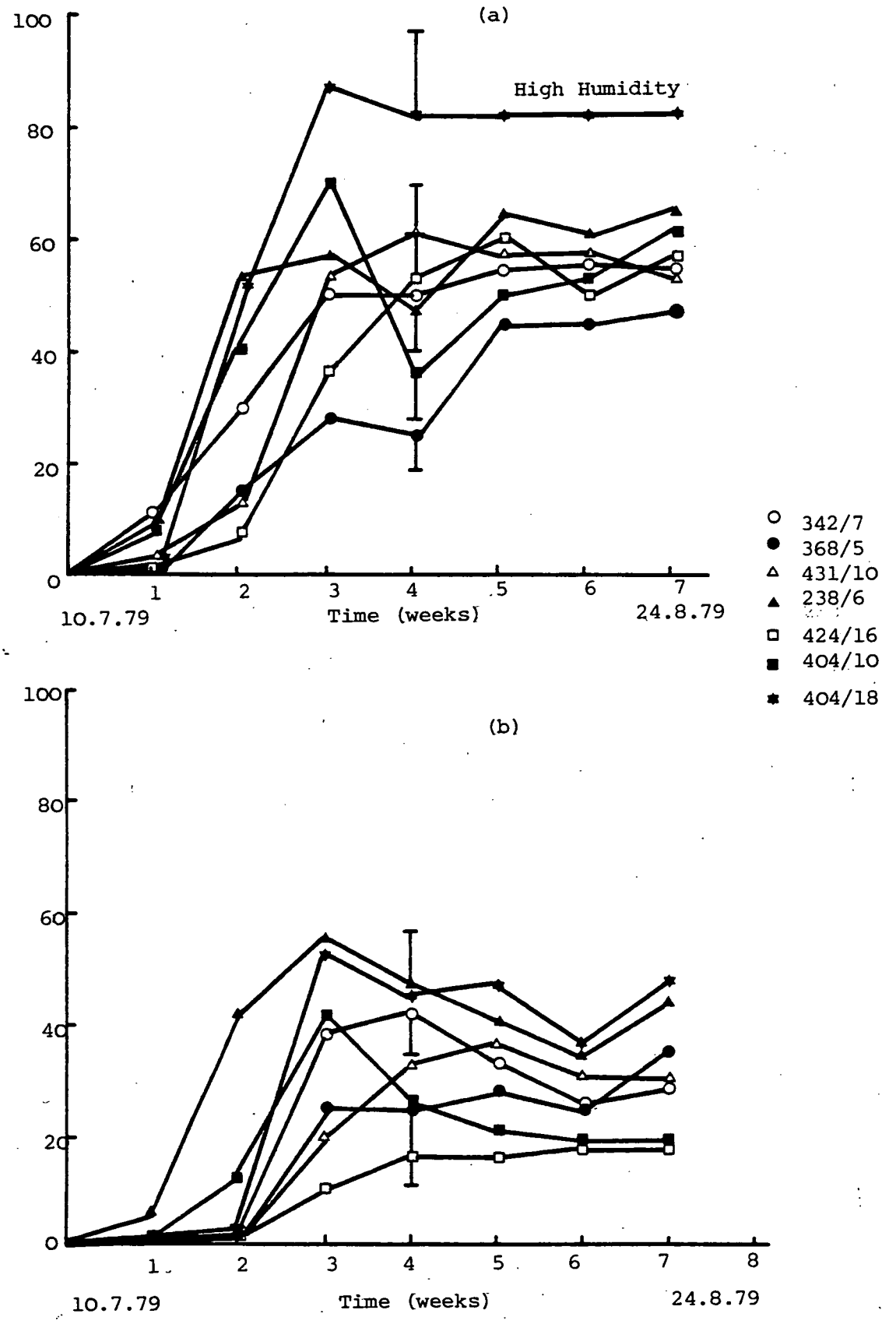
Fig. 25



Effect of high and low humidity on bud activity in decapitated *T. scleroxylon*.

(Means of 54 plants (8 x 7 clones) per treatment, O = High Humidity, ● = Low humidity and Standard Error (±SE) inserted for weeks 3 & 4).

Fig. 26



Effect of high and low humidity on axillary bud activity in decapitated clonal plants of *T. scleroxylon*. (Fig. 26a = High, Fig. 26(b) = Low humidity treatments and standard error bar(±SE) for weeks 3 and 4 inserted).

Table 9a : Effect of humidity on mean leaf production, n = 8, * = n = 6 (with standard error (± SE) in parentheses).

Clone	Mean Leaf Production	
	High Humidity	Low Humidity
238/6	26.0 (4.1)	16.0 (3.6)
368/5	17.0 (4.6)	10.3 (2.1)
342/7	21.0 (6.8)	9.3 (1.3)
404/10	20.6 (5.1)	6.0 (1.8)
404/18	36.0 (5.0)	9.8 (1.4)*
424/16	20.0 (5.8)	6.5 (1.5)
431/10	15.0 (2.6)	9.3 (1.9)
Mean	22.1 (2.6)	9.6 (1.2)

Table 9b : Effect of humidity levels on mean shoot production n = 8 (Top 3 axillary shoots, with standard error (±) in parentheses). * = n = 6.

Clone	Mean Shoot Production	
	High Humidity	Low Humidity
238/6	118.4 (10.4)	89.4 (5.6)
368/5	140.1 (18.4)	78.1 (9.6)
342/7	81.2 (9.3)	72.0 (7.0)
404/10	80.6 (2.3)	41.2 (6.6)
404/18	166.8 (8.4)	94.6 (9.4)*
424/16	93.4 (12.4)	51.7 (3.5)
431/10	120.1 (14.6)	80.3 (6.8)
Mean	114.5 (12.1)	72.5 (7.4)

clone 404/18 produced highest bud activity and clone 368/5 the lowest. At the low humidity, highest bud activity was produced by clones 404/18 and 238/6 while clone 424/16 had the lowest (Fig. 26 a,b). Clone 404/18 had a mortality rate of 25 % at the low humidity while other clones no losses were recorded.

There was no relationship between mean leaf number produced and mean shoot produced by the 3 uppermost lateral shoots (r = +0.53) while a significant relations (r = +0.76) at P = 0.05 existed between them at low humidity.

5.5.4 Discussion

The results of this investigation agree well with those reported earlier from similar experiments in *Pisum sativum* (Remy 1968; McIntyre 1971), in *Phaseolus vulgaris* (McIntyre 1972) and in *A. repens* (McIntyre 1979) in which he demonstrated that a reduction in humidity from 100 % to 98 % at 20 ^{o}C caused complete inhibition of bud activity. McIntyre (1979) suggested that this extreme sensitivity to humidity occurred as a result of the development of water stress, though no measurement of water potentials were presented. However often workers have found that many plant processes, at a fundamental biochemical level are very sensitive to small water deficits in the tissue (Hsiao 1973). In more comparable work, McIntyre (1973) demonstrated in *Phaseolus vulgaris* grown at humidities of 30, 60 and 90 %, that each reduction in water stress, as measured by leaf turgidity, caused a highly significant increase in growth of the cotyledonary buds (which served as a measure of apical dominance). In this, (McIntyre 1973) and his report on *A. repens* (McIntyre 1979) indicate that the effective level of humidity that may affect apical dominance may vary from one species

to the other, and also that other factors such as light and nutrition may interract with the reduction in water potential caused by low humidity. However the possibility that competition for moisture between the apical and axillary buds may be responsible for correlative inhibition is becoming more acceptable, but the involvement of reduced stomatal conductance, thense photosynthesis and thus reduced carbohydrate may also be important.

On the clonal variation in this study, the higher bud activity in clone 404/18 at high humidity (Fig. 26 a,b) suggests this clone is probably less adapted to drier environments than the others, which is also responsible for its high mortality (25 %) at the low humidity treatment; while the similarity between other clones at this treatment suggests that they probably all have relatively strong apical dominance although genetically different in their reaction to high humidity, and perhaps also moisture conditions. Furthermore, the ranking of individual clones (426/18 and 368/5 in particular), varied under the different regimes suggesting the involvement of other factors probably light which according to McIntyre (1981) may interact in a complex manner with humidity. It was explained that light-induced inhibition is due primarily to a reduction in the water potential of the tissues resulting from an increase in transpiration. The significant relationship between mean shoot length and mean leaves produced at low humidity, although not significant at the high humidity suggests a close relationship between them and the phenomena of apical dominance.

From a practical standpoint, the results of this study emphasises the importance of adequate and reproducable humidity conditions when tests are done to elucidate the true genetic variations between clones in their levels of apical dominance. Adequate levels are considered to be 70 % RH at a temperature of 30 ^{o}C.

5.6 Effects of high temperature on bud activity in decapitated plants

5.6.1 Introduction

Temperature is known to exert a strong influence on all living processes. Optimum temperature for plant growth may vary between different organs on the same plant and even between two sides of the same organ (Rorison, 1981).

In woody plants, a diurnal alteration of high dry temperatures and low night temperatures is often more favourable than a constant temperature for the maintenance of continued growth of the terminal apices (Precht *et al*, 1973). This has been recognised in a number of temperate trees (Kramer 1957; Hellmers 1966; Hellmers *et al*,1970; Longman and Coutts 1974), while amongst tropical trees, *Gmelina arborea, Terminalia superba, Chloraphora excelsa, Ceiba pentardra,* and *Triplochiton scleroxylon* were notably sensitive to differences in temperature even when temperature was varied only at night in a 13 hour photo-period. For example, lower night temperature brought about the temporary cessation of terminal shoot growth in *Gmelina arborea*, whilst in *Triplochiton* longer leaves were formed at a 20°-day 130 ° night regime than at 20°/20° or 30°/30° C regimes. (Longman 1978). It has further been shown that for most tropical trees, optimal temperatures for growth are above 30 °C and that temperatures higher than 40 °C or lower than 10 °C can be lethal (Kwakwa 1964, Longman 1978). Scurfield (1961) and Blake (1976) investigated the response of *Eucalyptus* spp to temperature, and its effects on branching, and they similarly reported that high day and night temperatures (28 °C) inhibited elongation of the main-stem but not branches in *E. obliqua* seedlings. Moreover, Blake (1976) demonstrated that a wide thermoperiod with night chilling (28°/5° C and 24°/5° C day/night temperature) increased branch number and

levels of cytokinin - like growth substance. Blake (1976) explained this effect in terms of apical dominance mediated through temperature effects on the amounts of growth promoting and inhibiting substances in the stem. Temperature effects on correlative inhibition has also been reported in the South African Sugar Association Report (1967 - 1968) where heat treatment of 4-8 node stalks of *Saccharum* spp (against Ratoon stunt disease) increased the activity of the buds (lower apical dominance). Leakey *et al*, (1978) in one study in *Agropyron repens* investigated the effects of temperature on bud activity and the development of dominance in rhizone fragments - a system very similar to that studied here. They reported that high temperature (33 ^{o}C) delayed the re-establishment of dominance.

Hardwick *et al*, (1979), Hardwick and Andrews (1980), also demonstrated with *Phaseolus vulgaris* that low temperature of 15^{o}/15^{o} C night/day in controlled environments supressed the growth of lateral branches thus increasing apical dominance. This however could be interupted by raising the temperature by about 6 ^{o}C with bud heaters. They concluded that the temperature effect is mediated by the buds themselves rather than by any effect of temperature on the supply of some factor.

The present work with *T. scleroxylon* investigates the effect of high temperature on bud activity of decapitated clonal plants, as part of continuing investigations of factors affecting apical dominance in this species.

5.6.2 Material and Method

The experiment was carried out at FRIN - Nigeria in July 1979. 10 plants of each of 6 clones (410/3, 410/12, 432/2, 432/11 and 446/1) ranging from 65 - 75 cm in height, 14 to 18 nodes and with 5 leaves

were selected. They were divided into two groups (5 plants per clone) and individual plants were completely randomised within a single block at the two treatments : high day time temperature (40 ^{o} ± 5 ^{o}C) and low (ambient) temperature (30 ^{o} ± 2 ^{o}C). Plants were decapitated by the removal of the 2 top nodes and assessment of lateral shoot growth were made weekly after. To provide the high temperature treatment, a clear polythene tent, thereafter called the 'heat' tent was built in the open and stood on two layers of building blocks with their openings partially blocked with clean cloth to allow adequate gas exchange (Fig. 27a). Temperature within this structure was monitored, and found to be fairly stable with a day temperature of 40 ^{o} ± 5 ^{o}C and a night temperature of 30 ^{o}C ± 3 ^{o}C. As a result of its thermal mass, the structure tended to even out the natural fluctuations in temperature. The cooler temperature treatment was provided by the ambient temperature of the nursery about 2 metres from the 'heat' tent. Temperatures recorded by a thermohydrograph showed that during the day, temperatures were 30 ^{o} ± 2 ^{o}C while at night they dropped to 25 ^{o} ± 1 ^{o}C. Humidities at both sites were very similar at night, with about 5 % difference at noon (95 % night and 75/80 % at noon). Characteristic traces of temperature and humidity are illustrated in Figs 27 bi,ii.

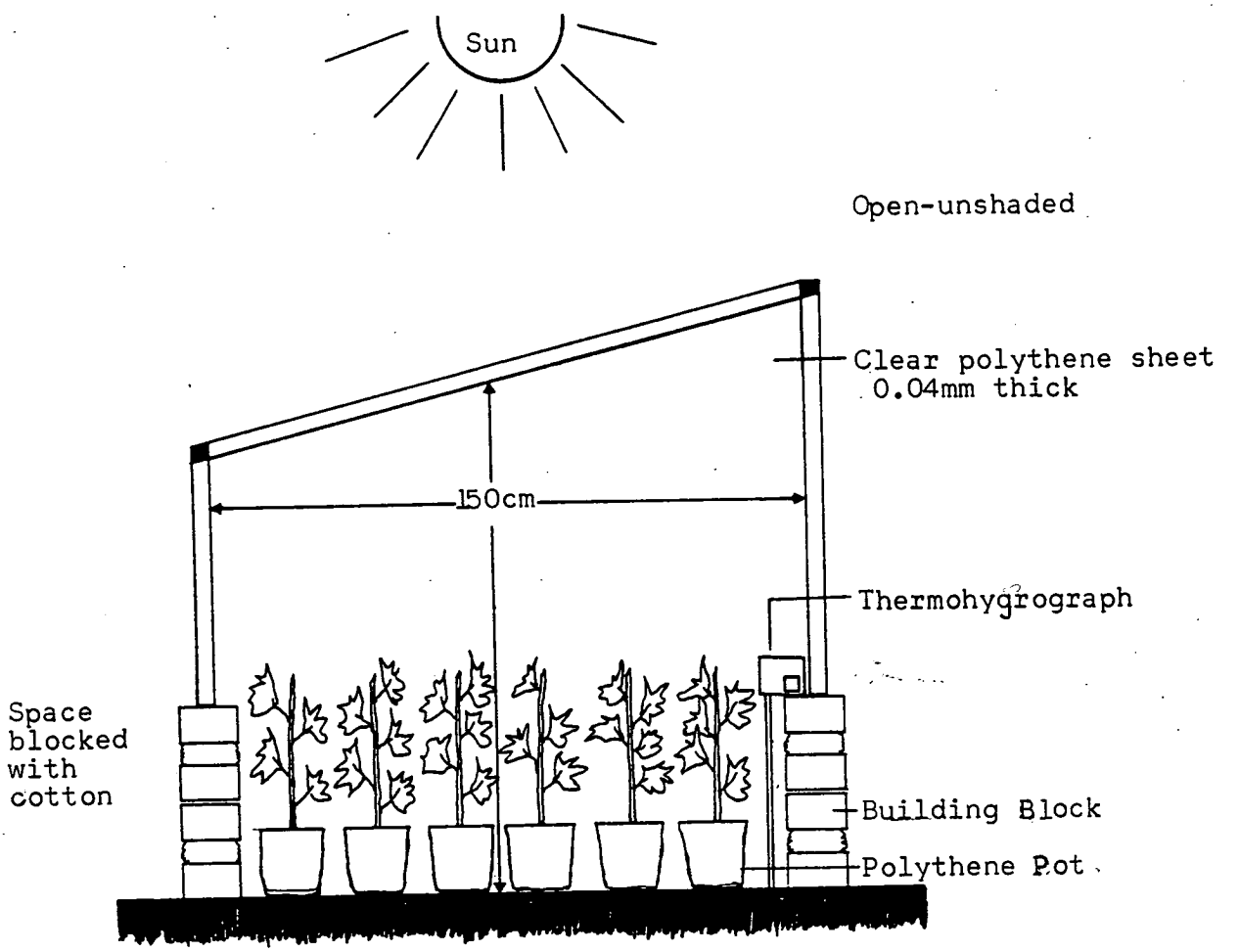
A year after, branching patterns (primary, secondary and tertiary) were re-assessed in clone 446/1.

5.6.3 Results

The rate of bud activity was greater in the first 3 weeks at high temperature than at low temperature, although the overall level attained by week 4 did not differ much between treatments (Fig. 28 I & II).

Although the ranking of different clones changed slightly with treatment, there were few significant differences in performance.

Fig. 27a



Showing 'heat tent' used to provide the high temperature treatment.

(Wooden frame covered with plain polythene sheet).

Fig. 27b

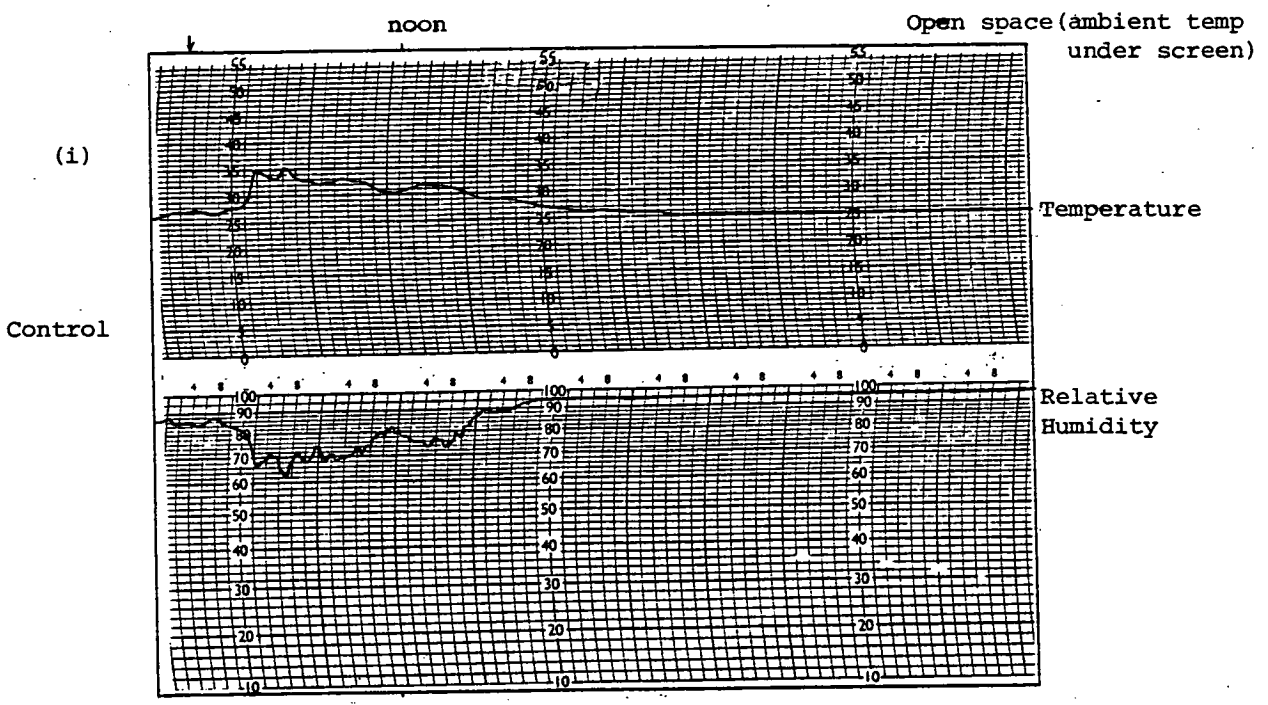
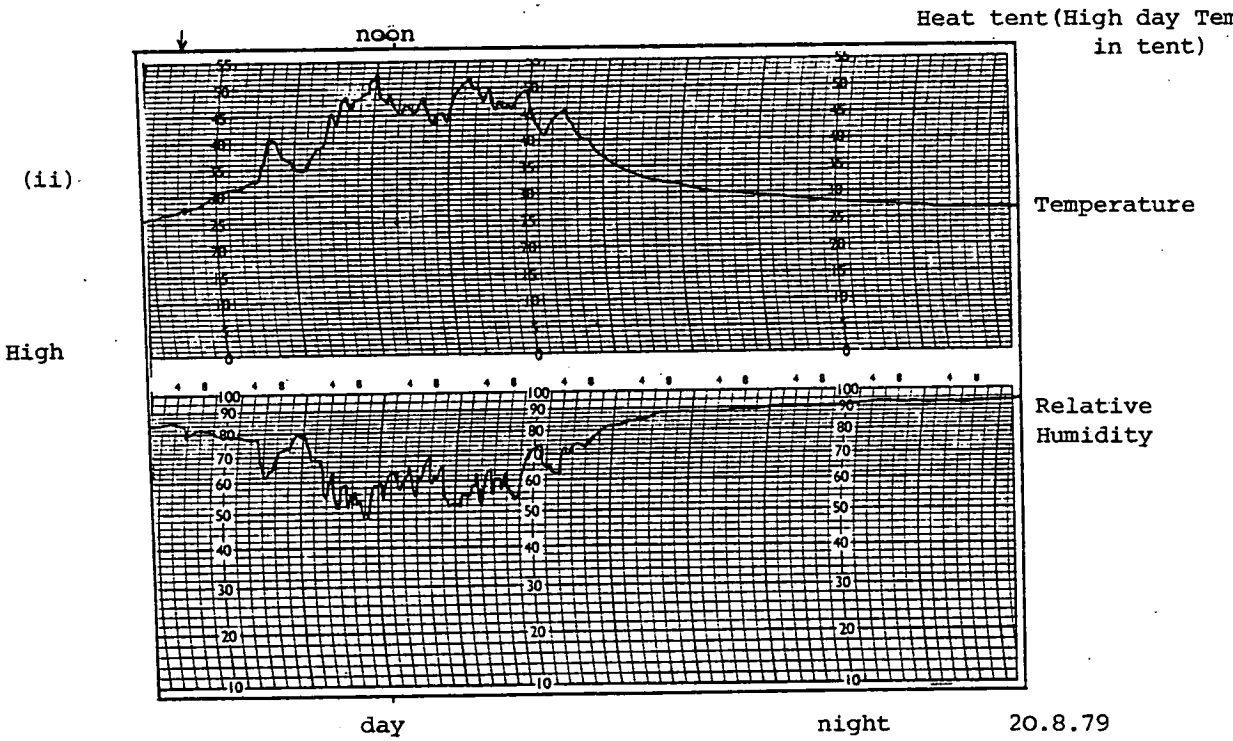


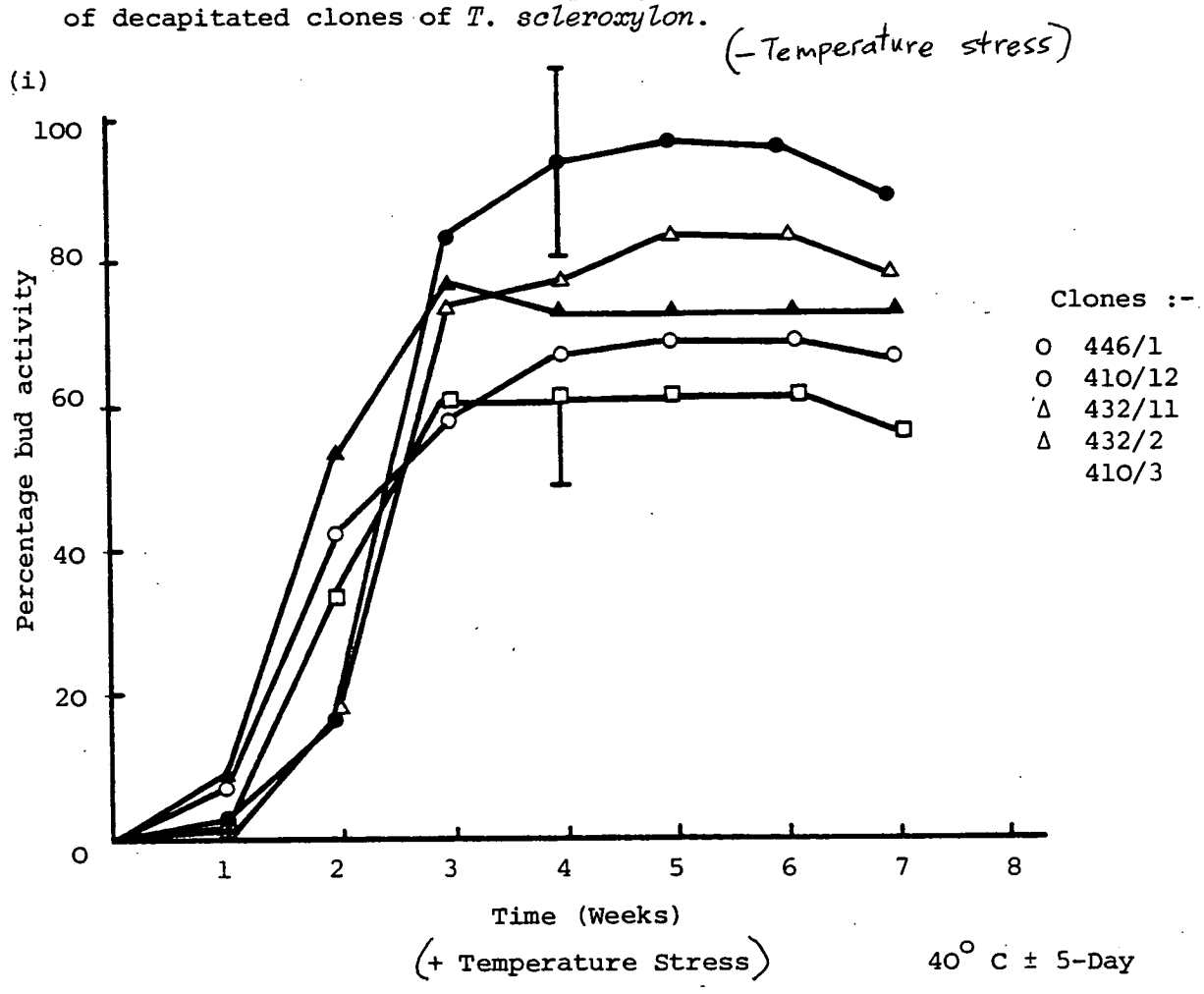
Fig. 27c

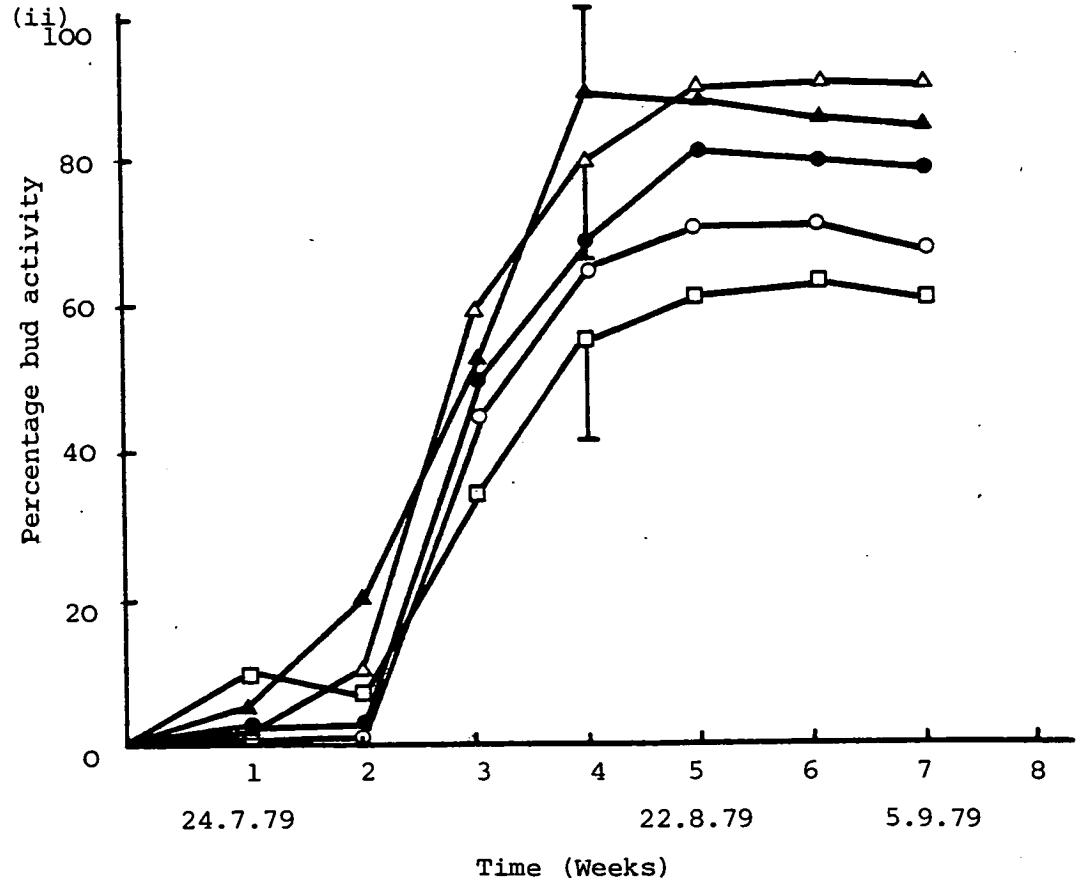


Temperature and relative humidity levels at the control and High temperature treatment conditions at FRIN 20.8.79.

Fig. 28

Effect of normal temperature and high temperature on bud activity of decapitated clones of *T. scleroxylon*.





At 40 °C, the two clones of seedlot 410 did have significantly different levels of bud activity, clone 410/3 being the least active at both temperatures.

Mean lateral shoot length per plant was not significantly affected by temperature for example in clone 410/2 values were 55.4 ± 12.0 mm for ambient and 48.6 ± 11.2 mm for high temperature. However, there was a dramatic reversal of shoot polarity at high temperature (Fig. 29). At 30 °C the pattern of lateral shoot production was similar to that occurring in vertical plants of all other experiments in which lateral shoots are longest at the apical region and shortest at the basal region (Fig. 29a). A second major effect of heat treatment was the reducing of leaf size from about 165 cm^{-2} to 22 cm^{-2} (Fig. 29b).

Furthermore, although primary branch number remained constant at the two treatments over the subsequent years, secondary and tertiary branches were considerably more numerous in heat treated plants (Fig. 29c).

5.6.4 Discussion

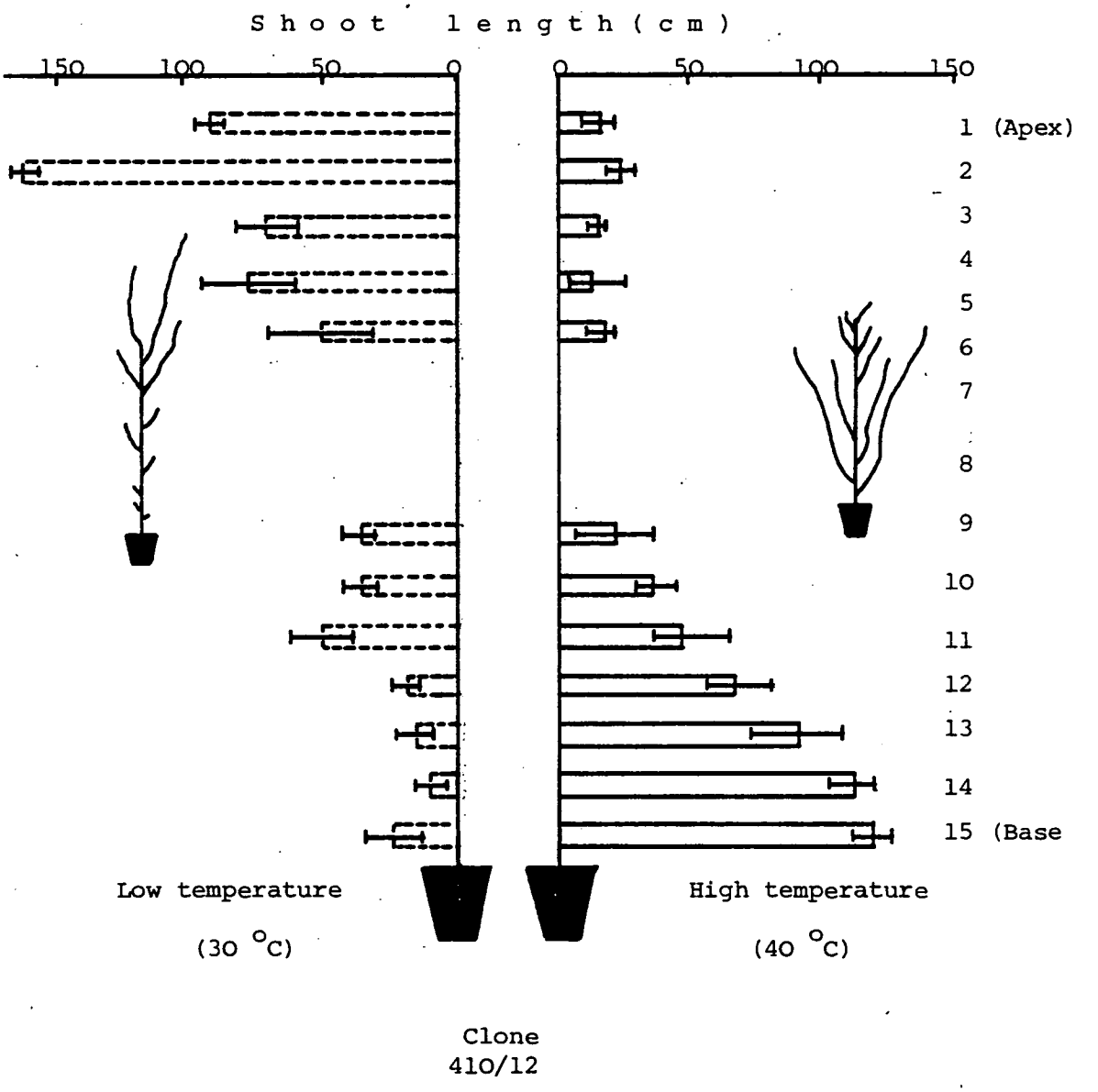
Although high temperatures have been found to affect the re-establishment of dominance in rhizomes of *Agropyron repens* (Leakey *et al*, 1978) and sugar cane stems, it was not possible to see an effect in *T. scleroxylon* in the present study for dominance seems not to become reasserted in *T. scleroxylon* under the conditions of the FRIN nursery. High temperatures did not however affect dominance in this experiment, but some effect of high temperature does however influence the early pattern of budbreak and there are many more secondary and tertiary branches on the primary branches. This loss of apical dominance agrees well with the reports of Scurfield (1961)

in *Eucalyptus polyanthemos* where an increase of temperature from 20/17 °C to 27/24 °C substantially increased number of axillary branches; Blake (1976) in *Eucalyptus obliqua* where high temperature (28 °C) increased branch number or a wide temperature day-night range which also increased branch number; It further agrees with the reports of Hardwick *et al*, (1979), Hardwick and Andrews (1980) who also demonstrated that high temperature enhances axillary branch growth in *Phaseolus vulgaris*, thus decreasing its apical dominance.

High temperatures have affected polarity of lateral shoot production through some major effect which gives basal buds the competitive advantage over apical buds and changes the whole gradient of shoot production. Similar effects on shoot polarity (where there were more basal branches at 28 °C), have also been reported by Scurfield (1961) and Blake (1976) with *Eucalyptus* species.

In attempting to explain the mechanism of high temperature effect on apical dominance, Leakey *et al*,(1978), suggested that the lack of correlative inhibition at 33 °C in *A. repens*, was possibly a result of degradation of the inhibitor. Hardwick and Andrews (1980) on the other hand suggested that the effect of temperature on lateral meristems was the result of some effect on the rest of the plant. Contrary to this, and to the conclusions of McIntyre (1973) who suggested that the supply of some factors, such as water and nutrients from the rest of the plant is responsible for correlative inhibition, is the work of Andrew and Hardwick (1981). They showed, using heaters, in which they could overcome lateral bud suppression as a result of low temperature (15 °C) by raising the temperature to 21 °C, that temperature effect is mediated by the buds themselves rather than by an effect of temperature on the supply of other factors. Ethylene is known to be produced by stressed plants Liberman (1979) and Field (1981) up to certain temperatures (36 °C for *Pisum sativum*), thus an

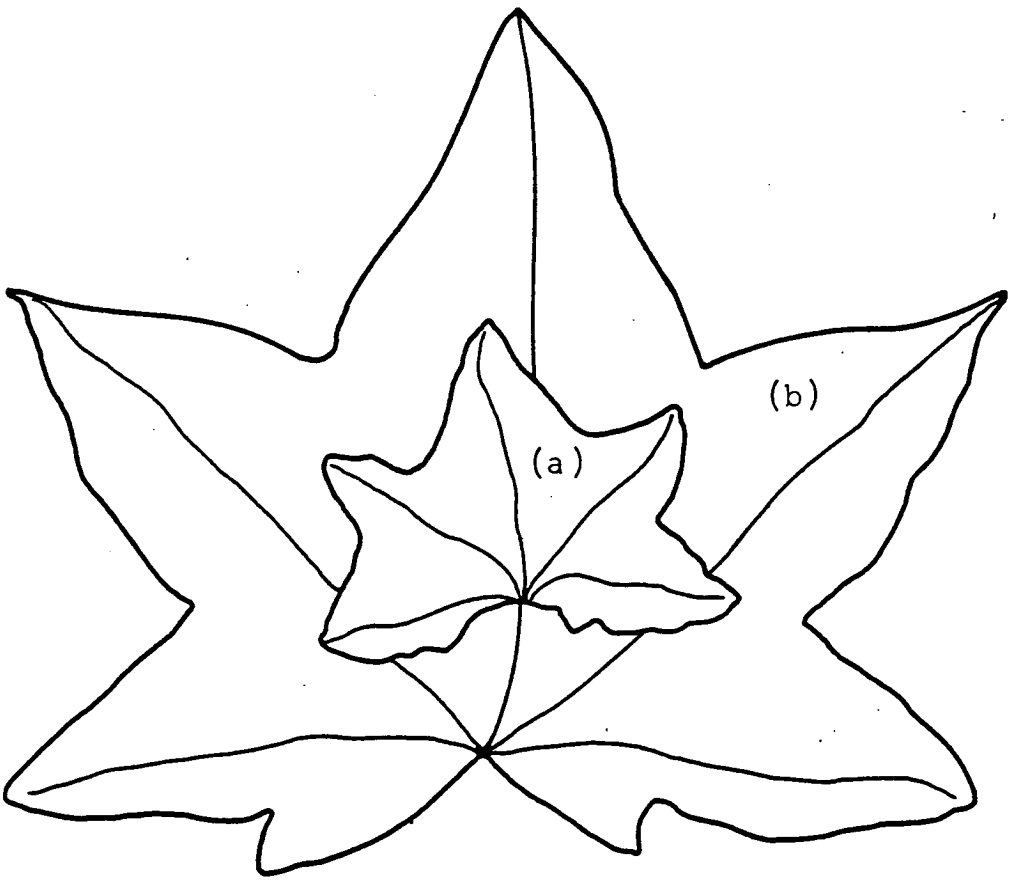
Fig. 29a



Effects of high temperature on lateral shoot growth of a cecapitated clone of *T. scleroxylon*.

(Vertical line on each bar denotes ±SE, n = 5 per treatment)

Fig. 29b

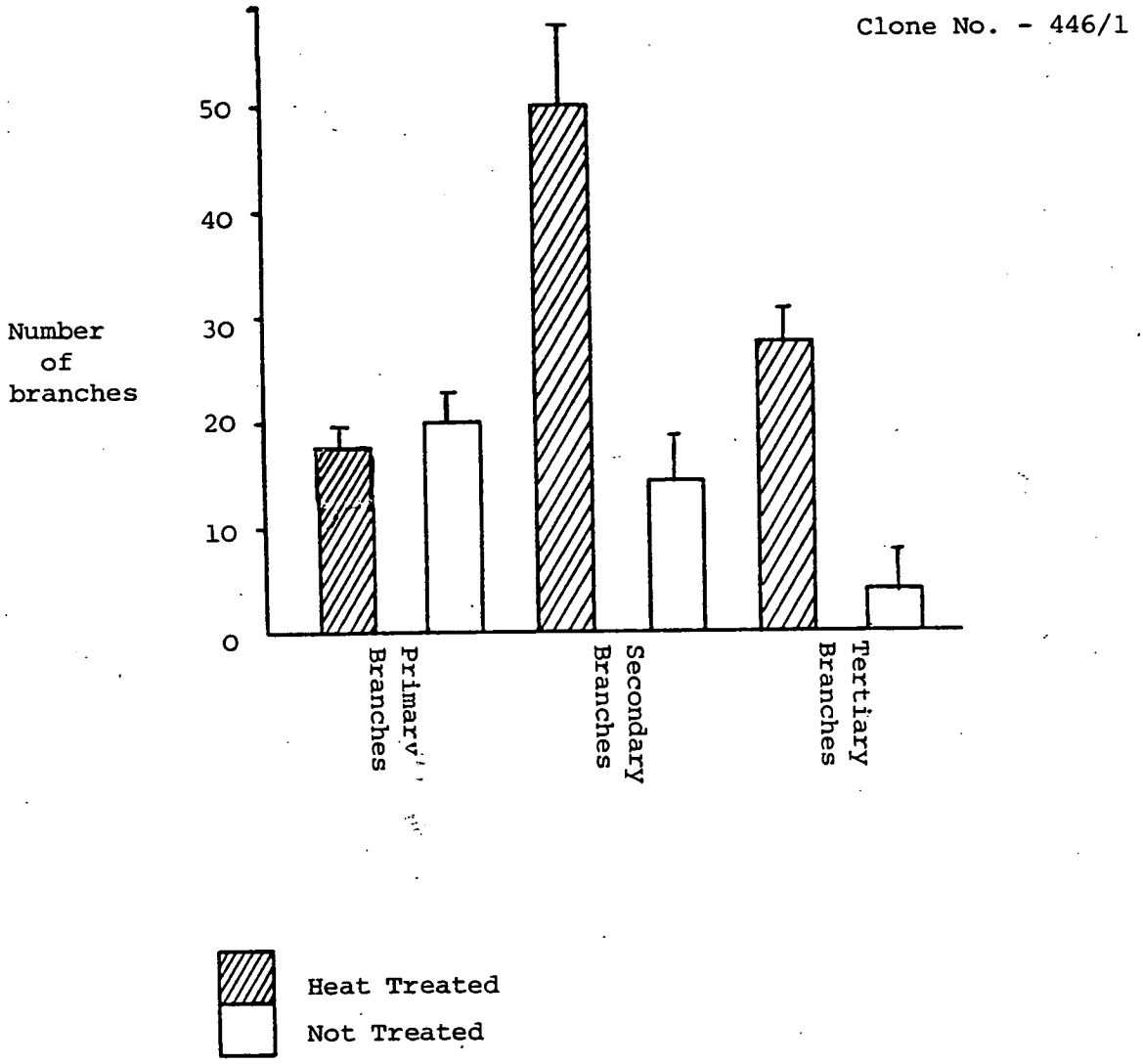


Effect of high daytime temperature on leaf size in Obeche Triplochiton scleroxylon. (n = 50 leaves)

(a) High temperature treated (40 ° ± 5 °C): mean leaf area = 22.3 cm^2
(b) Ambient temperature (30 ° ± 2 °C) : mean leaf area = 165 cm^2

Area: (a) 22.3 sq. cm.
(b) 165 sq. cm.

Fig. 29c



Effects of high temperature (40 ^{o} ± 5 ^{o}C) on the mean numbers of branches of *T. scleroxylon* clone 446/1, 12 months after treatment. (n = 5 plants, vertical lines = ± SE)

alternative hypothesis, is that at around 35 °C the bottom of the plant is producing ethylene while at the warmer top (40 °C) production has ceased. The suggestion of the involvement of ethylene here is supported by the marked reduction in leaf area (Fig. 29b) in the high temperature treatment; a typical response in ethylene treated plants (Hillman and Yeang 1979). Also, further a temperature gradient within the 'heat' tent enhanced by leaf shading could result in lower temperature at the pot level, thus allowing the basal part of plants to have a lower temperature, so possibly increasing its production of ethylene. Hillman and Yeang (1979), Yeang and Hillman (1981) have demonstrated that ethylene is effective in releasing lateral buds from suppression or correlative inhibition, thus perhaps allowing the greater development of basal branches rather than the upper ones in the *T. scleroxylon* plants under test.

This hypothesis is presented diagramatically in Fig. 30. The need for assessing apical dominance under well controlled - ambient temperature conditions is well demonstrated in this study.

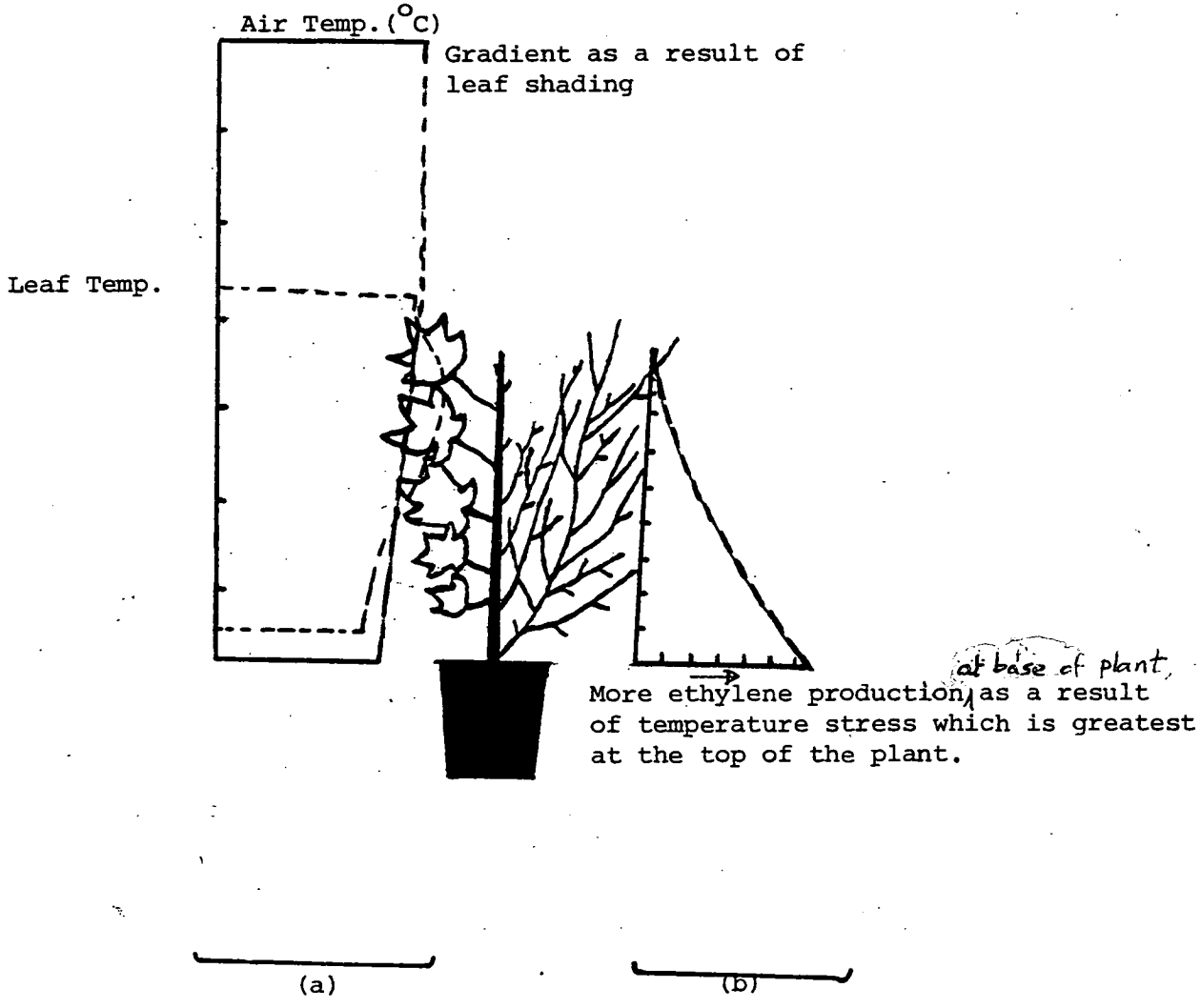
5.6.5 A note on the implications of heat treatment to practical forestry

The environmental factors which influence the relative development of branches and the tree bole are likely to affect the commercial value of the species. An understanding of the effects of environment on the tree form is thus important, particularly when plantations outside the natural range of species are anticipated.

The natural distribution of *T. scleroxylon* extends into the fringes of the semideciduous forest belt of West Africa and into outliers in the Guinea savannah areas.

In 1976, clonal experiments and gene banks of *T. scleroxylon* were established at Afaka Experimental Station near Kaduna in the Guinea Savannah Grassland zone of Nigeria where temperatures frequently reach 40 °C in the open. In the light of the findings, in this

Fig. 30



A hypothetical explanation for the effect of high temperature on basal axillary branch dominance, and its effect on form development in *T. scleroxylon.*

((a) = plant form at time of treatment, (b) Form development 12 months after treatment.)

Plate 3

Heavy basal branching of *T. scleroxylon* at Afaka in the savannah belt of Nigeria.

experiment on high temperature effect, it is interesting to note that many plants growing at Afaka have a form like those of this experiment (plate 3), which although unsuitable for commercial forestry may be useful as clonal seed orchards. These plots also represent ex-situ conservation away from natural pests and diseases. It is also possible that plants heat-treated in this way could be ideal for studies of floral initiation, producing a compact crown on a small plant, with many more sites for reproductive spars and thus potentially a greater fruit yield per tree.

5.7 Effect of daylength on bud activity in decapitated plants of *T. scleroxylon*

5.7.1 Introduction

Despite the small daylength variation in the tropics (e.g. in Ibadan-Nigeria, 11 hours 40 mins in December to 12 hours 33 mins in June), photoperiod is a physiologically-active factor in the control of shoot extension in some native plants, both herbs (Njoku 1958), and trees (Kwakwa 1964; Longman 1966). For example in *Terminalia* spp.,*Chlorophora excelsa*, and *Chlorophora repia* it was demonstrated that increasing the photoperiod beyond those normally experienced increased shoot growth (Longman 1978). The effect of daylength on the apical dominance in tropical species has however not been reported, but in contrast, there are many reports of its effect in temperate species. In Pea seedlings, Kitamura and Kudo (1952) demonstrated that daylength had marked effects on the magnitude of apical dominance. They concluded that short days (SD) promote axillary bud and branch growth and long day (LD) enhanced apical dominance. These photoperiodic effects, apart from their influence

on photosynthesis may be mediated through changes in hormonal balance (Phillips 1975). This is supported by observations in *Perilla fructescens* where Beaver and Woolhouse (1973) observed that short day treatment markedly increased the flux of cytokinin from root to shoot. However daylength has also been found to interract with (a) temperature in *Pisum sativum* (Nakamura 1965), (b) nutrients in *Pisum sativum* (Nakamura 1965) and *Linun ussitatissimun* (Gregory and Veale 1957), in their effects on apical dominance.

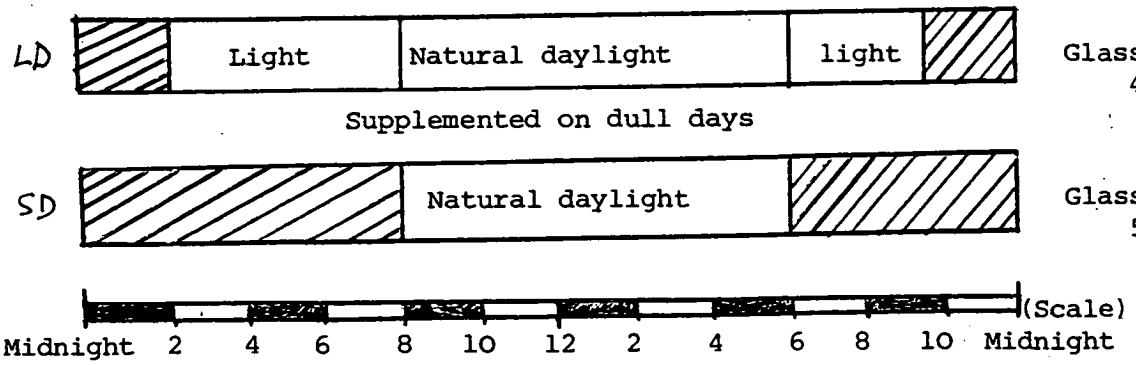
The present investigation concerns the effects of daylength on bud activity of decapitated plants of *T. scleroxylon*, thus being seen as an expression of apical dominance.

5.7.2 Materials and Methods

After 1 week's acclimatization, 15 to 18 plants of each of 5 clones (8038, 8047, 8053, 8035 and 8049), about 60 cm tall, with between 18 - 22 nodes were decapitated by removal of top two nodes, thus reduced to between 16-20 nodes with 4 leaves left on each plant.

Half the plants of each clone were then randomised to form two blocks in 2 different glasshouses in which daylength was maintained at either 10 hours for short day (SD) or 19½ hours for long day (LD), artifical lights providing the extension to a natural daylength of 8 hours and supplementing it on dull days (Fig. 31).

Fig. 31 Showing duration of light providing photoperiod treatments.



Black polythene sheets prevented the receipt of unwanted light from the surrounding glasshouses during the dark periods. Photon flux density at both treatments, during the light periods was about 650 $\mu E\ m^2\ s^{-1}$, and as close to total darkness as possible during dark periods.

Assessment of lateral shoot length were made weekly over 9 weeks. At the end of the experiment, leaf area was assessed with the Lambda Leaf Area Meter (Model 3100) and shoots were ovendried to constant weight at 90 ^{o}C for 24 hours for the determination of their dry weight.

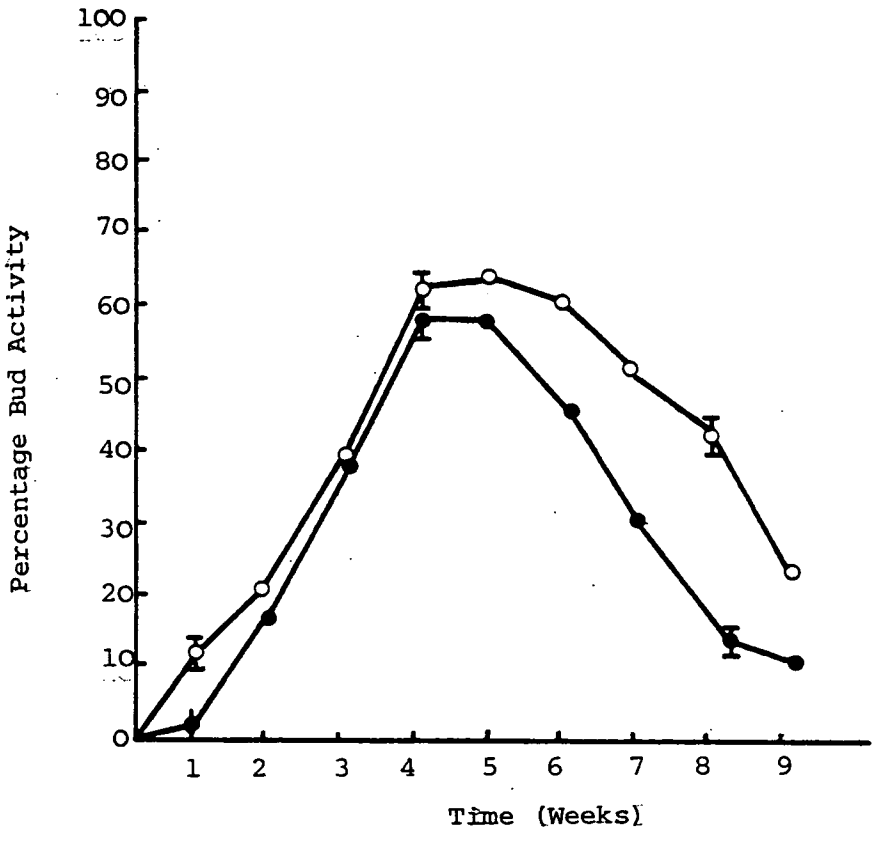
5.7.3 Results

There was no significant effect of daylength on the peak level of bud activity, reached 4 weeks after decapitation, but significant effect existed at week 1 and at the second phase of bud activity after maximum bud activity, when reassertion of dominance was earlier in the short day treatment than at the long day (Fig. 29).

Clones maintained their ranking at both treatments, with clone 8038 and 8047 having the greatest and least bud activity respectively (Fig. 32b).

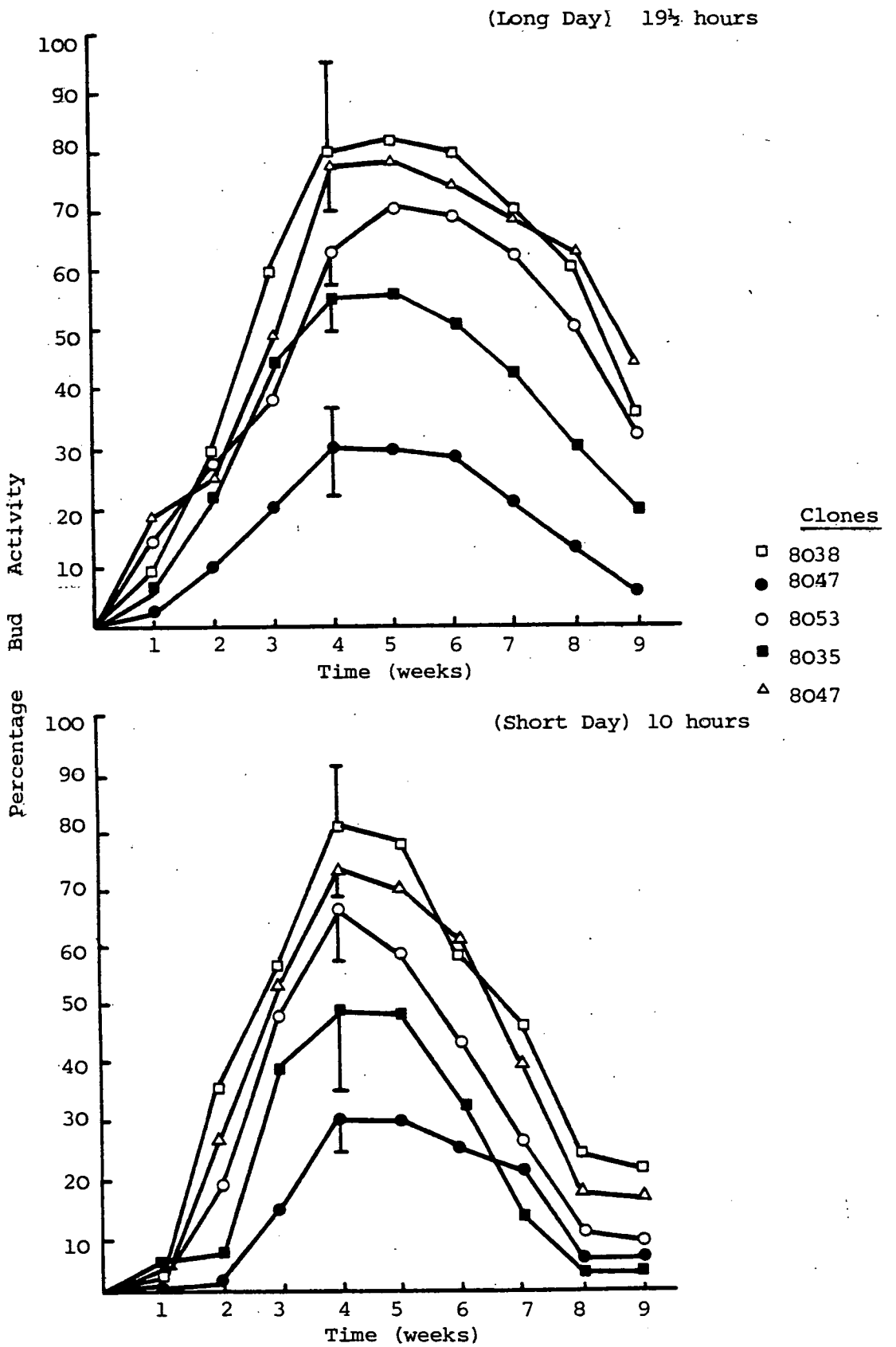
Under long days shoot length was significantly greater that at short days (375 mm and 180 mm respectively). Similarly, both leaf area and leaf number were greater under long days. At a clonal level, clone 8049 produced most leaves (66) while clone 8053 produced greatest area of leaf Lamina (161.2 cm^{-2}) at long days. On the other hand with short days clone 8038 produced most leaves (37) while clone 8047 most leaf area (93.0 cm^{-2}) (Table 10). On a dry matter basis, the long day treatment also produced more shoot dry matter (5.4 g.) than short day treatment (2.3 g) and similarly in leaf dry weight (0.65 g -LD, 0.45 - SD). At a clonal

Fig. 29



Mean treatment effect of daylength (10 hours - SD/19½ hrs. LD) on axillary bud activity in decapitated *T. scleroxylon*. (○ = Long day, ● = Short day with standard error (±SE) as vertical lines. n = 35 for each treatment.)

Fig. 3.2b



Effect on daylength on axillary bud activity in decapitated plants of 5 clones of *T. scleroxylon*. (Means of ⅛ plants per clone, with vertical lines representing (±SE) Standard Error week 4).

level, clone 8038 produced both the greatest amount of shoot and leaf under long days (8.9 g and 1.10 g), while under short days clone 8049 produced the most shoot (2.7 g) and clone 8053 the most leaf (0.55 g) (Table 10).

There was no significant relationship between leaf number and leaf area at both LD and SD (r = +0.31, and - 0.48) and neither was there a significant relationship between shoot and leaf dry weights at both LD and SD (r = +0.57 and -0.04).

Table 10 : Effects of daylength on final leaf number and leaf area (CM^2) produced by decapitated plants of *T. scleroxylon* (figures in parentheses are (±) standard errors, n = 7 or 8 plants per clone).

Clones	Mean leaf number produced		Mean leaf area (cm^2)	
	LD Long days	SD Short days	LD Long days	SD Short days
8049	66 (6.0)	32.0 (4.0)	132.2 (6.3)	88 (5.1)
8038	58 (3.3)	37.0 (4.5)	113.4 (6.8)	78.6 (2.1)
8035	48 (4.8)	32.0 (4.6)	110.5 (8.9)	68.8 (5.0)
8053	43 (2.6)	23.0 (3.0)	161.2 (9.3)	73.8 (4.6)
8047	33 (1.8)	14.0 (5.9)	143.9 (9.0)	93.0 (3.4)
Mean	49.6(5.7)	27.6 (4.1)	132.2 (9.5)	804. (0.19)

Table 10 : Effects of daylength on mean shoot and leaf dry weight (g) at final day of assessment in decapitated plants of *T. scleroxylon*. (figures in parentheses are (±) standard errors, n = 7 or 8 plants per clone).

Clones	Mean Shoot dry weight (g)		Mean Leaf dry weight (g)	
	LD Long days	SD Short days	LD Long days	SD Short days
8038	8.9 (1.6)	2.8 (0.09)	1.10 (0.15)	0.49 (0.08)
8049	5.8 (0.4)	2.7 (0.5)	0.44 (0.065)	0.47 (0.05)
8047	4.7 (0.6)	2.3 (0.24)	0.31 (0.08)	0.42 (0.03)
8035	4.0 (0.8)	2.0 (0.04)	0.44 (0.13)	0.36 (0.02)
8053	3.7 (0.6)	1.70(0.7)	0.84 (0.02)	0.55 (0.03)
Mean	5.4 (0.9)	2.3 (0.19)	0.65 (0.14)	0.46 (0.03)

5.7.4 Discussion

The greater bud activity under long days both at early and late stages of this experiment does not agree with the findings of Kitamura and Kudo (1952) in *Pisum sativum* . They reported substantial effects of daylength on apical dominance, with long days enhancing apical dominance in undeca-pitated plants while short days weakened apical dominance. The opposite of this can only be said for weeks 1 and after the 4th week where long day delayed the establishment of apical dominance and short day enhanced it. However, the suggestions of Phillips (1975), that photoperiodic effects may be mediated through their effects of photosynthesis and probably a change in hormonal balance, is favoured. In this case less shoot and leaf production or dry weight accumulations in short day treated plants (Table 10a and 10b) indicate a limitation to this primary process of photosynthesis which was then a major indirect factor in the day length response. These results also do not agree with those of Gregory and Veale (1957) in undecapitated Flax, in which long days 17½ hours enhanced apical dominance while short day 10 hours decreased apical dominance, at both high and low nitrogen levels. It should however be acknowledged that perhaps apical dominance *per se* and dominance development in decaped plants are something different. However in a recent work (Leakey and Longman, in press), with *T. scleroxylon* (plants similar to the ones in this experiment), at 25 °C, the effect of daylength (11, 13 and 15 hours) on the maximum level of bud activity was not significant and this agrees with the present work. Further agreement was that dominance was not re-established under long day treatment even after the 9th weeks. Furthermore at 25 °C, mean shoot length and total leaf area of the top shoots, under long days were considerably greater than under shortdays. There is similarity

between these findings and those of Longman (1978) in *Terminalia* spp. and *Chlorophora excelsa*, where increasing the photoperiod substantially increased shoot growth rates and leaf area; and also in some other West African trees (Longman and Jenik 1974).

Furthermore, the lack of strong relationships between (i) the number of leaves produced and their leaf area or (ii) shoot dry weight and leaf dry weight, suggest some other underlying factors which might be involved in the effect of photoperiod, such as the effect of short day treatment in the flux of cytokinin from the root to shoot as demonstrated in *Perilla fructescens* by Beaver and Woolhouse (1973).

At the practical level, as far as maximum bud activity in decapitated plants is concerned, if other factors such as temperature are rigidly controlled,photoperiod is not a critical factor. On the other hand, attempts to make comparisons between clones in relation to other growth responses like total shoot length, and the size and number of leaves, would require the standardization of photoperiod.

5.8 EFFECTS OF EDAPHIC ENVIRONMENTS ON BUD ACTIVITY IN DECAPITATED PLANTS OF *T. scleroxylon*

It is well established that in addition to the aerial environments to which growing plants are exposed, their edaphic environments are also of great importance to their development.

Nutrient status and soil water conditions seem the most important provided temperature and aeration are adequate. The effects of various factors on apical dominance have also been extensively investigated recently (see Review by Phillips 1975), with particular attention paid to the importance of inorganic and organic nutrients, as well as water (see McIntyre 1964; 1968; 1971; 1977; Fletcher and Dale 1974). It is not clear exactly how these affect lateral bud development, but it is now generally accepted that root factors

influence correlative inhibition, and this has been demonstrated in *Solanum andigena* where cytokinins from the roots induced lateral shoot growth in decapitated plants (Woolley and Wareing 1972), and in other similar investigations.

The present study considers the effects of nutrient status and soil moisture on the sprouting of decapitated plants of *T. scleroxylon*, as these factors are viewed as a further set of plant and environmental variables affecting apical dominance, to be added to these aerial factors already reported in the earlier parts of this chapter.

5.8.1 EFFECTS OF NUTRIENTS ON AXILLARY BUD ACTIVITY IN DECAPITATED PLANTS OF *T. scleroxylon*.

As well as nutrients exerting an overall influence on plant growth, there is some evidence that certain nutrients particularly nitrogen affect the intensity of apical dominance.

The Nutritive theory of apical dominance, which states that the competition for nutrients is the main factor in correlative inhibition has stimulated much work since it was developed in 1900 by Goebel. In recent years, effects of nutrient concentrations on apical dominance have been studied in Flax (*Linum ussitatissimum*) by Gregory and Veale (1957); McIntyre (1968a); McIntyre and Larmour (1974), *Solanum sisymbrifolium* (Wakhloo 1970), *Agropyron repens* (McIntyre, 1965; 1969; 1971; 1972; Leakey *et al*, 1978) and in *Phaseolus vulgaris* (Phillips 1968; Shein and Jackson 1972; McIntyre 1973). All these workers agree that nutrition greatly affects apical dominance, the majority suggesting that high levels of nutrients release axillary buds from correlative inhibition, while Leakey and Longman (in press) considers that high nutrient levels

may prevent the buds from becoming inhibited.

The work reported here investigates the effects of nutrients on the correlative inhibition in *T. scleroxylon*. Also, following claims that vascular bundles may be absent in inhibited buds (Sorokin and Thimann 1974), anatomical investigation of stem-bud relationship from decapitated and non-decapitated plants was made to observe the connection between buds and the vascular system in the stem.

5.8.1.1 Materials and Methods

20 plants of each of clones 8038, 8049, 8053, 8046 and 8055 were selected (of varying heights) and repotted into 7" diameter pots and grown in the standard environment of the ITE tropical glasshouse (see Chapter 3).

Nutrient treatments, following removal from the standard 1 % Solufeed Solution, were either 0.004 % or 4.0 % 'Solufeed' (23: 19.5:16; N:P:K.), given twice weekly to 10 plants of each clone, starting 32 days prior to decapitation. Plants were then randomly allocated into 3 blocks, and to compensate for differences in stature, some plants were raised up on inverted pots to the same level as the others and appropriately spaced out to prevent shading and competition between plants.

Six leaves were retained on each plant following decapitation and thereafter assessed for lateral shoot length at weekly intervals for 10 weeks. Shoots were considered active if extension exceeded 2 mm $week^{-1}$, as described in Chapter 3.

5.8.1.2 Results

Mean lengths of the top four shoots were significantly greater from plants at 4 % Solufeed than from those at 0.004 %, one week

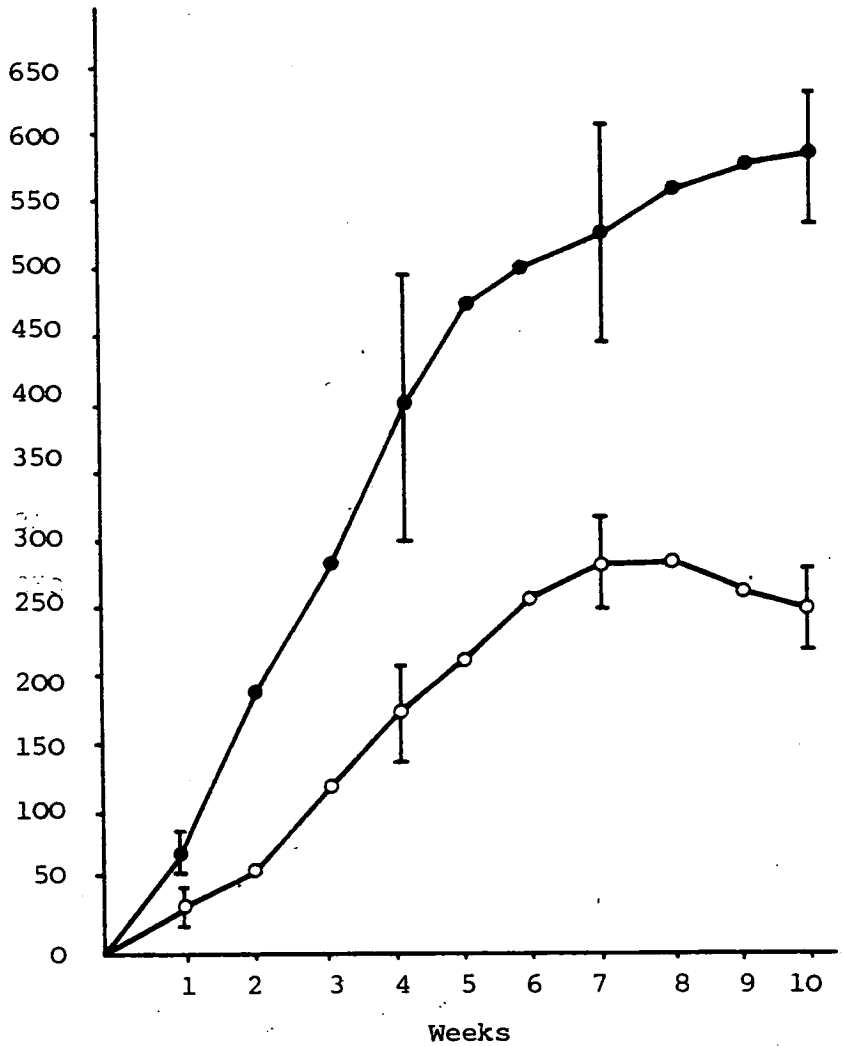
after decapitation (Fig. 33a). In addition, bud activity at the higher concentration was greater (Fig. 33b) and although some buds were subsequently re-inhibited most (66 %) made continued growth. At the lower concentration of nutrients bud activity started late and dominance was quickly re-established, being complete by Week 8.

Although clones responded differently to treatment, there were no significant differences at the low concentration of nutrients and only clones 8038 and 8053 differed significantly from clone 8049 at the high concentration at Week 4 (Fig. 33c).

5.8.1.3 Discussion

Nutrient status had an immediate effect on the growth of lateral shoots, which was significant within a week. However unlike other studies, nutrient treatment was started before decapitation, and plants may have accumulated nitrogen. This result supports the idea that nutrients are important in the phenomena of correlative inhibition, and agrees with the reports of Gregory and Veale (1957) in *Linum ussitatissimum* where high nitrogen level increased axillary branch growth more than at the low nutrient treatment. It agrees also with the work of McIntyre (1967) in the same species (flax) where he showed that the inhibiting influence of a dominant shoot was inversely related to the nutrient level and that an inhibited shoot could be released from inhibition by increasing the nitrogen level. It also agrees with the findings of McIntyre (1977) in *Pisum sativum* who reported that when plants were grown under favourable nutrient levels (nitrogen and carbohydrate) axillary buds were released from inhibition. In decapitated plants of *Agropyron repens* Leakey *et al* (1978b) also demonstrated that the application of exogenous supply of nitrogen

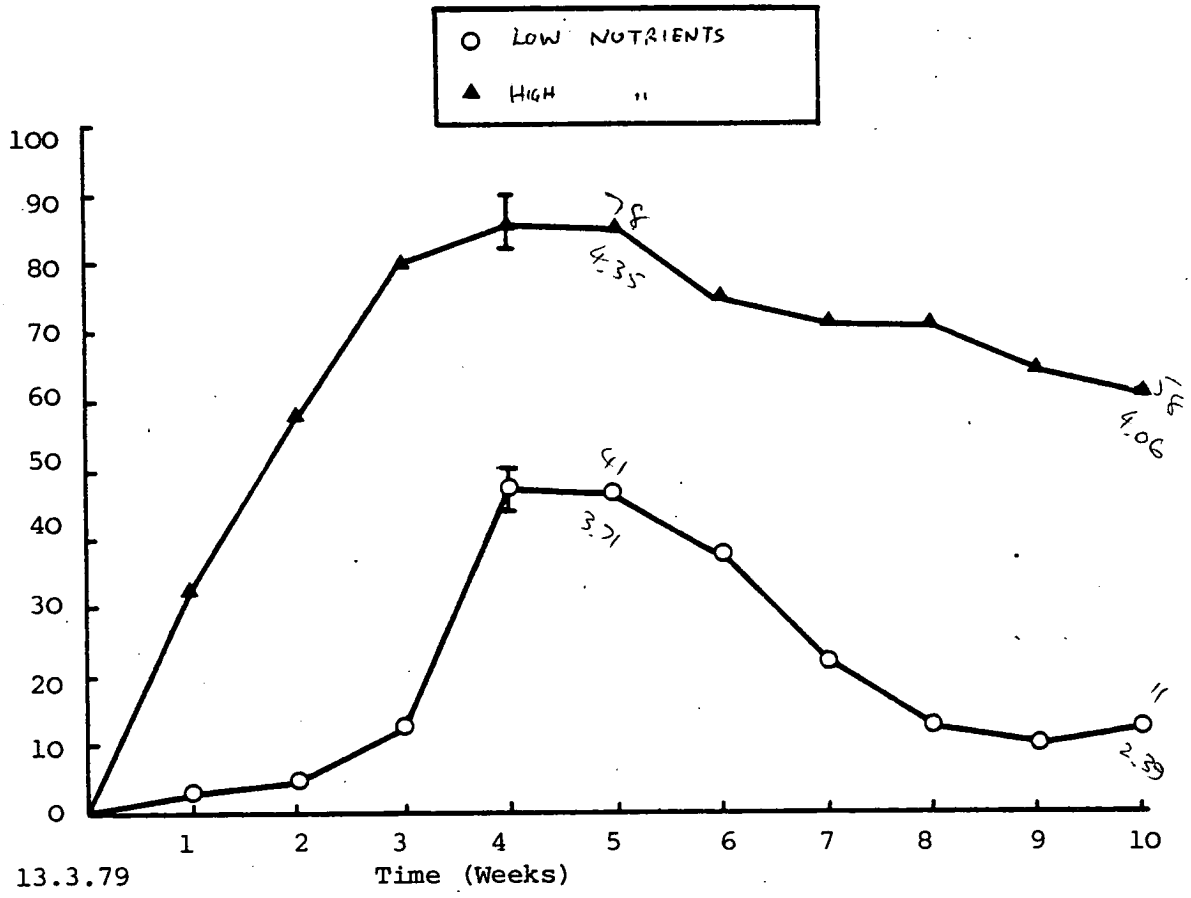
Fig. 39a



Effects of nutrient levels (● = 4 % Solufeed; o = 0.004 % Solufeed) on the mean shoot growth (1st-4th only) of decapitated plants of *T. scleroxylon*.

(Vertical bars are Standard Error (±SE). n = 50 plants).

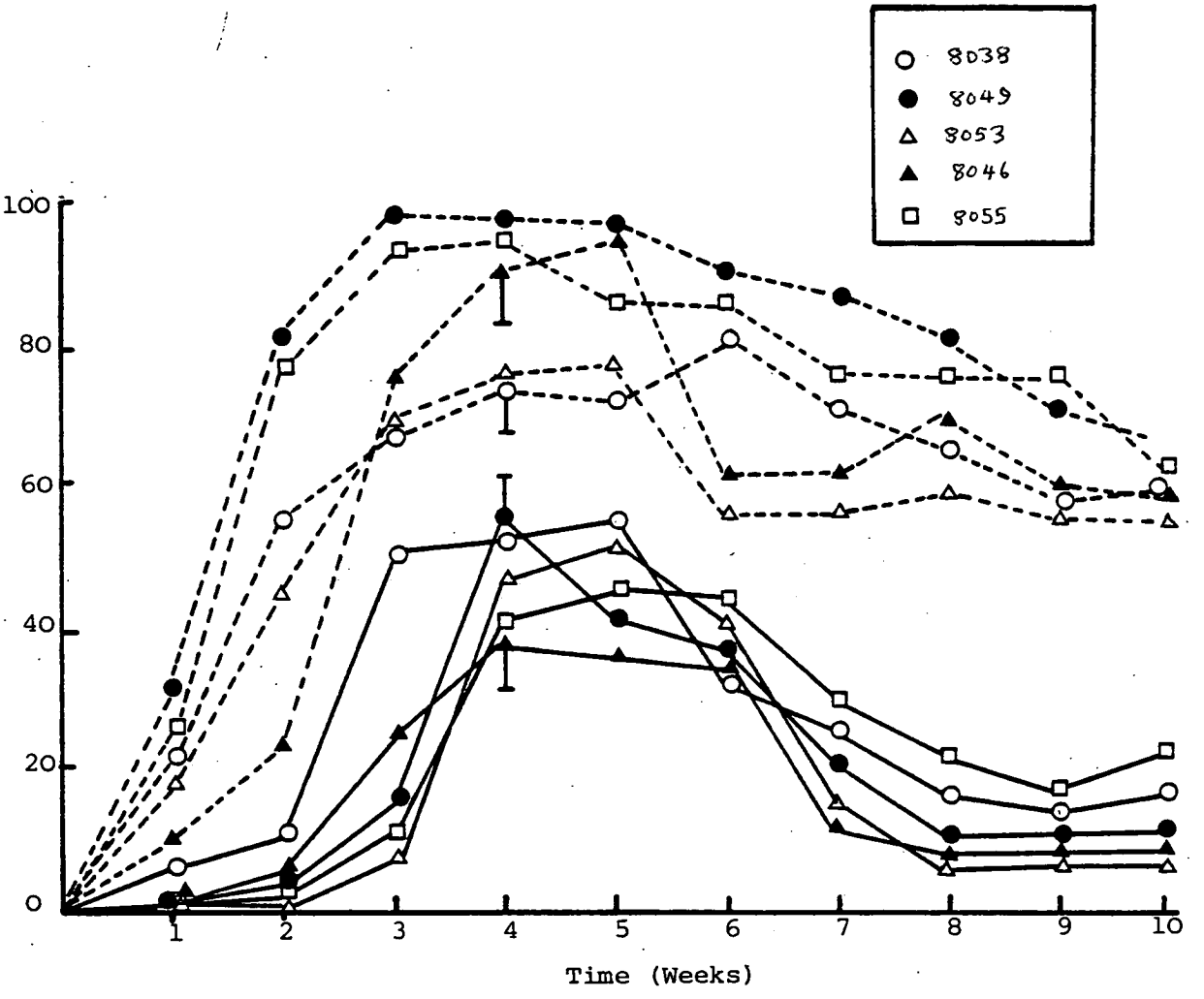
Fig. 33b



Effects of nutrient levels (▲ = 4 %, O = 0.04 % Solufeed) on bud activity following decapitation of *T. scleroxylon* plants.

(Mean of 5 clones x 10 plants with Standard Error (±SE) for Week 4).

Fig. 33c



Variation in % bud activity in decapitated clones of *T. scleroxylon* with high (4.0 % Solufeed fertilizer hatched lines) and low (0.004 % Solufeed fertilizer unbroken lines) applications.

(Clones - O = 8038, ● = 8049, Δ = 8053, ▲ = 8046, ▫ = 8055, with Standard Error (±SE) for week 4. n = 10 plants per clone/treatment).

(KNO_3) delayed the onset of dominance, as was also shown in the present study. Perhaps as suggested by Leakey *et al* (1978b) the greater growth rates of basal buds prevented their inhibition. In the present study in contrast to Leakey and Longman (in litt) who used similar plants of *T. scleroxylon* grown at less extreme nutrient status's, which were not started prior to decapitation, an immediate effect of nutrients on sprouting was also shown, implying that the nutrient status prior to decapitation probably affected their response to decapitation. It thus appears that stored nutrients enhanced bud activity and growth so delaying or preventing their inhibition. This agrees with the suggestions of Leakey and Longman (in press) that high nutrient levels particularly nitrogen, may prevent buds from becoming inhibited rather than releasing them from inhibition, as proposed by Gregory and Veale (1957).

As the fertilizer used in the present study was a mixture of N.P. & K, the effects of the other elements should be considered. In *Linum ussitatissimum* McIntyre (1967) demonstrated that phosphorus also had effects on dominance between shoots. He varied the amount of phosphorous given to decapitated plants (0.25 ppm - 1.0 ppm in the culture medium) and reported that bud activity was positively related to phosphorus concentrations. In a similar way, Wakhloo (1970) demonstrated that Potassium had similar effects in *Solanum sisymbrifolium*. The involvement of Potassium in apical dominance has very recently been supported by work in *Bidens pilosus* (Kramer *et al* 1980) where microanalysis and election microscopy revealed that K^+ were apparently accumulated in the stem tissue around nodes after decapitation. The presence of K^+ was interpreted in terms of its possible role in bud growth initiation and regulation. It is therefore possible that these other elements may have affected

dominance relationships of *T. scleroxylon* and could have had additive effects on bud activity.

Although the clonal differences in the present study were not great, it is reasonable to suppose that *T. scleroxylon* clones might differ in the ability to take up mineral nutrients in a way similar to that found in *Betula* clones (Mason and Pelham 1976), and that, following a Hormone Balance theory for apical dominance, this could effect bud activity in decapitated plants.

To conclude, in the light of these results and those of Leakey and Longman (in press), the need to standardize nutrient status for a predictive test of branching habit is very important and needs careful control.

5.9 EFFECTS OF WATER STRESS ON BUD ACTIVITY IN DECAPITATED PLANTS

Kozlowski (1958, 1971) Zahner (1968) and many others have emphasised that moisture stress, more than any other single factor, (soil-plant-atmosphere continuum), restricts plant growth. It is accepted as a major ecological factor in the distribution of vegetation types over the world land surface.

An indication of its influences on growth correlation was discussed by Wilson (1948) who suggested that shoot apices and other meristematic tissues have the competitive ability to obtain water at the expense of the older parts. Earlier, Loeb (1918) concluded in his work with *Bryophyllum calcycinum* that moisture could be a major factor in correlative inhibition, but only recently has its role in the phenomena of apical dominance been re-investigated.

Hussain and Link (1966) observed in *P. sativum*, that inhibited buds showed shrinkage, indicating that water was perhaps being diverted from them to more active ones. Remy (1967) using the same

species subsequently demonstrated that the degree of water stress within decapitated shoots determined the position of dominant shoots. This was done by altering the direction of water movement within plants using a miniature aspirating pump which allowed him to direct water to either of the two cotyledonary shoots. Later McIntyre (1971), in work on isolated rhizomes of *Agropyron repens*, suggested that inhibition of the lateral buds subjected to various levels of water stress, largely depended on the availability of water and nutrients, both of which could act as a limiting factor. He later tested this hypothesis in *Pisum sativum* (McIntyre (1971) in which the relation between transpiration, leaf turgidity, and lateral bud growth was investigated and he found that water stress measured as leaf turgidity was closely related to bud activity. He thus concluded that water stress could contribute to correlative inhibition. He subsequently went on to propose that the very rapid increase in bud length following decapitation of the apex was due primarily to cell extension resulting from an increase in water potential in the buds (McIntyre, 1973; 1977). This view was to some extent substantiated by the findings of Yeang and Hillman (1981) in *Phaseolus vulgaris*, but they further reported that subsequent growth could not be attributed to increase in cell length since other factors, such as cell division became involved in the process.

Apart from the above information on herbaceous plants, little seems to be known on the specific effects of water stress on correlative inhibition in forest trees. The present work concerns the effects of 3 levels of water stress on the bud activity of decapitated *T. scleroxylon* plants and their effects on leaf size and shoot length.

5.9.1 Materials and Methods

30 plants, 50-60 cm tall, of each of 5 clones (8038, 8045, 8047, 8049 and 8053) were repotted into 7" pots and kept under standard conditions for one week before being allocated to treatments and randomized into 3 blocks. All plants were reduced to 6 leaves, and to reduce water loss from the soil surface, each pot, standing in its own saucer, was covered by a polythene bag, tied around the plant stem but slit at the base to allow water uptake (Plate 4). Some aeration was allowed by two 15 mm diameter holes on the upper surface of the bags. To avoid splashing and thus "cross-contamination" of treatments, the plants of each block were all treated similarly. When all plants had recovered from repotting the following treatments were applied:-

(i) 250 mls Daily

(ii) 250 mls at 3-day intervals

(iii) 250 mls at 12-day intervals

starting 12 days before plants were decapitated: Thereafter assessments of lateral shoot length was then made at weekly intervals, additionally at the end of the first 12 day cycle, 2 leaves were taken from two plants of each clone (Leaf No. 3 & 4) to determine their water potential using a pressure bomb (see Hellkvist *et al*,1974). The angle of leaf 1 was also measured from the pulvinus, as this angle provides a rough, visual, measure of turgor. At the end of the experiment (Week 12) 4 leaves from the uppermost dominant lateral shoot of 4 plants per clone were measured with a Lambda Leaf Area Meter to assess leaf area.

5.9.2 Results

Preliminary investigations showed that water potentials (ψ) (Table 11) as measured with the pressure bomb and leaf angles at pulvinus, at 10 a.m. were closely correlated under the 1, 3 and

Experimental plants of *T. scleroxylon* in ITE glasshouse on the 1st day of water stress experiment.

12 day watering regimes used. (i.e.)

i, Number of days before watering against water potential:

r 2 0.98 ($P<0.02$)

ii, Water potential against leaf droop at 10 a.m.:

$r = -0.96$ ($P<0.05$).

Water stress (12 day watering regime) affected bud activity marginally in the sprouting phase, but under both 3 and 12 day regimes dominance development among shoots was delayed and possibly prevented (Fig. 34b). Under the severe treatment bud activity fluctuated in sequence with the watering cycle (Fig. 34a).

Table 1

	Treatments (250 mls)	Leaf angle at Pulvinus	Mean water Potential	Observations
1	Daily	90 ^{o}	- 7 (bar)	Not wilted
2	3 d.interval	45 ^{o}	-19 (bar)	Wilted at 3rd day
3	12 d.interval	>18 ^{o}	-38 (bar)	Wilted at 3rd day

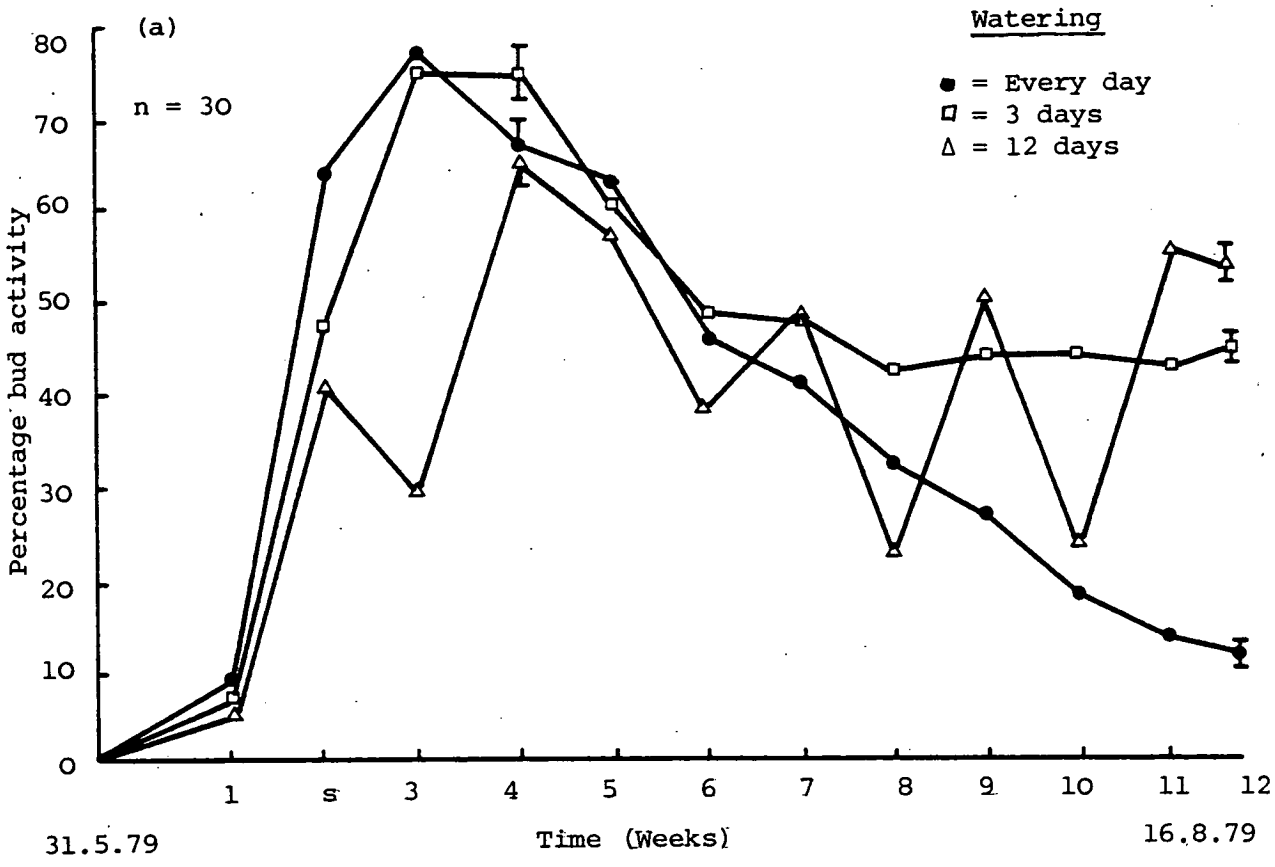
Treatment effects (1d, 3d and 12d watering intervals) and corresponding values of leaf angle, water potential (bar) and general observations.

Clones differed in their response to the watering regimes (Fig.34c), in three major ways - those relating largely to treatments :-

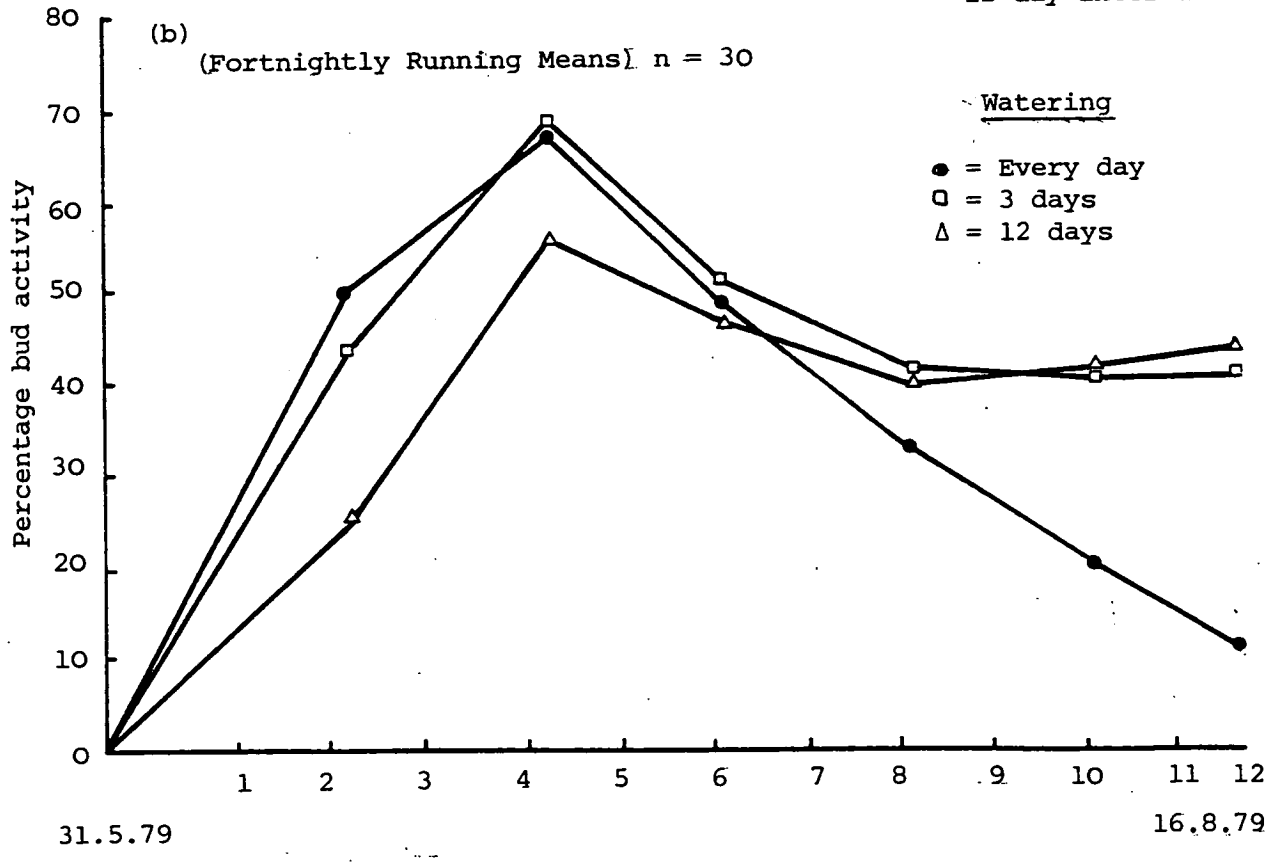
(i) With daily watering, there appeared to be genetic differences in the proportions of buds released from correlative inhibition. All clones re-established dominance at about the same time.

(ii) With watering every3rd day, bud activity during the sprouting phase was less variable, but clones subsequently differed during the

Fig. 34 a,b



- Time of watering for 12-day interval treatme



Effect of different watering regimes on axillary bud outgrowth of decapitated clonal materials of *T. scleroxylon*

(a) Mean values

(b) Running means, to show treatment effec on plants

dominance-re-establishment phase, there being two major groups, those in which co-dominance was established by the 2-3 uppermost laterals, and those in which almost all shoots made continued growth. These groups were, clones 8047, 8049, 8053 and 8038, 8045 respectively.

(iii) With watering every 12th day, clones differed in both their sprouting and dominance-development phases; one clone (8047) in particular responding quite differently from the rest. With the exception of this clone, the response was similar to that of the group under the 3rd. watering regime, in which dominance was not re-established. In all these clones bud activity fluctuated in sequence with the watering cycle (Fig. 34c. III).

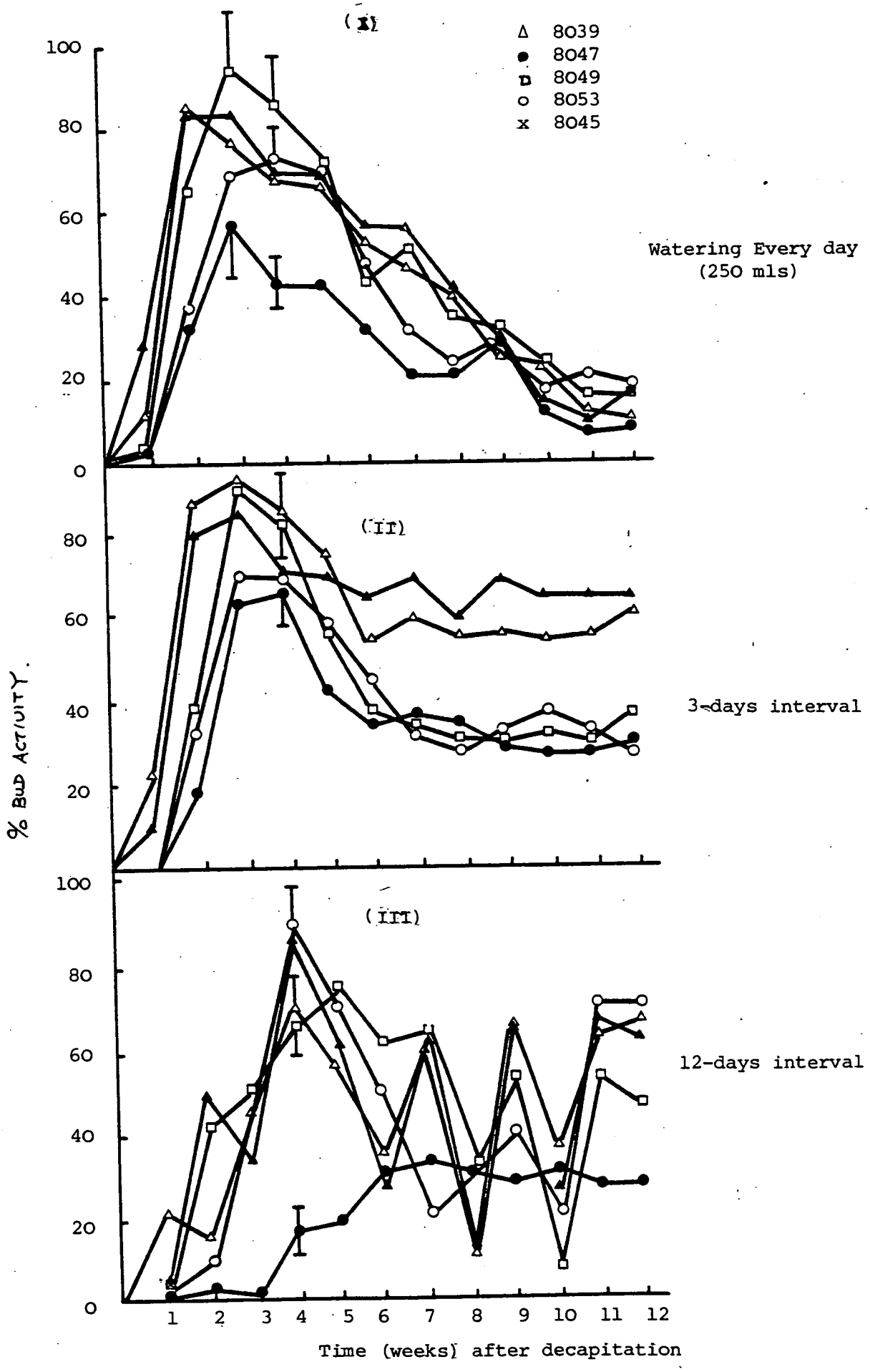
In complete contrast, however, clone 8047 was very slow to sprout under this watering regime and its bud activity was generally lower than the other clones but maintained an equilibrium which was sustainable throughout the period of test.

Watering regime also affected leaf size, the leaves being smaller the greater the water stress. There was clonal variation in leaf size, with clone 8047 having significantly smaller leaves than the other clones under the 3rd and 12th day watering treatments. Similar clonal differences are apparent in mean shoot length (Fig.35), this correlating with bud activity at 4 weeks, $r = +0.5$ ($P = 0.05$), and with mean leaf area, $r = +0.72$ ($P = 0.01$), both being highly significant.

5.9.3 Discussion

Peak bud activity was reached by weeks 3 - 4 in all treatments by which time, even the plants watered every 12 days had received 2 cycles of watering, and this peak was very similar in all treatments,

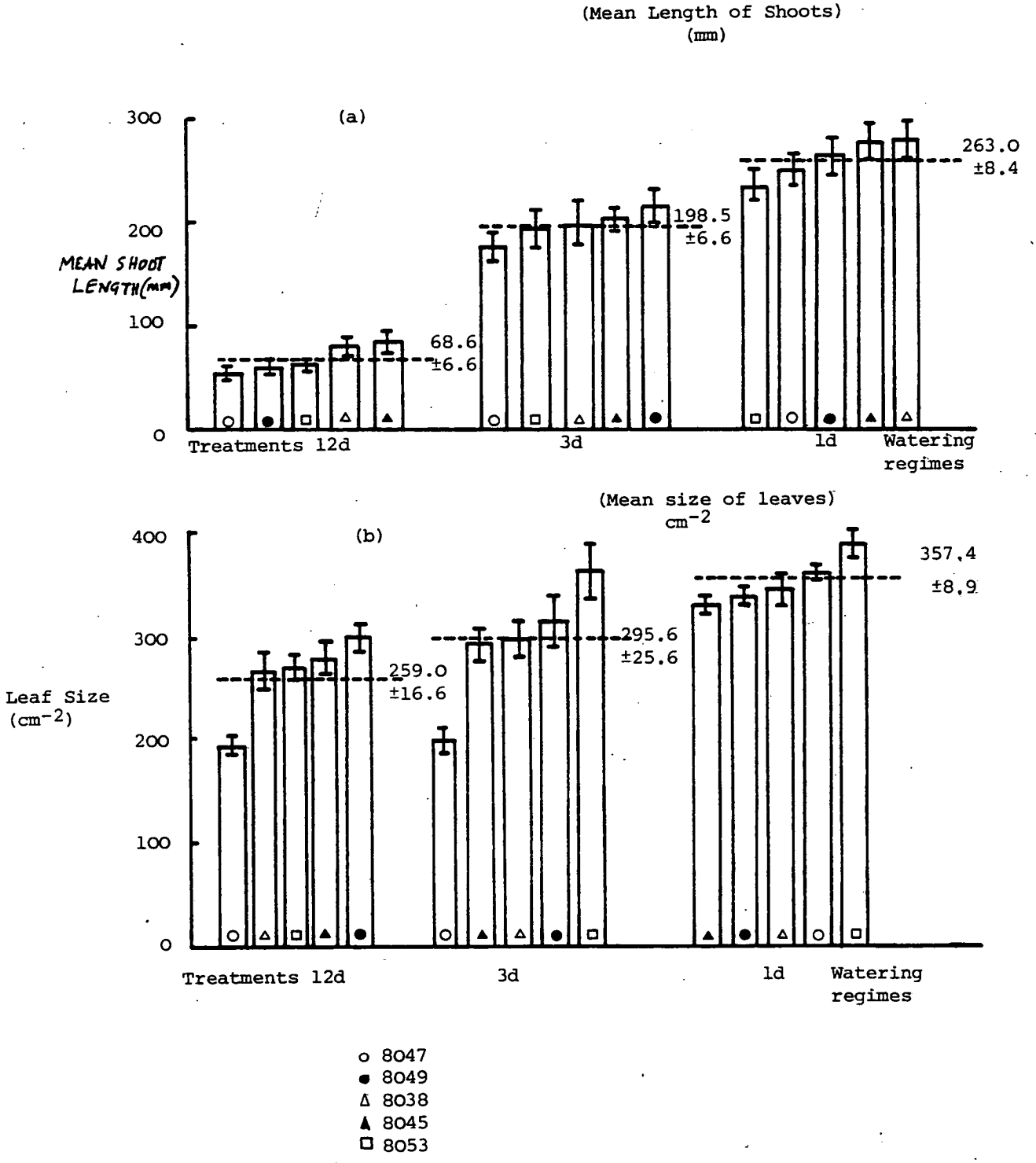
Fig. 34c



Effects of different watering regimes on clonal materials of *T. scleroxylon*

(n = 10)

Fig. 35



Effects of water stress on leaf size, and mean shoot length produced after 12 weeks under 12 days, 3 days and daily watering regimes in decapitated clonal plants of *T. scleroxylon* (clones o = 8047, ● = 8049, Δ = 8038, ▲ = 8045 and □ = 8053, vertical bars represent ± Standard Errors. n = 40 for shoot length and n = 16 leaves per clone in leaf size).

the lower mean (Fig. 34b) for the 12 day cycle being probably attributable to the atypical response of one clone (8047), as will be discussed later. However, although initial bud outgrowth was lower in the 12 day watering cycle (Fig. 34c), it appears that watering regime does not greatly affect the level of bud activity at the end of the sprouting phase. This is rather surprising in the light of the findings of McIntyre (1973) in *Phaseolus vulgaris*, where he domonstrated that outgrowth of cotyledonary buds was correlated with the degree of water stress as measured by the relative turgidity of the leaves, and as demonstrated by other workers. However it is not known in what way response to decapitation in *T. scleroxylon* would differ if done at a different point in the watering cycle. Furthermore, it is quite possible that cyclic water stress, as experienced in this experiment, may have rather different physiological effects on such processes as apical dominance than for example a constantly maintained level of water stress, as used by McIntyre (1973).

The sensitivity shown by clone 8047, one of the clones from the drier rainfall zone to the watering regimes of the present study probably reflects a genetic ability to tolerate water stress, as it produced the least leaf lamina area of all clones. This evidence supports the views of McIntyre (1976) who suggested that plants can adapt to the degree of water stress normally experienced in the field, and that this is likely to influence their mechanism of bud inhibition. In the instance of clone 8047, it appears that to a considerable extent its tolerance to water stress was due to its ability and perhaps its rate of growth to equilibrate with water availability. This could be a useful trait in drier areas. In this case, it suggests that it

may display a lower transpiration rate on a per plant basis, and perhaps also, thicker leaves with a greater water storage capacity. Its ability to control effectively its stomatal pores may have contributed to this also, while the other clones were not able to adjust their vegetative growth to match the availability of water, and thus produced too many leaves, which were large. Consequently they transpired more and suffered from water stress, while clone 8047 did not.

The ranking of clones in the daily watering treatment was maintained at each assessment, at least within the limits of statistical error. In the other two treatments the ranking was altered, clone 8047 always sprouting the least and 8049 being always one of the highest sprouters. This is not unexpected considering that they are genetically different. These two clones 8047 and 8049 are however useful marker clones for future work.

Generally, watering regime affected mean leaf size in all clones and this was probably the cause of the differences in mean shoot length ($r = +0.72$), this being largely a result of the reduction in photosynthetic surface area and the consequent reduction in carbohydrates available for shoot growth. This is comparable to the effect of shading reported earlier in the chapter.

In the case of the delay in the re-establishment of dominance, it was indicated in the nutrient experiment earlier in this chapter that more rapid growth of lower laterals may delay their inhibition, as in *A. repens* (Leakey *et al*, 1978b) and the same may be true in this water stress experiment because under the 12-day watering regime growth of apical shoots was also poor. This observation agrees with McIntyre (1979) in *A. repens*, earlier grown under low N level, but

which when subjected to water stress exhibited a basipetal pattern of shoot growth as observed in the present work. He explained this situation as a consequence of the basipetal distribution of N. concentration which on analysis showed a close relationship to shoot development (McIntyre 1972), and revealed the interraction between the effects of N and water stress.

It is clear that shoot extension and bud activity in decapitated plants of *T. scleroxylon*, are sensitive to water status and thus in tests to compare clones response to decapitation, great care must be taken to water all plants regularly and uniformly. It is probably also desirable to standardise the size of the pot, as this is likely to affect water stress in plants that are rapidly transpiring.

5.9.4 GENERAL CONCLUSIONS ON THE EFFECTS OF PLANT, AND ENVIRONMENTAL FACTORS ON BUD ACTIVITY IN DECAPITATED *T. scleroxylon* PLANTS

The results presented so far suggest that a considerable amount of within-clone variation can be prevented by rigorously standardising the conditions under which decapitation tests are done. Particular attention to the following points should be made:-

i) Decapitation should remove only the top 2-nodes and preferably plants should be part of a regular batch.

ii) Only 4-6 leaves should be retained

iii) Day lengths should be about 12 hours, but extension to 19.5 is acceptable providing temperatures exceed 25°C.

iv) Light intensities should be between 650 and 1500 $\mu E\ m^{-2}\ s^{-1}$.

v) Temperature should be around 30 °C, within range 25 - 35 °C.

vi) Careful and regular daily watering should prevent water stress.

vii) Only extreme nutrient levels seem to seriously affect peak bud activities, although the dominance phase appears to be more sensitive. John Innes compost with 1 % liquid fertiliser

(Solufeed) seems to be very suitable

ix) Ranking in clonal variation is sometimes affected by environmental factors, so to monitor this "marker clones" should be included in all screening tests.

x) At least 15 plants should be used to enable reasonable discrimination between clones.

Most of these conditions can be met in both the tropical glasshouses at ITE and the nursery at FRIN, although in the latter the temperature and humidity requirements cannot easily be arranged in either the dry season or the hammattan periods when temperatures may reach 35 ^{o}C and air svpd can rise to 40 mbar on occasions.

SECTION 3

PERFORMANCE OF CLONES IN PLANTATION

Based on the experiences gained in the work with *Betula pubescens*, field assessments on 4-year old trees of *T. scleroxylon* were done in Nigeria to elucidate clonal variations in growth, branching characteristics and later the effects of these on crown variation.

CHAPTER 6

6. GROWTH OF *T. scleroxylon* CLONES IN NIGERIAN PLANTATIONS

In *T. scleroxylon* as in other forest trees, lack of flowering during the juvenile period, and the infrequency of fruiting of mature trees, (Longman and Coutts 1974), have posed great problems to plantation establishment and tree improvement (Longman 1976). Recently however, the development of vegetative propagation techniques using juvenile cuttings has provided foresters with a new source of planting stock, with the added advantage that by selecting clones foresters can potentially increase yields from forest plantations.

With the realisation of this potential methods of propagation have been developed for many forest species, including some like *T. scleroxylon* which were formerly considered difficult-to-root, and now this important advance is becoming a reality (Libby 1974, Longman 1976).

However there are still many problems to be solved, as for example how to select clones, the width of the genetic base, the selection intensity etc. Many of these have been discussed by Kleinschmit (1979) who emphasized the need to conserve the genetic variation of indigeneous populations, and to beware of the hazards of disease and pests if the genetic base becomes too narrow. He advocates generous selection intensities and the use of mixtures containing large numbers of selected clones.

Extensive literature now exists on the study of clonal variation in many forest species, such as: *Pinus radiata* (Wilcox *et al* 1975), *Picea abies* (Kleinschmit 1973), *Populus deltoides* (Farmer

and Wilcox 1968) and *P. euamericana* (Gordon and Promintz 1976). From these, estimates of genetic parameters (heritability values) have been calculated for various traits (Hinds and Krugman 1974) and the genotypic value of individual clones (mean performances) have been estimated (Burdon and Shelbourne 1974; Korster 1977).

The vegetative propagation of *T. scleroxylon* in Nigeria (FRIN) and Scotland (ITE) Leakey *et al* in press) has allowed the establishment of various clonal field trials, including those used in the present study.

Earlier reports of clonal variation in this species, include those of Bowen (1975), Howland and Bowen (1977), Howland *et al* (1978) Longman (1978) and Ladipo *et al* (1980) who all reported appreciable clonal variation in rate of height growth and branch production from 18 months after planting. The present study extends these early investigations to a later stage of growth.

6.1 Materials and Methods

Between June and September of 1979, extensive field assessments were made at Gambari Forest Reserve near Ibadan.

Three experiments (3/75, 5/75 and 7/75) were used, all previously set up with well replicated single tree plots by the West African Hardwood Improvement Project in June 1975 (Howland and Bowen 1977). In the studies presented not all the clones of these experiments were assessed. Rather, clones were selected to encompass the range of diversity. They had been raised from 12 half-sib seed sources, now represented by between 1 to 7 clones. The origin, culture and treatments have earlier been described (Chapter 3). However, parent trees were from neighbouring and geographically separate sources and in some instances from different rainfall

zones (Table 12).

Table 1 :

Seedlot/Clone Number	Origin of Seedlot (Nigeria)
137/9	Olokemeji
139/6, 7, 9	Olokemeji
142/10, 12	Omerelu
144/1, 4, 5, 7, 9	Igbo-ora
161/3, 5	Owo
166/1, 3, 8	Azukala
175/1, 2, 5, 6, 7, 8, 10	Igbado
177/10	Ilugun
224/1, 7, 11	Ede
225/8	Ede
261/4	Iyamyong
505/2	Ikere

All experiments were hand weeded to prevent competition and shading from weeds, to allow all plants to grow at their best, exhibiting their full genetic potential.

6.1.1 Experiment 3/75

This experiment was planted between 23rd and 24th July, 1975 at an espacement of 4.9 m.

It consists of clones from seedlots 142, 166 and 175 which were represented by a variable number of ramets (20 - 30), and fully randomised into 2 blocks (A and B) about 50 yards apart, surrounded by 3 rows of 'fillers'.

6.1.2 Experiment5/75

This was planted between the 18th and 21st July, 1975, also at 4.9 m spacing. It consists of clones from seedlots 139, 144 and 224. Each clone from each seedlot was represented by 12 ramets in randomised blocks with each clone represented once per block; 2 filler rows surrounded the experiment.

6.1.3 Experiment 7/75

This is the largest experiment of the 1975 plantings consisting of all the other seedlots (14), and those in the above experiments. Clones were planted at 2 sites (A and B), about 500 yards apart consisting of 9 and 6 blocks respectively. Each clone was fully randomised within the 15 blocks with each tree represented once per block. 3 filler rows formed surrounds at each part of the experiment. After 12 months, survival was 98 % (Howland *et al* 1978) and later, plants in 3 blocks of Experiment 7/75B were pruned below 1.25 m, so removing strong basal branches.

In June 1978, certain clones were selected for their variability on the basis of early performance and marked with tree paint to facilitate easy identification. In June 1979, assessments of branching characteristics were made on these selected clones, (see Appendix 1) on the basis of experience obtained from study of *Betula pubescens* reported in Chapter 4 (see plate 7).

Data analysis was computer-processed, using the programe OYE (see Appendix 2) to give mean values and standard errors for each clone and parameters. Following Burdon and Shelbourne (1974) it was assumed that these mean values are estimates of total genotypic potential. This assessment is known to be valuable if commercial multiplication is to be vegetative; as it is in the case of *T. scleroxylon*.

Abscission index (percentage of branches self pruned) was determined for each clone from the formula :

$$\text{Abscission Index (AI)} = \left(\frac{Sm}{Sm + Bm} \times \frac{100}{1}\right)$$

where Sm = Branch scars per metre and Bm = Branches per meter and values presented as %.

Plate 5

Field assessment (Expt. 7/75A of *T. scleroxylon* at Gambari Forest Reserve in Nigeria in June 1979 when trees were 4 years old.

Diameters at breast height (dbh), which are generally accepted as a comparative measure of wood production, are presented for each clone. Stem taper based on diameter measurements at 0.1 m (db) and 1.3 m (dbh), are presented to give an indication of clonal variation in stem quality (form quotient). This was computed from the well known formula :

$$q = \frac{dbh}{db}$$

where q is taper (form quotient)

6.2 Results

6.2.1 Narrow spacing (2.5 m)

Mean tree height ranged from 8.1 ± 0.43 m for clone 175/5 to 5.9 ± 0.62 m for clone 166/1, these being the tallest and shortest clones respectively (Table 13a).

Multistems were frequent, but their incidence varied from clone to clone, with clone 166/1 having 2.1 stems while many other clones had only one stem.

Furthermore, diameter (dbh), height to the lowest living branch, mean branch number, forking, number of heavy branches including form and vigour scores were significantly different between clones. (Table 13a).

Clones differed significantly in their natural branch shedding, as shown by the abscission index (AI), with clone 175/9 having the lowest score (42.6) and clone 144/5 (76.0), the highest (Table 13 b(i)). Stem quotient (bole taper) also differed between clones (Table 13 b(ii), with clone 166/1 having the least (0.58) and clone 175/6 having the highest value (0.80). Coefficient of variation for these two parameters were 12.2 and 7.4 respectively.

As done for *Betula* spp in Chapter 4, polygonal graphs are used to represent 7 clones. Highly variable 'fingerprints' exist between

TABLE 13a

Table 13a: Analysis of growth 4 years after planting of clones of *T. scleroxylon* planted at 2.5 m spacing in Gambari Forest Reserve, Nigeria - Expt. 7/75A (Br = branches, L.Liv = lowest living and Standard Errors (SE) in parenthesis, C.V = co-efficient of Variation).

	Clone No.											
	137/9	139/6	139/9	144/1	144/4	144/5	144/7	144/9	161/3	161/5	166/1	166/3
1. Height (m)	6.9(0.36)	6.8(0.33)	7.8(0.34)	6.3(0.32)	6.4(0.36)	6.1(0.28)	6.6(0.28)	7.7(0.26)	6.9(0.33)	7.3(0.36)	5.9(0.62)	6.9(0.41)
2. Stem No.	1.0(0.002)	1.0(0.03)	1.1(0.2)	1.0(0.004)	1.2(0.02)	1.0(0.002)	1.0(0.002)	1.1(0.1)	1.0(0.06)	1.0(0.1)	2.1(0.2)	1.5(0.3)
3. Stem Diam. (dbh-cm)	99.8(6.0)	93.3(2.3)	93.4(3.4)	85.7(7.2)	83.8(4.6)	75.0(5.1)	87.6(4.8)	95.0(9.1)	115.0(4.3)	101.4(6.1)	73.0(5.6)	97.0(5.6)
4. Height L.Liv.Br.(cm)	17.4(5.1)	21.4(3.8)	15.1(1.1)	27.7(2.3)	35.3(4.5)	28.5(5.1)	22.5(4.7)	25.8(6.6)	30.0(3.1)	18.9(4.3)	7.1(3.5)	35.4(5.0)
5. Syllepticity (1-5)	2.3(0.2)	1.6(0.3)	2.0(0.2)	2.4(0.4)	3.2(0.2)	2.1(0.3)	2.6(0.3)	2.5(0.4)	1.0(0.06)	2.3(0.3)	2.1(0.3)	1.5(0.1)
6. Total Branch No.	30.6(3.4)	24.0(2.1)	29.0(1.6)	27.9(2.6)	16.9(1.8)	13.9(1.2)	16.6(2.1)	29.7(2.6)	29.0(1.6)	21.0(2.6)	13.0(1.0)	26.0(3.1)
7. Branch/meter	4.4(0.6)	3.5(0.6)	3.7(0.5)	4.4(0.9)	2.6(0.2)	2.2(0.09)	2.5(0.5)	3.8(0.4)	4.2(0.2)	2.9(0.4)	2.2(0.1)	3.7(0.3)
8. Total Scar	39.6(1.8)	44.0(3.1)	30.0(1.6)	55.1(4.8)	40.0(3.4)	44.1(2.1)	37.0(1.4)	41.6(4.6)	46.0(3.1)	27.0(1.3)	35.1(2.1)	40.0(1.8)
9. Scar/meter	5.7(0.5)	6.4(1.6)	3.8(0.8)	8.7(1.3)	6.2(1.3)	6.6(0.54)	5.5(0.8)	5.4(0.8)	6.6(0.5)	3.7(0.2)	6.0(0.6)	5.8(1.4)
10.No. Fork	0.85(0.05)	0.65(0.1)	2.1(0.8)	0.5(0.07)	0.8(0.04)	0.9(0.03)	0.5(0.04)	0.6(0.04)	0 (0.0)	0.8(0.1)	2.4(0.4)	0.5(0.03)
11.No Attempted fork	1.7(0.05)	1.1(0.03)	3.1(0.5)	1.3(0.04)	0.8(0.03)	0.9(0.05)	1.8(0.03)	1.3(0.1)	2.0(0.03)	1.3(0.04)	2.0(0.03)	1.8(0.04)
12.No Heavy Br.	3.3(0.4)	1.6(0.5)	1.3(0.3)	1.6(0.7)	1.8(0.5)	0.9(0.3)	2.2(0.6)	2.3(0.4)	0 (0.0)	2.0(0.6)	1.2(0.3)	1.8(0.4)
13.Form (1 - 10)	4.8(0.3)	4.3(0.4)	4.1(0.5)	5.3(0.6)	5.5(0.4)	5.1(0.8)	4.8(0.5)	5.6(0.8)	7.0(0.9)	3.3(0.2)	2.6(0.4)	2.6(0.3)
14.Vigour (1-10)	4.7(0.4)	4.5(0.3)	6.2(0.7)	4.5(0.6)	4.8(0.5)	4.4(0.3)	4.8(0.4)	4.8(0.6)	6.0(0.5)	5.1(0.6)	4.0(0.5)	4.3(0.4)

(Continued below)

	175/1	175/2	175/5	175/6	175/7	175/8	175/9	175/10	177/10	224/7	225/8	Average	C.V.%
H	7.6(0.50)	7.4(0.60)	8.1(0.63)	7.8(0.58)	7.8(0.51)	7.4(0.26)	7.1(0.41)	7.0(0.40)	7.0(0.30)	7.0(0.26)	6.1(0.28)	7.04	8.8
Stem No.	1.0(0.04)	1.0(0.004)	1.3(0.2)	1.3(0.2)	1.0(0.004)	1.0(0.1)	1.0(0.1)	1.1(0.1)	1.0(0.01)	1.0(0.1)	1.0(0.04)	1.1	22.4
d	115.4(5.6)	123.0(6.3)	109.0(6.4)	115.0(6.1)	105.0(9.6)	118.0(6.2)	84.5(3.4)	87.0(9.2)	93.1(5.4)	110.0(6.8)	85.0(3.1)	97.6	14.5
	20.6(4.3)	31.1(3.2)	38.2(7.2)	21.3(4.5)	30.1(4.9)	39.0(7.2)	20.3(3.2)	28.0(4.6)	21.7(5.3)	31.0(2.1)	20.0(2.8)	25.5	30.8
Sy/	3.4(0.3)	2.0(0.3)	2.5(0.3)	2.7(0.3)	2.3(0.3)	1.5(0.2)	2.1(0.3)	1.7(0.3)	2.6(0.4)	1.6(0.2)	3.0(0.2)	2.2	26.0
	30.0(2.1)	26.2(3.4)	32.2(3.0)	27.2(2.4)	27.4(2.3)	30.4(1.6)	32.0(1.6)	19.2(1.3)	21.4(1.5)	30.0(2.8)	20.0(2.6)	25.0	24.0
B/m	3.9(0.2)	3.5(0.1)	3.9(0.2)	3.4(0.2)	3.5(0.3)	4.1(0.4)	4.4(0.9)	2.7(0.1)	3.1(0.1)	4.3(0.2)	3.2(0.1)	3.5	20.2
(Continued)	40.0(3.1)	55.3(3.8)	56.0(4.4)	37.0(1.1)	44.0(1.7)	38.0(1.6)	23.0(1.1)	34.1(1.5)	33.0(1.8)	48.0(2.3)	23.0(1.0)	39.6	23.1
S/M	5.3(1.4)	7.4(0.9)	6.8(1.2)	4.7(1.4)	5.6(1.1)	5.1(1.0)	3.3(0.9)	4.9(1.3)	4.8(1.0)	4.1(0.3)	3.7(0.6)	5.5	23.8
F	0.6(0.06)	0.6(0.2)	0.80(0.07	0.8(0.03)	0.8(0.03)	0.4(0.2)	0 (0.0)	0.8(0.3)	1.1(0.4)	1.1(0.2)	2.0(0.3)	0.8	70.6
	1.6(0.04)	0.8(0.3)	1.0(0.03)	1.2(0.02)	1.3(0.4)	0.7(0.1)	2.5(0.1)	1.4(0.04)	1.8(0.03)	0.8(0.03)	3.0(0.2)	1.5	44
HB	3.1(0.4)	3.1(0.4)	1.6(0.4)	1.6(0.4)	1.7(0.4)	3.6(0.4)	1.6(0.6)	2.3(0.3)	2.1(0.6)	1.3(0.3)	2.0(0.3)	2.0	43
	5.3(0.5)	5.8(0.4)	6.0(0.6)	5.3(0.5)	5.1(0.6)	6.5(0.2)	5.8(0.6)	4.5(0.3)	4.9(1.0)	4.8(1.0)	4.0(0.8)	5.0	22.2
	6.5(0.5)	6.2(0.4)	6.8(0.6)	5.9(0.5)	6.2(0.6)	7.4(0.2)	5.8(0.3)	4.0(0.8)	5.6(0.3)	4.8(0.4)	5.2(0.8)	5.3	17.3

(narrow spacing = 2.5 m)

(n = 8 - 10 per clone)

Largest value

Smallest value

Table 13b: Variation in intensity of natural branch abscission (AI) and stem taper (stem form quotient) between clones of *T. scleroxylon*, 4 years after planting at Gambari Forest Reserve near Ibadan.

((a) = narrow spacing, (b) = wide spacing).

(i) Expt. 7/75A (Narrow spacing) 2.5 m

Clone	AI %	Stem Taper
137/9	56.8	0.77
139/6	65.0	0.66
139/9	51.0	0.71
144/1	66.0	0.65
144/4	71.0	0.75
144/5	76.0	0.62
144/7	69.0	0.72
144/9	58.6	0.69
161/3	61.0	0.72
161/5	56.0	0.64
166/1	73.0	0.58
166/3	61.0	0.71
175/1	57.0	0.65
175/2	67.8	0.76
175/5	63.5	0.69
175/6	58.0	0.80
175/7	61.5	0.68
175/8	55.0	0.70
175/9	42.6	0.73
175/10	65.0	0.74
177/10	60.0	0.69
224/7	61.5	0.69
225/8	55.0	0.65
Average	61.4	0.70
CV %	12.2	7.4

(ii) Expts. 3/75, 5/75 (Wide spacing) 4.9 m

Clone	AI %	Stem Taper
139/9	39.0	0.67
142/10	26.9	0.65
144/1	44.0	0.65
166/8	33.7	0.63
175/1	33.0	0.68
175/5	27.0	0.70
175/10	24.0	0.58
177/10	29.4	0.70
224/1	25.1	0.70
Average	21.5	0.66
CV %	31.3	6.03

Table 14: Analysis of growth 4 years after planting of clones of *T. scleroxylon* planted at 4.9 m spacing in Gambari Forest Reserve, Nigeria Experiments 3/75 and 5/75.

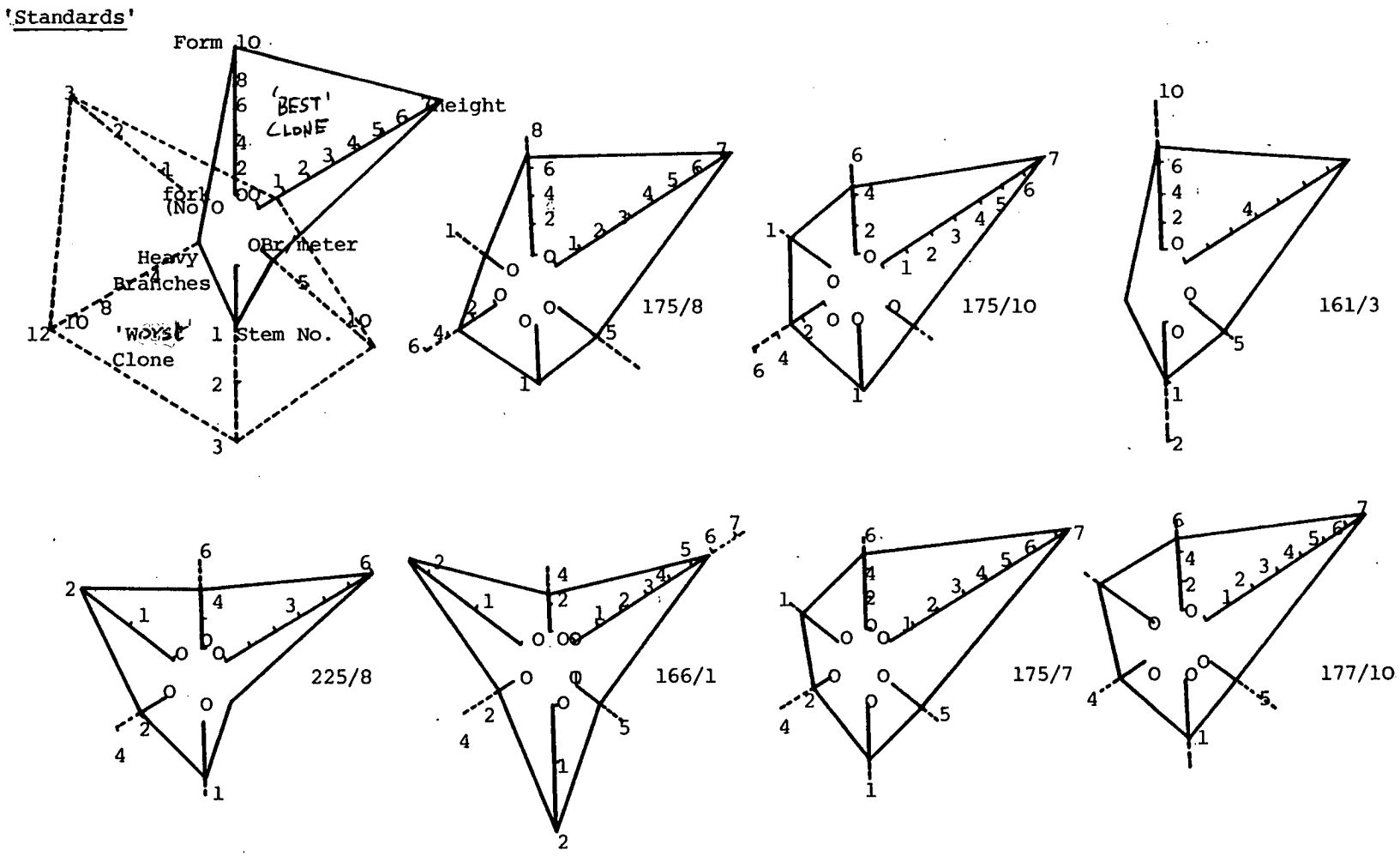
(Br. = Branches, L.Liv = Lowest living, Standard Error (±) of mean values in parentheses and CV = co-effic. of Variation).

Parameter	139/9 ✓	142/10	144/1 ✓	166/8	175/1 ✓	175/5 ✓	175/10	177/10 ✓	244/1	Average	CV %
1. Height (m)	6.1(0.26)	6.3(0.40)	5.4(0.33)	6.5(0.38)	6.7(0.28)	5.8(0.28)	5.8(0.16)	6.2(0.38)	7.8(0.31)	6.2	11.1
2. Stem No.	1.0(0.005)	1.0(0.11	1.0(0.004)	1.2(0.1)	1.1(0.08)	1.0(0.06)	2.0(0.02)	1.2(0.2)	1.0(0.004)	1.16	27.8
3. Stem Diam. (dbh-mm)	117.0(6.9)	109.7(9.6)	102.0(6.2)	106.0(5.9)	130.9(8.7)	106.6(6.2)	95.0 (3.1)	120.5(6.8)	172.6(2.9)	118.0	19.6
4. Height L.Liv.Br. (cm)	17.4(1.2)	7.2(2.0)	19.1(1.5)	10.2(0.9)	10.0(1.4)	6.7(1.0)	6.0(0.8)	7.9(1.1)	11.3(1.7)	10.6	43.9
5. Syllepticity (1-5)	3.1(0.2)	3.8(0.2)	2.7(0.2)	2.5(0.3)	3.0(0.4)	2.6(0.4)	3.0(0.2)	2.8(0.3)	4.6(0.4)	3.12	21.5
6. Total Branch No.	35.0(1.8)	41.4(4.0)	30.0(2.4)	36.3(2.6)	49.0(3.6)	37.2(2.8)	33.0(1.3)	37.0(4.1)	57.6(8.1)	39.5	21.9
7. Branch/meter	5.7(0.8)	6.5(0.9)	5.5(0.2)	5.5(0.4)	7.2(0.5)	6.1(0.7)	5.6(0.5)	5.0(0.7)	7.4(1.3)	6.16	11.7
8. Total Scar No.	22.2(2.4)	15.2(1.7)	24.0(3.6)	18.2(2.5)	24.2(4.0)	14.0(1.8)	11.0(1.6)	15.5(4.6)	18.7(3.3)	18.0	25.8
9. Scar/meter	3.6(0.1)	2.4(0.5)	4.4(0.2)	2.8(0.3)	3.6(0.6)	2.3(0.3)	1.8(0.1)	2.5(0.2)	2.3(0.3)	2.9	29.2
10. No. Fork	0.5(0.01)	0.5(0.08)	0.5(0.01)	1.0(0.2)	0.5(0.1)	0.5(0.1)	2.0(0.04)	1.2(0.3)	0(0.0)	0.75	78.0
11. No. Attempted Fork	0.4(0.2)	0.6(0.3)	0.7(0.02)	0.3(0.06)	0.7(0.3)	0.2(0.01)	0(0.0)	0.3(0.02)	0(0.0)	0.36	76.0
12. No. Heavy Branches	4.8(0.8)	2.6(0.4)	3.7(0.6)	1.5(0.3)	2.0(0.4)	1.3(0.4)	1.0(0.2)	2.4(0.4)	13.3(1.8)	3.6	106.1
13. Form score (1-10)	6.1(0.7)	5.1(0.7)	5.7(0.3)	6.2(0.4)	7.0(0.4)	6.1(0.5)	5.0(0.3)	5.9(0.5)	6.9(0.3)	6.0	11.5
14. Vigour Score (1-10)	7.2(0.3)	6.6(0.5)	6.4(0.5)	6.6(0.4)	7.6(0.3)	6.3(0.4)	5.0(0.2)	6.1(0.6)	7.3(0.8)	6.6	12.5

———— Largest value (Wide spacing = 4.9 m)

---------- Smallest value (n = 14-21 per clone)

Fig. 36



Polygonal graphs showing variation between 7 selected clones of *T. scleroxylon* based on 4th year data from Expt. 7/75A planted at narrow spacing (2.5 m) in Nigeria

clones (Fig. 36), against hypothetical models of 'good' and 'bad' clones.

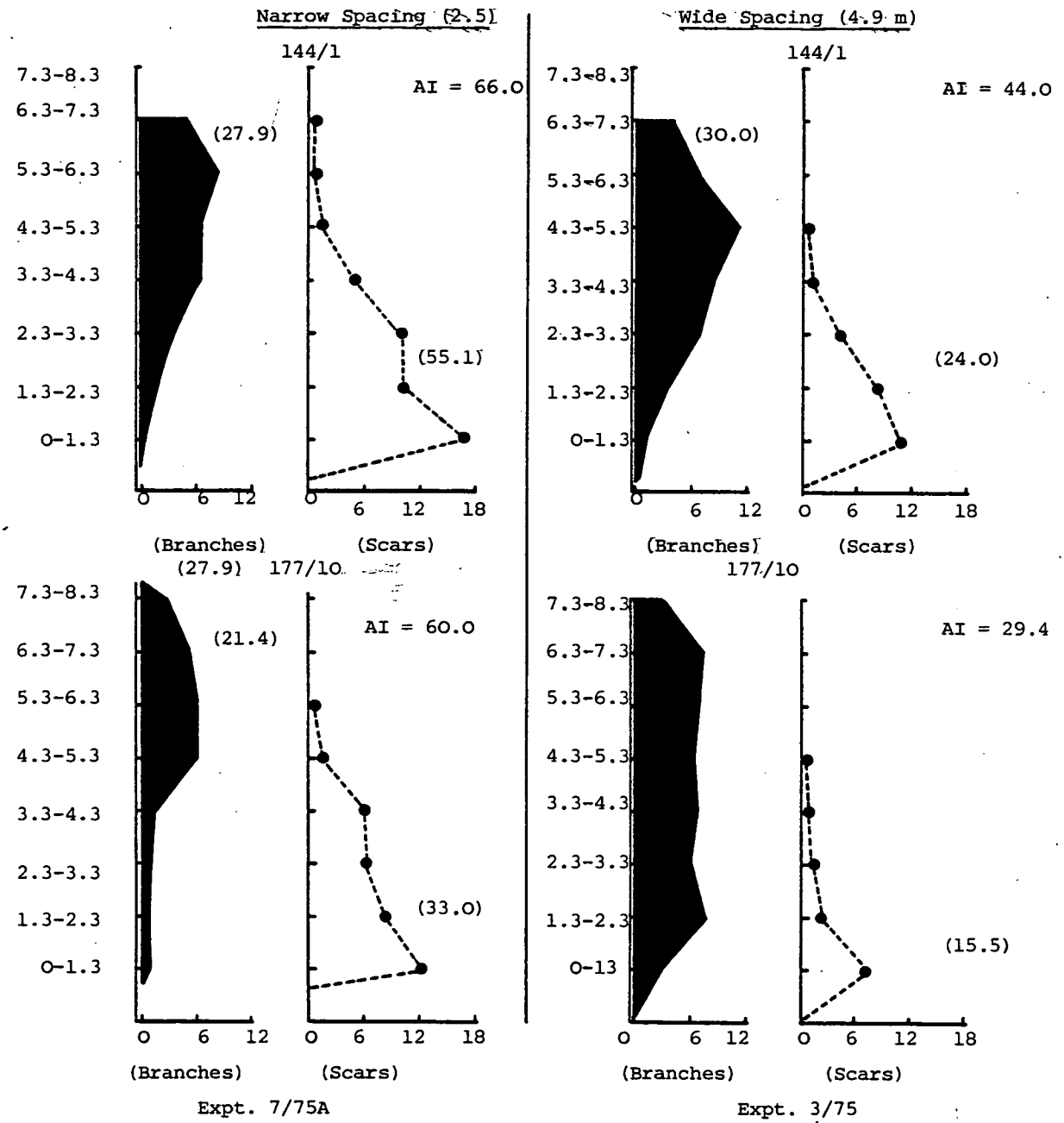
6.2.2 Wide Spacing (4.9 m)

Mean heights of clones differed significantly as in the case for narrow spaced plants. This ranged between 5.4 ± 0.33 for clone 144/1 which was the shortest and 7.8 ± 0.31 m for clone 224/1, the tallest (Table 14); comparable differences were also found for stem number, branch number and the other parameters examined. Abscission index at this planting density was lower than at higher densities but also differed significantly between clones, this ranging from 24.0 (clone 175/10) to 44.0 (clone 144/1). Stem form quotient on the other hand was unaffected by plant spacing, ranging between 0.58 (clone 175/10) to 0.70 (clones 177/10 and 224/1), (Table 13b(ii)).

Examples of the variations in frequency distribution of branches and branch scars are shown for 2 representative clones (144/1 and 177/10). Also shown is the effect of spacing (2.5 and 4.9 m) on these characters, which shows that more branches and less natural abscission takes place at wide spacing than at narrow spacing (Fig. 37). Furthermore, as shown by the mean values for all clones, height after 4 years at 2.5 metre spacing was 9.8 % greater than at 4.9 m spacing. Total number of branches and total number of scars were 58.0 % greater and 54.5 % less at wide spacing respectively, and there was also a greater tendency to heavy branching (47 %) and the retention of lower branches (Fig. 38). Stem diameter, by contrast, was less influenced by spacing, being only 17.2 % greater at wide spacing.

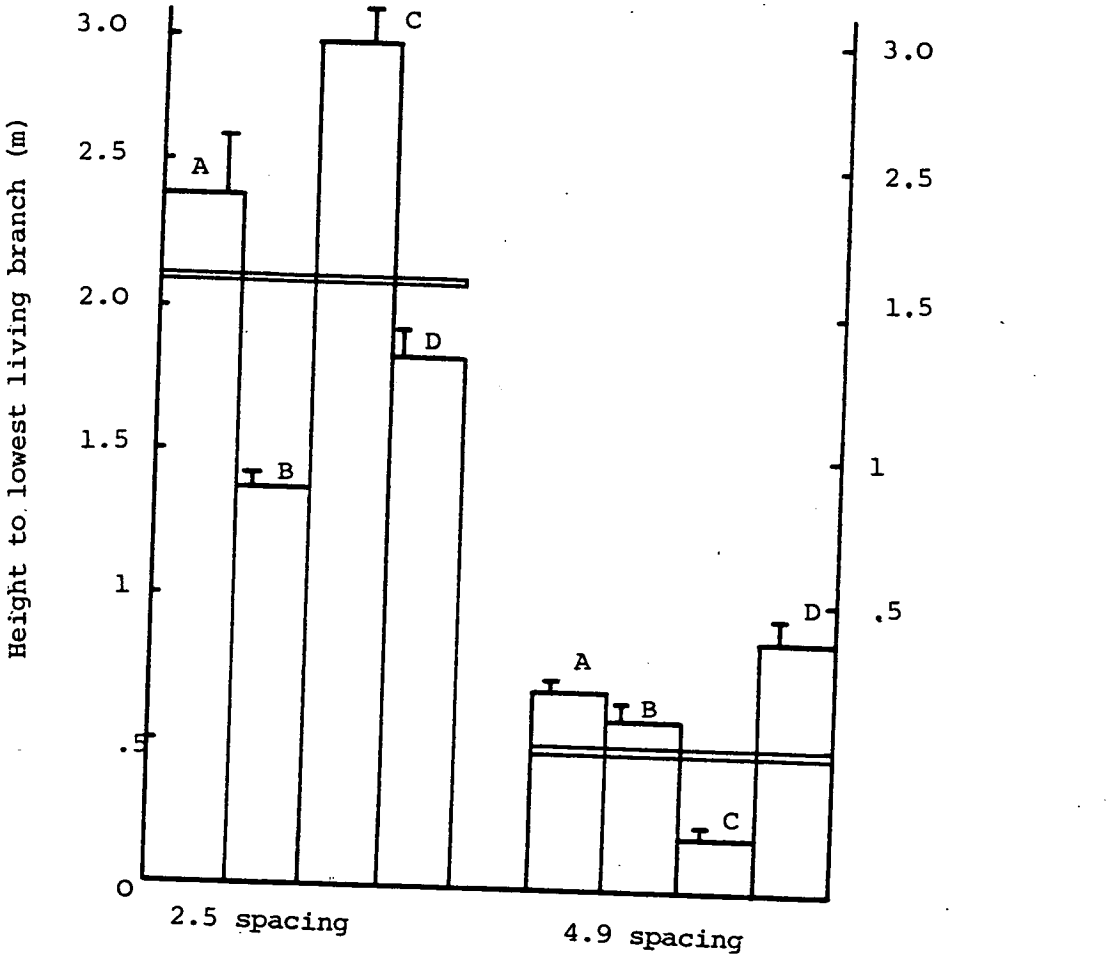
The effect of pruning lower branches at 1-year after planting was to increase both branching (9.3 %) and multistem production (15%),

Fig. 3·7



Variation in the frequency of branches and scars per meter rank of height in two clones of *T. scleroxylon* planted at narrow (2.5) and wide (4.9) meter spacing after 4 years at Gambari-Nigeria.
(AI = abscission index, and total scar and total branches in parentheses).

Fig. 38



A Clone 175/5
B " 175/10
C " 144/1
D " 177/10

Effect on spacing (2.5 m, 4.9 m) on clonal variation in height to lowest living branches in *T. scleroxylon*, 4 years after planting at Gambari-Nigeria. (means from Expt. 3/75 A & B (4.9 m spacing) Expt. 7/75A & B (2.5 m spacing) Horizontal line means average for all clones, vertical lines = SE ±)

particularly in clones 137/9 and 144/5 (Table 15). Significant differences were not detectable in other parameters as shown in Table 14 at 4 years despite pruning at age 1 year.

Correlations between the means of 15 parameters values, from the experiment 7/75A (2.5 m spacing) are presented in a matrix form in Fig. 39. There is a high degree of positive correlation between some parameters. Mention will be made of some of the most important relationships: there were good correlations between diameter and height ($r = +0.76$, $P = 0.001$), Stem number and number of forks ($r = +0.59$, $P = 0.01$), Total branches and number of branches per meter, ($r = +0.94$, $P = 0.001$), Height and total branches ($r = +0.71$, $P = 0.001$), and total branches and diameter (dbh) ($r = 0.66$, $P = 0.01$) and total branches and Abscission Index which was negatively related and highly significant ($r = -0.71$, $P = 0.001$).

At wide spacing (Fig. 40), diameter and height was also significantly related ($r = +0.91$, $P = 0.001$), stem number and number of forks ($r = 0.95$, $P = 0.001$), total branches and branch per meter ($r = +0.96$, $P = 0.001$), total branch and diameter (dbh) was significant at $P = 0.01$, Total branch and Abscission Index were not related at this spacing ($r = -0.44$). In contrast to the case of narrow spacing, height and total branches were significantly related ($r = +0.93$, $P = 0.001$), and so was height and syllepticity ($r = +0.75$, $P = 0.02$), but height was not related to scar number ($r = +0.12$).

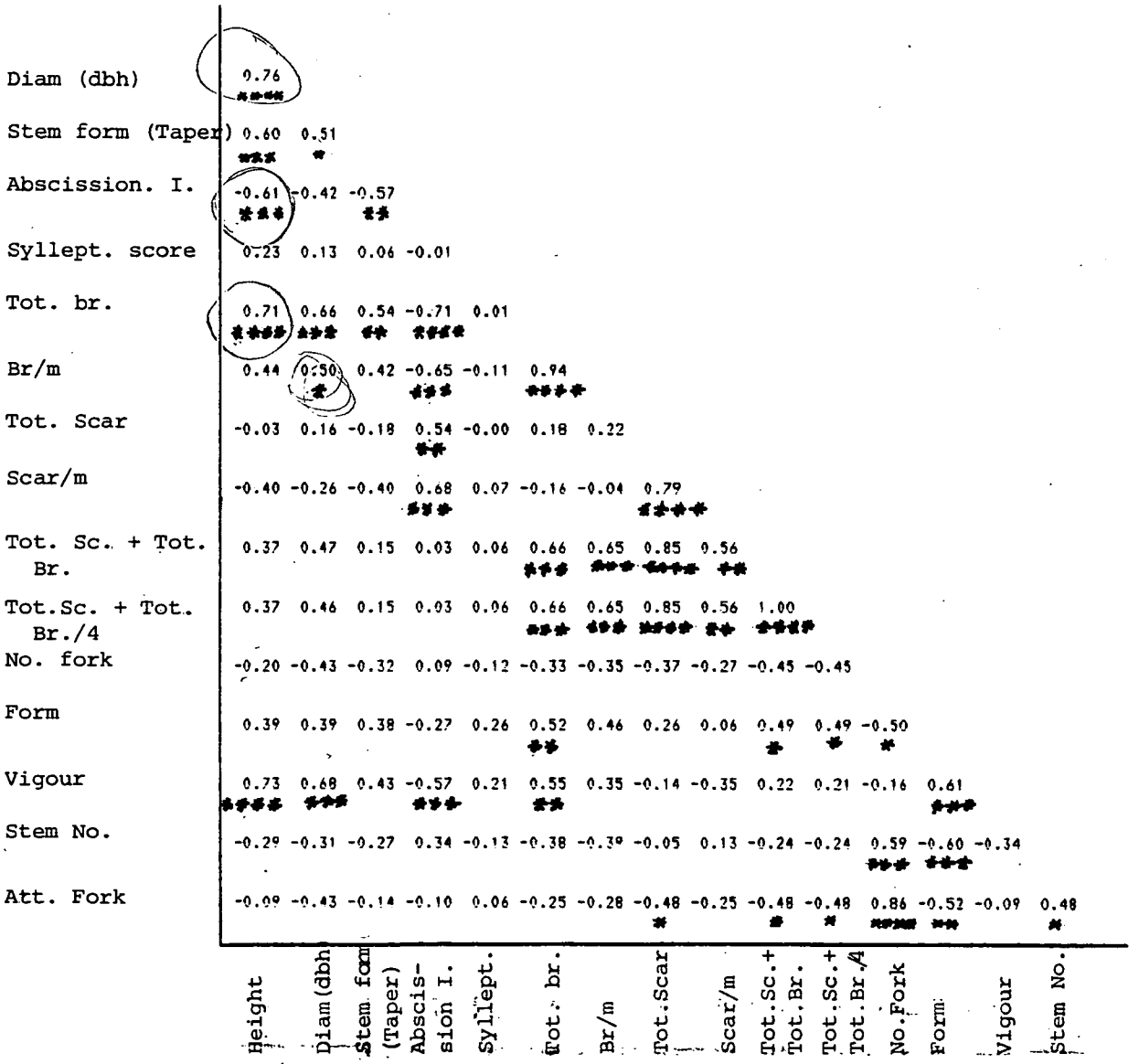
6.3 Discussion

The mean growth data presented above for *T. scleroxylon* clones show substantial variation in the attributes investigated. This confirms the growth data collected at 18 months from the same experimental plantings (Howland and Bowen 1977, Howland *et al* 1978, and Ladipo *et al* 1980). Variation of this magnitude has been reported

Table 15: Effect of removing branches and multistems to a height of 1.25 m in July 1976 (one year after planting), on growth of *T. scleroxylon* in Gambari, Nigeria, 3 years later (Expt. 7/75B - 2.5 m spacing, n = 4 plants per clone at each treatment.

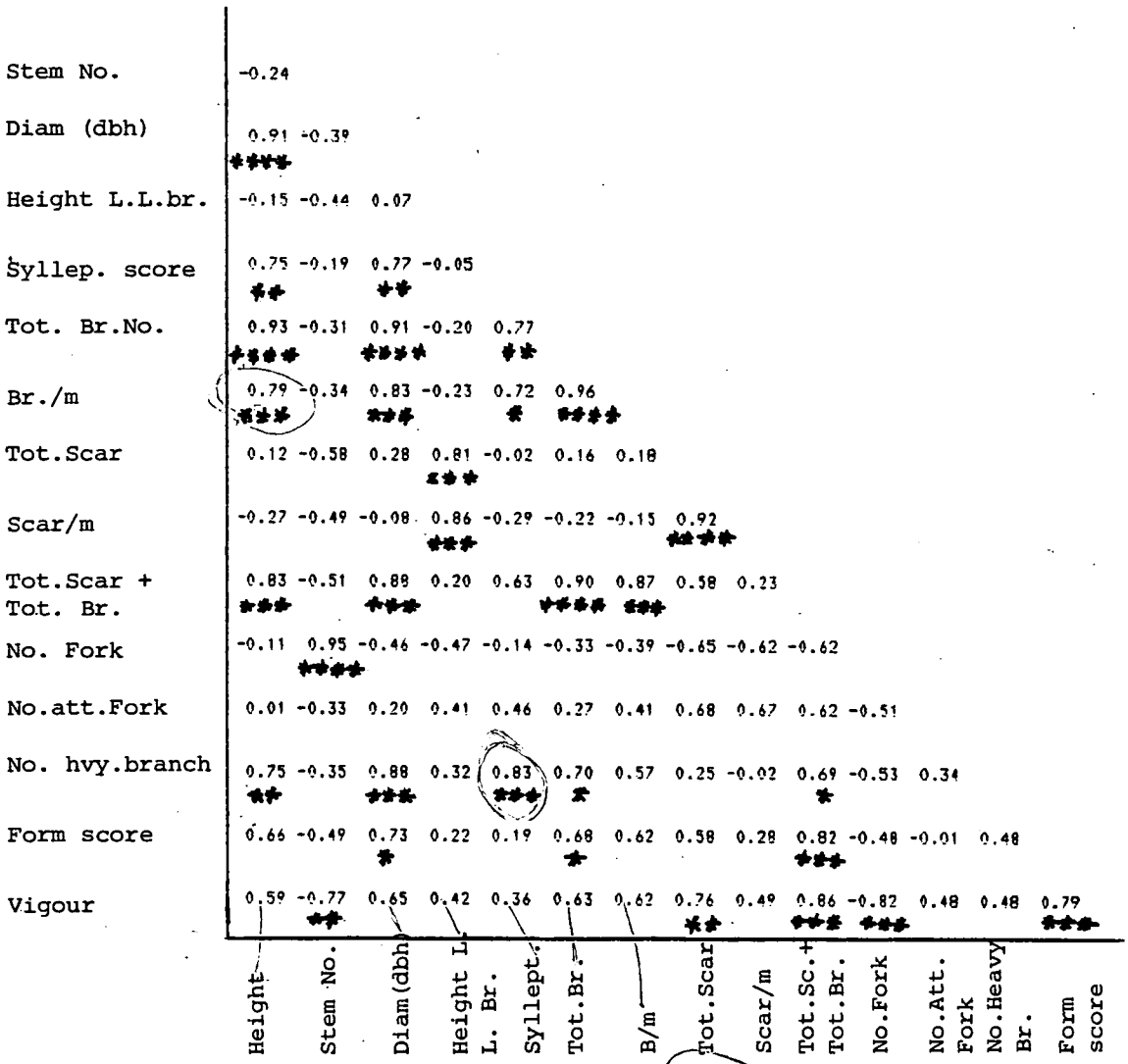
Parameter	Unpruned				Pruned			
	Clone 137/9	Clone 144/5	Clone 175/2	Clone 175/7	Clone 137/9	Clone 144/5	Clone 175/2	Clone 175/7
Height (m)	5.9(0.43)	4.7(0.60)	5.7(0.45)	5.9(0.40)	6.4(0.32)	4.4(0.46)	5.7(0.50)	5.9(0.65)
Stem No.	1.0(0.003)	1.0(0.02)	1.0(0.01)	1.0(0.01)	1.3(0.03)	1.3(0.02)	1.0(0.002)	1.0(0.001)
Height L.Liv.Branch	16.0(3.2)	22.0(2.0)	22.8(3.5)	28.7(4.8)	15.6(4.6)	14.9(1.6	36.0(6.5)	22.3(8.3)
Total Branches	29.0(2.6)	19.5(3.5)	25.0(1.8)	28.5(3.1)	29.3(2.9)	19.6(3.1)	33.5(1.5)	30.0(4.5)
No. of Forks	1.0(0.08)	1.0(0.02)	0(0.0)	0.7(0.03)	0(0.0)	0.6(0.08)	0(0.0)	1.0(0.08)

Fig. 39



Correlation matrix for various parameters of growth after 4 years in plantation at Gambari Forest Reserve, Nigeria, at normal spacing 2.5 m. (= non significant, * = significant at P = 0.05, ** = Sig. P = 0.02, *** = Sig. P = 0.01 and **** = Sig. at P = 0.001, df = 17)

Fig. 40.



Correlation matrix for various parameters of growth after 4 years in plantation at Gambari Forest Reserve, Nigeria at wide spacing 4.9 m (= non significant, * = Sig. at P.0.05, ** = Sig. P 0.02, *** = sign. at PO.01 and **** = Sig.at P=0.001, df = 8).

KEY

(Key to abbreviations on Figs.39 and 40)

A.1	= abscission index
Att. fork	= mean number of attempted forks
B/M	= mean total number of branches per metre of stem
Dia (dbh)	= Diameter at breast height (1.30 m).
Fork No.	= mean number of forks on stem
Height.L.Liv.br.	= Height to lowest living branch
No. Hvy. br.	= mean number of heavy branches
Scar/m	= mean total number of scars per metre of stem
Stem No.	= mean number of stem (multiple stems)
Syllep.	= Syllepticity score (1-5)
Tot. branch	= mean total number of branches on mainstem
Tot. Scar	= mean total number of scars on mainstem

between clones of other species such as *Pinus radiata* (Shelborne and Thulin 1974) where the importance of such variation was fully discussed.

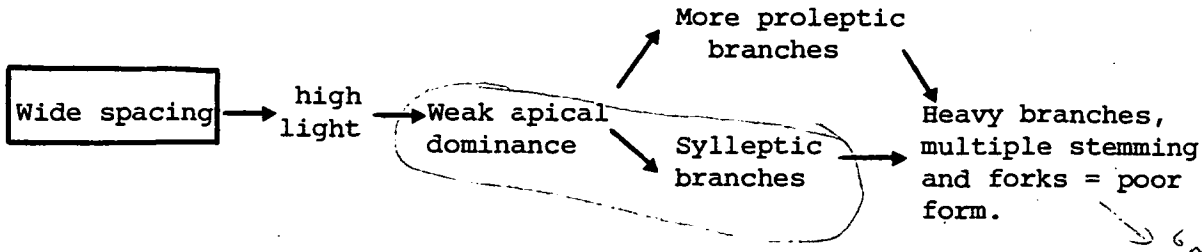
One of the early observations made which has influenced the present work, was that branching pattern is a major determinant of height (Ladipo *et al* 1980). As height is closely related to yield, it seems that the hypothesis for further investigation ought to be that branching is related to yield. Indeed, the basic approach, involving a study of apical dominance at an early stage of growth, and subsequently correlating this with tree form in the plantation, seeks to test this hypothesis.

However, before we pass to this part of the work, which is the subject of the next chapter, we should first examine the extent to which this early observation is substantiated.

At wide spacing, where the earlier indications were obtained, the relationship between height and branching was indeed substantiated. Using the correlation coefficient as a measure of the strength of the relationship, it can be seen that the relationship is very strong : $r = +0.79$ for the correlation between branches per metre of stem and height. This relationship is further improved when scars as well as branches are included : $r = 0.83$.

However, at narrow spacing these relationships are not evident. This indicating that different factors probably operate at the two spacings. This view is supported by the differing roles of syllepticity in the two cases: at wide spacing height is strongly correlated with syllepticity but not so at narrow spacing.

As the production of sylleptic shoots is to be regarded as an indication of low apical dominance, we may postulate the following causal relationships at wide spacing:



The net effect of this is that the number of heavy branches at wide spacing is much greater than that at narrow spacing (2.0 per tree, as against 0.36, see Fig. 38).

As reported by Howland and Bowen (1977) and Ladipo *et al* (1980), spacing also seems to influence stem characteristics in *T.scleroxylon*. Thus the difference in height 44.1 % between wide and narrow spacings reported at 18 months (Ladipo *et al* 1980) has now (4 years) been reduced to 9.8 %. This decrease in height difference is probably as a result of competition at narrow spacing and indicates a need for thinning in these stands. The increased branching and the reduced incidence of abscission at wide spacing is probably as indicated earlier the lack of mutual shading and the longer and bigger branches being retained for a longer period.

The different performance of clones at the two spacings tested here clearly indicates that clonal evaluation must be done under the silvicultural conditions that are to be followed in commercial plantings, both with regard to spacings and to thinning regimes. In this respect, it is interesting to note that in the Ivory Coast, *T. scleroxylon* in the World Bank Plantation Project is being grown initially at 3.75 m spacing. This is to be thinned later on. It may however be useful to also impose high density selection to test attributes which under normal conditions would not be prevalent until later in the rotations.

From a practical point of view it is worth noting that many of

the attributes that display clonal variation are indeed important ones as far as selection for superior trees is concerned. The large variation reported here in the abscission index (Table 13b) indicates that the ability of *T. scleroxylon* clones to shed lower branches is highly variable and can probably be selected for. This applies also to the stem form quotient (taper), which is another important index of wood volume in mensurational work. It therefore appears that selection for natural abscission, large stem diameters (dbh) and low stem taper would probably result in considerable gains in yield and stem quality in the species. Furthermore, taking diameter at breast height as a rough index of timber yield, the data presented in Table 12a suggest that a quite modest selection programme, taking the top 10 % of clones, should produce a gain of about 20 % in relation to the present-day average. More rigorous selection from a larger number of clones, would probably produce even greater returns (c.f. Kleinschmidt 1974). Previously, it was shown that 18 months after planting, a 10 % selection operated at 18 months might produce a potential increase in height of at least 16 % (Ladipo *et al* 1980).

Clearly, a priority in a selection programme would be to eliminate clones with grossly undesirable characteristics, such as forking and formation of multiple stems. Furthermore, the close relationship between stem number and the number of forks (at both spacings) indicates that the undesirable characteristics are probably under common genetic control and thus, selection against one of them will indirectly improve the other.

The use of the tree form diagrams (Fig. 37), which represents 6 parameters graphically illustrates the potential variation and will help to identify ideotypes for *T. scleroxylon*.

As regards the silvicultural practice of pruning clones, it

seems that, rather than overcome the production of unwanted branches, it stimulated sprouting from basal nodes. This may be because it was done in July at the peak of the growing season before the canopy had closed and when they were clean weeded. A similar occurrence has been reported in the fast growing topical tree *Simaruba amara* (Schulz and Vink 1966), in which only regular pruning during early periods of field growth was necessary to produce the desired form. This sort of operation will probably be more useful and economical if done in the dry season or later when the canopy was closed (i.e. 3rd year) so accelerating self-pruning.

Finally, the large variations between clones in the characters investigated in this study with *T. scleroxylon* - a basically out-breeding species; provides a useful tool which can be effectively utilized for improvement by selection. The following chapter further investigates the variations in branch characteristics in a few clones. It also attempts to assess crown attributes and the variation in crown shape among these clones.

CHAPTER 7

CLONAL VARIATION IN BRANCH CHARACTERISTICS AND EFFECTS ON CROWN FORM IN *T. scleroxylon*.

7.1 Introduction

The crown form of a tree is basically determined by a combination of the persistence of main stem and a number of branching characteristics; including the number of branches and their individual characteristics. The latter includes the angles of inclination, length, inter-branch distance, number and orientation of secondary and tertiary branches, and the ratio of branch lengths. Such characteristics have sometimes been considered as adaptive strategies for light interception (Horn, 1974; Brünig 1976) and are expected to be under strong genetic control, although they can be influenced a great deal by environmental factors (Pickett and Kempf 1980).

Evidence for the involvement of apical dominance (Phillips 1969), and apical control in the relation of branching (Brown *et al* 1967) has been discussed extensively, and it is generally recognised that these can probably account for most of the variation in branching habits and crown development between different species of tree.

Branch angle is known to be influenced by the main stem apex and the presence of other shoots on the tree (Jankiewicz 1973): an example of a correlative influence *sensu* Münch (1938). The following main factors have been identified as influencing branch angle :-

(a) Negative geotropism - causing faster elongation on the lower side of a shoot and thus causing upward growth.

(b) Geoepinasty - induced by prolonged geotropic effects,

giving rise to faster growth on the lower side of a branch probably as a result of auxin accumulation (Lyon 1971).

(c) Mechanical pressure - generated by growth of tissues situated in the crotch, at least in apple tree branches (Jankiewicz 1964) and

(d) Weight - this being caused by the increase in branch weight with development (Baranetsky 1901).

Through these influences and some related morphological variations, branches are classified as orthotropic (erect or partly erect) or plagiotropic (more or less horizontal), the latter varying between persistently plagiotropic and non-persistent plagiotropic. In *T. scleroxylon*, branches are basically of the orthotropic or non-persistent plagiotropic types. The branching pattern of *T. scleroxylon* conforms to Rauh's model, Halle *et al* 1978), which is one of the 23 basic architectural models of tropical trees. Apart from this basic classification, little is known of its branching characteristics, except from descriptions by Jones (1969) and some recent preliminary observations of clones growing in Nigeria (Howland *et al* 1978).

Branch length has been suggested to be influenced more by internode elongation, which depends on vigour and correlative influences (Champagnat, 1965, Plich *et al* 1974). Attempts have been made to determine the relationship between branch characteristics (branch angle, branch length and branch diameter) and general crown shape of trees (Shinozaki *et al* 1964, Honda and Fisher 1979), including the use of computer models, as for example in *Terminalia catappa*, and *Cornus alternifolia* (Honda *et al* 1981).

To characterise the shape of the crown, it is necessary to measure a number of crown parameters, as Curtin (1970) has shown. In *T. scleroxylon*, the mode of growth is such that the lower branches are longest and the overall crown shape is quite distinctive and may be described as a blunt cone. Such a situation occurs in many trees, for example

Eucalyptus obliqua (Curtin 1970).

The present study investigates clonal variation in the critical characteristics which define the dimensions and proportions of the *T. scleroxylon* crown in a 4 year-old plantation at Gambari in Nigeria at narrow spacing. These characteristics are required in Chapter 8, where their relationship with apical strength (measured by the decapitation test) is investigated.

7.2 Materials and Methods

Assessments were made on the 5 lowest branches from 8 trees of each of clones 137/9, 144/1, 144/4, 144/5, 144/7, 166/1, 175/1, 175/2, 175/5, 175/6, 175/7, 175/8 and 177/10 in June 1979 from Experiment 7/75B at Gambari near Ibadan. Critical measurements required to define the dimensions and proportions of the *T. scleroxylon* crown included :

(i) Height at which each primary branch arises on main stem

(ii) Length of primary branch

(iii) Number of nodes on primary branch

(iv) Mean internode length (derived from ii and iii).

(v) Diameter of primary branch (1 cm from main stem)

(vi) Angle between stem and primary branch, and

(vii) The number of secondary branches on primary branches, (see Fig. 41).

A set of precision callipers was used to measure branch diameters, whilst a protractor was used to determine angles, as done by Franklin and Callahan (1970).

Data analysis from the above measurements, was done using the computer program 'IBAZ' (see Appendix 3) which gave means and corresponding Standard Errors for each clone.

Many workers have assessed the horizontal and vertical components of tree crowns as was done for *Eucalyptus obliqua* (Curtin 1970), but in the present work, a slightly different approach is taken. The projection of the characteristics of the lower 5 branches, enabled the crown to be estimated (see Fig. 41). This is possible because of the distinctive form of the crown (see Plate 9).

The crown forms estimated from the measurements described above were later drawn and measured with a Lambda area meter to give an index of the cross-sectional areas for each clone, while a crown index (CI) was calculated from the formula

Ca x ba x bl, where Ca = estimated crown area (m^2)

ba = branch angle and bl = branch mean length.

7.3 Results

Mean height to the 5 basal branches differed substantially between clones, ranging from 3.41 m for clone 144/1 to 1.48 m for clone 144/9 (Table 16).

Mean branch length also differed between clones with 177/10, and 175/8 having the longest branches (2.18 m) while clone 144/4 had the shortest (1.25 m). Despite their identical mean branch lengths, clones 175/8 and 177/10 differed in mean branch diameter, being 3.15 cm and 2.86 cm respectively. The incidence of secondary branches differed significantly between clones; clone 175/8 again having the greatest number while clone 144/9 had the least number (16.1 and 8.2 respectively). In contrast to mean branch lengths, the mean numbers of nodes per branch were greatest in clone 175/6 (41.3) and least in clone 144/1 (25.1). Mean internode length also differed (Fig. 42), with clone 144/7 having the greatest, and clone 144/9 the least (6.15 and 4.21 cm respectively).

The overall result of all these different characteristics was

Fig. 41

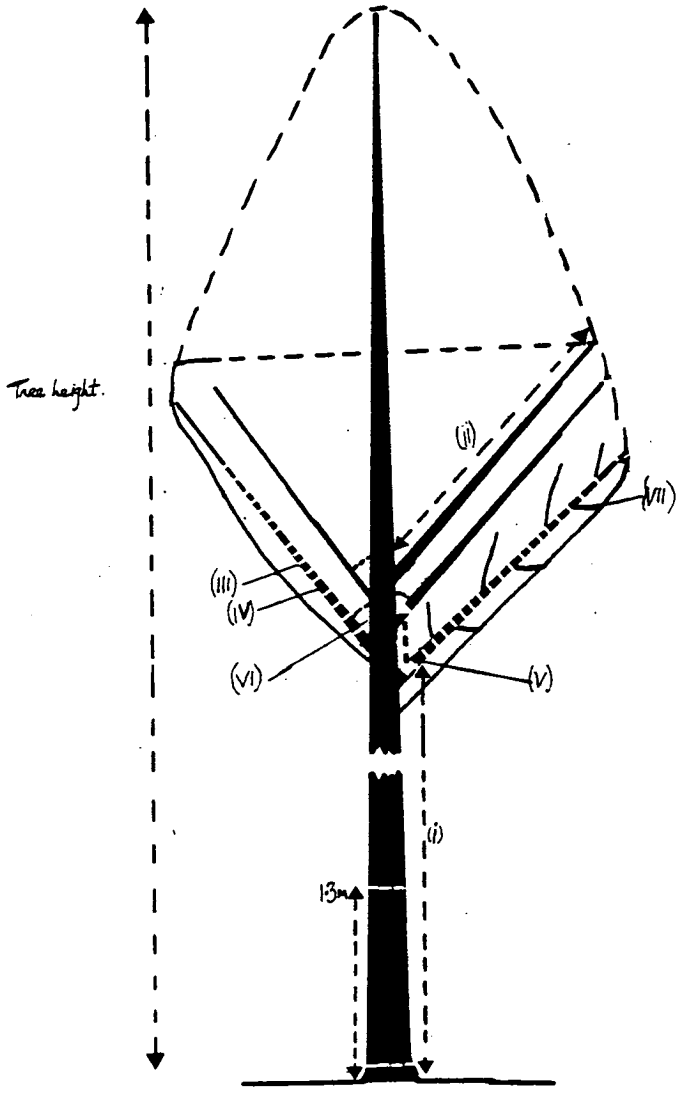
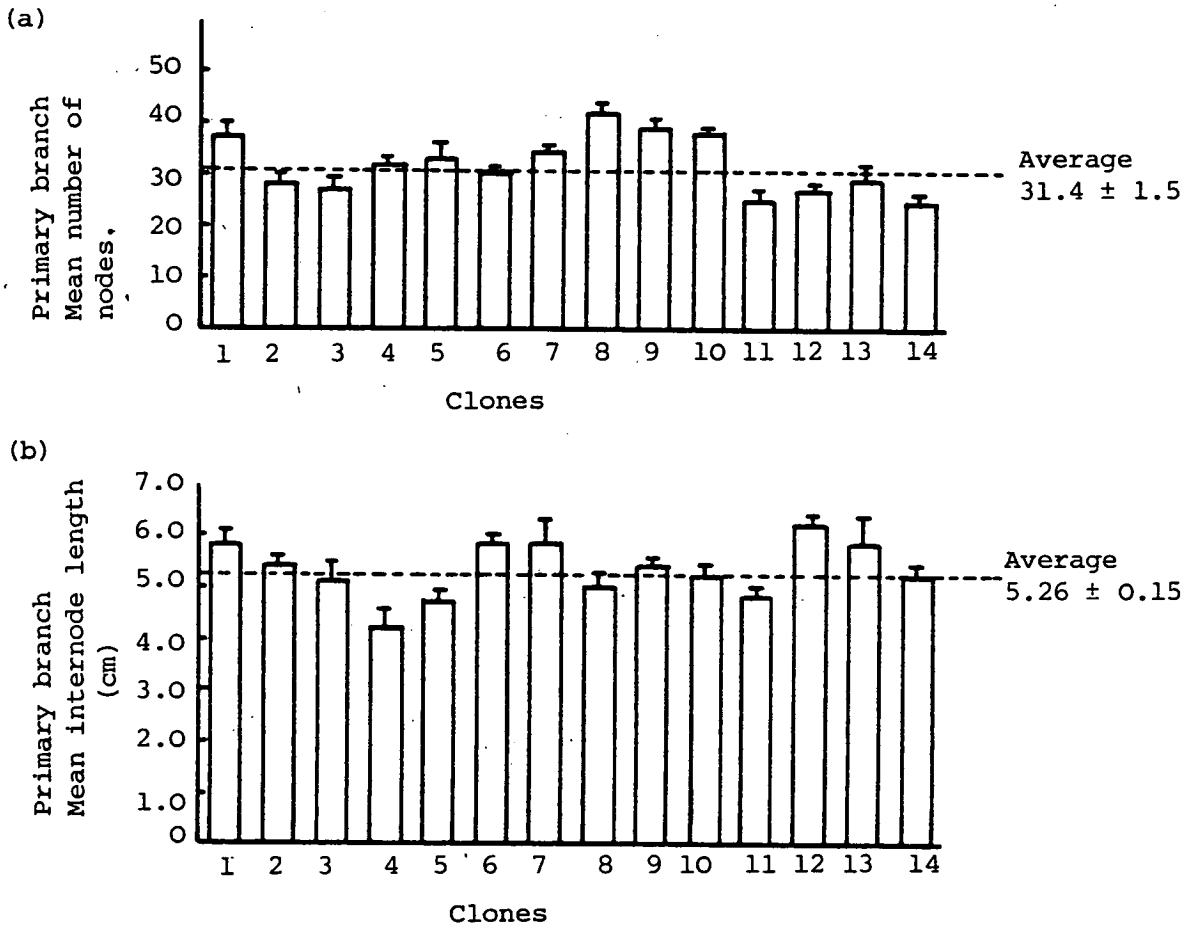


Diagram illustrating measurements carried out to define shape of the crown of *T. scleroxylon* clones, after 4 years growth at Gambari-Nigeria. (see text for symbols).

Table 16: Variation in branching characteristics of *T. scleroxylon* clones, 4 years after planting at Gambari, Nigeria at narrow spacing 2.5 m.

Clone	Mean height to branches 1-5 (m)	Mean Branch angle (°)	Mean Branch length (1-5)	Mean Branch Diameter (1-5)	Mean Number Secondary branches on 1-5.
137/9	2.21 ± 0.13	53.8 ± 1.4	2.0 ± 0.035	2.93 ± 0.03	10.3 ± 0.68
144/1	3.41 ± 0.12	44.4 ± 1.8	1.32 ± 0.18	2.16 ± 0.22	11.75 ± 0.91
144/4	2.58 ± 0.11	58.8 ± 1.86	1.25 ± 0.07	2.04 ± 0.13	9.25 ± 0.1
144/5	2.25 ± 0.22	63.0 ± 2.6	1.59 ± 0.22	2.57 ± 0.25	13.27 ± 1.01
144/7	2.30 ± 0.08	61.6 ± 2.0	1.65 ± 0.03	2.28 ± 0.07	11.05 ± 0.81
144/9	1.48 ± 0.15	40.1 ± 1.8	1.36 ± 0.05	2.50 ± 0.22	8.6 ± 1.01
166/1	2.41 ± 0.35	44.9 ± 3.5	1.76 ± 0.23	2.56 ± 0.23	10.8 ± 1.33
175/1	2.33 ± 0.16	49.8 ± 5.5	1.46 ± 0.11	2.24 ± 0.11	12.86 ± 0.97
175/2	2.87 ± 0.10	59.3 ± 1.5	1.77 ± 0.014	2.76 ± 0.11	13.8 ± 0.58
175/5	3.21 ± 0.14	59.8 ± 1.06	1.99 ± 0.14	2.88 ± 0.66	15.3 ± 0.93
175/6	3.15 ± 0.17	50.0 ± 2.7	2.08 ± 0.10	2.80 ± 0.11	15.05 ± 1.28
175/7	2.84 ± 0.17	60.2 ± 1.7	1.54 ± 0.05	2.52 ± 0.03	11.79 ± 1.5
175/8	2.73 ± 0.11	62.8 ± 1.63	2.18 ± 0.05	3.15 ± 0.13	16.1 ± 1.3
177/10	2.38 ± 0.34	53.3 ± 2.9	2.18 ± 0.27	2.86 ± 0.35	12.4 ± 0.65
Mean	2.59	54.6	1.72	2.60	12.5
SE	0.13	2.0	0.09	0.09	0.58

Fig. 42



Branching characteristics of *T. scleroxylon* clones, 4 years after planting:-
(a) Variation in mean numbers of nodes on primary 5 lower branches and
(b) Variation in mean internode length on same branches. (June 1979)

Clones

1 - 177/10	8 - 175/6
2 - 175/7	9 - 175/8
3 - 175/1	10 - 137/4
4 - 144/9	11 - 144/4
5 - 144/5	12 - 144/7
6 - 175/2	13 - 166/1
7 - 175/5	14 - 144/1

Table 17: Estimated Crown area and Crown Index of 14 clones of *T. scleroxylon* after 4 years growth at Gambari, Nigeria. Crown Index (I) calculated from Crown area (m^2) x mean branch angle x mean branch length (cm).

Clone	Estimated Mean Crown Area	Crown Index (I)
175/7	7.7	6.0
177/10	13.2	13.4
175/1	11.5	7.0
144/9	6.4	3.1
144/5	6.8	5.7
175/2	7.6	6.7
175/5	11.5	11.6
175/6	11.3	9.9
175/8	12.8	14.8
137/9	10.6	9.6
144/4	5.1	3.2
144/7	7.5	6.5
166/1	7.3	4.8
144/1	3.8	1.9
All clone mean	8.8 ± 0.8	7.4 ± 1.05
CV %	33.7 %	53 %

that there were substantial differences in estimated crown area between the clones, in which clone 177/10 was largest (13.2 m^2) and clone 144/1 the smallest (3.8 m^2). This also strongly influenced the crown index (Table 17), which showed similar variation. Mean crown form is best summarised by scale drawings of the basic field measurements (Figs. 43a and b). From these it is evident that some trees have relatively tall and thin crowns whilst others are more spreading (Figs 43a and 43b).

Finally, of all the parameters assessed, significant correlations existed only between branch length and node number ($r = + 0.85$ - $P = 0.001$), and between branch position and branch angle ($r = + 0.67$ - $P = 0.01$).

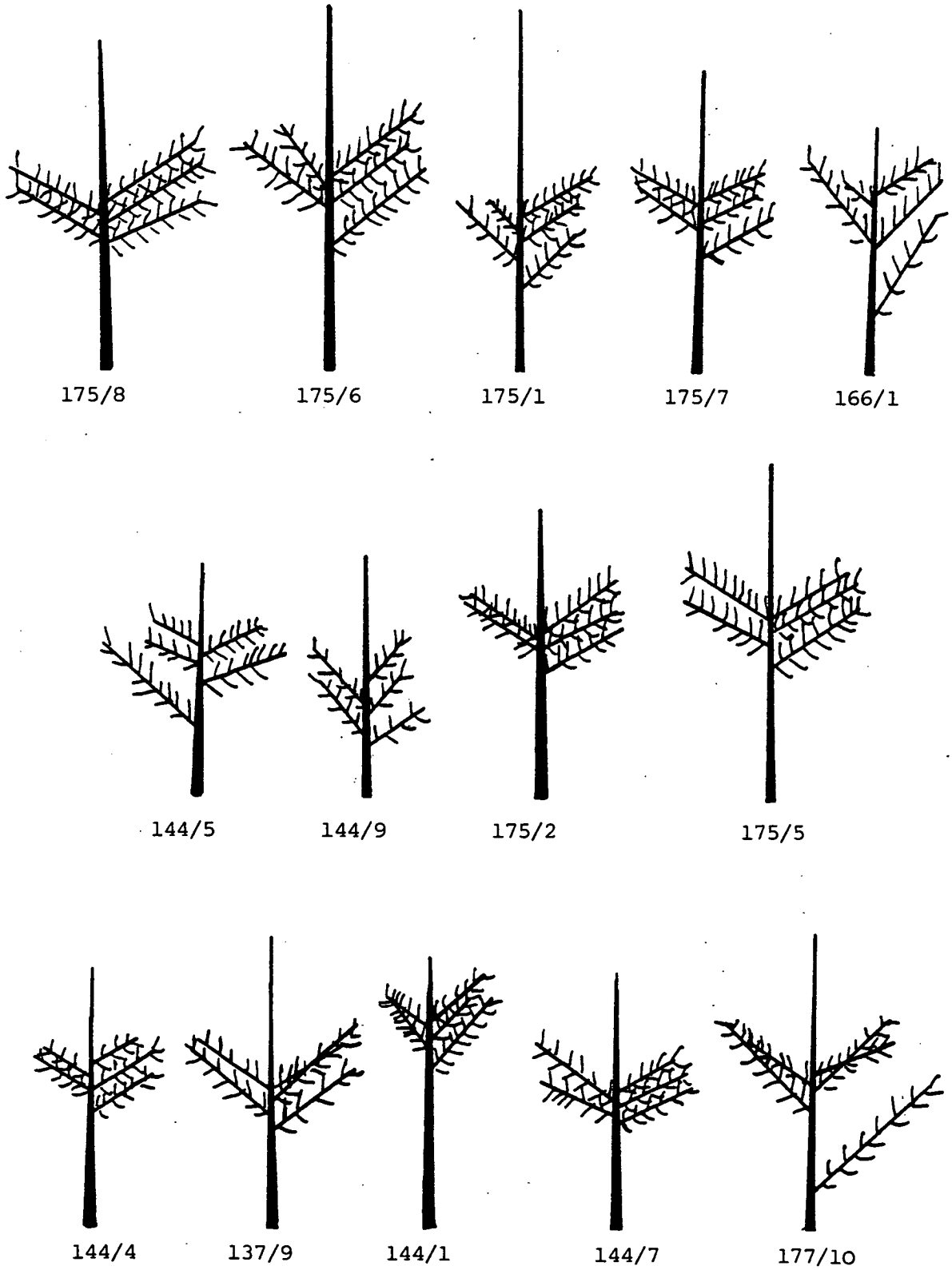
7.4 Discussion

Crown development takes place freely, without competition, in open spaces. In closely spaced plantations, on the other hand, competition between neighbours may affect lateral spread of individual trees (Ovington 1956), or the persistence of lower branches.

Despite these modifications of phenotype (see Chapter 6) the branching characteristics, and crown shape of clones in plantations are still strongly influenced by genetic differences (Downs 1949). Certainly, this seems to be so in *T. scleroxylon* when planted at 2.5 m spacing for clones had identifiable crown characteristics. Similar variation is evident in the work of Pickett and Kempf (1980) in *Viburnum* spp, in which natural vegetative propagation occurs. In this spacing intraspecific variation in branch attributes were found between the various natural clonal populations and also in *Populus* spp where Dickmann (1975) found clonal variation in branch attributes.

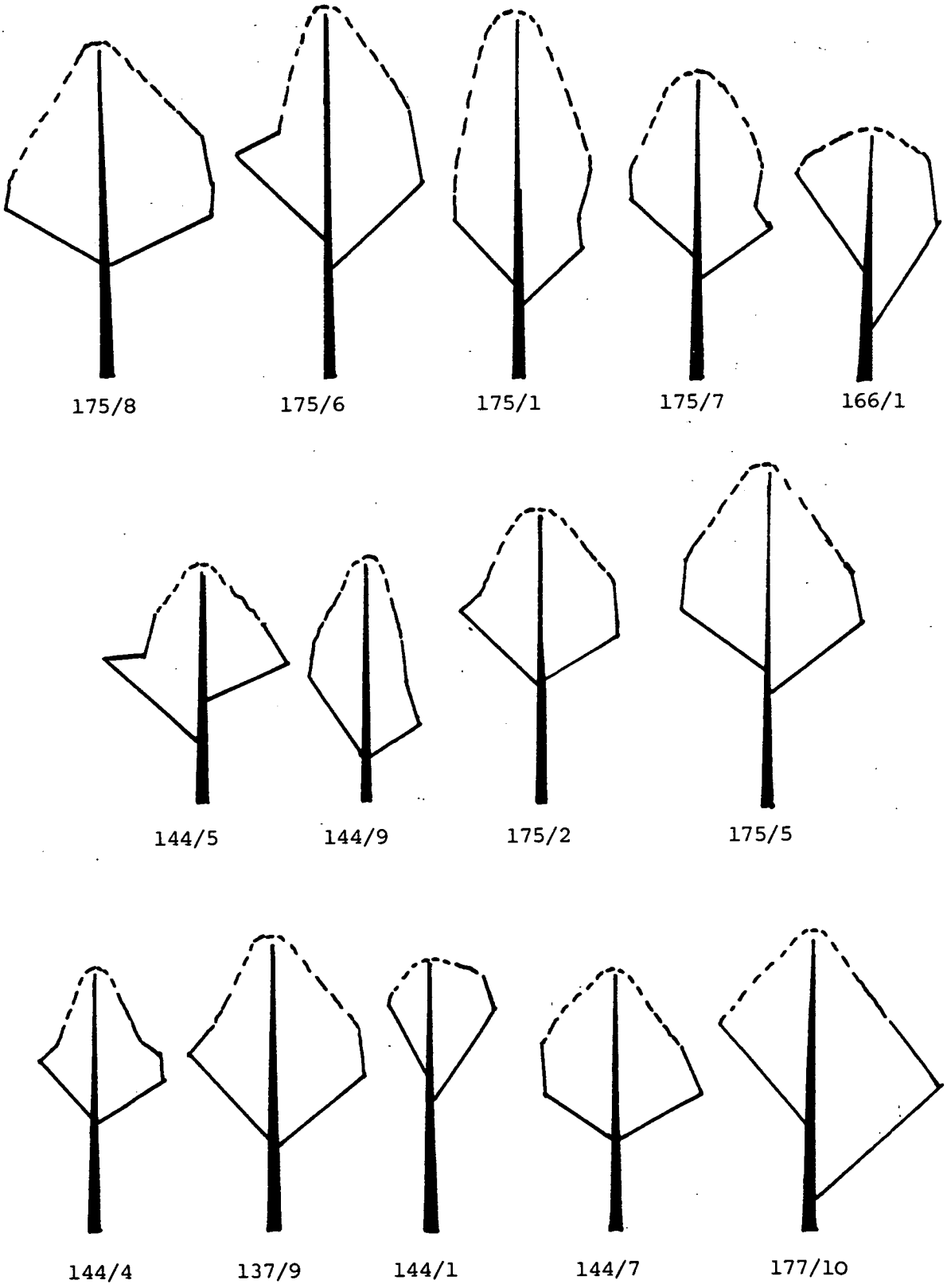
In relation to possible selection for improvement, Dickmann (1975)

Fig. 43a



Scale drawings of clones of *T. scleroxylon* showing : Variation in the characteristics of 5 lowest branches. (scale = 1 mm = 1.19 m. secondary branches not to scale).

Fig. 43b



Scale drawings of *T. scleroxylon* clones showing: an extrapolation of crown shape from height and lengths of 5 lowest branches to indicate differences in crown shape of 4 year old plants at Gambari-Nigeria (Expt. 7/758) planted at 2.5 m spacing. (Scale 1 mm = 1.19 m).

favoured steep branch angles, which gave compact crowns. This suggestion does not agree with present views for *T. scleroxylon*, where erect branches are frequently of large diameter, as in clones 144/9 and 175/8, and may compete with the main axis to form forks, while wide angle branches tend not to be of this kind. (Plate 8). Small branched clones are also favoured according to Karki (1979) for *Pinus sylvestris* , thus increasing the allocation of resources to mainstem production. He thus selects narrow crowned clones.

The considerable variation in node number and internode length reported here for *T. scleroxylon* clones is similar to that found by Koster (1971) for *Populus deltoides*. It is difficult to relate such structural characteristics to photosynthetic functions within canopy, but short internodes increase the packing of leaves and so increases their mutual shading. However, in *T. scleroxylon* this could to some extent be circumvented by the presence of long leaf petioles with a pulvinus at each end so that the leaves are relatively mobile and heliotropic. The presence of more secondary branches in some clones also may imply a denser canopy (plate 9).

Although mean branch height (all 5 branches) was not closely correlated with mean branch angle, the individual positions of each of the 5 lower branches were related to their respective angles ($r = +0.67$ - $P = 0.01$) in all clones. This agrees with the work of Jankiewicz (1972) in young apple trees where he recorded a close relationship between the height at which branches arise and their angles of inclination, this increasing from top to basal branches. However, the lack of relationship between the other attributes is an interesting occurrence in *T. scleroxylon*, which implies that other crown attributes are independent of each other and so may be selected for individually.

Crown form in *T. scleroxylon* varied from narrow to broad and from deep to short (Fig. 43b). Karki (1979) following his studies of the advantages and disadvantages of similar crown forms in *Pinus sylvestris*, concluded that narrow, short and thin branched trees are more desirable in plantation forestry because this tends to :

(i) increase the sawlog percentage, from total wood harvest,

(ii) increase stemwood percentage from total assimilation product,

(iii) decrease the need for uneconomic early thinnings, and

(iv) increase the number of plants that can be planted per hectare.

Larson and Gordon (1969a) emphasized the importance of a compact or dense crown in *Populus*. In the case of *T. scleroxylon*, a tall tree with narrow, lax crown, having few small diameter branches and held horizontally seem to be a more favourable ideotype. So, on the basis of the conclusions and demonstrations of Karki (1979), and the findings in this chapter, it seems that clones 175/6, 144/1, 175/7 and 144/4 have better shaped crowns than clones 175/8, 175/1, 137/9 (which have many branches) and 177/10 which have broader crowns. Furthermore, according to Brown *et al* (1967) although they were talking of between species variations, trees with decurrent crowns have weak apical dominance, but strong apical control, and the converse applies to excurrent crowns. In this work, as illustrated by crown shapes (Fig. 43b), it seems that there is considerable variation in apical control. It remains to be seen if the inverse relationship between apical dominance and apical control hold true for the variation in crown development within this species.

7.4.1 Limitations of the 'crown-form' projection method

(1) Since crown outlines are often 'distorted' (Curtin 1970), and rarely completely smooth, the direct extrapolation method used here

Plate 8

Variation in branch angle and branch size in 3-year old clonal plants of *T. scleroxylon* (Expt. 1/76) planted at 2.4 m spacing at Gambari, Nigeria.
(Top = narrow angled, large diameter branches. Bottom = wide angled, narrow branches).

Plate 9

Variation of crown form in 3-year old *T. scleroxylon* clones at Gambari, Nigeria (Expt. 1/76).

(left = short compact crown. Right = open extended crown) planted at 2.5 m spacing.

(based on the characteristics of the 5 basal most mature branches) may not fully represent the crown outline, even when it is known that branch lengths decrease gradually with height on the tree bole.

(2) The crown-tip may vary in degree of bluntness, a feature which cannot be recorded without climbing scaffold.

(3) There may be a regular decrease in mean angle of branches with passage up the tree. This could not have been estimated in this case without felling the trees.

However, the present work, despite the above limitations, aided by visual observations, can give an indication of clonal variation in form, and may be useful for selection purposes in a tree improvement programme aimed at commercial plantation establishment, as is the case in *T. scleroxylon* in Nigeria.

SECTION 4

PREDICTION OF BRANCHING HABIT

The decapitation test was applied to a range of clones of *T. scleroxylon*, to measure the strength of apical dominance. Numerical values thus obtained were correlated with field performance of the respective clones at 4-years.

This approach is shown to be a promising one for selecting clones at an early age. It is hoped that it will make a practical contribution to plantation forestry in Nigeria.

CHAPTER 8

THE DEVELOPMENT OF A 'PREDICTIVE TEST' FOR BRANCHING HABIT

8.1 Introduction

It is clear from the work already presented that clones of *T. scleroxylon* have individual growth and branching characteristics when grown in plantation at wide and close spacing. It is known that branching and form in woody plants is usually associated with the phenomena of apical dominance (Phillips 1975) and apical control (Brown *et al* 1967). When small plotted plants are decapitated, the genetic characteristics of the different clones are expressed in relation to bud activity. This seems to be a measure of apical dominance. The aim of the present chapter is to see if there is a relationship between apical dominance as determined by the Decapitation Test and field performance and branching habits.

As the performance of trees at maturity and the form in particular are of prime importance to foresters, the value of selection on the basis of 'juvenile' traits or performance depends very much on the correlation between such traits and suitable measures of form in the mature tree. An early selection based on good juvenile/mature correlation, refered to as 'indirect selection' has been known to be very useful (Von Weissenberg 1976). In the case of branching, the genetic basis in general is not yet clearly understood, but if the form of the tree results from the intensity of apical dominance, then perhaps it is possible to predict the final shape of the tree or its form and branching from a study of apical dominance in young plants in the nursery.

Lambert (1980) enumerated the advantages of early selection which included :

(a) Smaller genetic tests of 'juvenile' materials at closer spacing than in usual large field trials.

(b) Genetic gains can be achieved more quickly at higher efficiency (Nanson 1968)

(c) Measurements and assessments can be done more easily and cheaply, and

(d) The breeder can be more responsive to changes in demands for improved products or new cultural methods.

The disadvantage however is : Flower induction is more difficult in young plants, and also costly (this disadvantage may not be tenable any longer in *T. scleroxylon* as more effective methods of flower induction and pollen handling in 'juvenile' plants are developed; Leakey *et al* 1981).

The application of correlative response in early selection is more common in agricultural crops. Here, yield has received most attention as in *Theobroma cacao* (Toxopeus 1964) where pod production and growth attributes in the first year of fruiting was related to later yield performance, and in *Hevea brasiliensis* (Alika 1978; 1980) who reported a good relationship between latex yield over 8 years. Among forest species emphasis has been placed more on growth performances. In this instance, reports are known on Loblolly pine and Douglas-fir (Cannell *et al* 1978; Lambeth 1979; Waxler 1980), *Pinus taeda* (Waxler and Buijtenen 1981) and in Broad leaf species, *Populus deltoides* (Cooper and Ferguson 1974). In early selection against disease or pests however, a different approach has usually been taken (Strobel 1975). Here, the biochemical analysis of plant extracts have been used; such as in *Pinus strobus* (Wilkinson 1980) where a close relationship was found between chemical properties of white pine oleoresin (containing monoterpenes) with resistance of weevil attack (*Pissodes strobi*).

The first part of this chapter is concerned with the measurement of apical dominance in juvenile clonal material. The second part

examines the correlation between these measurements and the form of the tree in plantations and leads to the development of a predictive test for branching habit which may enable superior clones to be selected at an early age.

8.2 Materials and Methods

The origin of clones, their culture and treatments are as described in Chapter 3.

Three sets of clones were screened in 1980. The first two were done at ITE and these included :

i) Clones 144/9, 175/1, 175/5, 175/6, 175/9, 8047 and 8049, and

ii) Clones 137/9, 139/9, 144/1, 144/7, 166/1, 175/6, 175/7, 175/8 177/10, 261/4, 505/2 and 506/14.

The following clones were represented in the third screening at FRIN Nursery :-

Clones 139/6, 144/6, 161/5, 166/3, 166/5, 224/3 and 224/7.

As far as possible, plants were of equal size, ranging from between 60 to 80 cm tall, but in some cases plants about 50 cm tall, with 5 retained leaves had to be used.

The top 2 nodes from each plant were removed. Spacing was sufficient to prevent appreciable shading (plate 10). There were 8 replicate plants at ITE and 15 at FRIN, these being randomised in two blocks. The numbers were dictated by availability of plants. All plants received weekly applications of 1 % 'Solufeed' at ITE and 1 % 'Wellgro' in Nigeria.

Assessments of lateral shoot length were done weekly over 9 weeks.

8.2.1 SCREENING OF NIGERIAN CLONES BY DECAPITATION

In Chapter 5, the effects of various factors on apical dominance, including the effects of the condition of the plant, the edaphic and

Plate 10

Screening of clones in Edinburgh (ITE glasshouse) in March, 1980. Note that smaller plants were raised to prevent shading by larger plants.

the aerial environments were investigated. The results from these tests, which were summarised at the end of that chapter, were used here to provide the standard environments for the Decapitation Test in Edinburgh and Ibadan respectively.

8.2.2 Data analysis

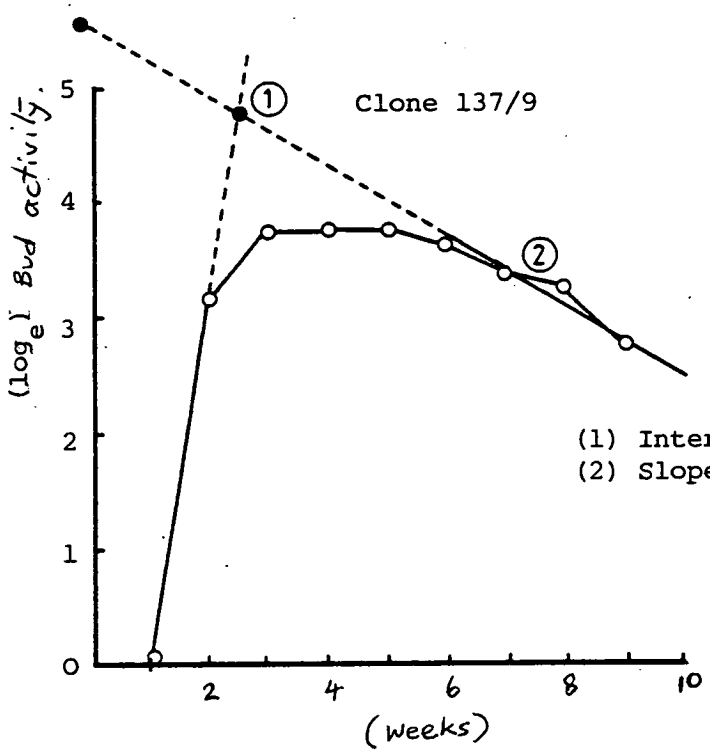
Bud 'activity' and the standard error values were calculated as described earlier, and presented as percentage values. The maximum bud activity usually occured at 4 weeks. It is this value, which by established tradition at ITE, has been used as a measure of apical dominance. However, further parameters can be obtained when the raw data is subjected to certain graphical analysis (Fig. 44). When the experimental values are converted to natural logarithms, it was nearly always possible to clearly distinguish two phases.

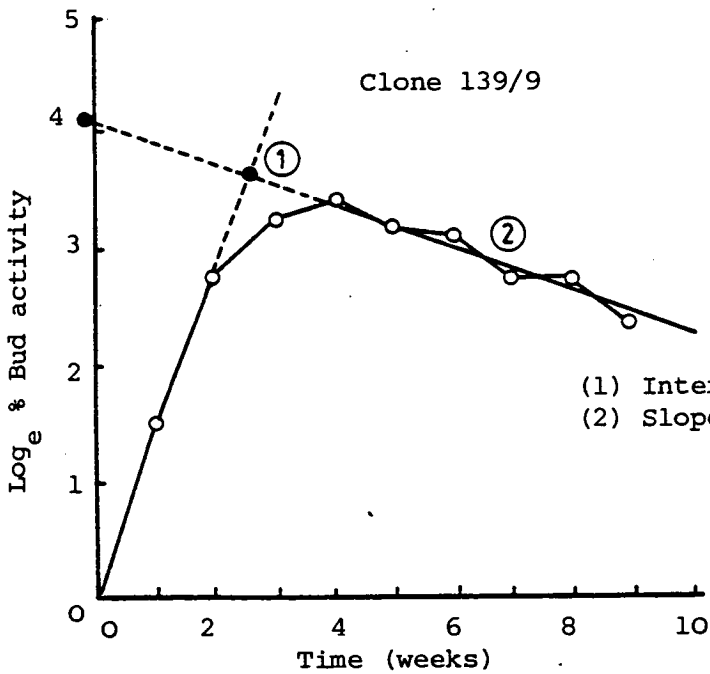
The first phase is that of rapidly increasing bud activity while the second phase was that of a rapid decline in bud activity, this being associated with the reassertion of dominance by the uppermost shoots (Fig. 44). Between these two phases is a transition region, usually occuring between weeks 3 and 4 - the period of maximum bud activity.

Using linear regression, it was possible to fit a straight line to the second phase, henceforth known as the Reassertion phase. This slope expresses the rate at which the uppermost shoots gain dominance, and so appears to be a possible candidate for an index of apical control. No attempt was made to estimate the standard error of the slope, as the values are not independent of each other, and significance testing is thus not possible.

Several other attributes of the graph seemed possible as candidates for an index of apical dominance. It was postulated that the intercept

Fig. 44





Showing analysis of bud activity slopes. (1) = reassertion of dominance, (2) = point of intercept on axis, and (3) potential bud activity for clones 137/9 and 139/9.

(labelled 1 on Fig. 44) could be regarded as a 'potential bud activity'. It might also be postulated that the initial slope be regarded as a useful measure of apical dominance. However, only the maximum bud activity, potential bud activity and the reassertion slope were used in the present exercise.

Clones were ranked according to their level of maximum bud activity, in an attempt to show their relative intensity of apical dominance from low activity, being considered to be indicative of strong apical dominance to high activity or weak apical dominance.

Data from the above were correlated with those from field data reported in Chapters 6 and 7, using the program MCORR 2 (Appendix 6).

8.3 Results

The 'intensity' of apical dominance in *T. scleroxylon* clones within each of the 3 screening experiments differed significantly.

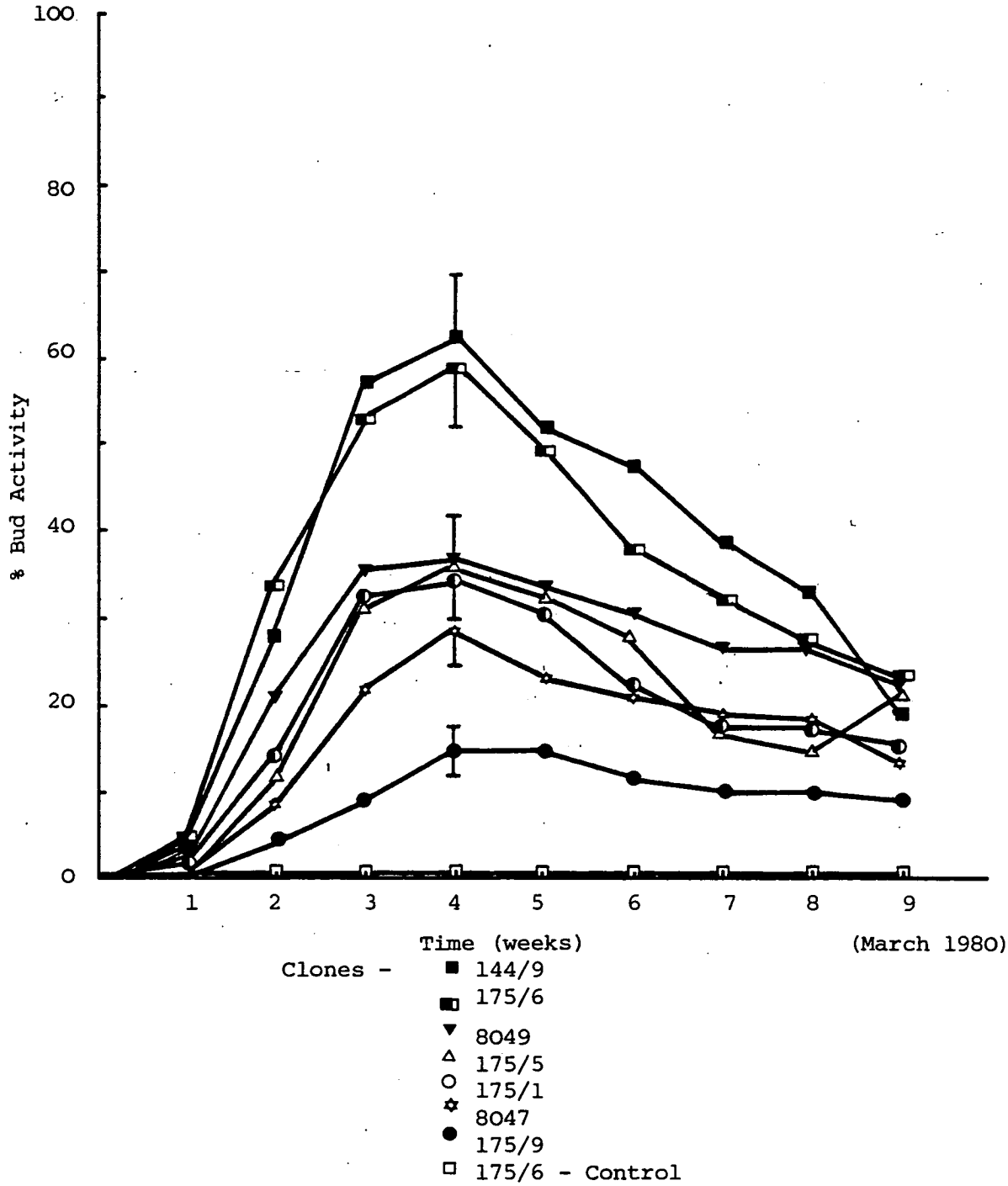
In screen I, clones 175/5 and 175/1, produced the highest bud activity at 4 weeks (62.7 % and 59.2 respectively) while clone 8047 produced the least (13 %), a difference of about 75 % (Fig. 45).

In screen II, clones 505/2 and 144/1 produced the highest bud activity at 4 weeks (83.1 % and 70 % respectively) while clone 144/7 produced the least (17.2 %), a difference of about 79 % (Fig. 46). The control undecapitated clone 175/6 did not show bud activity in either of these two screenings.

In screen III, clones 224/7 and 139/6 produced highest bud activity at week 4 (70 % and 65 % respectively) while clone 161/5 produced the least (18 %), and a difference of about 74 % (Fig. 47) based on maximum bud 'activity' at week 4, clones were ranked from low bud 'activity' to high bud 'activity'; in other words from strong apical dominance to weak apical dominance respectively (Table 18 a).

Fig. 45

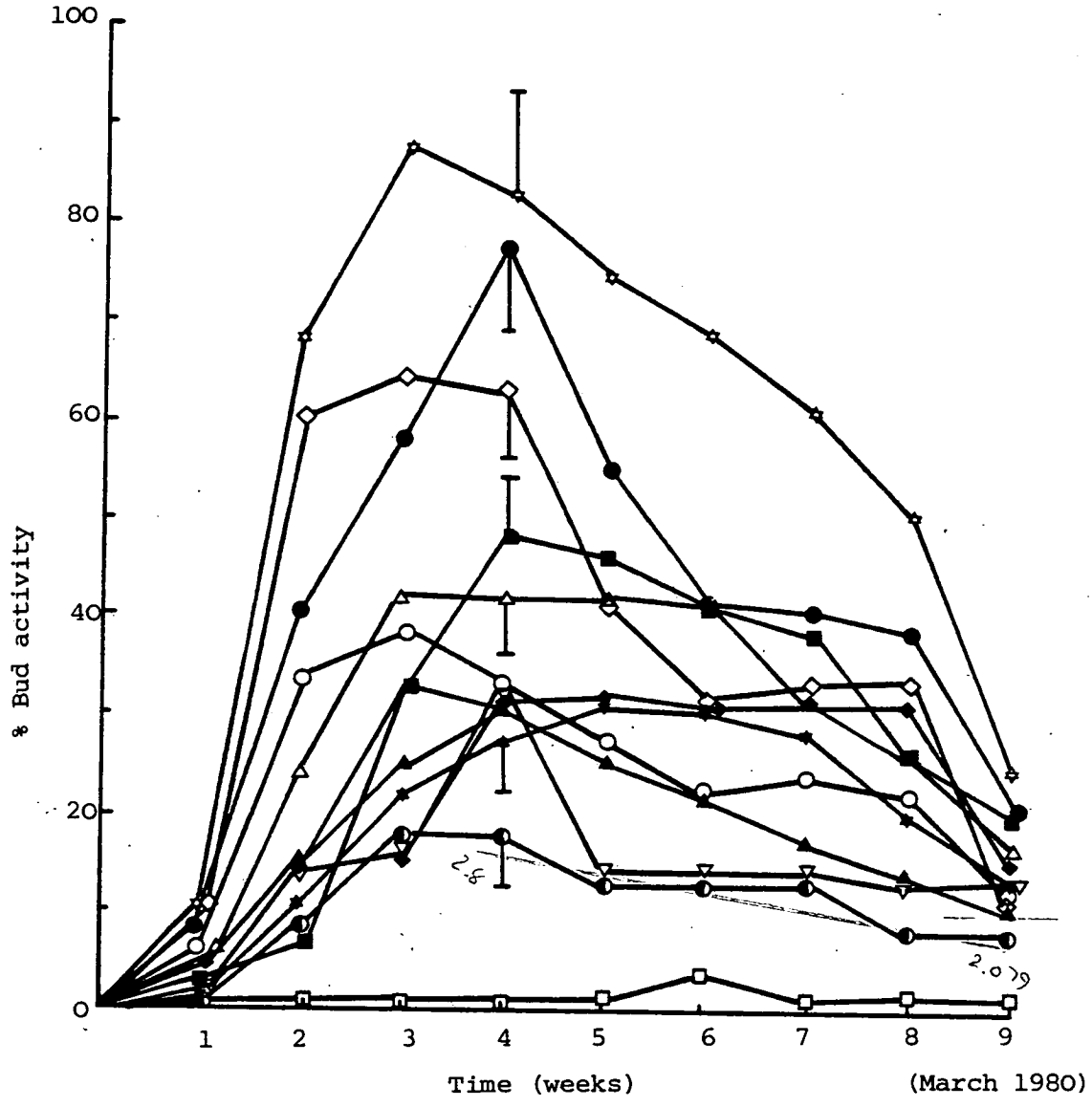
Screen I (ITE)



Variation in bud 'activity' between decapitated plants of *T. scleroxylon* clones screened under uniform conditions.

Fig. 46

Screen II (ITE)

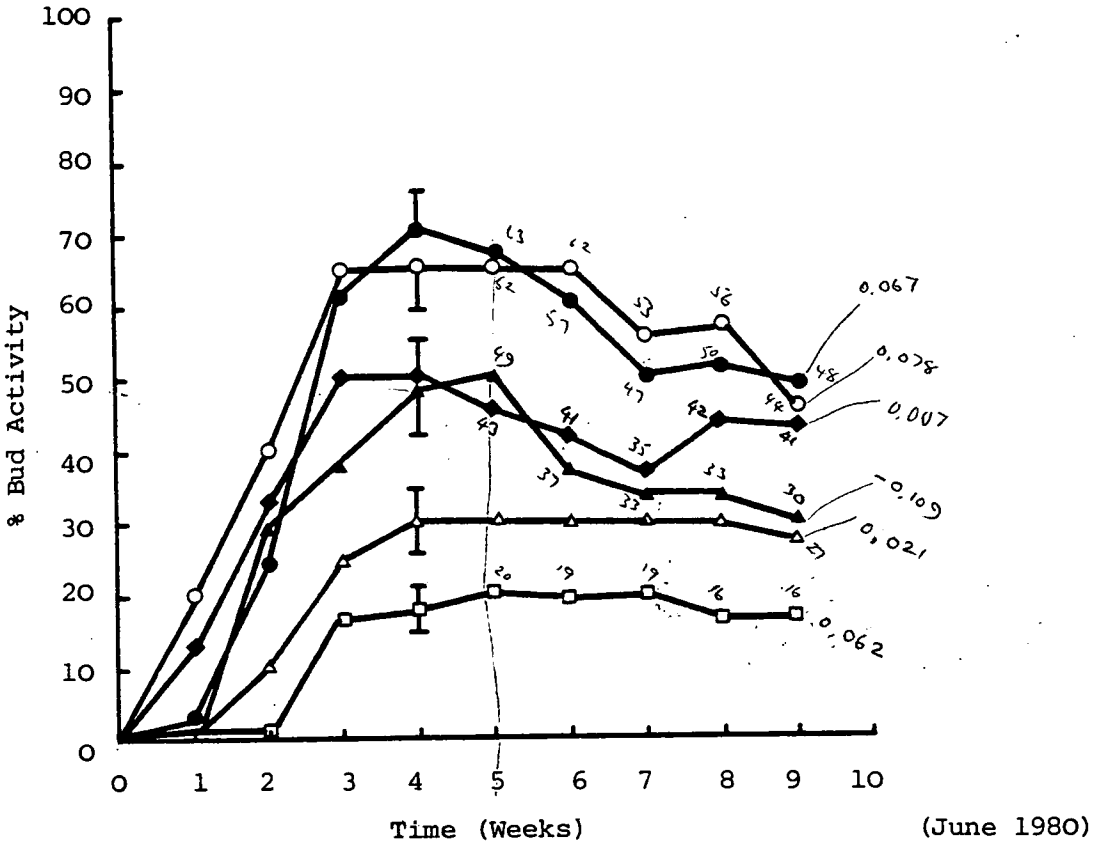


Clones -
- 505/2
- 261/4
- 144/7
- 177/10
- 137/9
- 139/9
- 144/1
- 166/1
- 175/7
- 175/8
- 506/14
- 175/6 - Control

Variation in bud activity between decapitated plants of *T. scleroxylon* clones, screened under uniform conditions.

Fig. 47

Screen III (FRIN)

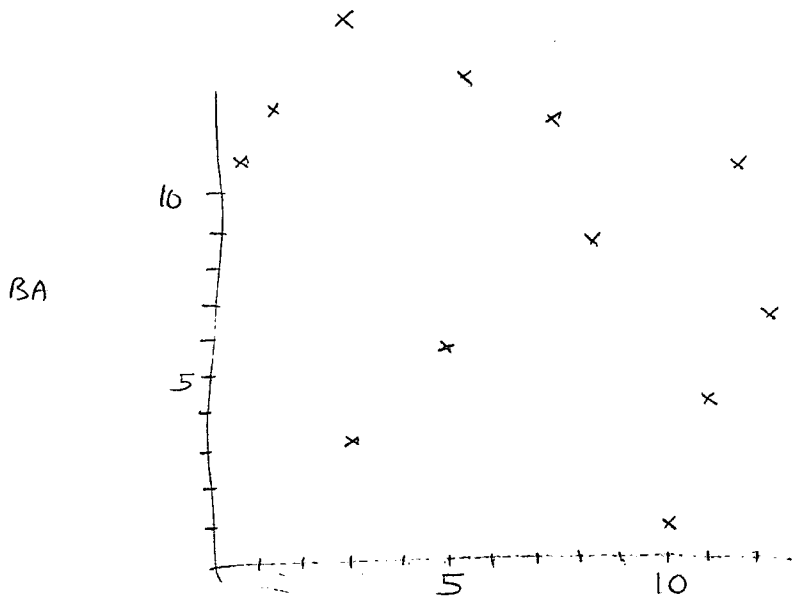


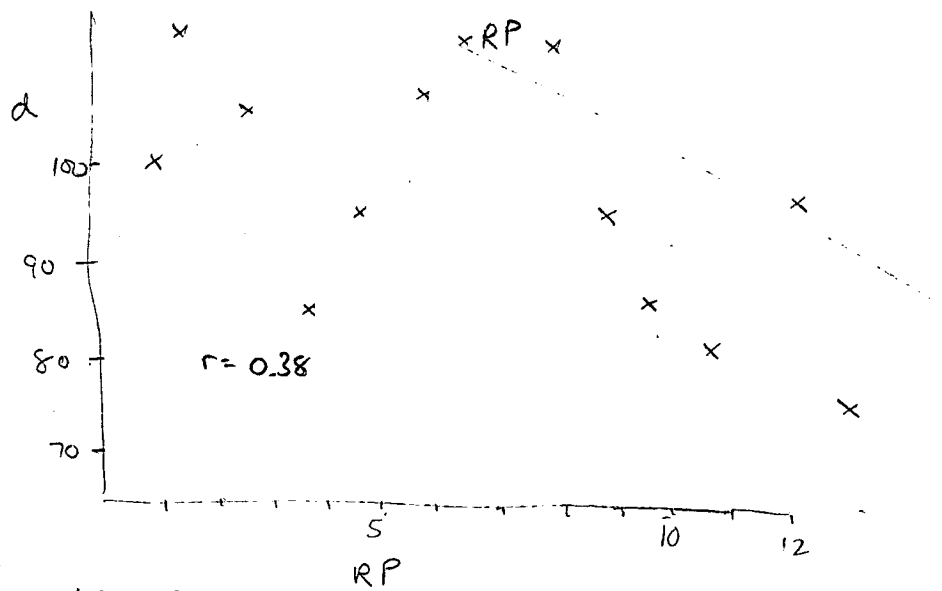
Clones -
- 224/7
- 166/5
- 166/3
- 224/3
- 139/6
- 161/5
- 144/5

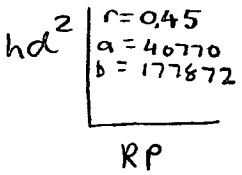
Variation in bud 'activity' between decapitated plants of *T. scleroxylon* clones screened under uniform conditions.

Table 18a: Ranking of *T. scleroxylon* clones based on maximum number of buds released from apical dominance by decapitation at 4 weeks in potted clonal plants tested in Edinburgh and Ibadan.

Rank	Clone	% Bud Activity at 4th Week			Remarks
		Screen I	Screen II	Screen III	
15-30	144/7		17.2		High 'apical dominance'
	161/5			18.0	
	175/7		28.3		
	175/9	28.8			
	506/14		30.0		
	166/3			30.0	
	139/9		30.1		
	166/1		32.0		
	177/10		33.0		
31-60	144/5			35.0	Average
	144/9	38.5			
	137/9		42.8		
	175/8		52.3		Low 'apical dominance'
	175/1	59.3			
	175/5	62.7			
	224/7			65.0	
60-90	139/6			70.0	
	144/1		70.0		
	505/2		84.0		


BA
10
5
5
10


RP
d
100
90
80
70
r= 0.38
5
10
12
RP


hd²
r=0,45
a=40770
b=177672
RP

Analysis of the reassertion phase (Phase 2) revealed differences in slopes between clones in the 1st and 2nd screens (Table 18b and Figs. 48(a) and (b)), this varying from -0.302 for clone 137/9 to clones 177/9 and 166/1 (-0.098), being steepest and least steep respectively.

Table 18b :

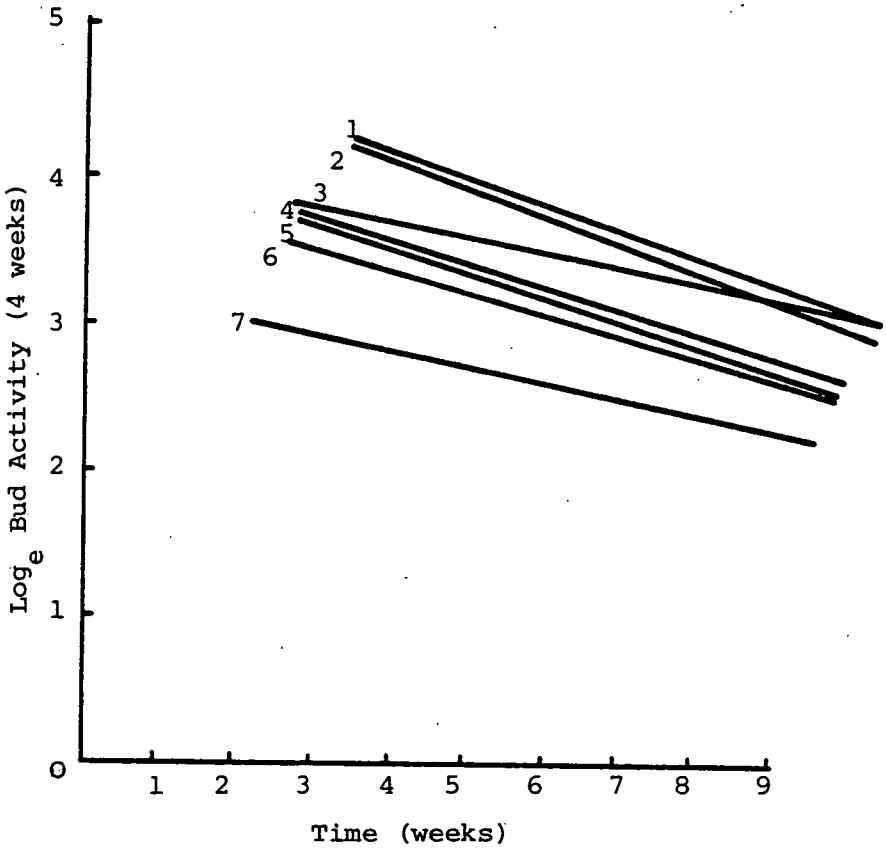
Clone	Screen I	Screen II
137/9		-0.302
175/8		-0.267
261/4		-0.254
505/2		-0.205
175/7		-0.201
144/1		-0.200
139/9		-0.192
175/5	-0.186	
175/6	-0.174	
175/1	-0.165	
8049	-0.142	
177/10		-0.141
144/7		-0.134
175/9	-0.117	
8047	-0.106	
144/9)	-0.098	
166/1)		-0.098

Variation in the regression coefficients of the reassertion phase in decapitated clones of *T. scleroxylon* ranked according to steepness of slope (from high to low slope).

'Potential bud activity', the projected point of interception between the two phases of bud activity also differed greatly between clones in these two screens. Furthermore, Table 19 shows the variation in potential bud 'activity' ($\log_e$) at week 4. In

Fig. 48a

(Screen I)

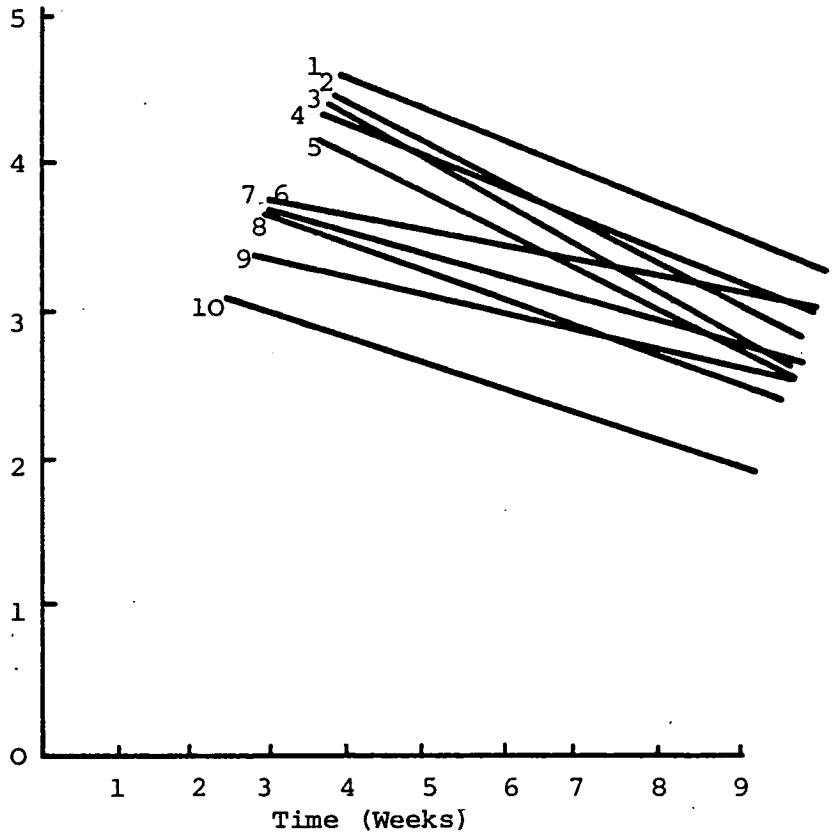


Clone : 1. 175/1
2. 175/5
3. 144/9
4. 9049
5. 175/6
6. 175/9
7. 8047

Variation in restoration slopes of 7 decapitated clones of Obeche - *T. scleroxylon* K.Schum.

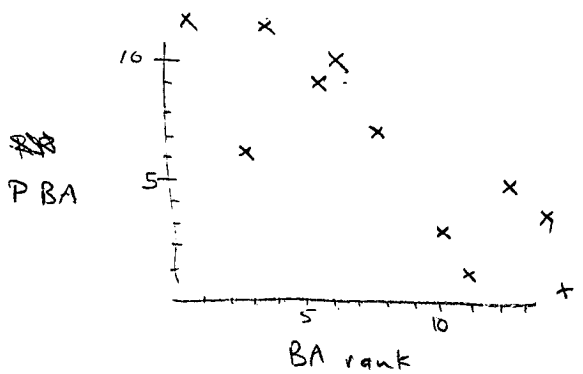
Fig. 48b

(Screen II)



Clones :
1. 505/2
2. 137/9
3. 261/4
4. 144/1
5. 175/8
6. 166/1
7. 177/10
8. 506/14
9. 139/9
10. 144/9

Variation in restoration slopes of 10 decapitated clones of Obeche - *T. scleroxylon* K. schum.


P BA
10
5
5
10
BA rank

this case clone 505/2 had highest bud activity (4.8) while clone 8047 had lowest (2.8).

Table 19:

Clone	Screen I	Screen II
505/2		4.8
137/9		4.7
144/1)		4.6
144/9)	4.6	
261/4		4.3
175/5	4.2	
175/1	4.1	
175/7		4.0
177/10		3.8
8049)	3.7	
175/6)	3.7	
139/9		3.6
166/1)		3.5
175/9)	3.5	
144/7		3.1
8047	2.8	

Variation in Potential bud 'activity' ($\log_e$) between decapitated plants of *T. scleroxylon* (Based on % bud 'activity' over the two phases of bud activity in two screens).

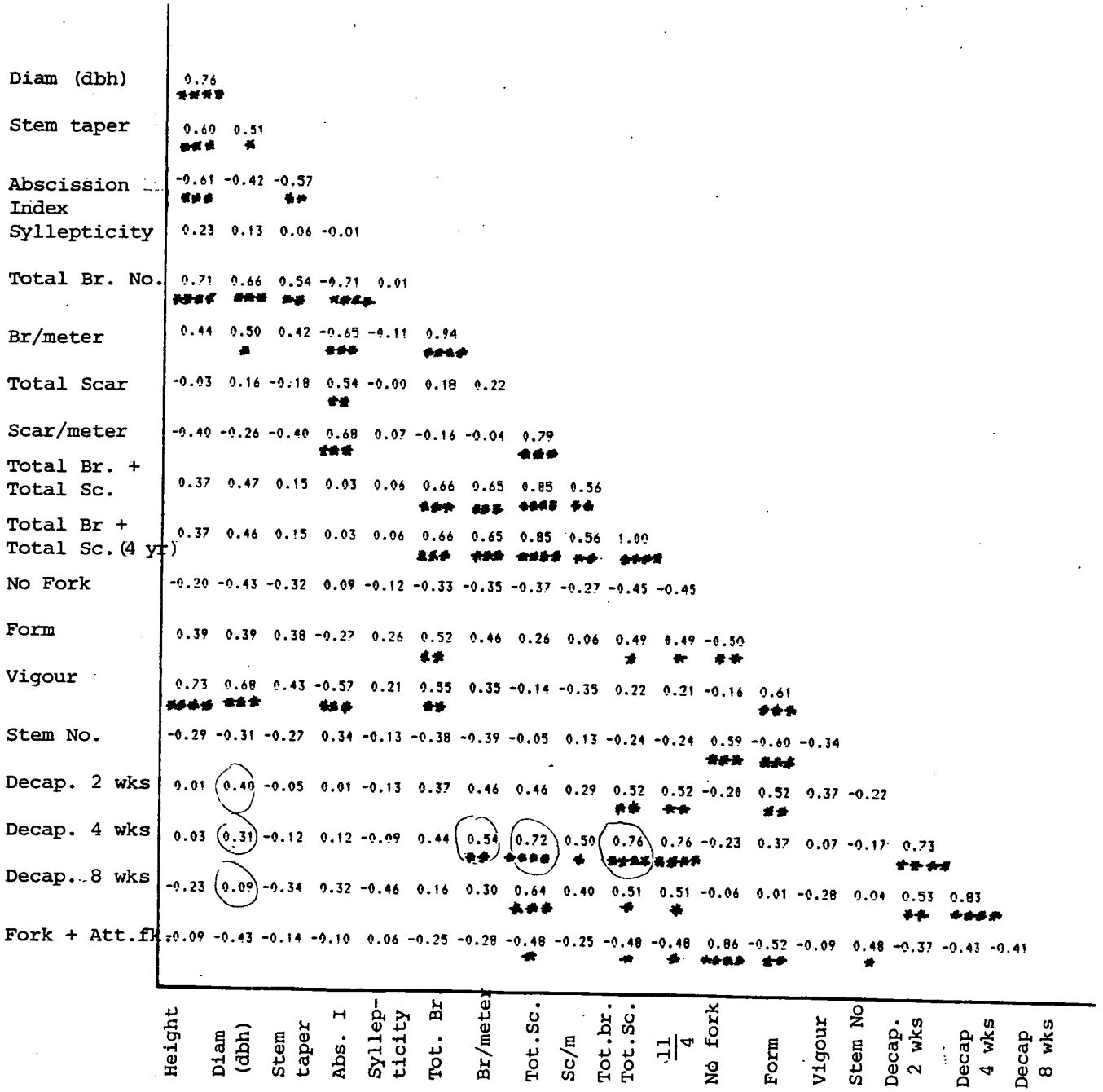
8.4. CORRELATIONS BETWEEN BUD ACTIVITY IN SMALL DECAPITATED PLANTS AND GROWTH CHARACTERISTICS OF SOME CLONES GROWN IN PLANTATION AFTER 4 YEARS

Mean bud activities at 2, 4 and 8 weeks, regression coefficients of the reassertion phase, and the estimated bud activity from juvenile plants of *T. scleroxylon*, after decapitation were correlated against appropriate field data for different growth and branching parameters.

Better relationships existed between the parameters and the 4th week decapitation values than in the 2nd and 8th week.

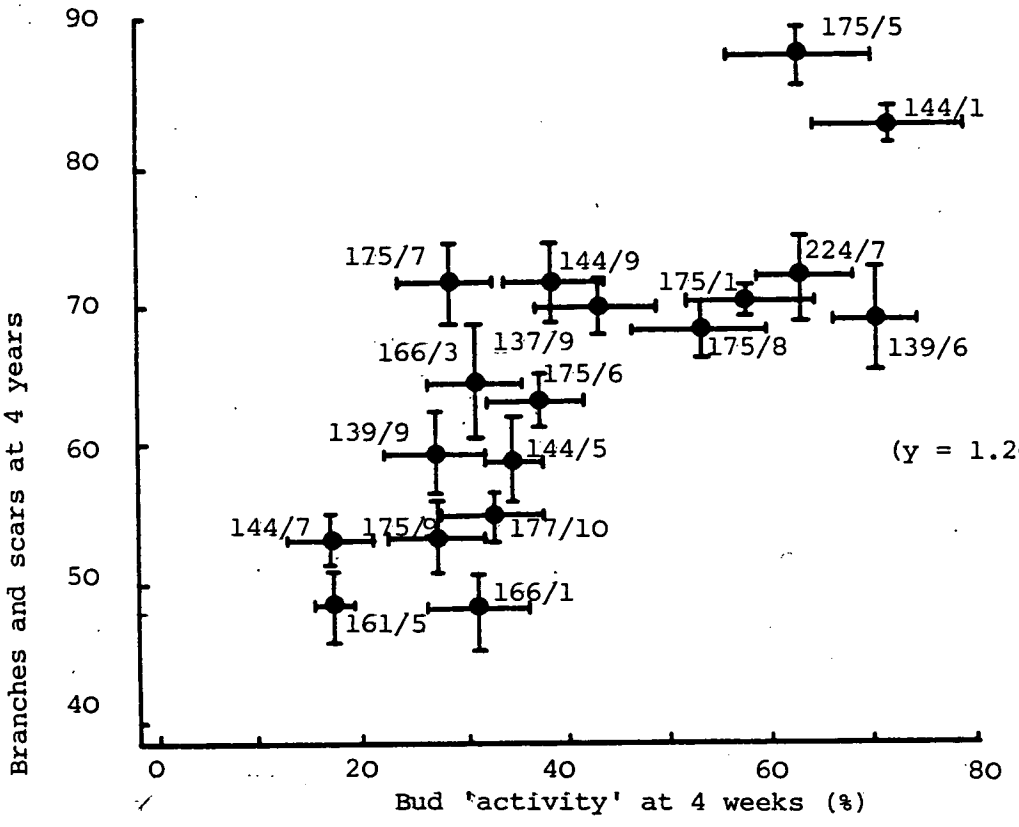
Fig. 49

Narrow Spacing



Correlative response between some 'adult' parameters from Nigerian field experiments and bud activity at 2, 4 and 8 weeks from glasshouse experiments at ITE and FRIN (at narrow spacing 2.5 m. figures without * are not significant, * = Sig. at P.0.05, ** = P-0.02, *** = P-0.01, and **** = P-0.001, df = 17)

Fig. 50

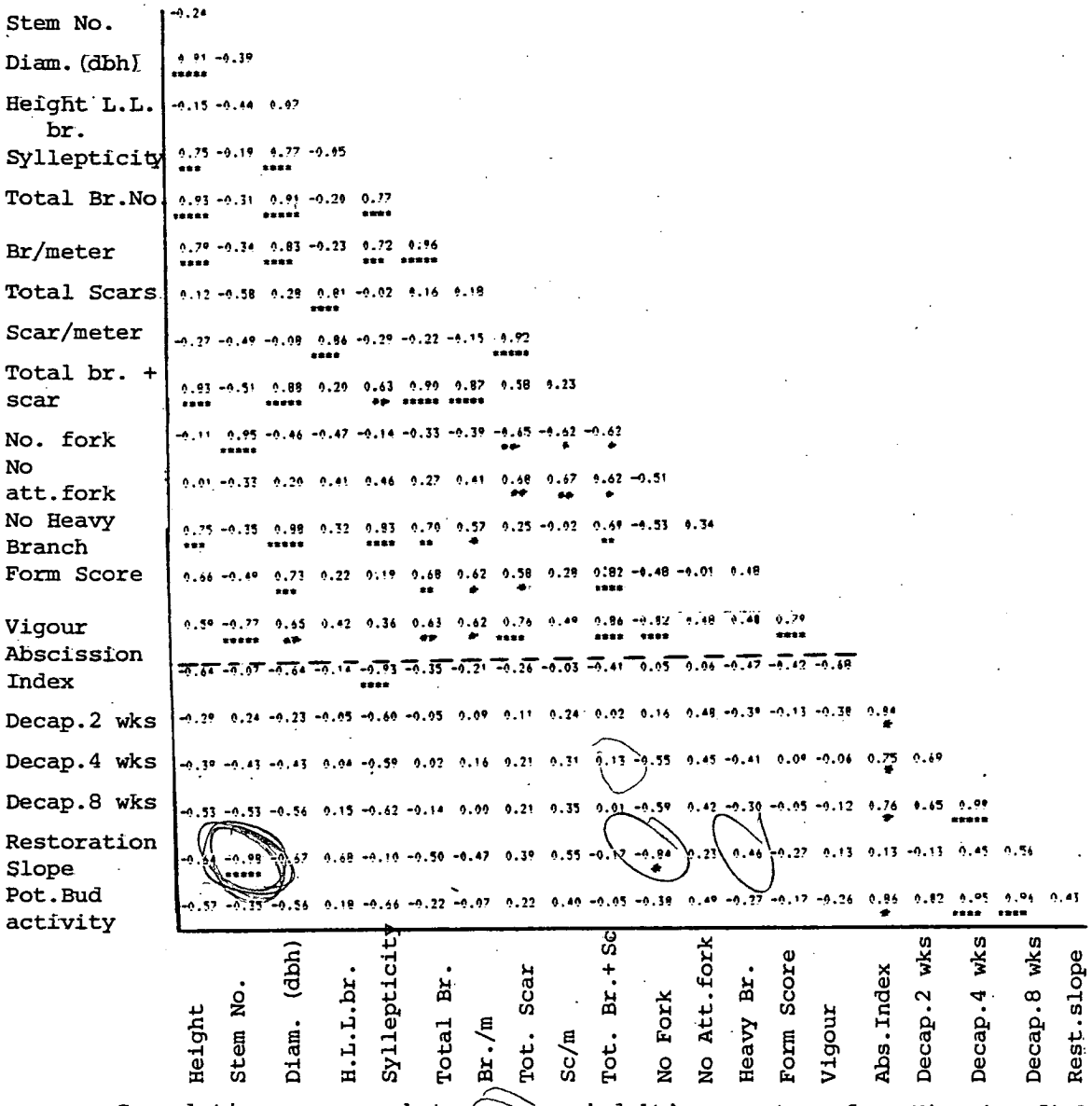


Bars represent standard errors
Correlation co-efficient +0.76 2222
Significance level - 0.001 % P (d.f - 17)

Relationship between bud 'activity' at 4 weeks with mean total. number of axillary shoots produced in 4 years growth in plantation at 2.5 m spacing.

Fig. 51

Wide Spacing



Correlative response between some 'adult' parameters from Nigerian field experiments (3, 4 and 4/75 at 4th year of growth and bud activity at 2, 4, and 8 weeks from glasshouse experiments at ITE and FRIN (Corr. Co-efficient above dashed line in matrix has 8 d.f. and below is 4 df. Figures without * are non-significant, others with *, **, ***, ****, and ***** have P = 0.10, 0.05, 0.02, 0.01 and 0.001 respectively. Data for wide spacing 4.9 m).

Significant relationships (r = >+0.70) were recorded between bud activity 4 weeks from small decapitated potted plants in glasshouse or nursery and the branching frequency in 4-year old plantations at 2.5 m spacing (Figs. 49 and 50).

At wide spacing (4.9 m), no such relationships were found between bud activity and branching (Fig. 51), nor were crown attributes (Chapter 7) at 2.5 m spacing (Expt. 7/75B) related to 'bud activity' (Fig. 52).

Potential bud activity was also related to branching at narrow spacing, (r = >+0.60). Reassertion slopes (regression coefficients of the second phase) also showed good relationship with parameters such as Diameter (r = +0.53 - P = 0.05), and branching (r = >+0.45), at narrow spacing (Table 20).

At wide spacing, no relationship existed between potential bud activity or reassertion slope and most parameters, with the exception of stem number which was closely and negatively related to it (r = -0.98, P = 0.001), (Fig. 50).

Table 20:

Parameters	df	r	P(sig.)
Reassertion slope with Diam(dbh)	12	+0.53	0.05
" " with height	12	+0.19	ns
" " with Absc.Index	10	-0.54	0.10
" " with No.branches	12	+0.48	0.10
" " with No.branch scars	12	+0.28	ns
" " with br. + scars	12	+0.46	0.10
Potential bud activity with Diam.	12	+0.43	ns
" with height	12	+0.18	ns
" with branch No.	12	+0.60	0.05
" with Scar No.	12	+0.54	0.05
" with branch + scars	12	+0.71	0.01

Relationships between reassertion slopes and Potential bud activity with some growth parameters at 2.5 m spacing. (Expt. 7/75) after 4 years in plantation.

Fig. 52

Crown and Branch Characteristics

(Narrow Spacing)

	Branch angle	Branch length	Crown area	Crown index	Potential bud activity	Restoration Slope
New Branch length	0.29					
Estimated Crown area	0.24	0.83 ****				
Crown Index	0.44	0.92 ****	0.93 ****			
Potential bud activity	-0.14	-0.05	0.03	0.08		
Restoration slope	0.45	0.37	0.32	0.44	0.61 ***	
Bud activity at week 4	-0.24	-0.10	0.06	0.04	0.67 ***	0.37

The relationship between crown, branch attributes and bud activity at week 4, potential bud activity and the restoration slope of 14 clones of *T. scleroxylon*.

(Blank space = non-significant, * = sig. P 0.05, ** = sig. at P 0.02, *** = Sig -P -0.01, and **** = sig. at P = 0.001).

(Data from Expt. 7/75 10 df, narrow spacing 2.5 m)

8.5 Discussion

The large variation reported between clones in their axillary bud activity after decapitation is similar to the findings of Longman (1978) and Leakey and Longman (in press). They reported variations between decapitated seedlings of *T. scleroxylon* even when the latter were from the same seedlot. The present result agrees also with preliminary observations of Bowen *et al* (1977) who reported substantial variations between clones of *T. scleroxylon*.

Fielding (1953; 1960) had earlier reported variation between *P. radiata* clones in apical dominance and branching. More recently, Cannell (1974) found variation in branching between provenances of Sitka spruce and Lodgepole pine. He explained the differences in branching and leader shoot extension in terms of apical control, this being large or small in different genotypes.

The variation recorded in the present study in reassertion slopes (Table 18) is comparable with the conclusions of Longman (1978) who did not analyse the reassertion slopes of the *T. scleroxylon* seedlings he tested, but did identify that the rate of dominance reassertion differed greatly between seedlings, even within the same seedlot. This parameter (the reassertion slope) is probably related to apical control, as the correlative influences between the shoots or branches leading to the domination or reassertion of dominance by one of the anterior shoots can be likened to the situation in growing trees where the apical bud influences the amount of growth of the lower branches, leading to a definite crown form.

The ranking of clones on the basis of axillary bud activity (Table 17), allows for easy classification of clones on the basis of their potential to sprout or produce branches - a measure of their intensity of apical dominance. A close relationship between 'juvenile'

traits, either morphological or physiological, and 'adult' characters is clearly useful for early selection of superior clones in an improvement programme. At narrow spacing, best correlations of this type were between bud activity at 4 weeks and the total number of branches and scars (Fig. 50) produced over 4 years field growth ($r = +0.76$, $P = 0.001$). This correlation was slightly better than against scars alone ($r = +0.72$, $P = 0.001$); the relationship between bud activity and total branches being not significant ($r = +0.44$).

This suggests that bud activity following decapitation is a good predictor of the production of branches, but that branch shedding results in a living crown which has no relationship with the production of branches, i.e. the control mechanisms are different. On the basis of the relationship between bud activity amd branches and scars (Mean branches produced in 4 years), the early selection of clones for branching habit in *T. scleroxylon* as ranked on Table 17 is practicable, this being possible within the first 6 months of the life of the tree. The advantages of this scheme of early selection rather than the usual long term silvicultural field tests, have been enumerated earlier. It is however important to mention here that a early predictive method is more econimical, as it is less expensive and not open to the various natural or human hazards i.e. wind, pests and fire to which field tests are usually exposed. Difficulties involved in this method will however be discussed later.

The lack of relationship at the wide spacing between bud activity and branching may be a result of more branches, especially included sylleptic ones being produced in response to light, and perhaps other environmental effects, consequent on spacing. More information is needed here, especially in relation to the role of

spectral shifts in the incident radiation. However, on the basis of the relationship at narrow spacing, between bud activity and branching (Fig. 50) clones 161/5, 144/7, 166/1, 175/9, 177/10, 144/5, 139/9, 166/3 and 175/6 produce fewer branches, having stronger apical dominance than the others, and represent half the total sample of clones. At this 50 % selection intensity, predicted improvements in branching habit will be 15.7 %, which is an appreciable gain (Table 21). This appreciably high gain at this early stage supports the calculations of Nanson (1968) who discussed the high returns and the high efficiency involved in early selection, as compared to long-term silvicultural methods.

Table 21: Units refer to the total branch production in 4 years.

Character	Overall mean	Mean of selected clones	Selection differential	%	Gain %
Branching habit	64.9 ± 2.6	56.1 ± 2.1	8.8	14%	15.7%

Selection differential and predicted gain from selecting the 9 (50 %) least branching clones (high apical dominance) out of 18 based on the correlated response between bud activity at 4 weeks and field branching in Nigeria in *T. scleroxylon* (based on Shelbourne and Thulin 1974)

Earlier assessments of Experiments (Ladipo *et al* 1980) at wide spacing suggested that branch production, as assessed by the number of branches per metre, was probably related to height, and thus

that yield was a function of branching habit. At narrow spacing, this relationship is not strong as in the wide spacing, nor is it with scars per metre, but mean branch number was related to height ($r = +0.71$, $P = 0.001$) while mean scar number was not. However, reassertion slope was related to diameter, ($r = +0.53$, $P = 0.05$) and number of branches ($r = +0.48$. $P = 0.1$), but not with scar alone although it was also weakly related ($r = +0.46$, $P = 0.1$) with both branches and scars (mean). This thus suggests that apical control is probably involved in diameter increment or stem volume production and so it is probably a determinant of yield. On the other hand the close relationship between height and diameter ($r = +0.76$, $P = 0.001$) indicates that they are inter-related and so indirectly substantiating the earlier hypothesis that branching is indeed a function of yield. In this case, this conclusion agrees with those of Toxopeus (1964) who in young seedlings of *Theobroma cacao* found that yield at later age was related to growth attributes of juvenile plants.

8.5.1 Genetic basis of branching and 'apical dominance'.

Shein and Jackson (1971) suggested that growth of mainstem and laterals may depend on the balance of hormones, while Phillips (1975) favoured a hormone directed nutrient transport theory as responsible for correlative inhibition and branch development.

The close relationship reported here between 'apical dominance' and field branching does not of course disprove any of these views, but it does underline the genetic control of apical dominance. Practically-orientated programmes like the present one frequently throw up useful material, of extreme response, which present opportunities for the testing of hypotheses in the future. It is

hoped that comparative studies on the mechanism of apical dominance may in future be carried out on half-sib clones which differ markedly in their strength of apical dominance. This being based on the suggestions that, clonal variations in the levels of hormone balance or its concentration, influencing nutrient transport, are under genetic influence, and thus responsible for the variation in branching habits in *T. scleroxylon* clones.

Taking a geneticists viewpoint, and adopting the explanations of Von-Weissenberg (1976) for the basis of genetic correlation between parameter pairs, three possible explanations are suggested.

i) Linkage - two different genes controlling each trait (apical dominance and apical control) but close to each other on one chromosome and therefor inherited together.

ii) Pleiotropy - one gene controlling both traits, and

iii) Both linkage and pleiotropy occuring simultaneously.

However, if the relationship between these parameters (traits) are dependent on linkage, and assuming that epistasis between genes does not occur, then the genetic correlations between them will ultimately decline by repeated sexual cycles as a result of breaking up of the linkage block during breeding. But as vegetative propagation for *T. scleroxylon* is well established (Howland 1975b), the use of vegetative multiplication of selected clones for commercial forestry will not allow this link breakage. On the other hand, if the relationship is due to pleiotropy, the genetic correlations will remain unchanged over many cycles of selection.

Further studies are required to verify the situation in *T. scleroxylon*.

8.5.2 Probable difficulties involved in the 'Predictive test'

Although an attractive alternative to silvicultural field tests, the early indirect method of selection needs to be carefully approached for the following reasons:

(1) It is only at the final stage of rotation that conclusive remarks can be made on tree form.

(2) A clone with a high degree of bud activity following decapitation may have a high natural branch abscission rate and so produce useful boles. Thus the elimination of clones of this type may result in loss of a potentially good clone.

(3) A clone with a low degree of bud activity following decapitation may develop heavy branches which reduce the economic log value. On the other hand, the lack of any close relationship between heavy branching and bud activity suggests this problem does not normally occur (Fig. 52).

(4) Pests and diseases may be specific to certain clones. As a precaution, methods for screening clones for pest and disease resistance may be required. Forests of the future may contain carefully selected mixtures of clones, so that even if one clone is devastated, the others will survive. In this respect, it is clearly essential to identify large numbers of good clones, so that clonal forests may diverse. This may be achieved either by an intense selection of a very large initial batch of clones, or by a generous (50 %) selection from a relatively small batch.

(5) Wood quality of selected clones may not be favourable in terms of wood density and mechanical quality, and

(6) The photosynthetic efficiency in relation to shading and water stress is an additional factor which requires attention. Already there are rapid field methods for measuring photosynthesis *in situ* (Griffiths, pers. comm.) and, in practical forestry, there is no reason why such equipment should not be run on site. Controlled by a microprocessor, very little technical expertise would be required to make such a system effective.

In conclusion, although the above problems may be real ones, the possibility of early selection, based on the screening for intensity of apical dominance will be a useful predictive method in the early selection of clones for plantation establishment.

The need for such an economic and gainful technique will be vital to the re-afforestation of the landscape, especially in the tropical moist forest zones, where problems of forest destruction is becoming of universal importance. The added advantages of managed plantations over natural ones, particularly in the tropical zones are well known (Johnson 1976). Here, the longer growth period coupled with early selection for form, will result in economic and faster rotations thus a quicker revival of the high productivity for which the tropical forests have been known in past years.

SECTION 5

FURTHER STUDIES OF CLONAL VARIATION IN *T. scleroxylon*

On the basis of the results with clones from the earlier part of this thesis, further tests on seedlings were carried out. The effect of site on growth, branching and clonal variation in photosynthesis were also investigated.

CHAPTER 9

VARIATION IN DEVELOPMENT, BRANCHING AND 'APICAL DOMINANCE' IN HALF-SIB, AND FULL-SIB SEEDLING POPULATIONS OF *T. scleroxylon*.

9.1 Introduction

Unlike temperate species, few workers have attempted to study intraspecific variation in the developmental characteristics of tropical forest species. However, many reports have been made on the general aspects of growth of some of these forest species, such as *Gmelina arborea, Terminalia superba, Terminalia ivorensis,* and *Chlorophora regia* (Longman, 1966; Okali 1971).

The first part of this chapter investigates the variation in early seedling development under relatively uniform tropical glass-house conditions between two half-sib seedling populations of *T. scleroxylon*. The material used originated from extreme parts of the species natural distribution.

Earlier studies in this thesis have examined clonal variation in apical dominance of young plants, following decapitation, as a possible indicator of later branching patterns. Preliminary study of two half-sib progenies has suggested that there is considerable variation in apical dominance between half-sib seedlings of *T. scleroxylon* (Leakey and Longman 1976).

The purpose of the second part of this chapter was to further investigate genetic variations in apical dominance by decapitating half-sib and full-sib progenies. This chapter further looks at the occurrence of branching without decapitation in very young seedlings, particularly, that occurring at the cotyledonary nodes, and its relationship with bud activity after subsequent decapitation.

The propensity to form branches at this stage in development is considered to be an undesirable trait, as the mature tree unless pruned may exhibit forking or multisteming which will adversely affect its commercial value.

9.2 Materials and Methods

Seedlings were raised from two half-sib seedlots (S533 and 535) transported from Nigeria to Edinburgh. They originated from different vegetational zones:

(1) Derived Savannah - (533)

(2) High rain forest - (535) (Table 22)

Seeds were sown in sand, at a depth of about 2 mm and adequately watered once daily with temperature set at about 28 ^{o} ± 2 ^{o}C around the germination trays. In 2 weeks, about 90 % had germinated, and they were all pricked out into 2" pots and after 1 month repotted into 5" plots. All seedlings were carefully labelled before being transfered to another part of the glasshouse where they were spaced out ready for assessment. In the first experiment 15 seedlings from each sample were thereafter studied for 5 months at monthly intervals starting 2 weeks after germination (18.11.80 - 22.5.81), in the Tropical Glasshouse, on a growth bench. Light was supplied by 8 fluorescent tubes, giving 540 μE m^{-2} s^{-1} light at the plant level. Plants were arranged in a completely randomised block design consisting of 3 blocks of 10 plants per seedlot. Growth parameters considered included height, node number, internode length, leaf number and the number of branches produced by these undecapitated plants. In the second experiment, another set from this batch (28 plants per progeny) were decapitated by the removal of 2 nodes only. Average number of leaves was kept at 5. This was done after two

months when they were 45 cm tall and with about 14 nodes. Weekly assessments of bud activity started after this and continued for the next 9 weeks.

Table 22: Origins of half-sib seedling populations of *T. scleroxylon.*

Source No.	Location	Latitude	Longitude	Rainfall Zone ($mm.\ yr^{-1}$)	Expl. Site
533	Elele (Owerri-Porthacokut Rd.) Nigeria	5^{o} 00 N	7^{o} 20 E	2000-2500	ITE
533	Ayangba, Nigeria	7^{o} 40 N	7^{o} 10 E	1300-1500	ITE

For the third experiment, the second batch of seedlings (full-sibs) originated from cross pollinations between plants of 3 clones (8001, 8002 and 8057), the latter being from a mature cutting of grafted plus-tree, produced at FRIN (Table 23 a & b) Leakey *et al* (1981). Progeny from the above cross pollinations are listed in Table 23

Seeds were germinated in modified Fisons controlled environment cabinets (Fisons 140 G2 mkIII), illuminated by 8 incadescent bulbs (40 watts) and 6 fluorescent tubes (warm white) at a proportion of 20 to 80 % respectively. After two months these plants were transfered into the tropical glasshouse where assessments continued. Observations before decapitation on 9.3.79, and 31.1.79 included the observation of cotyledonary branch development, branching from other axillary nodes and the development of forks. Following decapitation, in which two apical nodes were removed, assessments of bud activity were made at weekly intervals.

As in the other experiments of this kind, shoots were considered

Table 23(a): Origins of the parent plants of ITE full-sib seedlings.

Source No.	Location	Latitude	Longitude	Rainfall Zone	Exptl. Site
8001	Ilaro, Nigeria	6° 54 N	3° 06 E	2000-2500	ITE
8002	Ilaro Nigeria	6° 54 N	3° 06 E	2000-2500	ITE
8057*	Igieke Nigeria	6° 42 N	5° 46 E	2000-2500	ITE

* Provisional plus tree originating from mature graft at FRIN(VV 79).

Table 23(b): Details of parentage of ITE full-sib seedlings (Produced 1978 Summer)

Plant No.	Parents	Exptl. Site
8100	8057 x 8001	ITE
8093	8057 x 8002	ITE
8112	8057 x 8001	ITE
8089	8057 x 8002	ITE
8092	8057 x 8002	ITE
8095	8057 x 8002	ITE
8108	8057 x 8001	ITE
8082	8057 x 8002	ITE
8088	8057 x 8002	ITE
8101	8057 x 8001	ITE
8090	8057 x 8002	ITE
8107	8057 x 8002	ITE
8087	8057 x 8001	ITE
8085	8057 x 8002	ITE
8083	8057 x 8002	ITE
8086	8057 x 8001	ITE
8081	8057 x 8002	ITE
8110	8057 x 8001	ITE
8084	5057 x 8002	ITE
8114	8057 x 8001	ITE
8099	8057 x 8001	ITE
8103	8057 x 8001	ITE
8102	8057 x 8001	ITE

to be actively growing if their length increased >2mm week^{-1}. Most seedlings had re-established dominant shoot within 8 - 9 weeks.

9.3 Results

9.3.1 Experiment 1

There were significant differences in the height growth of seedlings from the two half-sib seed lots (plate 11) with seedlot 535, the rainforest seedlings achieving greater height, this being 36 % more than those from seed lot 533 which originated from the drier savannah zone (Fig. 53a). Despite these differences in height there was no differences between them in the number of nodes or leaves produced (Fig. 53 b, c). In contrast numbers of branches and internode lengths did differ significantly, with progeny 533, the savannah seedlings, producing more branches while progeny 535, the rain forest seedlings, produced greater internode lengths (Fig. 43 d,e).

9.3.2 Experiment 2

Following decapitation these same seedlings showed considerable variation in bud activity. Those from the rain forest collection (535) having the least bud activity throughout the test period. Within these two populations also, the frequency distribution in the strength of apical dominance (% bud activity) was remarkably different, with the greatest number of seedlings having a bud activity between 90 + %, and 21 - 60 % in seedlots 533 and 535 respectively. The respective mean values for sprouting between these seedlots were 61 % and 40 % (Fig. 55, plate 12).

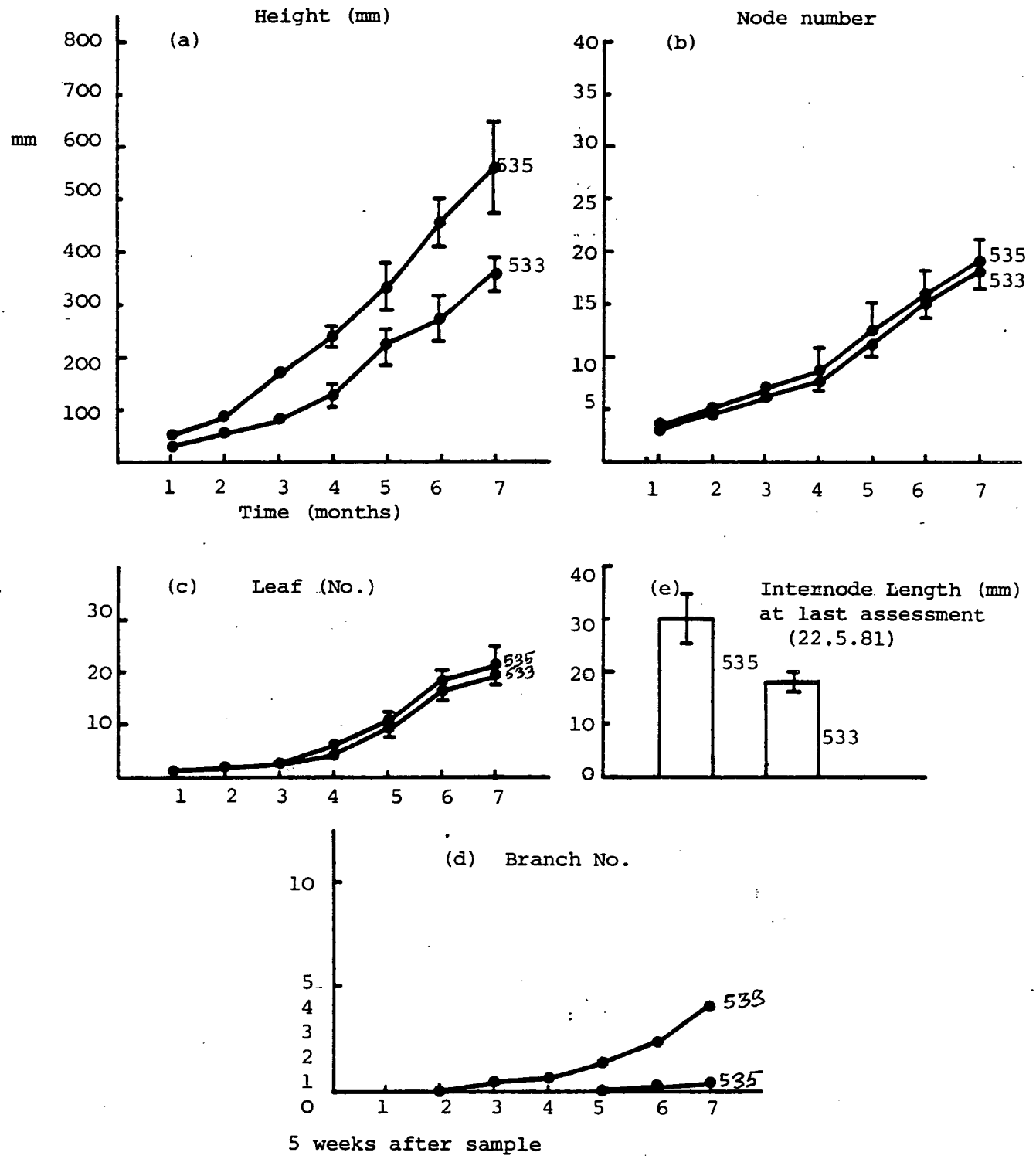
9.3.3 Experiment 3

Bud activity in the two full-sib batches of seedlings (Parents 8057 x 8001 and 8057 x 8002) both showed considerable variation between

Plate 11

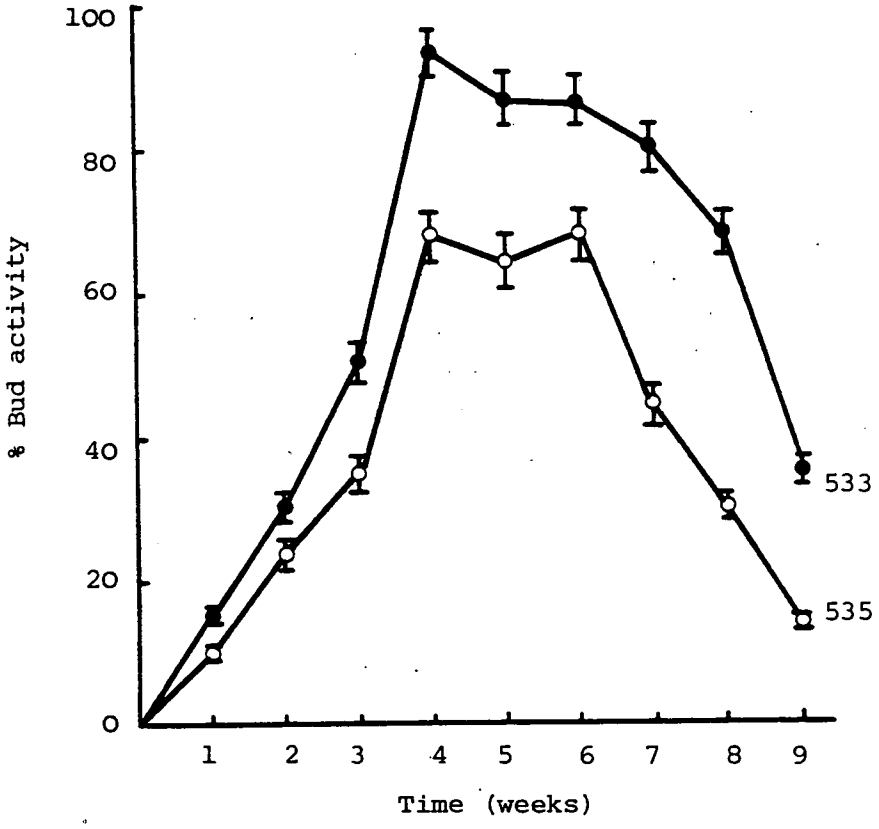
Showing representative plants from S535 (Elele) and S533 (Ayangba) on 22.5.81, 5 months after sowing.

Fig. 53



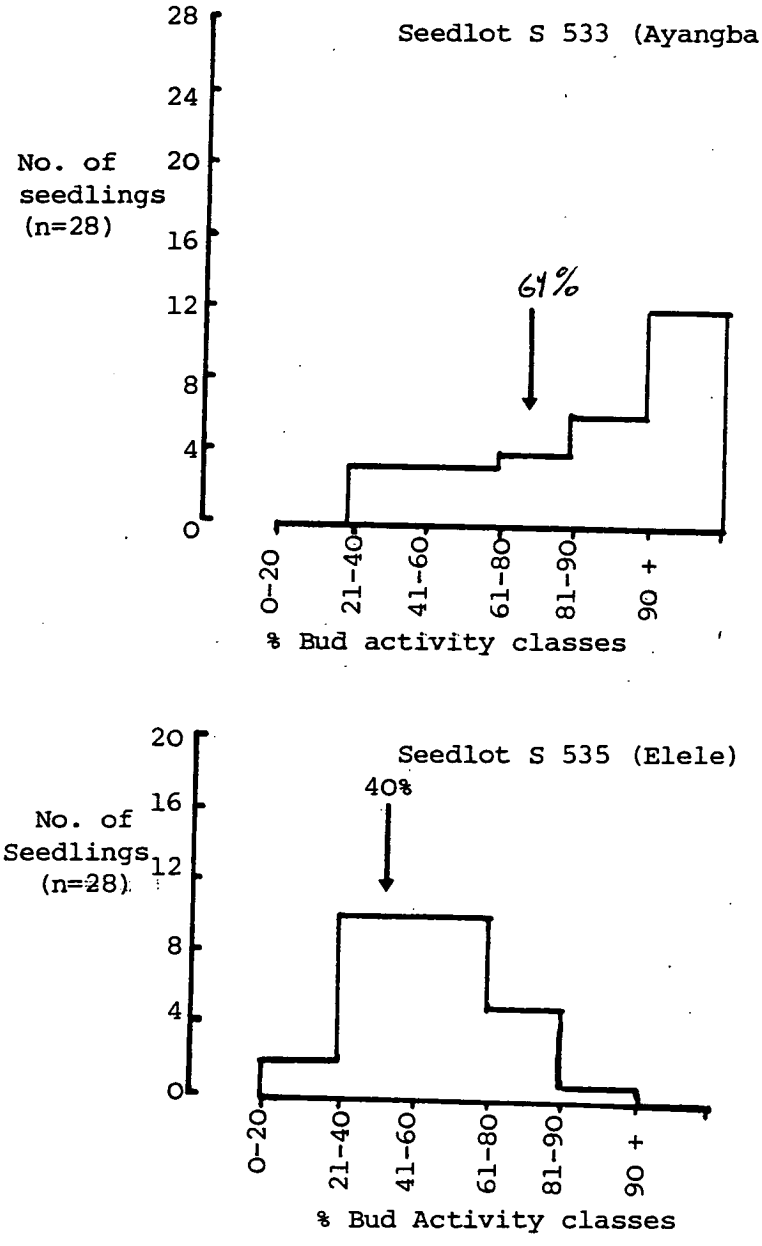
Variation in growth characteristics between populations of *T. scleroxylon* seedlings collected from the rain forest (535) and the savannah(533), (n = 15 per progeny, a = height (mm), b = node number, c = leaf number produced, d = branch number and e = internode length, vertical lines represent standard error (±) for each point).

Fig. 54



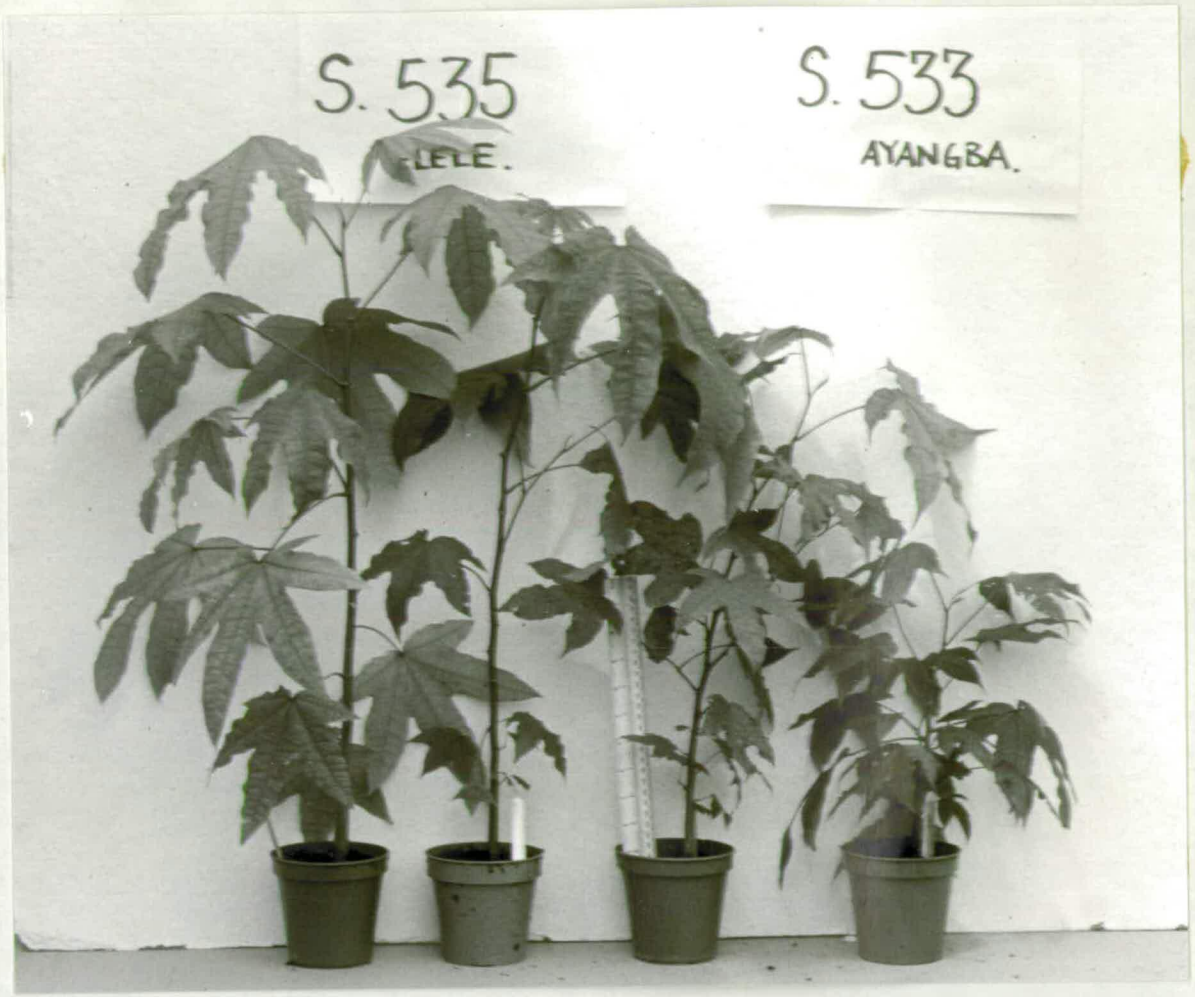
Variation in bud activity between two populations of *T. scleroxylon* seedlings collected from the savannah (533) and the rainforest (535).
(n = 28 plants per progeny, vertical lines are standard error (±) for each point on graph).

Fig. 55



Frequency distribution of *T. scleroxylon* seedlings with different strengths of apical dominance as indicated by lateral bud activity following decapitation - two seedlots treated S 533 (Savannah Collection) and S 535 (Rain forest collection). Arrows indicate mean % bud activity over 9 weeks.

Plate 12



Showing representative plants for S.535 (Elele - High forest) and S.533 (Ayangba - savannah) plants on final day of assessment after decapitation. (Note intensity of branchiness between the two lots).

Fig. 56

Variation in bud activity before and after decapitation at 4 months old in *T. scleroxylon* full-sib seedlings (clone 8057 x clone 8001) raised at ITE. Each line represents the activity of one individual seedling.

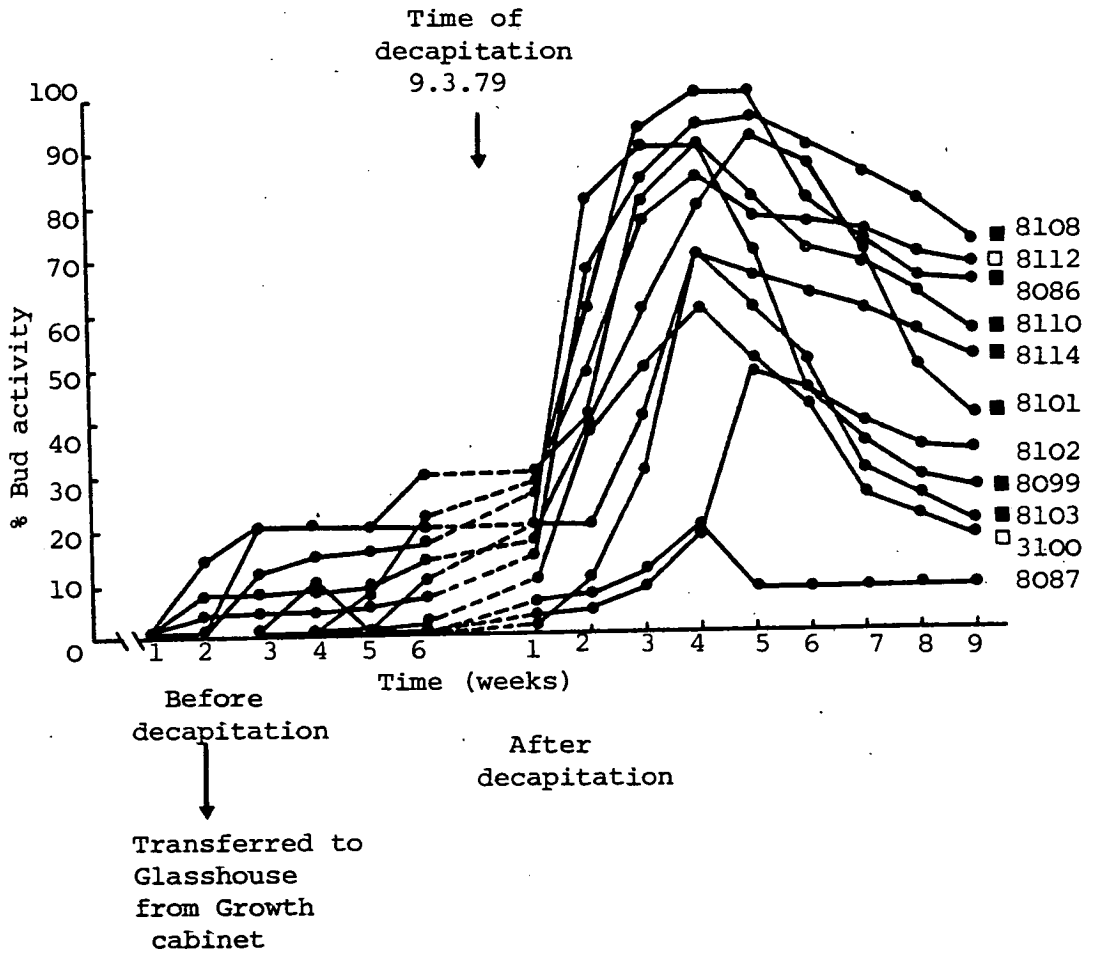
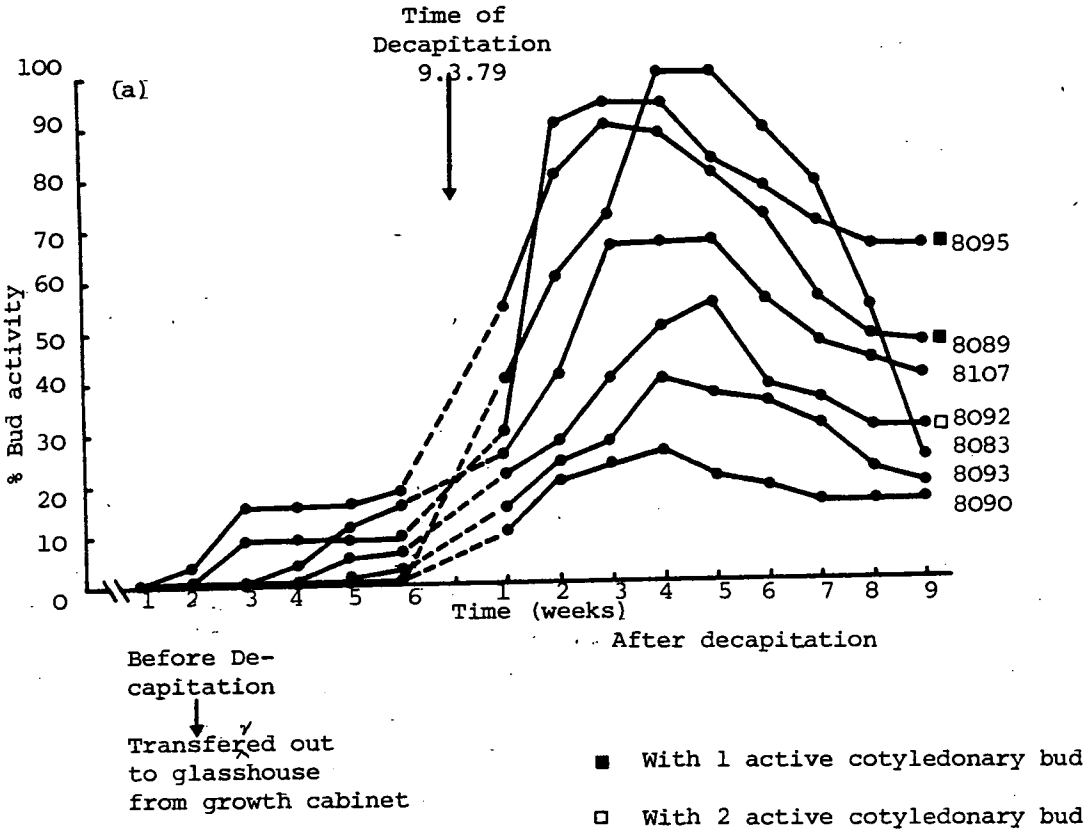
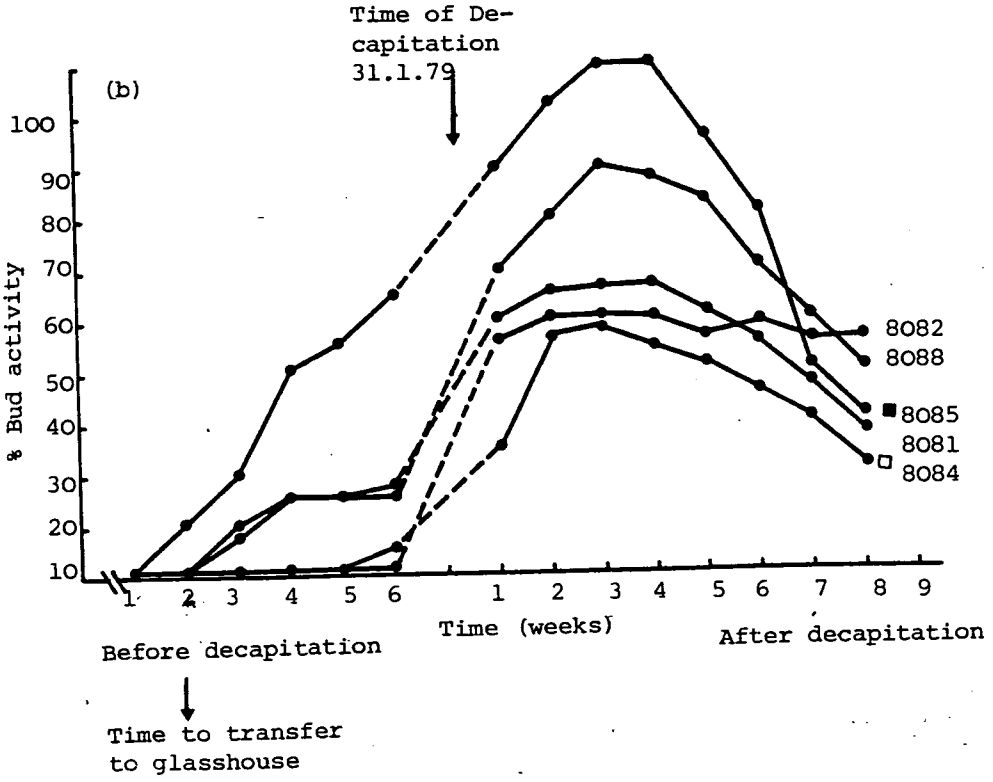


Fig. 57

Variation in bud activity before and after decapitation at 4 months old in *T. scleroxylon* full-sib seedlings (clone 8057 x clone 8002) raised at ITE (each line represents activity of one individual seedling).





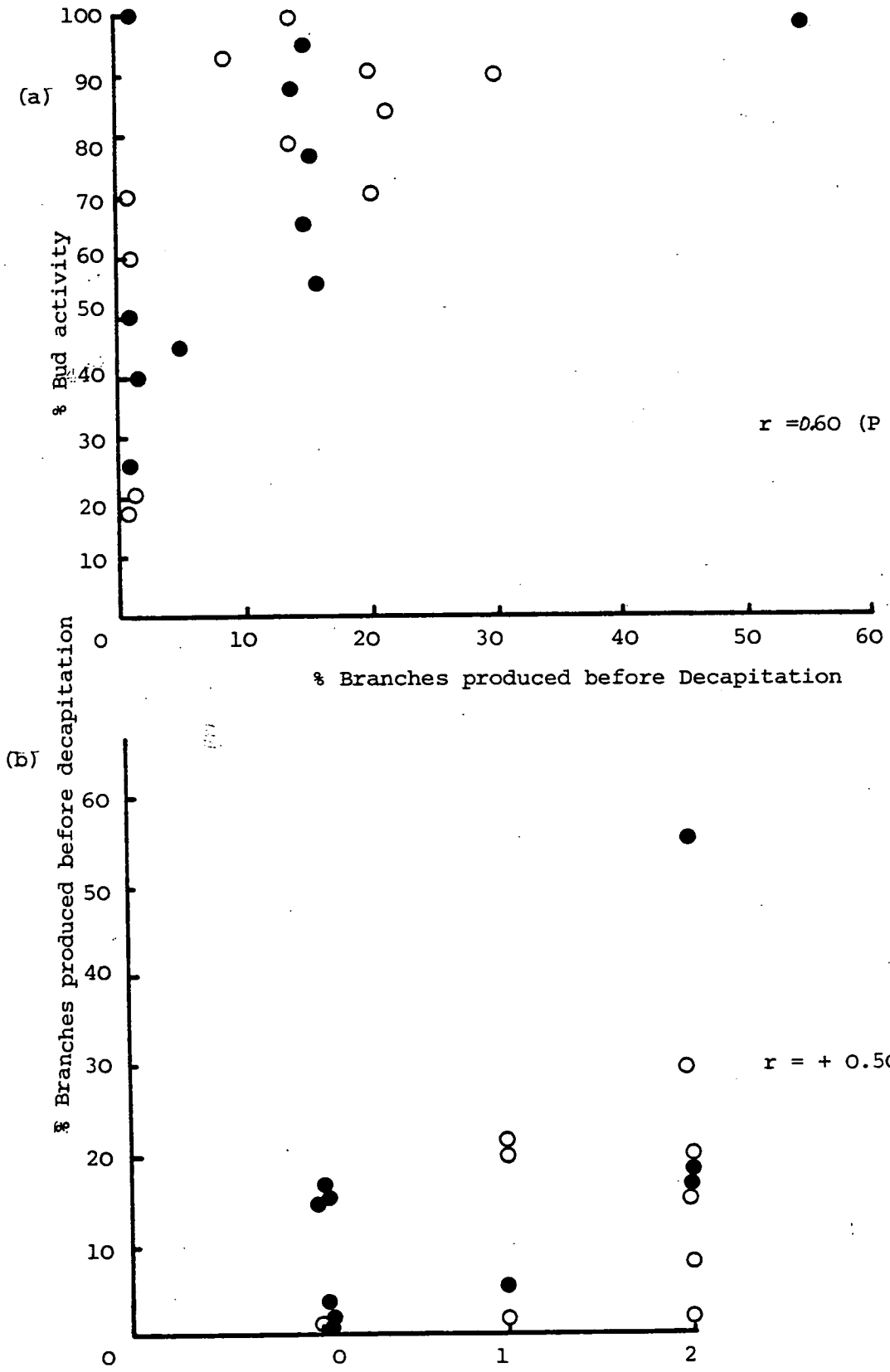
seedlings despite their identical parentage (Figs. 56 and 57 a,b) with, in many instances, some loss of apical dominance before decapitation. This resulted in branches arising from cotyledonary nodes (Fig. 53d), reported earlier as in the seedling population 533 (Savannah population). It is interesting to note a similar occurrence in the records of the pollen donor parents 8001 and 8002 which were randomly collected seedlings from Ilaro in Nigeria (see Table 23 a).

Finally, there were significant relationships between the various parameters investigated among the full-sib seedlings. Here, bud activity 4 weeks after decapitation was closely related to the production of branches before decapitation ($r = + 0.60$, $P = 0.01$). The occurrence of active cotyledonary buds was also strongly related to bud activity at 4 weeks ($r = + 0.64$, $P = 0.01$) but less significantly to the production of branches before decapitation ($r = + 0.50$, $P = 0.02$); (Figs 58 a and b and Fig. 59 , respectively).

9.4 DISCUSSION

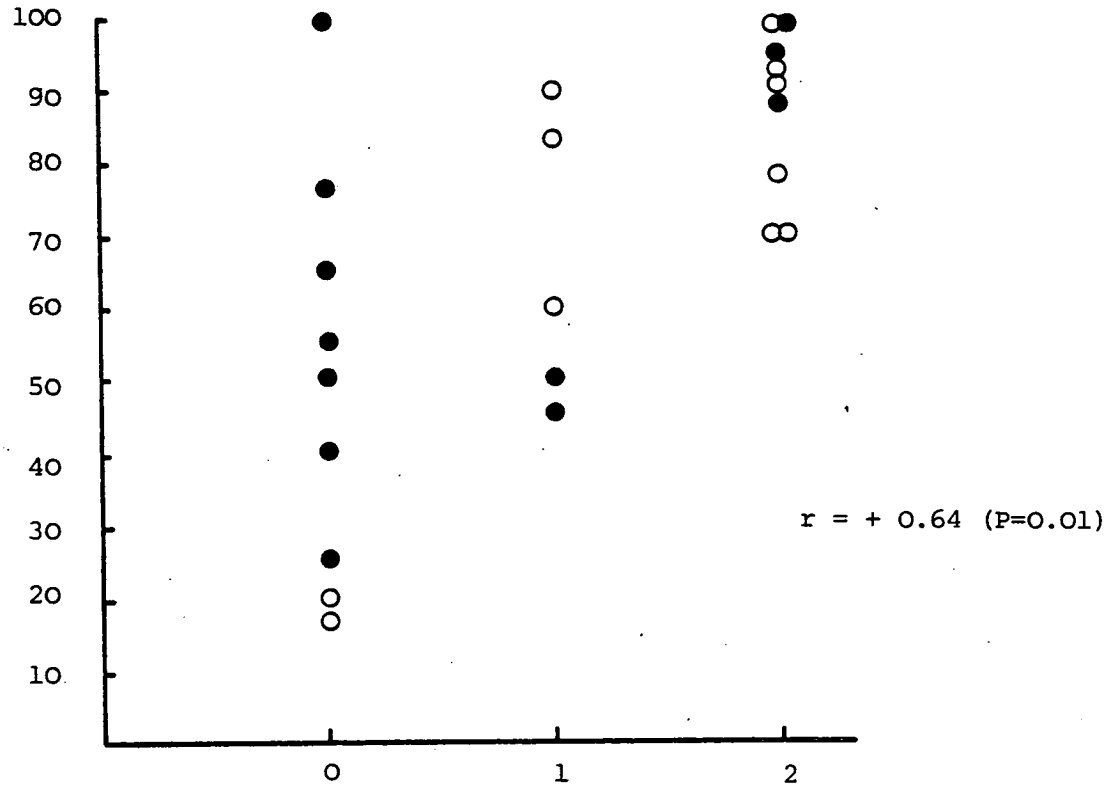
Okali (1971) reported that leaf production and duration were important factors in differences in growth of the seedlings of some tropical trees. The present study, on provenance variation in one species, shows that differences in leaf production are small. Thus the main differences were not caused by differences in leaf production; but internode elongation and occurrence of branching. Further, differences in photosynthetic rates may also be important. It is possible that the differences in internode length may be attributable to differences in endogenous gibberellin (GA_3) contents, for GA_3 is generally recognized as being important in the control of extension growth (Fulford *et al* 1968). However, measurements of Gibberellin

Fig. 58



The relationships between (a) bud activity at 4 weeks and branches produced before decapitation (b) percentage branches produced before decapitation and number of cotyledonary branches present before decapitation.
(n = 23, 8057 x 8001 = 11 seedlings and, X 8002 = 12 seedlings. CBO = Cotyledonary bud outgrowth).

Fig. 59



The relationship between Cotyledonary bud outgrowth and bud outgrowth 4 weeks after decapitation.
(Full-sibs of *T. scleroxylon* seedlings raised at ITE Edinburgh, parents, o = 8057 x 8001, ● = 8057 x 8002, CBO = Cotyledonary bud outgrowth).

content unfortunately have not been made in the present study. Alternatively perhaps the greater branching of 533 seedlings reduced their limited reserves at this early stage of growth.

As regards branching between the half-sib seedlings, the branchy seedlings of 533 which also had higher overall level of bud activity showed weak apical strength on the decapitation test. This supports the hypothesis that the tendency for the tree to be a heavy brancher, forked or a multistemmer may be detected by applying the decapitation test at an early stage. This also supports the hypothesis that response to decapitation is a measure of apical dominance, and it is interesting that the taller and more vigorous seedlot (535) seems to have a greater measure of correlative inhibition.

Although only one population from each provenance was examined, there is a strong ecological variation between these batches of seedlings, in that the more branchy individuals that are of short stature originate from the savannah while the less branch taller ones come from the rain forest. There appears to be wide ecological amplitude in *T. scleroxylon*, which can only be accertained by the study of more seedling collections all over the range of this important West African hardwood forest species.

The most important differences between these seedlots as far as the present study is concerned, however is the considerable variation in branching frequency, especially from the cotyledonary nodes. This implies that the genetic differences in apical dominance detected by the decapitation test, may in fact be discernable at an even earlier age. Such differences may perhaps have developed in response to selection pressures peculiar to their sites of origin, but care should be taken not to over-emphasise such findings for the dangers of juvenile-mature correlations are well known (Sziklai 1974). These findings do,

however, warrant further investigation.

In the case of the full-sib seedlings, it is important to consider the characteristics of the parents. As mentioned earlier, clone 8001 and 8002 showed cotyledonary node activity when previously studied in 1974, while the adult 8057 was earlier selected as a plus tree because of its good form and favourable branching habit. The occurrence of cotyledonary bud activity and branching in the seedling offsprings of both crosses (8057 x 8001 and 8057 x 8002) before and after decapitation, further indicates that early cotyledonary bud activity is under genetic control and probably a dominant trait, which thus needs to be discriminated against in early selection. The substantial relationships between the presence of cotyledonary bud activity before decapitation, with branching before decapitation, and bud activity after decapitation suggest an underlying link between these characteristics. It is not known at present whether this link is of a genetic nature or whether all three parameters are controlled by apical strength in some way. After decapitation, the substantial variation between individual seedlings in these controlled full-sibs in dominance reassertion supports the conclusions of Leakey and Longman (1976) that a wide range of variation exists within *T. scleroxylon* which can be utilized by vegetative propagation and suggests that recombination of genes controlling this characteristic occurs during meiosis.

From a practical point of view, as better flower induction methods are developed and more viable seeds are produced (Leakey *et al* 1981), the possibility of procuring sufficient for reforestation programmes cannot be ruled out. In this case, a modest selection in seedlings to favour seedlings without cotyledonary bud activity may also be an indirect way of establishing better seedling plantations with stock of desirable branching characteristics.

CHAPTER 10

PROGENY-CLONE X SITE INTERACTION IN *T. scleroxylon*

10.1 Introduction

The genotype of an individual can be assessed only from its phenotype or that of its parents or relatives, under uniform site conditions.

When grown in two or more environments, relative performance at the sites may differ (Squillace 1970). This variation is known as Genotype X Environment (G.E.) interactions and changes in gene expression, as a result of GE are known by plant breeders to be important sources of phenotypic variation within plant species. Screening of plant performance in several environments is clearly desirable, as some genotypes may express themselves in useful ways in a broad range of environments, whilst others may have more limited use. Identification of those genotypes which give rise to a useful phenotype is clearly of great practical value in clonal forestry, as such genotypes might form the 'back-bone' of a clonal mixture over a wide geographical zone whilst other, less wide-ranging, forms could be added according to the location.

Compared to annual crops, (Finlay and Wilkinson 1963) few reports are known on GE interaction in forest trees (Shelbourne 1972). No published records are known on *T. scleroxylon*, but in another tropical tree, *Gmelina arborea* Ojeniyi and Agbede (1980) reported substantial effects of edaphic conditions (soil organic matter and nitrogen) on diameter growth at 3 sites in Nigeria. In some temperate conifers, King, (1965), Squillace, (1969), Shelbourne,

(1972), Johnson and Samuel (1978), and Burdon (1980) have agreed that ignoring GE can seriously reduce genetic gains, or the effectiveness of tree improvement efforts.

In a temperate broad leaf genus (*Populus* spp.), conflicting results are known. In first year growth and wood characteristics at 2 sites Farmer and Wilcox (1968) did not find significant clone-site interaction. Randall and Mohn (1969) on the other hand, found substantial GE interaction for height and diameter at ages 1 to 4 on the same sites. Mohn and Randall (1973) found significant GE interaction in height, diameter, and number of 1st year branches at 6 sites in Mississippi. They indicated that site soil differences were responsible for this.

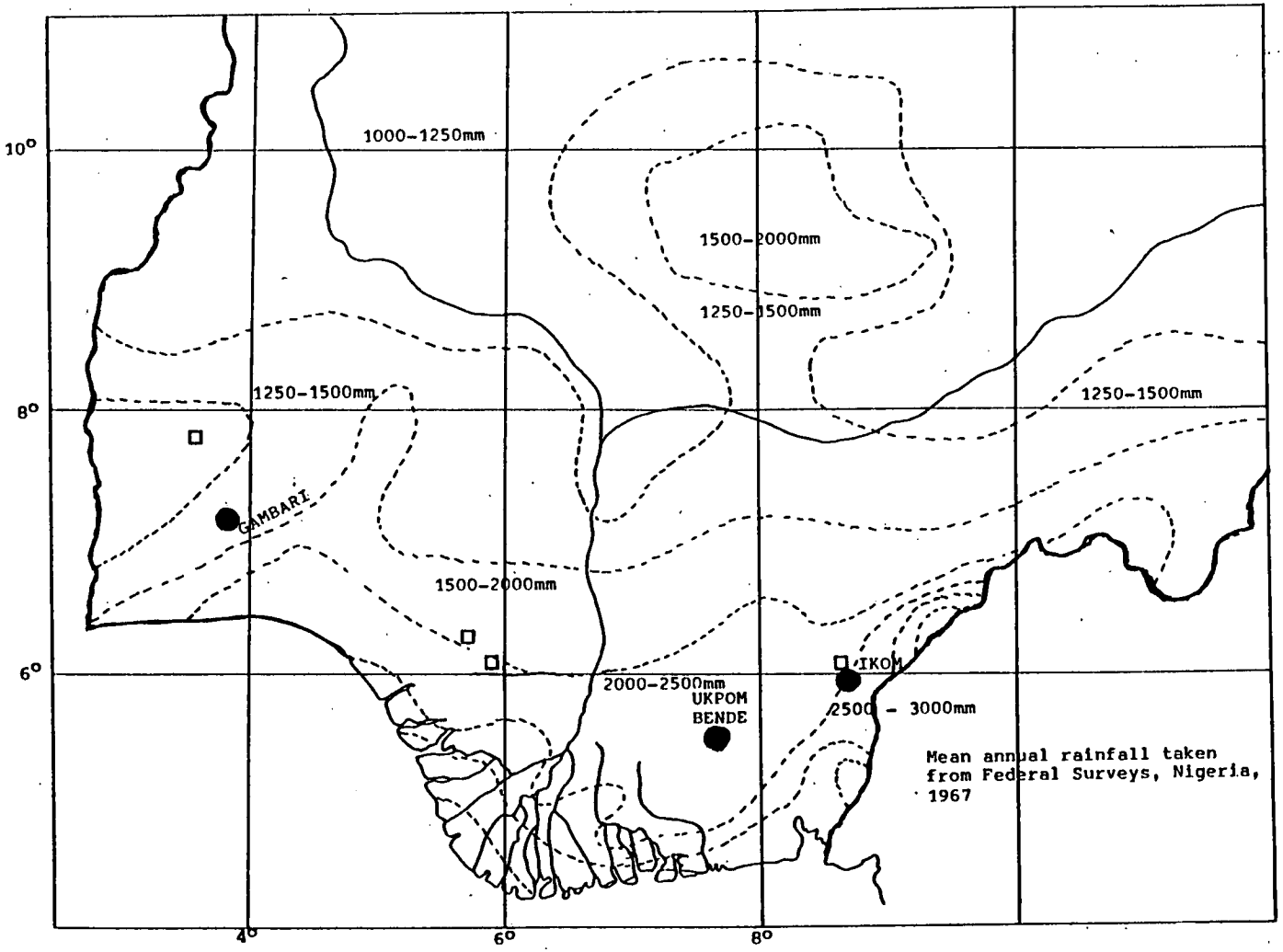
The present study investigates the responses of clones from 4 half-sib progenies (families) at 3 sites in Nigeria. The implication of the results are considered in relation to improvement of this important tropical hardwood species by selection.

10.2 Materials and Methods

T. scleroxylon progenies used in this work included Nos. 231, 259, 266, and 274, in the experimental planting 4/77 of the West African Hardwood Improvement Project in Nigeria. Each progeny was represented by between 10 to 12 clones, whose origins are presented on Table 24 and Fig. 60a.

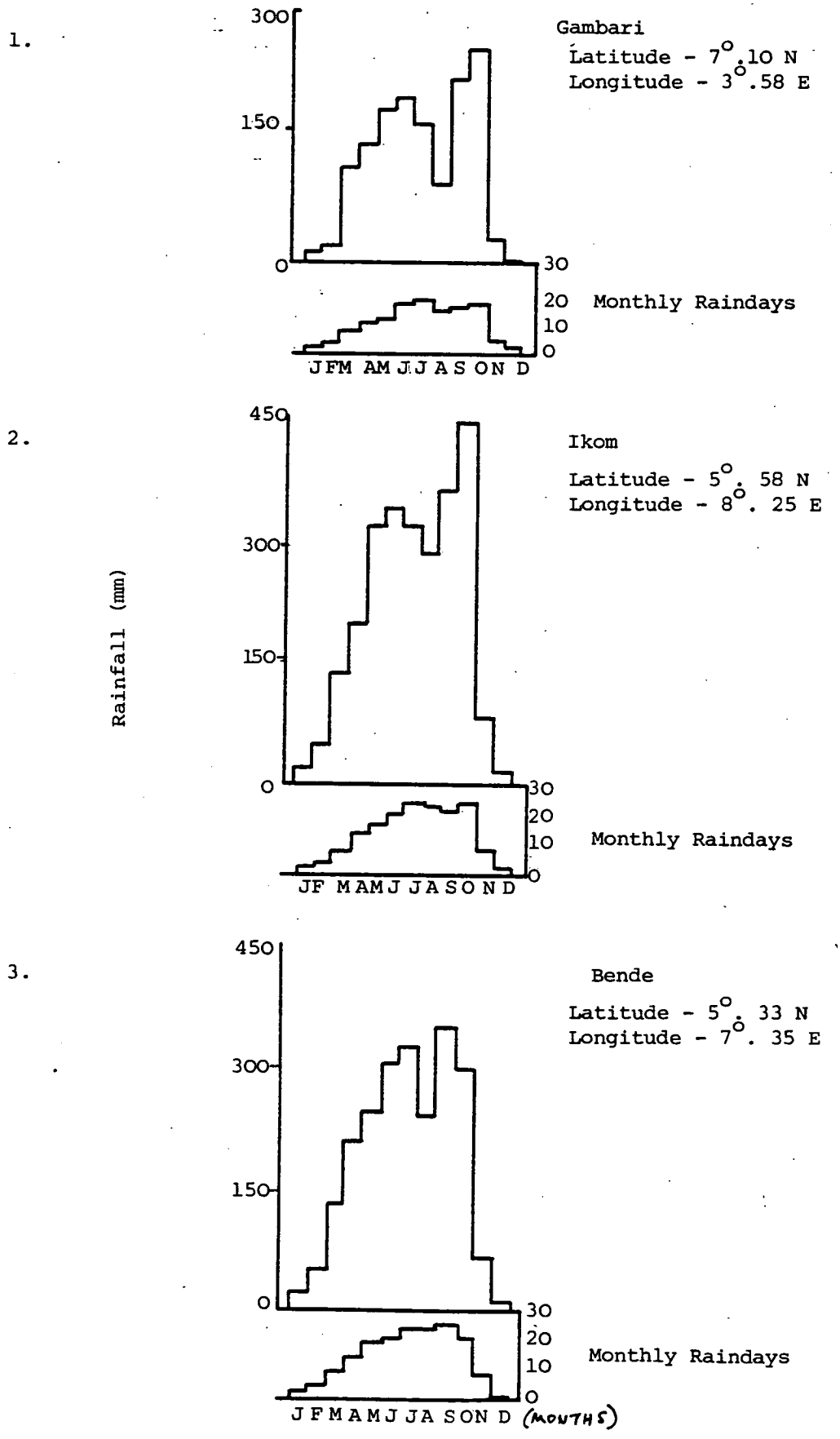
Details of culture, treatment and site preparation are as recorded for other field experiments reported in Chapters 6 and 7 of this thesis.

Fig. 60a



Showing the origins of half-sib progenies (□), and test sites (●), within the natural range of *T. scleroxylon* in Nigeria. (Expt. 4/77).

Fig. 60 b



Showing differences in rainfall distribution between the 3 test sites in Nigeria.

Table 24: Showing the location of progenies used in Progeny-clone site evaluation.

Source No.	Location	Latitude	Longitude
231	Ilugun	7^{o}. 24 N	3^{o}.49 E
259	Ikom	5^{o}. 57	8^{o}.37
266	Obille	5^{o}. 18	6^{o}.55
274	Sapoba	6^{o}. 04	5^{o}.51

Planting site, soil characteristic, and their locations are indicated on Table 25 with the rainfall range and distribution for each test site shown on Figs. 60a and b.

Table 25:

Test Site	Altitude	Rainfall, yr^{-1}	Soil	Forest Type
Gambari	190 m	Over 1500 mm	Yellow-red to brown loam	Moist semi-deciduous forest
Ikom	119 m	Over 2500 mm	Red clay loam	"
Bende	122 m	Over 2100 mm	Reddish loam to light-clay	"

Plants were planted out between June and July 1977 in a randomised block design. Each progeny was replicated 5 times at each site, with 36 plants (3 ramets per clone) within each plot. Espacement was 2.5 m (narrow spacing) and each trial at the 3

sites was surrounded by 2 rows of similar plants to minimise edge effects.

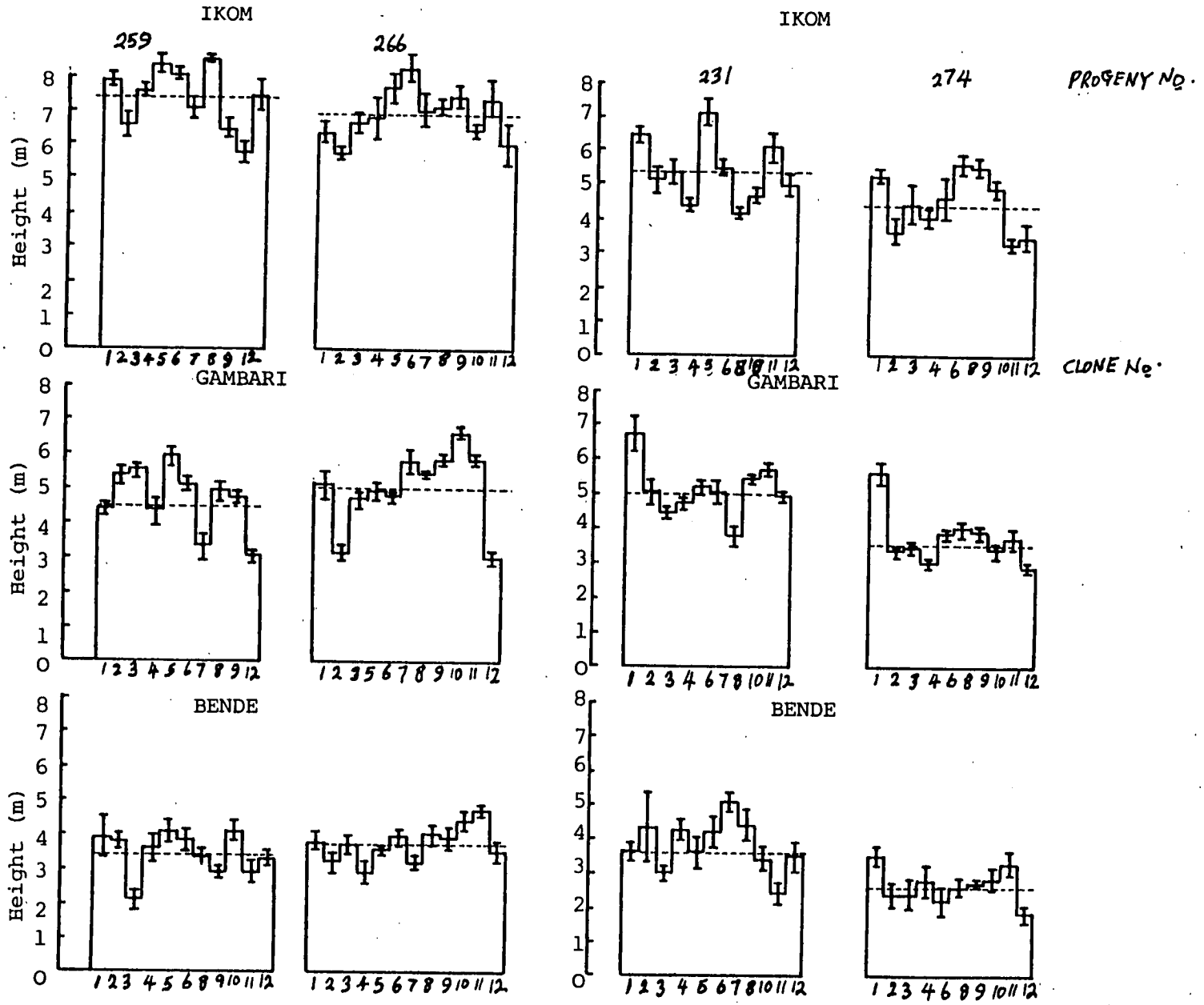
10.2.1 Assessment and Data analysis

Assessment of height, diameter, number of main stems and branching was done for each of these trials between June and August 1980, after 3 growing seasons. Data were processed with a computer program (LADON), which provided summary statistics. Following advice of Shelbourne (1972) analysis of variance was not attempted as the number of sites and sources was small, and quantitative estimates of the interaction components would have been imprecise. Mean values for each progeny and their individual clones, with their respective standard errors are presented. To assess the stability or consistency of each clone over the test-sites, diagramatic representation is presented of clonal performances in height and branching based on clonal ranking.

10.3 Results

Progenies were significantly different from each other in height, with 259 and 266 being generally taller than 231 and 274 (Table 25a). Height at Ikom was nearly double that at Bende and 25 % more than at Gambari. Significant differences were also found between the individual clones of each progeny and likewise between sites (Fig. 61). Diameter increment was also significantly different between the progenies, the least diameter being made by progeny 274 (56.6 cm). Greatest diameter was recorded by progenies at Ikom (Table 25b). Relative diameter growth at the 3 sites was very similar to that of height growth (Table 25b).

Fig. 61



Effect of site on height growth of clones from 4 half-sib progenies in Nigeria after 3 years growth (vertical lines are standard errors for each clone.

Table 25a: Variation in Progeny site interaction in height (m) after 3 years at Gambari, Ikom and Bende in Nigeria. ± refers to standard error.

Site	Progeny 259	266	231	274	Site Mean
Gambari	4.5 ±0.25	4.9 ±0.34	5.0 ±0.25	3.7 ±0.24	4.5 ±0.30
Ikom	7.3 ±0.29	6.8 ±0.21	5.4 ±0.29	4.7 ±0.27	6.05 ±0.60
Bende	3.4 ±0.19	3.7 ±0.15	3.8 ±0.23	2.6 ±0.16	3.3 ±0.27
Progeny mean for all sites	5.06 ±1.16	5.13 ±0.90	4.7 ±0.48	3.6 ±0.61	

Table 25b: Variation in progeny-site interaction in Diameter (cm) increment after 3 years at Gambari, Ikom and Bende in Nigeria. ± refers to standard error.

Site	Progeny 259	266	231	274	Site Mean
Gambari	69.3 ± 3.5	73.7 ± 3.6	71.4 ± 2.6	54.0 ± 5.7	67.1 ± 4.5
Ikom	125.9 ± 7.2	126.0 ± 5.0	89.2 ± 6.7	79.4 ± 4.8	105.1 ±12.2
Bende	56.8 ± 2.9	61.1 ± 2.95	60.3 ± 4.1	36.4 ± 2.9	53.7 ± 5.8
Progeny mean for all sites	84.0 ±21.3	86.9 ±19.9	73.6 ± 8.4	56.6 ±12.5	

There was marked significant differences within progenies, both in diameter and height (Figs. 62 and 63).

In the number of stems produced, only slightly significant differences were found between sites and between progenies (Table 25c).

Table 25c: Variation in Progeny/site iteraction at 3 sites in mean stem number after 3 years at Gambari, Ikom and Bende in Nigeria. ± refers to standard error.

Site	Progeny 259	266	231	274	Site Mean
Gambari	1.01 ±0.01	1.02 ±0.01	1.2 ±0.07	1.02 ±0.01	1.06 ±0.05
Ikom	1.2 ±0.13	1.43 ±0.10	1.5 ±0.11	1.2 ±0.06	1.3 ±0.08
Bende	1.27 ±0.06	1.46 ±0.09	1.46 ±0.08	1.3 ±0.06	1.37 ±0.05
Progeny mean for all sites	1.16 ±0.08	1.30 ±0.14	1.39 ±0.09	1.17 ±0.08	

The mean number of branches produced over 3 years, was significantly different between progenies, with progeny 274 producing the least branches (17.4). As in the number of stems, only marginal significance was apparent between test sites (Table 25d) while individual clones within each progeny produced significantly different amount of branches from each other in many cases (Fig.64).

A diagramatic representation of ranking, in the parameters height and branching enabled a visual evaluation of clonal consistency at test sites (Figs. 65 and 66). The ranking of clones in each progeny and site revealed a substantial variation in clone

Fig. 62

Diameter - showing effect on site on variation between progenies and clones in diameter increment after 3 years growth in field at Gambari, Ikom and Bende in Nigeria.

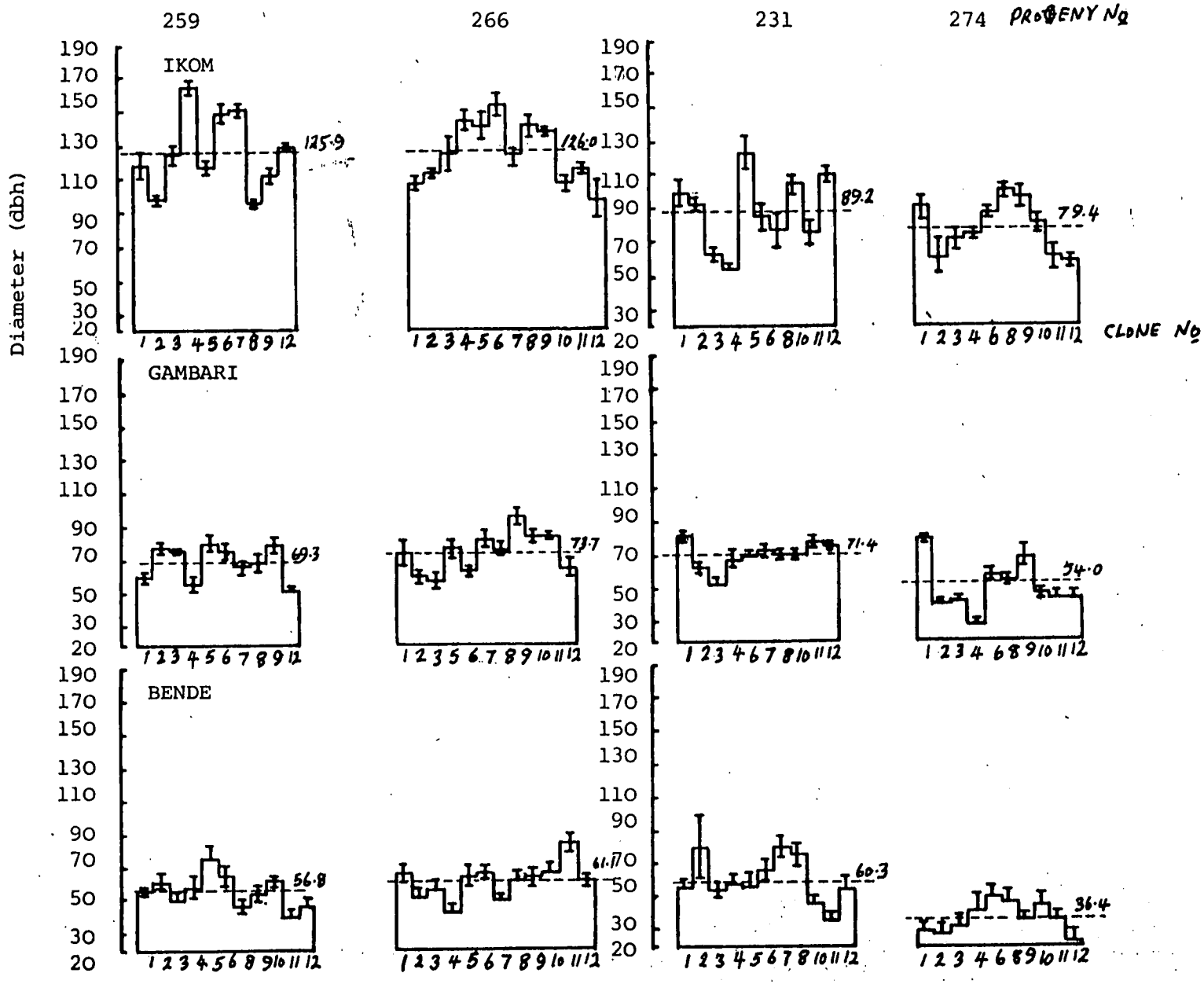
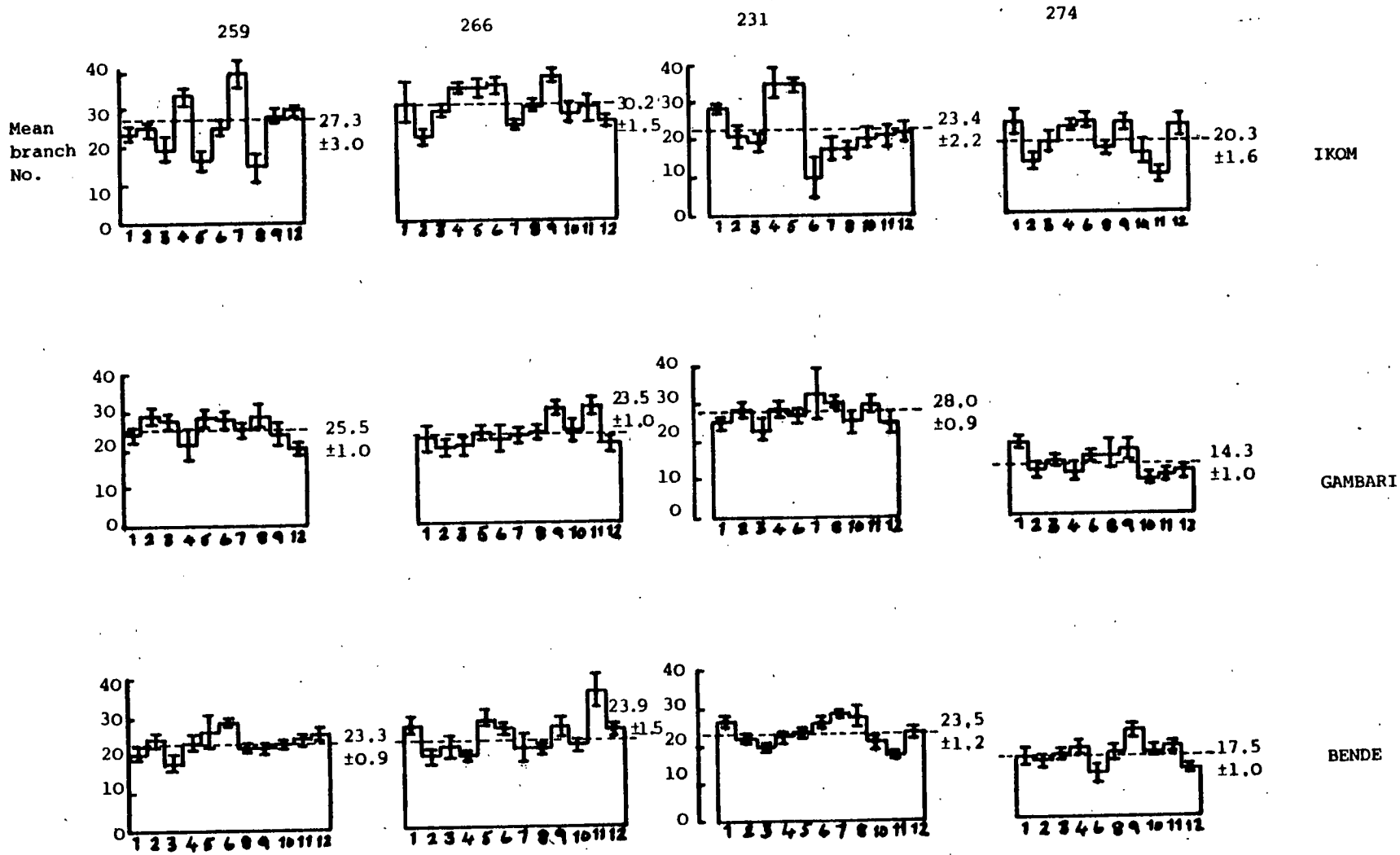


Fig. 63



Showing effect of site on variation between progenies and clones in mean number of branches produced after 3 years growth in the field at Gambari, Ikom and Bende in Nigeria.

Fig. 64

Effect of site on multiple stemming in 4 progenies of *T. scleroxylon* after 3 years growth in the field (Expt. 4/77).

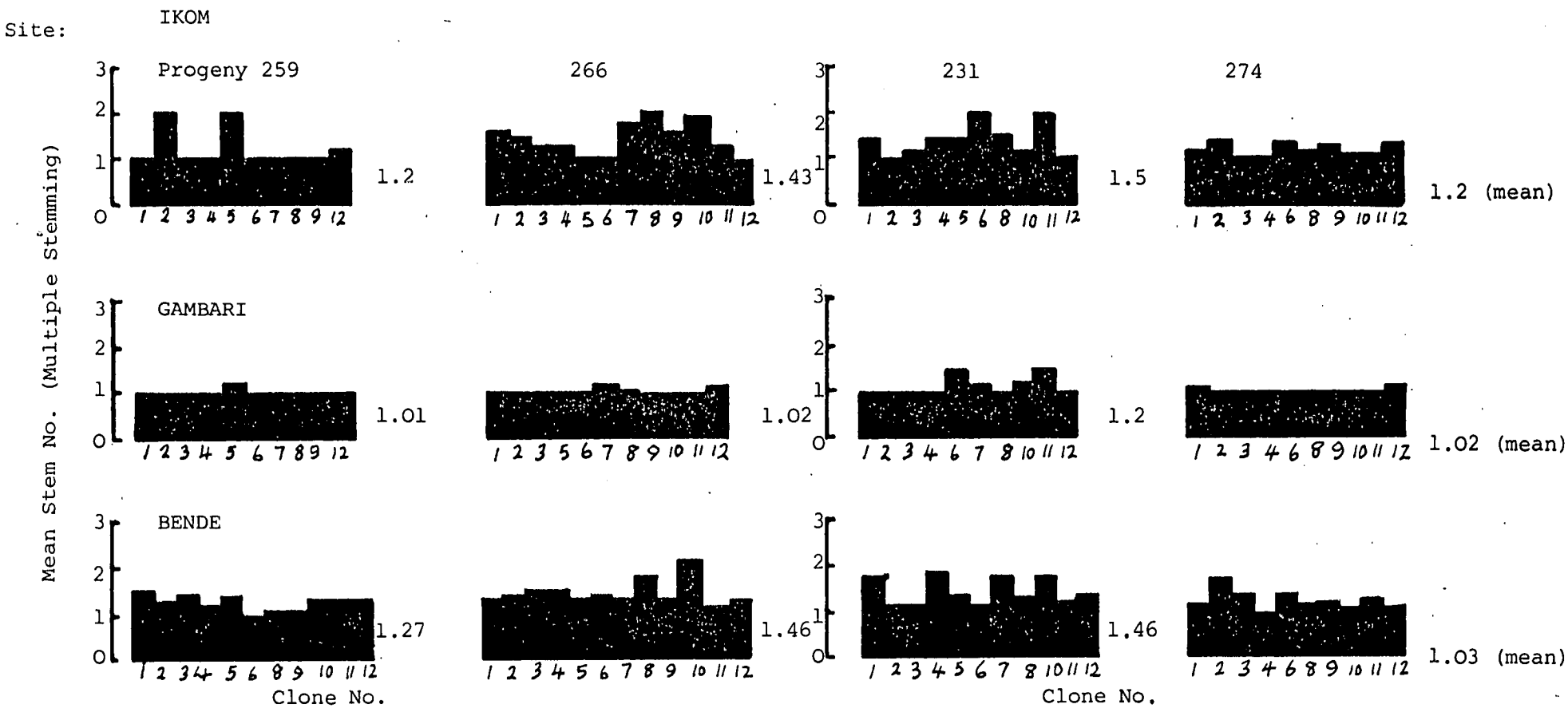
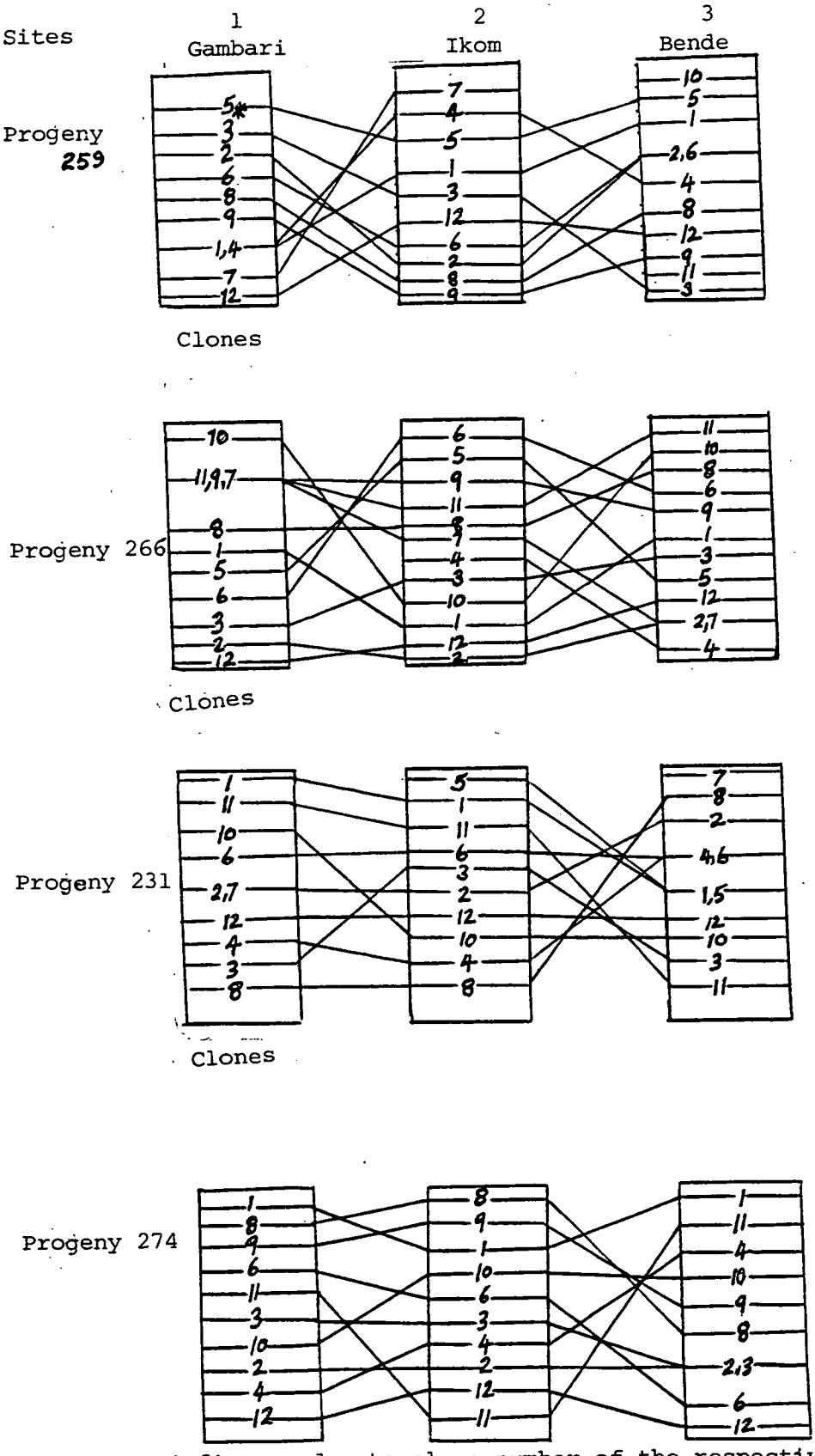


Fig. 65

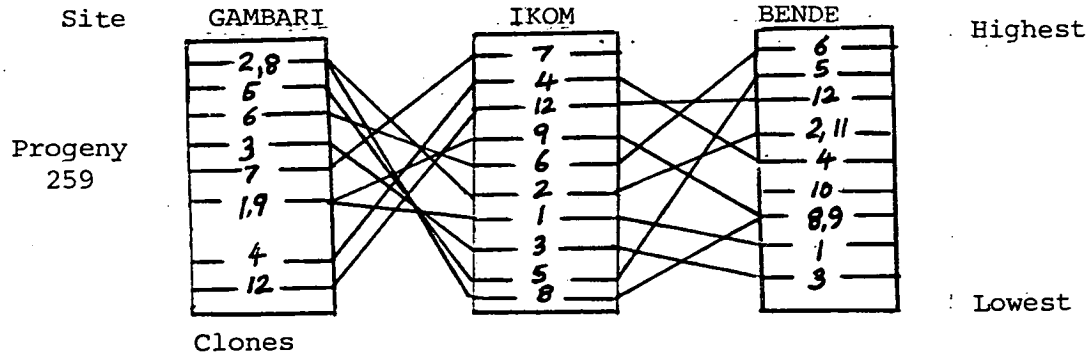
Effects of environment on ranking order in height, 3 years after growth in plantation at (1) Gambari, (2) Ikom, and (3) Bende, between clones from 4 half sib-sources in Nigeria.

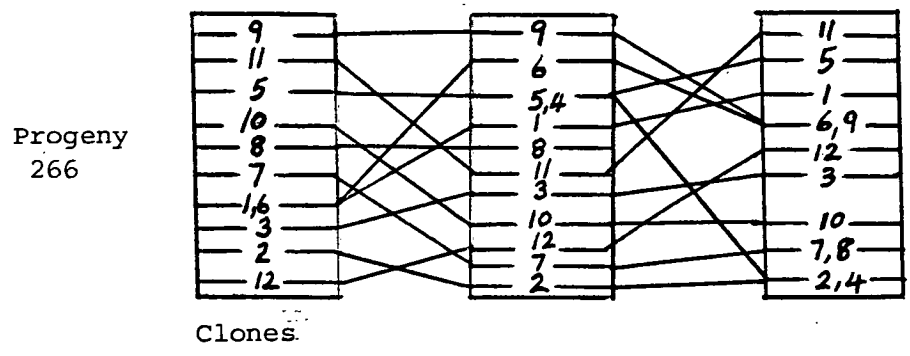


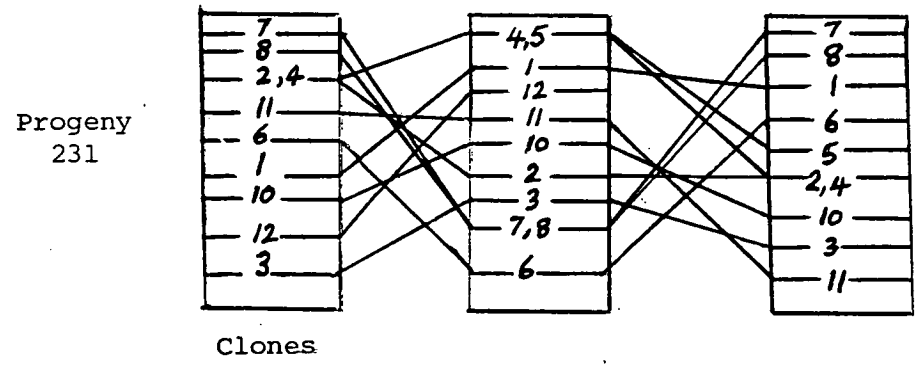
* figures denote clone number of the respective progenies e.g.259/5

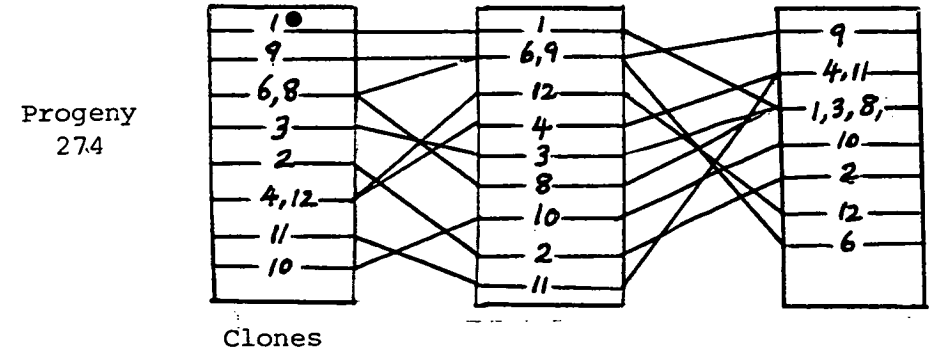
Fig. 66

Diagramatic representation of the effect of environment on ranking order in branching habit between *T. scleroxylon* clones from 4 half-sib sources after 3 years growth at Gambari, Ikom and Bende in Nigeria.









● figures denote clone number in the respective progenies, e.g. 274/1

performances in height and branching. The results reveal that about two thirds of the total number of clones in all progenies were roughly consistent in their ranking over 2 or 3 sites for height increment, while in the case of branching a rather larger fraction of the total clones from all progenies were consistent in their ranking over 2 or 3 sites. (Figs. 65 and 66).

Table 25d: Variation in progeny site interaction at 3 sites in Mean number of branches produced after 3 years at Gambari, Nigeria. ± refers to standard error.

Site	Progeny 259	266	231	274	Site mean
Gambari	25.5 ± 1.0	23.5 ± 1.0	28.0 ± 0.9	14.3 ± 1.0	22.8 ± 3.0
Ikom	27.3 ± 3.0	30.2 ± 1.5	23.4 ± 2.2	20.3 ± 1.6	25.3 ± 2.2
Bende	23.3 ± 0.9	23.9 ± 1.5	23.5 ± 1.2	17.5 ± 1.0	22.0 ± 1.5
Progeny mean for all sites	25.4 ± 1.2	25.9 ± 2.2	25.0 ± 1.5	17.4 ± 1.7	

10.4 DISCUSSION

Studies of the interaction between genotype and site form a basis for species siting in tree plantation establishment. Such studies provide the knowledge of relative progeny or clone productivity or form at each site, which the silviculturist may subsequently utilise, or which may help the breeder to re-

orientate his efforts towards developing the desired genotypes.

The consistently lower performances of progeny 274 at all sites in all the parameters examined emphasises the importance of careful choice of seed sources. It agrees with the findings of King (1965) who worked with Scots pine. He reported significant differences in height growth of progenies from 8 sources and associated consistently poor growth at all test-sites with particular sources. In a trial of *Gmelina arborea* at different sites within Nigeria, Ojeniyi and Agbede (1980) reported that Sapoba was the poorest in terms of soil organic matter and produced the least diameter growth. Onweluzo *et al* (1976) also drew attention to the sandy nature of these soils. As progeny 274 originated from this site, its poor performance in the present study may indicate a long history of adaptation to nutrient-deficient soils during which period slow growth rate may have been favoured by natural selection.

The substantial variation reported in progeny and clone performances at the 3 present test sites is similar to that reported by Farmer (1970), and Randall and Mohn (1969 and 1973) in *Populus deltoides*. Randall and Mohn (1969) found substantial clone X site interaction for height and diameter at ages 1 to 4 years among 79 clones grown on two sites in the same locality. Contrary to this, however, Farmer and Wilcox (1968) did not find statistically significant clone X site interaction for first year growth and wood characteristics between 100 clones on two sites in Mississippi.

In considering the causal factor in the variation in progeny and clone performances in the present study, it is most likely

that rather than wholly the differences in rainfall or its duration, soil fertility, or the organic matter content at these sites was principally responsible, as in the similar studies on *Pinus radiata* by Fielding and Brown (1961) and Burdon (1972). Further work is required to confirm this point. Differential responses to mineral nutrition are probably responsible for some of the more substantial changes in clone ranking at the different test sites in the present study. In the conclusion of a recent review by Shelbourne (1972), he reported that good evidence now exists, in crop plants, that stability in performance over a range of sites is a heritable character. He infered that selection for this, in forest trees on the basis of progeny tests in different environments should be effective. In this case, the ability of some clones to perform consistently at 2 or 3 sites rather than at only one, can be attributed to their genetic stability (*Sensu* Finlay and Wilkinson 1963) or ability to grow under changing conditions. Finlay and Wilkinson (1963) in their observations in barley varieties classified such genotypes as generally adaptable.

On the question of whether to select genotypes suitable for specific or a wide range of environments, Squillance (1969) advocated selection for specific sites, which he said could offset additional cost of breeding broadly adapted genotypes. In the case of *T. scleroxylon*, where immediate establishment of plantations are desired to alleviate the strain of exploitation on the natural stock, broadly adapted genotypes or clones, which can be identified by trials throughout the natural range, will be more useful and so

efforts towards this goal are required. Moreover, as environmental conditions tend to change from year to year, perhaps as a result of deforestation, emphasis on site-specific genotypes seems misplaced.

As regards the use of the decapitation test already reported in Chapter 8, it was unfortunate that there was insufficient juvenile stock to enable corresponding screening of the materials used in the present chapter. This aspect needs to be investigated in future.

CHAPTER 11

CLONAL VARIATION IN PHOTOSYNTHESIS, RESPIRATION, TRANSPIRATION AND RESISTANCE COMPONENTS TO CO_2 and H_2O VAPOUR TRANSFER IN *T. scleroxylon*.

11.1 Introduction

In a previous chapter, it was shown that response to decapitation has a practical potential as a predictive test for branching habit in *T. scleroxylon*.

While branching habit seems to be an important characteristic determing form and probably yield in this species (Ladipo *et al*, 1980), it is very likely that other attributes of certain clones could be highly desirable and that in the long term controlled tree breeding could combine these various attributes, thereby producing 'elite' clones.

One attribute worthy of consideration would be the rate of photosynthesis, particularly perhaps at low levels of light as this might be expected to be particularly useful in closely spaced plantations.

In this chapter, two basic questions are examined :-

(i) Are there differences between clones in their photosynthetic rates ?

(ii) If so, are these characteristics correlated with tree performance ?

To date, there are relatively few reported studies on the photosynthetic rates of tropical tree species; and even in temperate tree species, there have been relatively few demonstrations of clonal variations in their photosynthetic characteristics.

11.1.1 Assimilation in Tropical trees

The production of wood by forest trees depends on the photosynthetic capacity of each unit of leaf area; the total leaf area present; its display, duration, and physiological status; and the amount of assimilate expended in respiration (Okali 1977). The growth rate and the economic yield of trees is also decided by the proportion in which the assimilates are distributed to the various organs (Monsi and Murata 1969), particularly those relating to height and girth of the main stem.

One approach made with some W. African forest trees, *Terminalia ivorensis, Ceiba pentandra, Chlorophara excelsa* and *Theobroma cacao*, the latter being a tropical crop tree (Okali 1977), as by many earlier workers, has been to measure photosynthetic rates using the manometric technique. This requires that the leaf be subjected to quite unnatural conditions during the measurements, a procedure which is really only useful for comparative purposes (Wilson *et al* 1969). More realistic conditions can be obtained when attached leaves are exposed to light within stirred assimilation chambers, and an Infra-red gas analyser is used to measure the depletion of CO_2 from an accurately known flow of air containing normal concentrations of constituent gases (Jarvis & Cätsky 1971).

Extensive reviews by Larcher (1969) and Korner (1979) of photosynthesis and leaf conductances in trees include a few tropical species, such as : *Rhizophora mangle, Khaya senegalensis, Erythrophleum fordii, Combretodendron africanum,* and *Anthocephalus cadamba*, for which they reported maximum values of between 18 - 22 mg. CO_2 dm^{-2} h^{-1} (on leaf area basis).

Very few studies exist on community productivity (in situ) in

the tropical forests, and even fewer in forest plantations particularly of hardwood species. However Odum (1962) in Puerto Rico, estimated photosynthetic capacity for primary tropical rain forests, and reported rates of 6 mg CO_2 dm^{-2} h^{-1} for some dominant trees and 14 mg CO_2 dm^{-2} h^{-1} for pioneer species such as *Cercropia* spp. and between 2 - 5 mg CO_2 dm^{-2} h^{-1} for other constituent species. Other forests investigated include thos of Cambodia (Hozumi *et al*, 1965), Thailand (Ogawa *et al*, 1965), and more recently, the Pasoh forest of Malaya. In the latter, Koyama (1978) reported between 10 - 15 mg CO_2 dm^{-2} h^{-1} for the emergent layer species and 7.0 - 7.4 mg CO_2 dm^{-2} h^{-1} for the lower strata. These figures, which are considerably greater than those of Odum (1962) in Puerto Rico, suggest that community photosynthesis of S.E.Asian forests may be greater than that of Central Africa. This is further supported by measurements in *Shorea leprosula*, an emergent, which give a distinctively high value (24.4 mg CO_2 dm^{-2} h^{-1} = 0.068 µg Cm^{-2} s^{-1} = 0.68 mg m^{-2} s^{-1}), of all the 13 species evaluated (Koyama 1978). However, far more comparative studies are required before firm conclusions may be drawn.

It is clear however from the above review that rates of photosynthesis in tropical trees are not generally especially high. At least they equal those of herbaceous C_3 crops; though often, they are no greater than those of temperate species (see Larcher 1969 and Korner *et al*, 1979). Certainly they do not approach - on a leaf area basis - the high rates of 60 mg dm^{-2} h^{-1} which are characteristic of certain tropical graminaceous species (Korner *et al*, 1979).

11.1.2 Interspecific variation in photosynthetic characteristics

Studies of provenance differences in photosynthesis, respiration, transpiration and diffusion resistances, which began on herbaceous plants (Bjorkman & Holmgren 1963) have lately been extended to tree species (Ludlow & Jarvis 1971, Townsend *et al* 1972), and have included investigations of within-progeny variation (Ledig & Perry 1976). In temperate trees, interspecific variation is well known (Ferrell 1970, Hinkley *et al* 1978). Genetic variation in photosynthesis of food crops has also been established, (Moss & Musgrave 1971), but in this instance a consistant relationship between primary productivity and yield has not been found; this suggesting that productivity is a complex of numerous internal and external factors.

In coniferous species of the temperate zone, appreciable work has accumulated on clonal cuttings. These include in *Larix decidua* and *Larix leptolepis* (Polster & Weiser 1962), *Pinus taeda* (Ledig & Perry 1967), *Pinus sylvestris*, (Gordon & Gatherum 1968), *Pinus strobus* (Townsend *et al* 1972) and *Larix russica* (Ledig & Botkin 1974) where appreciable clonal variation has been reported. In temperate broad leaved species on the other hand, *Populus* has been extensively studied because of its potential for plantation culture, improvement, and the various uses of its wood and fibre (Cram 1960). Gordon & Promnitz (1976) reported over 30 % variation in photosynthesis between 4 clones of *Populus deltoides*, and Cuelemans *et al* (1980) observed substantial variations in maximum net CO_2 exchange rate in 8 clones of poplar hybrids, with associated variations in mesophyll and stomatal resistances and transpiration. They identified two clones which were full sibs and which were higher producing than the others. Typically

the other clones displayed rates of photosynthesis of only 0.17 mg m^{-2} s^{-1} whilst these two were 0.51 and 0.53 mg m^{-2} s^{-1}.

In the tropics, with the exception of *Pinus radiata*, only agricultural crop plants have been appreciably studied at a clonal level. These include *Camellia sinensis* (Barua 1970), *Hevea brasilhensis* (Samusiddin & Impens 1979) where significant differences were reported, in maximum photosynthetic rate and in most of its component processes, between 7 clones. Maximum photosynthetic values ranged from 0.40 to 0.67 mg CO_2 m^{-2} s^{-1} at light saturation. In *P. radiata* on the other hand, Bennett & Rook (1978) observed differences in photosynthetic rates between two clones of up to twofold. Earlier, Jackson *et al* (1972) working with 7 clones of the same species reported differences of up to 1.5-fold in transpiration rates between these clones. It was later found that the 'high transpiration' clone survived less well than the 'low transpiration' clones in the field after 7 years (Bennett & Rook 1978).

The present study, investigates photosynthetic characteristics in 6 clones of *T. scleroxylon*. Following Jarvis & Cätsky (1971) the rate of transpiration was measured simultaneously with photosynthesis, to enable analysis of the diffusion path of CO_2 into stomatal and mesophyll components.

11.2 Materials and Methods

11.2.1 Plant Material

For practical reasons only a small sample of all available clones could be investigated. Hence, 6 clones were chosen on the basis of contrast in branching and site of origin (see Table 26).

Table 26 :

Clone	Source (All Nigeria)	Rainfall
137/9	Olokemeji	1300 - 1500 mm
144/1	Igboora	1000 - 1300 mm
144/7	Igboora	1000 - 1300 mm
144/9	Igboora	1000 - 1300 mm
175/1	Igbado	1500 - 2000 mm
177/10	Iwgun	1300 - 1500 mm

Each clone was represented by 4 ramets, each about 60 cm tall, and raised as already described in Chapter 3. Ortets were transfered from the tropical glasshouse at ITE and grown under conditions described below, in a Growth Cabinet (Controlled Environments - Canada, Model E7), for 10 weeks before experimental assessments were made. All plants were supplied with 1 % nutrients (Solufeed) at weekly intervals, a treatment which had been continued since their propagation at ITE. Material was watered freely.

Because of the limited height in the Growth Cabinet, plants were decapitated by removing 2 top nodes, two weeks before measurements, and as a result of the limited space in the assimilation chamber, leaf tips were also trimmed two days before the experimental measurements were made. The first or second fully expanded leaf below the point of decapitation was used in all measurements.

11.2.2. Environment

Growth Cabinet environment was set to simulate as far as possible the peak growth period of *T. scleroxylon* in West Africa (June - July). Day and night temperatures were controlled at 30 ^{o}C ± 2^{o}C and 26 ^{o}C ± 2 ^{o}C respectively. Relative humidity set

at 80 - 95 % and illumination provided with 8 fluorescent (VHO F48T12) and 4 incandescent 60 watt bulbs, providing 400 μE cm^{-2} s^{-1} at 10 cms from lamps and a photoperiod of 13 hours.

11.2.3 Assessments

Plants were taken from the growth cabinet and the test leaf was placed in the assimilation chamber for measurement of CO_2 uptake and H_2O evolution.

The leaf temperature within this chamber (28 °C ± 2 °C) was kept constant using a thermostatically controlled bath and cooler, and sensed with a copper-constantan thermocouple (0.04 mm) stuck under the leaf with a small sellotape patch. Output was amplified and displayed on a digital meter constructed by M. Dixon of the Department of Forestry and Natural Resources, University of Edinburgh.

The rates of CO_2 and H_2O exchange were determined simultaneously at a range of 6 light intensities from dark to 1153 μE* m^{-2} s^{-1}. The total leaf areas were assessed and test leaf was put in an oven at 90 °C for 24 hours for the determination of dry weight.

11.2.4 Use of Apparatus

An infra-red Gas analyser (IRGA Hartman & Braun) which measures changes in CO_2 concentration in the air within the chamber, and a dew point hygrometer (model 880 - Cambridge) which measures the changes in absolute humidity between the incoming and outgoing air from the assimilation chamber (Fig. 67), was used to determine rates of net photosynthesis and transpiration. This was coupled with an 'Open gas' exchange system, as described by Jarvis & Cätsky (1971). The assimilation chamber, a hexagonal aluminium structure is as described by Wilson (1978). *T. scleroxylon* with

*1μE s^{-1} m^{-2} ≡ μMol s^{-1} m^{-2} ≡ 6.02 x 10^{17} photons s^{-1} m^{-2}

its long, slender and firm petiole was quite suitable for use in this chamber, with plastic putty put around the petiole to seal it in the special groove. The chamber was stood on a 50 cm wire frame in the water bath (Grant SE 35 thermocontrol) while the light source, a Wotam Power Star (HQl - T,250W) metal halide lamp and reflector stood 430 mm above the assimilation chamber.

10 mm of water in a transparent perspex bath separated the chamber and the lamp to absorb the infra-red radiation and minimise direct heating of the chamber. Light transmission to the leaf was maximised by the regular cleaning of the perspex window on the chamber.

The flow rate of air through the chamber was 7000 cm^3 min^{-1}, measured continuously with a precision flow meter (GAP - flowstat). Photosynthetically active radiation (PAR*) was determined with a quantum sensor (Ll-190 SR, Lambda l.Corp). For complete analysis of the diffusion pathway, some estimate of boundary layer resistance is required. Probably the most accurate technique available is that described by Grace *et al* (1980) in which the rate of cooling of a brass model is measured. To do this, a brass model of *T. scleroxylon* leaf was prepared and inserted in the chamber instead of the real leaf.

11.2.5 Air Flow System

The open positive pressure air system (Fig. 67) described by Šeštak *et al* (1971) was used. About 20 l min^{-1} of ambient air was drawn by a diaphragm pump from outside the building, three floors above ground level away from any exhaust outlet. The pump created a positive pressure within the system, preventing contamination from laboratory air. Air went into an air conditioning

* Photosynthetically Active Radiation (PAR) = 400-700 nm waveband

Key (to Fig. 67)

1a Air intake from outside building

1b Air stabilising jars (x 4).

2a Diaphragm pumps

2b Reference air pump 3 li/m

2c Sample air pump 3 li/m

3a Flow meter 10 li/m

3b Flow meter 0.5 li/min

3c Flow meter 10 li/m

4a Drying tower (silica gel granules)

4b Column of Na OH and $Ca(OH)_2$ to remove CO_2 in air

5 Humidifier (5 bottles in thermo-bath).

6 Blow off (with liquid paraffin)

7 Cooling unit in thermostatically controlled water bath

8 Assimilation chamber (with leaf inside)

9 Dew point hygrometer

10 Millivoltmeter

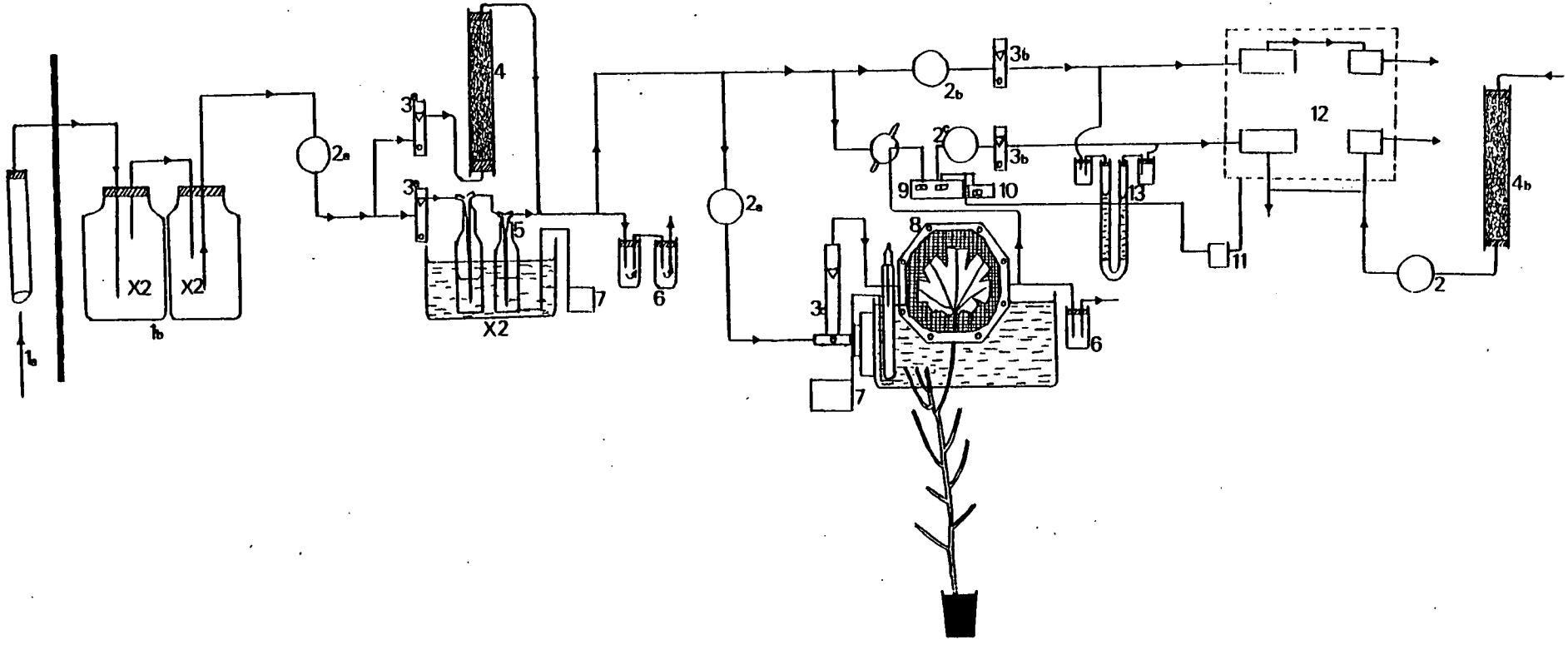
11 Chart recorder (fitted to IRGA and DPM)

12 IRGA

13 Differential monometer

Fig. 67

Gas exchange system used to determine rates of photosynthesis and leaf conductance to water vapour of individual attached leaves of *T. scleroxylon*.



Potted test plant of *T. scleroxylon*

system, which split into two, one going into the air drier (silica gel and anhydrous calcium chloride), while the other went into the air humidifying system, made up of 4 conical flasks in a thermostatically controlled water bath at 22 ^{o}C ± 4 ^{o}C. Airflow into the 'drier' and 'humidifier' were controlled with flostats and flow meters. By adjusting these flows appropriate mixtures of dry and wet air could be obtained to make any required humidity, to be directed to the assimilation chamber. This was adjusted to a standard value after each reading. A switch tap on the sample line made it possible to switch from 'ex-chamber' air to 'reference' air, thus reducing systematic errors during measurements. Differences between incoming and outgoing humidity were measured with a calibrated Dew Point meter (model 880 Cambridge systems). This, connected to a voltmeter, gave continuous readings, displayed on a potentiometric chart recorder (Model 28000, Bryans, Southern, Mitcham, Surrey). Air vents were provided at 3 points on this system to provide 'blow offs' where excess pressure was vented.

In monitoring the level of CO_2 from the chamber, air first went through the Dew Point Meter, where water vapour concentration and then through the sample line into the IRGA. Both reference line and sample lines were controlled through flow meters F3a and b (0.5 L m^{-1}) and a manometer stood between them and the IRGA to ensure that no appreciable pressure difference ever occurred between the lines.

11.2.6 Infra-red Gas Analyser. I.R.G.A.

The URAS-2 Infra-red Gas Analyser (Hartman and Braun) was used in differential mode to measure the difference in CO_2 concentration between the reference and sample lines. This equipment is fitted

with optical filters at 2700 nm. waveband, which makes it insensitive to water vapour. Sestak *et al* (1971) provides a detailed description of this.

Short and long cells make up the reference and sample tubes of this equipment. The sensitivity of the equipment was determined routinely by passing CO_2 free air through the short pathway of the reference cell (Fig. 67). Knowing the relative length of the cells, the sensitivity could be calculated (see Appendix).

11.2.7 The Dew Point Hygrometer

The Dew Point Hygrometer (Cambridge system Inc. Model 880) was used to measure the water vapour pressure of the air streams in and out of the assimilation chamber.

The instrument was calibrated with a water vapour generator (ADC-Herts) at the appropriate temperature.

The dew point of the outgoing rather than the ingoing air was controlled at 21 ^{o}C, this being the standard humidity in all the experiments (it is assumed that the outgoing, not the incoming air is at the same humidity as the air in the chamber).

11.2.8 The Experimental Procedure

In the measurement of photosynthesis and transpiration, the light response curve may to some extent depend on the exact procedure adopted in the experiment, as stomata may take some time to equilibrate completely and reach a slightly different aperture depending on whether the previous light conditions have been brighter or darker. For this reason, it is considered desirable to describe the actual procedure in detail.

(a) The whole system was run for 45 minutes to warm-up all electronic equipment, then ambient water vapour pressure and air flow rates were set.

(b) Equipment calibration was checked.

(c) Lamp switched on and allowed to warm up to produce maximum light.

(d) The plant for measurement was removed from the cabinet, placed on an adjustable stand so that the desired leaf was easy to place in the assimilation chamber.

(e) A thermocouple with its output connected to the chart recorder was attached to the abaxial surface of the leaf and held in position with thin adhesive tape. Thermocouple wires were run along the petiole in the special groove and held with plastic putty.

(f) The leaf was placed in the chamber and the chamber lid was screwed down, and the chamber fans (2) switched on.

(g) Air conditioning in the gas system was adjusted to get a dew point of 21 ^{o}C (66 % relative humidity at an air temperature of 28 ^{o}C) standard for all plants and leaves tested. The dew point meter output on the chart recorder was observed for steadiness.

(h) Temperature of the water bath was checked and the leaf temperature too, (28 ^{o}C ± 2 ^{o}C). The output of the IRGA (on the digital display panel and on a chart recorder was observed until the maximum level of assimilation was obtained (about 15 minutes).

(i) If all equipment and components were in good working order, readings of leaf temperature, ambient V.P.D. of leaf (sample and reference), air flow rate, and IRGA deflection were taken; After zeroing and calibrating with CO_2 free air the reading was taken. The CO_2 free air was disconnected and the tube from the assimilation chamber was fitted. The reading was now taken for CO_2 flux. All readings were taken only after

equilibration had been achieved, as on the chart recorder.

(j) A neutral filter was now interposed between chamber and light source. This operation continued with 6 filters of increasing densities corresponding to values of 1153 μE m^{-2} s^{-1}, 765 μE m^{-2} s^{-1}, 309 μE m^{-2} s^{-1}, 196 μE m^{-2} s^{-1}, 98 μE m^{-2} s^{-1} and 0 for all levels respectively. The temperature of the water bath was altered slightly to compensate for the effect of filters on the leaf temperature in the chamber, to maintain the temperature of the leaf at 28 ^{o}C.

After measurements are taken:

(k) The leaf was taken out of the chamber, detached from the plant, and measured with an optical area machine, (Lambda-L1-3100) after which the leaf was put in an oven for 24 hours at 90 ^{o}C before weighing on a Mettler balance for dry weight determination. Weights were checked twice for constancy.

A check for any diurnal fluctuation of leaf behaviour had been done previously. Observations of whole plants in the greenhouse and the growth cabinet had revealed a circadian rythm of Lamina movement. This started at about 4.30 p.m. every day. This was accompanied by a fall in CO_2 assimilation of about 5 % to 50 % later in the day.

Thus, all measurements were made from 7.45 a.m. to 3.45 p.m. everyday, after which dry weight determination of previous test leaves, or area measurements of the days leaves were done. Each ramet took about 2 hours to test.

11.2.9 Calculations

As a preliminary exercise before this experiment, the leaf surface (adaxial and abaxial) from a single clone (175/1) was investigated with an Electron microscope. This was to observe

the nature of stomatal distribution in this species.

Calculations of photosynthesis, respiration, and stomatal resistance were carried out using the computer programmes in Appendix .

The boundary layer resistance to heat loss was calculated using the method of Grace *et al* (1980).

Inter-conversions between aerodynamic resistance for heat, water and carbon dioxide were found by using the relationship in Grace (1981) while those for stomatal resistances were calculated from the ratio of the appropriate molecular diffusion co-efficients as first done by Gaastra (1959).

e.g. $r_s^{CO_2} = r_s^{H_2O} \times 1.56$

To calculate the mesophyll resistance (r_m), the value of r_a (0.0374 s^{-1} cm^{-1}, which was negligible, see Holmgren *et al* 1965) and r_s were substituted in the following equation:

$$\text{Rate of photosynthesis (g cm}^{-2}\text{ s}^{-1}) = \frac{CO_2 \text{ air} - CO_2 \text{ site g cm}^{-3}}{r_a^{CO_2} + r_s^{CO_2} + r_m^{CO_2}}$$

The CO_2 concentration of the air was taken to be 330 µl l^{-1} whilst that of the photosynthetic sites within the leaf were assumed to be 50 µl l^{-1}.

Water use efficiency (E_r) was calculated as the ratio of resistances to H_2O to those of CO_2 according to Holmgren *et al* (1965) and Osonumbi & Davies (1980), i.e.

$$E_r = \left(\frac{r_l^{H_2O}}{r_m^{CO_2} + r_s^{CO_2}}\right)$$

11.3 Results

11.3.1 Photosynthetic rate

The maximum photosynthetic rate per unit leaf area at light saturation was attained at around 765 μE m^{-2} s^{-1} by all clones, with no significant increase visible at the highest light intensity, 1153 μE m^{-2} s^{-1} (Fig. 68a).

There were however, substantial and statistically significant differences in photosynthetic rates between clones 144/9 and 175/1 which were the highest (0.032* μg cm^{-2} s^{-1}) and lowest (0.018 μg cm^{-2} m^{-1}) respectively of all the 6 clones studied. When photosynthetic rates are calculated on a unit dry weight basis (Fig.69) thre is an obvious re-ranking of clones, with clone 144/7 having the highest rate (9 μg g^{-1} s^{-1}). Clone 177/10 however is ranked second by both leaf area and on a dry weight basis.

The correlation of mean leaf dry weight and leaf area, for all clones ($r = +0.53$) reveals the disparity in leaf area and dry weight relations particularly in clones 144/1 and 144/9 (see Fig. 68b).

11.3.2 Respiration

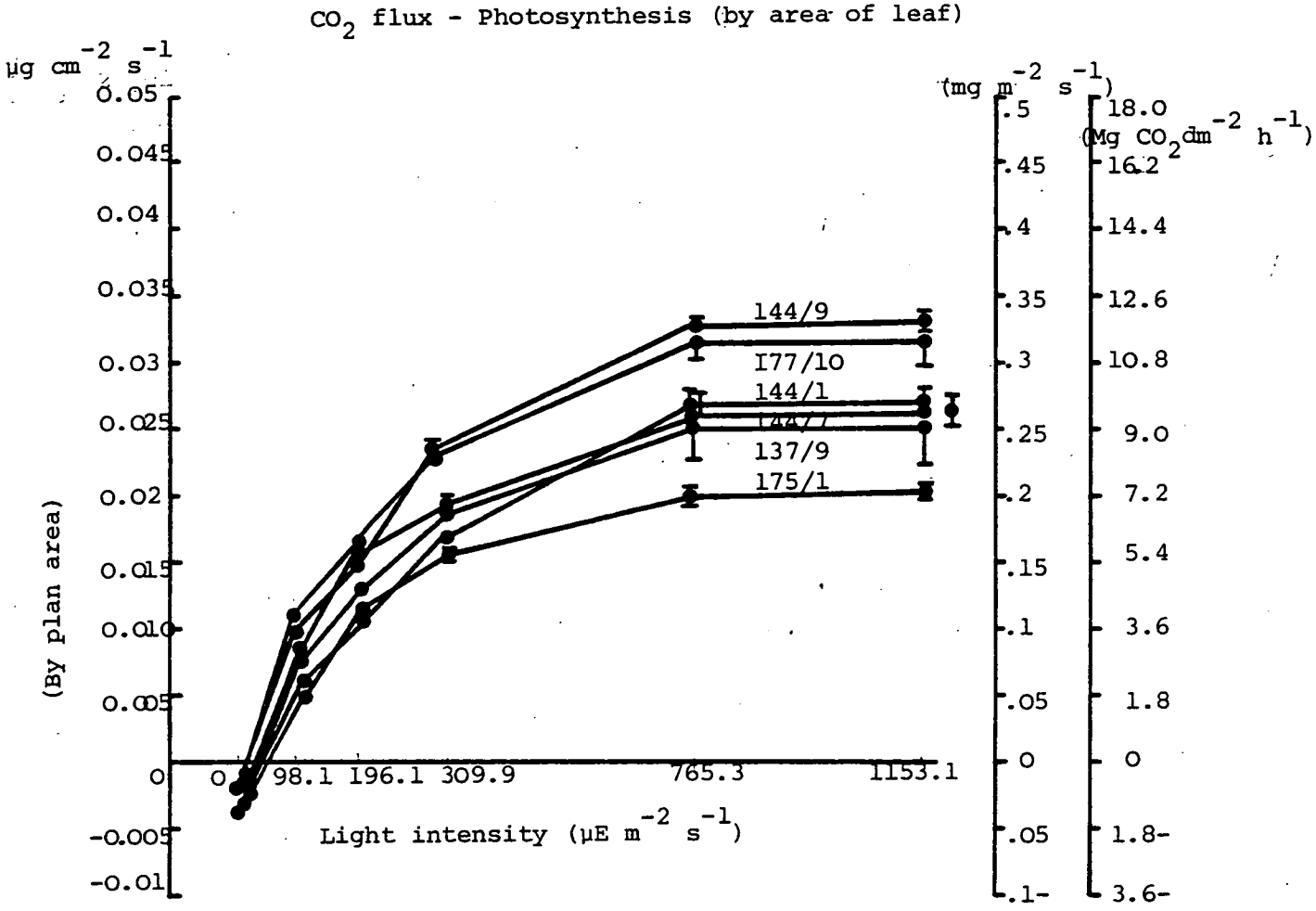
Respiration rates in the dark are also different between clones, with clone 177/10 respiring the most on an area basis (Table 27a) followed by 144/7, while the converse is true on a dry weight basis, (Table 27b).

11.3.3 Conductance to water vapour

Significant differences were found between clones in leaf conductances to water vapour. In this parameter, clones are more or less divided into 2 distinct and significantly different groups of low (clones 144/7, 175/1) and high (clones 144/9, 137/9 and 177/10 conductance. (Fig. 70).

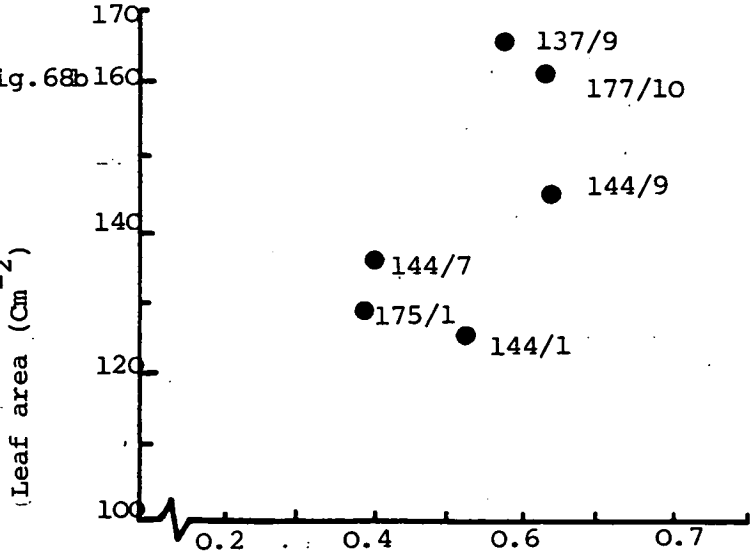
*The older units of mg dm^{-2} h^{-1} do not conform to S.I.nomenclature. However, they are frequent in the literature and have been quoted earlier in this Chapter. The units used here, μg cm^{-2} s^{-1}, are more acceptable. Conversions between units are shown in the appropriate figures (Fig.68a).

Fig. 6 8a



CO_2 flux - photosynthesis in 6 clones of *T. scleroxylon* at 6 light intensitites from dark (o) to 1153 µE m^{-2} s^{-1}. (Vertical lines represent Standard Error ±SE, n = 4 leaves per plant (4) per clone)

Fig. 6 8b

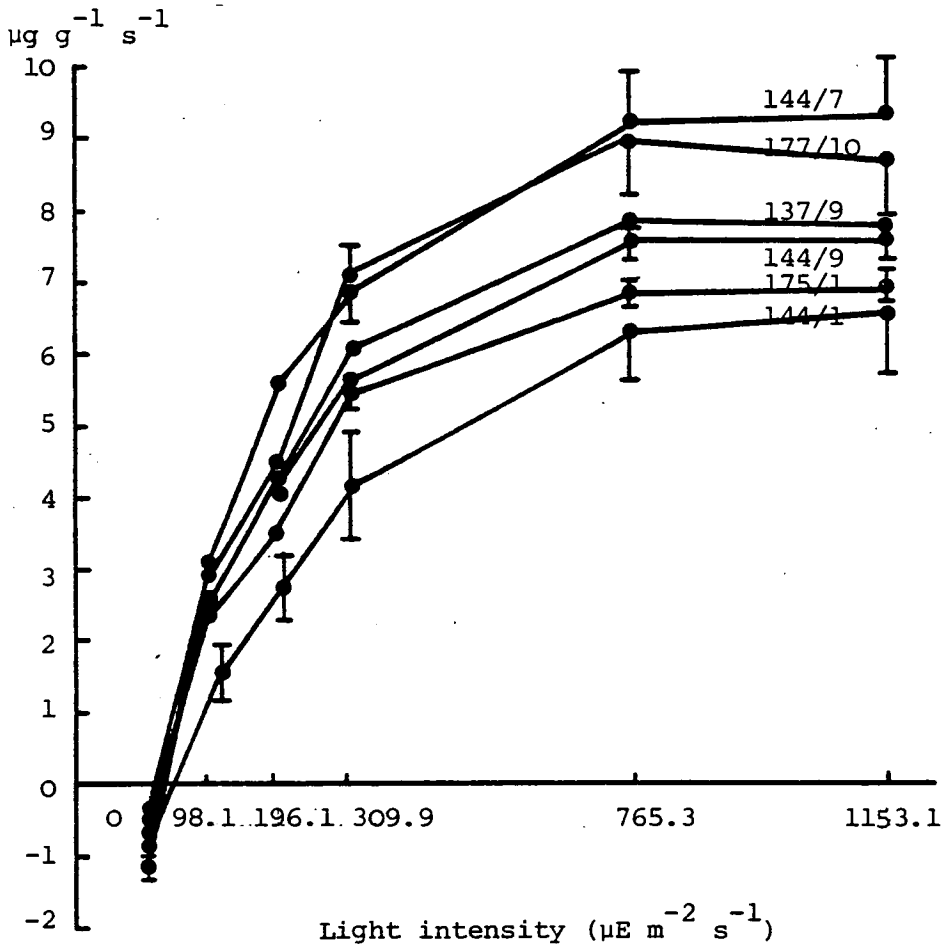


r = + 0.53 - ns

Showing the relationship between mean leaf area (cm^{-2}) and mean leaf dry weight in 6 clones of *T. scleroxylon* (n.s. = non significant. d f = 5).

Fig. 69

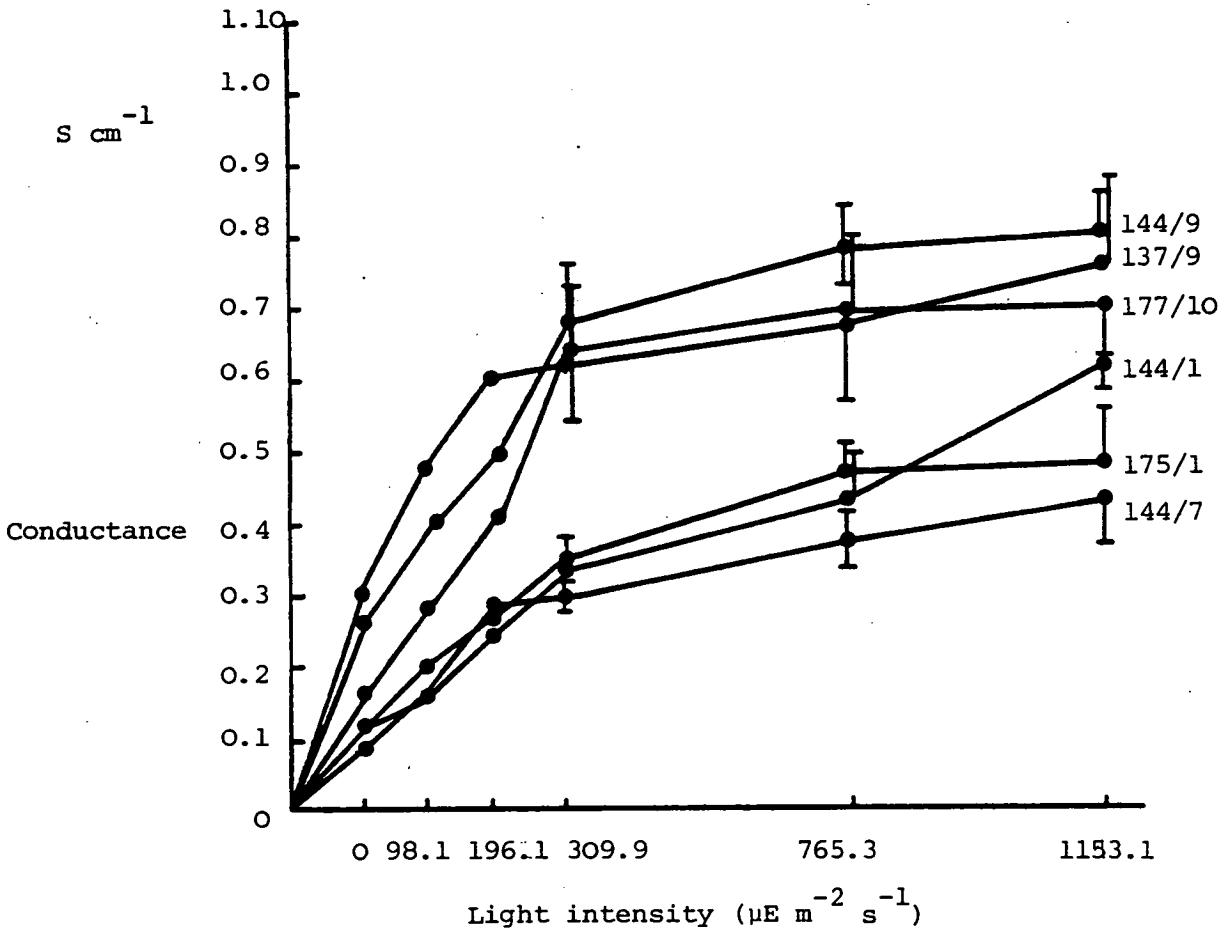
CO_2 flux (by weight of leaf)



Showing clonal variation in CO_2 flux by weight of leaf in *T. scleroxylon*

Fig. 70

Leaf Conductance (H_2O Flux)



Showing clonal variation in leaf conductance (H_2O flux) in *T. scleroxylon.*

Table 27a: Respiration at O % light on leaf area basis between clones of *T. scleroxylon*. ($\mu g\ CO_2\ Cm^{-2}\ s^{-1}$)

CO_2 Flux

Clone	Mean	± SE
144/1	-0.0026	-0.00004
137/9	-0.0019	-0.00057
177/10	-0.0034	-0.0002
144/9	-0.0021	-0.00030
144/7	-0.0031	-0.00034
175/1	-0.0014	-0.00022

Table 27b: Respiration at O % light on dry weight basis between clones of *T. scleroxylon*. ($\mu g\ g^{-1}\ s^{-1}$)

Clone	Mean	± SE
144/1	-0.615	-0.09
137/9	-0.58	-0.17
177/10	-0.896	-0.042
144/9	-0.499	-0.066
144/7	-1.078	-0.131
175/1	-0.467	-0.078

11.3.4 Stomatal Resistance to H_2O vapour

Stomatal resistances to water vapour in these clones is shown in Fig. 71. This is calculated simply as the reciprocals of the stomatal conductance to H_2O vapour. This figure is included here as many authors have presented such data as resistances, although conductances have been prefered lately as they are directly proportional to fluxes. However significant differences exist between clones only before light saturation is reached. In the dark clone 144/1 had the highest resistance (9) while clone 137/9 had the lowest resistance value (3.6 S cm^{-1}).

11.3.5 Stomatal and Mesophyll Resistances to CO_2

Mesophyll resistance to CO_2, calculated for high light intensity (1153 $\mu E\ m^{-2}\ s^{-1}$) revealed that from 8 - 14 % of the total resistance exhibited by clones to CO_2 transfer was accounted for as stomatal resistance, the remainder being mesophyll resistance (Table 28).

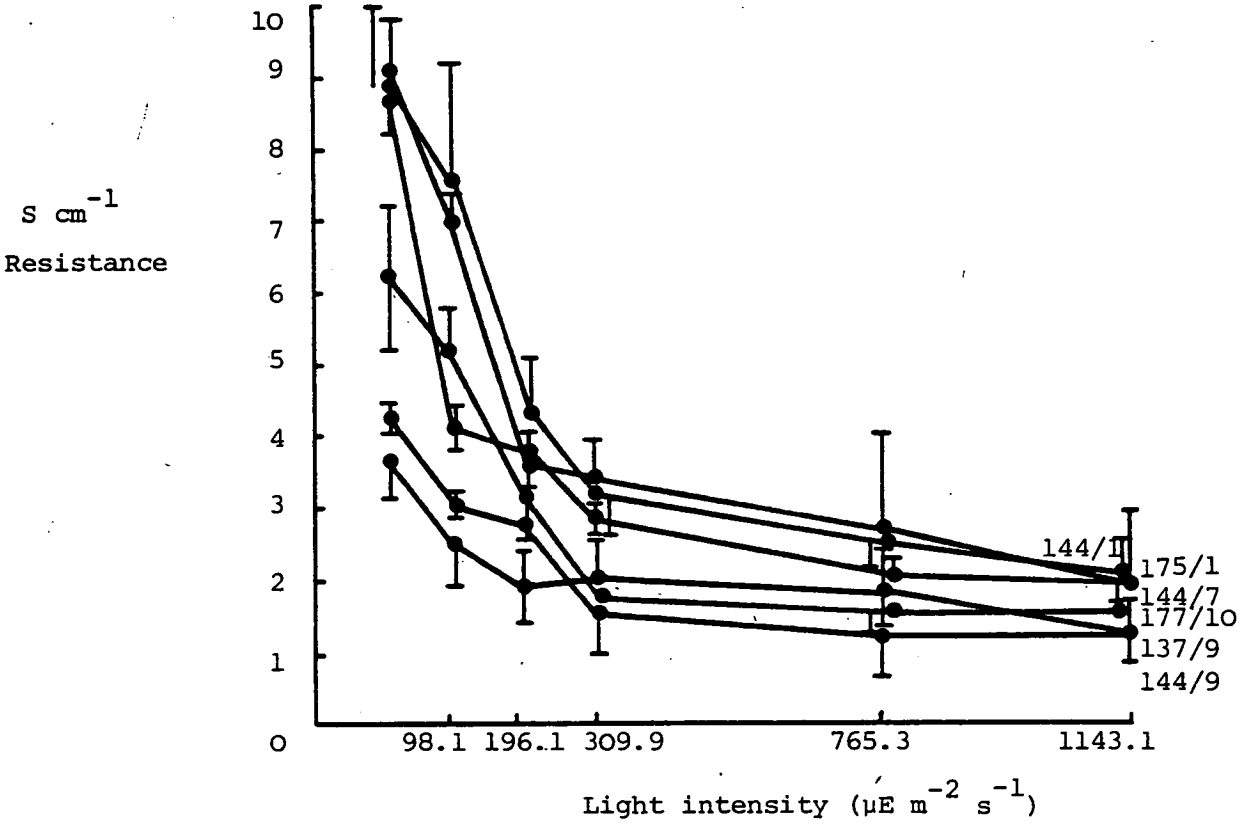
Boundary layer resistance in the well-stirred chamber was small enough to be ignored (see calculations). The variation between clones in the relationship between $r_s^{H_2O}$ to $r_s^{CO_2}$, representing water loss per unit of CO_2 fixed (as demonstrated by Holmgren *et al* (1965) and Osonubi & Davies (1980)) was also significantly different between clones (Table 29).

11.3.6 Relationships between photosynthesis and field growth parameters

Despite the clonal variation in all aspects of photosynthesis, there was no positive relationships between rates of maximum photosynthesis and the growth characteristics of trees of the same clones growing in Gambari Forest Reserve in Nigeria, although there was some indication ($P \simeq 0.1$) that clones with the most branches possess a lower capacity for photosynthesis on an area basis (Table 30).

Fig. 71

Stomatal Resistance to H_2O



Showing clonal variation in stomatal resistance (H_2O flux) in *T. scleroxylon*.

Table 28: Values of stomatal resistances (r_s) and mesophyll resistances (r_m) at high light intensity 1153 µE m^{-2} s^{-1} to CO_2.

($S\ cm^{-1}$)

Clone	$r_s^{CO_2}$	$r_s + r_m^{CO_2}$	$r_m^{CO_2}$	% r_s to $r_l^{CO_2}$
144/1	3.30	22	18.70	15.0
137/9	2.03	23.91	21.9	8.5
177/10	2.50	18.33	15.8	13.6
144/9	1.87	17.19	15.3	10.9
144/7	2.81	22.9	20.1	12.2
175/1	2.96	30.6	27.6	9.7
$\bar{x}$	2.58	22.5	19.9	11.65
sd-1	0.55	4.77	4.52	2.43
CV %	21.5	21.2	22.7	20.9

Table 29: Showing clonal variation in resistance ratio (water-use efficiency) of *T. scleroxylon*.

Clone	$r_s^{CO_2} + r_m^{CO_2}$	$r_l^{H_2O}$	Ratio $\frac{r^{H_2O}}{r^{CO_2}}$
144/1	22	2.1	0.095
137/9	23.9	1.3	0.054
177/10	18.3	1.6	0.09
144/9	17.19	1.2	0.07
144/7	22.9	1.8	0.08
175/1	30.6	1.9	0.06
		$\bar{x}$	0.075
		SD	0.016
		CV %	22.0

Table 30: Correlations between maximum photosynthetic rates and characters of maturing trees in field. (n = 6, ns* = very close to P = 0.1).

Variates	r	Sig.
Max. photosynthesis x height	= -0.40	ns
Max. photosynthesis x branch No.	= -0.58	ns*
Max. photosynthesis x diameter	= -0.54	ns

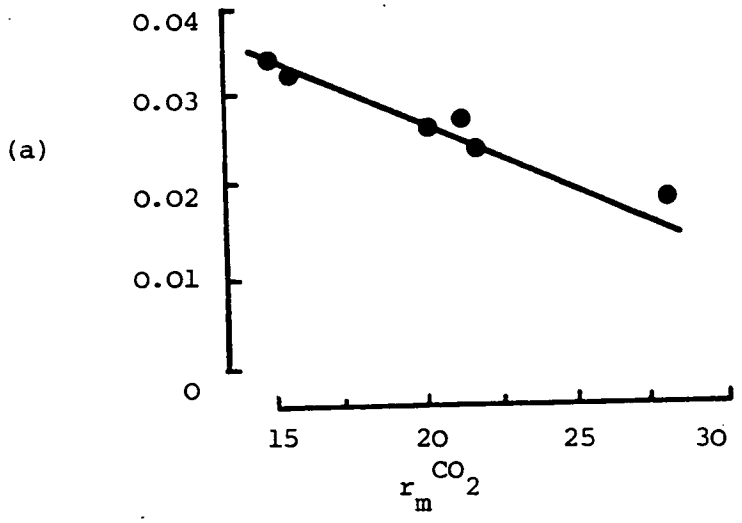
The relationship between maximum CO_2 flux and the derived parameters revealed that there was no relationship with $r_s^{CO_2}$ ($r = -0.074$.n.s.), but there was a very close relationship with $r_m^{CO_2}$ ($r = -0.99$, $P = 0.001$), (Fig. 72a and b).

11.4 Discussion

11.4.1 Comparison with other studies

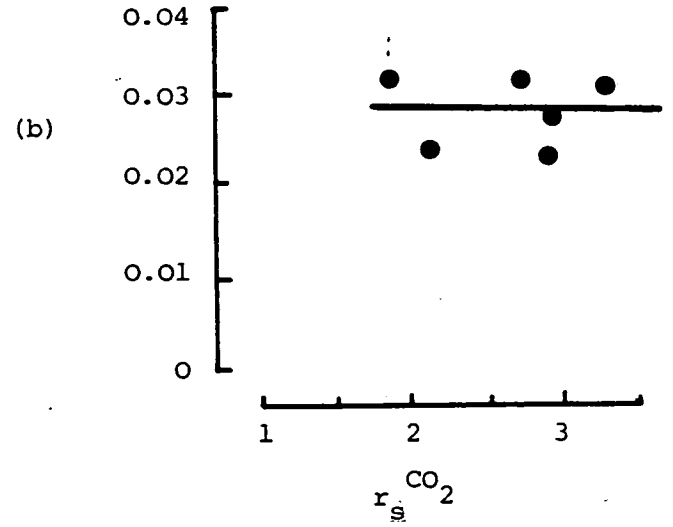
The maximum rate of photosynthesis and leaf conductance for a wide range of plant species have been reviewed by Korner *et al* (1979). He indicated that deciduous woody plants generally have somewhat greater photosynthetic capacity than evergreen species and that both of these are rather less efficient than herbs and grasses, particularly cultivated C4 plants. The general ranking of maximum leaf conductance in vascular plants is similar to that of photosynthesis (Fig. 73), but Whitehead *et al*, (1981), Grace *et al*, (in press) and Hinckley *et al*, (1981) have demonstrated that leaf conductances are much higher in some tropical forest trees, the value being over 10 times in some cases, compared to some temperate forest species.

Fig. 72a



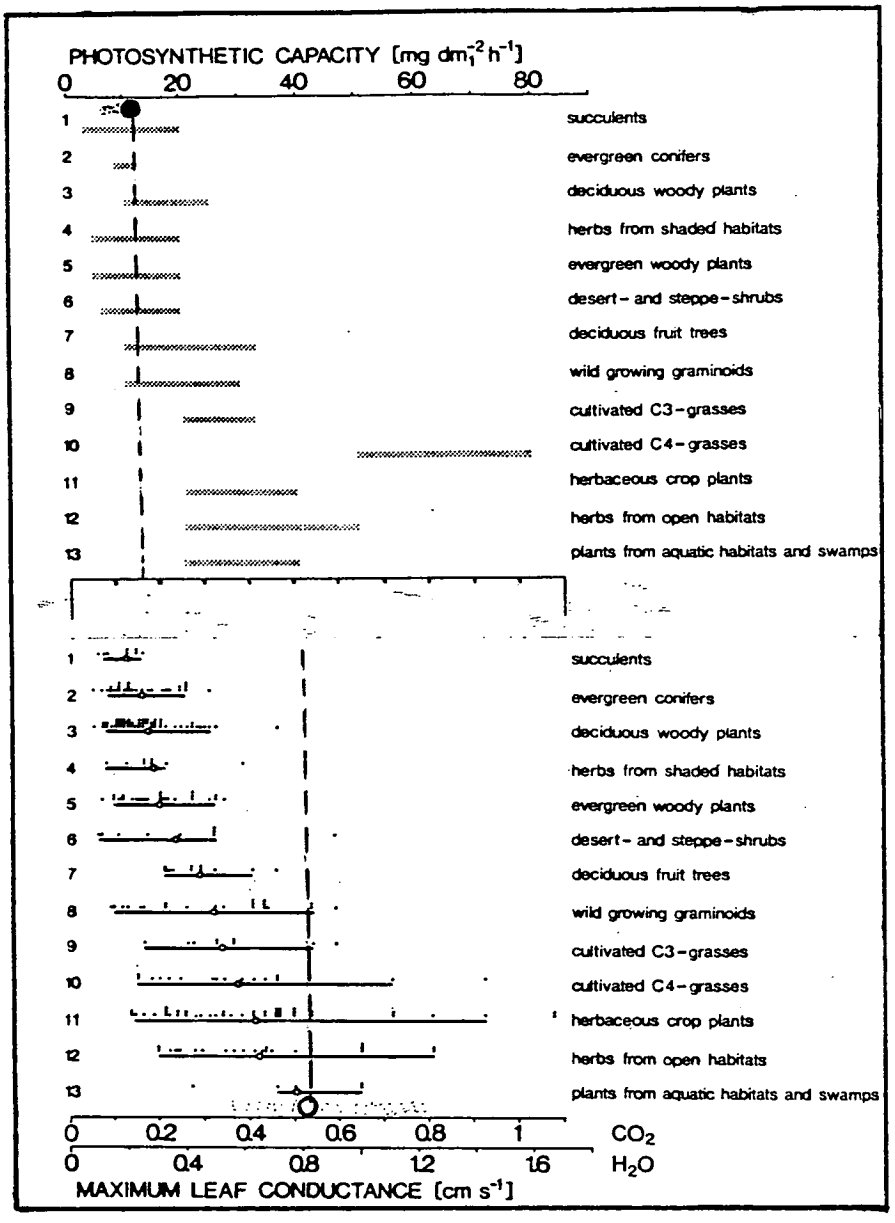
Showing the relationship between maximum photosynthetic rate and mesophyll resistance to CO_2 (r = -0.99).

Fig. 72b



Showing the relationship between maximum photosynthetic rate and stomatal resistance (r = -0.074, n.s.).

Fig. 73



Maximum photosynthetic rate (●) and conductance (o) to H_2O, of *Triplochiton scleroxylon* K.schum compared with those of other species. (adapted and modified from Korner *et al* 1979).

The photosynthetic capacity of *T. scleroxylon* (0.032 µg Cm^{-2} s^{-1} or 11.52 Mg CO_2 dm^{-2} h^{-1} or 0.32 mg Cm^{-2} s^{-1}), is relatively low for a deciduous tree, but in contrast, its maximum leaf conductance is fairly high and comparable with those of many herbaceous plants. Others have also found high conductances in tropical trees (Whitehead *et al*, 1981; Grace *et al*, (in press). Among tropical tree species, the photosynthetic capacity of *T. scleroxylon* seems to be above average, for Larcher (1969), and Koyama (1978) reported a range from 3-22 mg CO_2 dm^{-2} h^{-1} and 10-15 mg CO_2 dm^{-2} h^{-1} respectively. Furthermore, Edmisten (1970) found that *Ormosa krugii* averaged 10 mg CO_2 dm^{-2} h^{-1}. By contrast, Stephen (1968) working with *Anthocephalus cadamba* another fast growing tropical species, reported a lower rate of 8.8 mg CO_2 dm^{-2} h^{-1} which he commented to be much higher than rates for 3 other timber species reported by Allen *et al*, (1967). This may however reflect the fact that Stephen (1968) used excised leaves for his measurements. The values reported in *Gmelina arborea*, a faster growing tree than *T. scleroxylon*, 9.0 mg CO_2 dm^{-2} h^{-1} (Osonubi and Davies (1980) is also much lower than that reported for *T. scleroxylon* in the present study. In this instance, the lower rate may have been due to the 20 ^{o}C cultivation temperature which might have depressed photosynthesis.

T. scleroxylon, an emergent tree of the West African forest fits well into Lugo's sun plant group (10.6 - 11.0 mg CO_2 dm^{-2} h^{-1}) in Puerto Rico where he worked with juvenile seedlings (Lugo 1970).

With the reviews of Larcher (1969) and Korner *et al* (1979) and the results of other workers in tropical trees, including the present study in *T. scleroxylon*, it is evident that on rate basis, some temperate trees may truly be more efficient than most tropical trees.

However, the faster growth of tropical trees may probably be attributed to longer growth seasons, with less extreme variables; and the amount of leaves, sizes, and their efficiency in trappling more solar radiation (Cannell 1979).

11.4.2 Clonal variation in photosynthesis rate

Substantial differences between clones in the rate of photosynthesis were revealed, and this agrees with results using clones of other species such as *Populus deltoides* (Gordon & Promitz 1976), and *Pinus radiata* (Bennett & Rook 1978) in which between two clones, values ranging from 8 to 22 ng Cm^{-2} s^{-1} were reported. The dependance of ranking on whether calculations are referred to a leaf area or a leaf weight basis is probably due to the variation in leaf thickness or to a larger contribution of the leaf veins. On the other hand, the consistent high ranking of clone 177/10 (2nd) at both leaf area and leaf dry weight values, may reveal that this clone is superior to the other clones in this test.

The data of Samsuddin & Impens (1979) on clones of rubber (*Hevea brasiliensis*) photosynthetic rates i.e. 19.4 mg CO_2 dm^{-2} h^{-1} is much higher than those reported for *T. scleroxylon* which ranged between 7.2 to 11.52 mg dm^{-2} h^{-1}. This is however not unexpected since these rubber clones represent selected elite stocks and not wild stock which *T. scleroxylon* at this stage is. Similarly, in hybrid clones of poplar which previously had been selected for high growth in the field, Ceulemans *et al* (1980) reported substantial clonal variation in photosynthetic rates, ranging from 0.17 to 0.53 mg m^{-2} s^{-1}, this being higher than those in *T. scleroxylon* in this study, (0.2 - 0.32 mg m^{-2} s^{-1} or 11.5 mg CO_2 dm^{-2} h^{-1}).

The respiration rates reported here for *T. scleroxylon* are

comparable to those in *Magnifera foetida* (-1.65) and *Shorea parciflora* (-0.3 mg dm^{-2} m^{-1}, Yoda, 1978). Furthermore, it is comparable with the values for *Shorea macroptera* (-0.51 to -1.18) and *Shorea leprosula* (0.88 - 3.56 mg dm^{-2} h^{-1}) of the Pasha Forest in Malaya (Koyama 1978).

Leaf conductances to H_2O in the test clones, as indicated earlier, fall into 2 groups (low and high): Bennett & Rook (1978) demonstrated in *Pinus radiata* clones, that high transpiration rate was associated with poor survival of plants in the field, whilst low transpirers survived well. In the light of this, it was initially considered that the 2 groups might have arisen as a result of differences in selection pressures operating to obtain different water use efficiency in these genotypes. However, this view is not supported as the groups formed do not reflect any fundamental differences in the rainfall zones from which the clones originated. On the other hand, we cannot exclude the possibility of small scale variations in the pattern of soil water status.

11.4.3 Controlling resistance for CO_2 exchange

Clonal variations in CO_2 flux of *T. scleroxylon* seems to be more associated with variations in r_m than r_s (Fig 72a). This does not agree with the findings of Samsuddin & Impens (1979) who in rubber clones found good correlation between r_s and maximum photosynthesis. There is however agreement in that r_m is a more important factor in the over-all resistance to CO_2 flux; comparing with the conclusions of other workers such as Jarvis & Jarvis (1964) and Samsuddin & Impens (1980) in *Hevea brasiliensis*, where r_m was found to account for more of the resistances to CO_2 than any other resistance component.

Values for r_s reported by Samsuddin & Impens (1979) for rubber are similar to the values for obeche and especially for clone 144/7, but values for r_m CO_2 was however much larger. The values of r_m CO_2 in clones 144/7, 144/1, 144/9, 137/9, 177/10 and 175/1 are fairly well related to the rainfall of the zone from which they originate (r = +0.66). This is probably an indication that short season plants of the low rainfall zone (1000 - 1300 mm) require lower $r_m^{CO_2}$ for high photosynthesis.

Finally, clonal differences in water-use efficiency ratio were significant in *T. scleroxylon* (0.054 to 0.095) as has previously been reported for *Gmelina arborea* cuttings (Osonubi & Davies 1980). The water-use efficiency is generally held as being indicative of the ability of a plant to grow in a drier habitat. The higher water-use efficiency ratio of clones 144/1, 144/7 and 177/10 might thus be indicative of adaptation to dry conditions. Certainly, there is some indication of this as seedlot 144 originates from the dry zone. Moreover, clone 144/7 in Chapter 5 of this thesis was the clone least affected by the most severe water stress treatment. Thus this criterion seems useful for selection of materials for use in the drier habitats.

Further in conclusion and from the practical standpoint, the presence of clonal variation in maximum photosynthetic rate on both a dry weight and an area basis shows that many genotypes of *T. scleroxylon* possess an assimilation rate below the maximum for the species, and points to the possibility of improvement of the stock by selection for high rates of photosynthesis. This perhaps could be a useful supplement to selection on the basis of the result of the branching habit as suggested earlier.

On the other hand, some caution is desirable as correlations do not seem to exist between the rate of photosynthesis and the performance of a given clone in plantations. Indeed, it is known that photosynthesis in young material may be different from that of older trees and that the rate of photosynthesis may, to some extent, be modified by growing conditions prior to any measurement of photosynthesis, such as the trimming of the leaves. In view of the possibility of acclimation of the photosynthetic system to the prevailing growing conditions (Gordon & Promnitz 1976b), measurements made in the laboratory should ideally be related to similar measurements in the natural environment. In the present study, the conditions used were an approximation of those occurring naturally in West Africa; however, they may be important differences, and so results need to be confirmed in West Africa.

Moreover, the display of leaves towards the sun and sky is known to vary between clones, some of them being compact, while others are lax or columnar. This factor and the capacity of the leaf to adjust to shade, may well be just as important as the maximum photosynthetic rate of the leaf. Ultimately, even when experimental work is complete, the complex interraction between apical strength, form of canopy and the photosynthetic characteristics should be investigated through the use of some kind of computer model based on functional relationship. The present data, in as much as they represent potential selection criteria, may be regarded as preliminary information in the construction of such a model.

CHAPTER 12

SUMMARY AND GENERAL DISCUSSION

The work in this thesis has demonstrated that substantial variation exists between clones of *T. scleroxylon*. In particular, a stron relationship is reported between branching habit of clones in the field and apical dominance in juvenile clonal cuttings. This relationship should enable clonal selections to be made at a much earlier stage than usually practiced in silvicultural tests.

The main findings are listed below :

(a) Preliminary studies of *Betula pubescens*.

(1) Prior to field-work in Nigeria, preliminary studies on the form of *Betula pubescens* were carried out. Problems of bias in a scheme of assessment were demonstrated. Such errors arose where subjective judgement was required, but could be overcome to some extent by careful definition of the task, and most discrepancies between observers could be resolved by consultation.

(2) Differences in growth between and within provenances (Scottish and Norwegian) from different altitudes were identified. Within-provenance differences were also present, in dry matter production as in coppice regrowths of these provenances (Chapter 4).

(3) Experiences gained from the above work formed the basis for the later field assessments of *T. scleroxylon* in Nigeria, which formed an important part of this work.

(b) Factors affecting apical dominance.

(1) Following the removal of the top two nodes from the plants

(decapitation) the subsequent axillary bud activity was assessed. Two distinct phases of bud activity were identified: The phase of bud release which leads to maximum bud activity, and the phase of dominance reassertion. The phase of maximum bud activity was taken as a measure of the inherent intensity of apical dominance in clones. The effects of various factors on axillary bud activity (apical dominance) was investigated. This was done in order to establish a standard (optimal) condition in the glasshouse at ITE or the nursery at FRIN, under which genetic variation in apical dominance can be revealed (Chapter 5).

(2) Glasshouse and nursery experiments showed that only the two top nodes are to be removed from test plants, and that between 4-6 leaves are to be retained.

(3) Temperatures should exceed 25 ^{o}C, daylength should be between 12 to 19½ hours, and light intensitites should be between 650 to 1500 $\mu E\ m^{-2}\ s^{-1}$.

(4) Temperatures above 35 ^{o}C caused a reversal of the position of dominating shoot(s), these being basal instead of those near the top of the plant. Temperatures between 25 to 35 ^{o}C provide satisfactory test conditions.

(5) Humidity in the test environment should be between 70 - 90 % RH at 28 ^{o}C. The presence of water stress in test plants resulted in increase of apical dominance and reduction in axillary bud activity.

(6) Glasshouse experiment also showed that extreme nutrient

levels (4 %), increased peak bud activity while 1 % liquid fertilizer application reduced this response. (Chapter 5).

(c) Performance of clones in plantations.

(1) Field assessments showed that a wide range of differences existed between 4-year old *T. scleroxylon* clones in their heights, diameter (dbh), and number of stems.

(2) It was also revealed that clones differed in their branching habit, some branching much more than others. Natural branch shedding was also found to vary between these clones after 4 years growth in the plantation.

(3) Plant spacing (2.5 or 4.9 m) was found to affect height and branching, with more branches and sylleptic shoots produced under wide spacing, where branches were retained longer.

(4) The silvicultural treatment of branch pruning at early age, before canopy closure, was found to be ineffective. (Chapter 6).

(5) Branch characters or crown attributes from the 5 lower branches was found to differ between clones, there being differences in branch length, branch angles, number of secondary branches, number of nodes on branches and length of internodes. Extrapolation of the characters of the lower 5 branches provided a means of assessing crown shapes. There was substantial clonal variation in crown depth and width (Chapter 7).

(6) The relationships between the various attributes reported above revealed a complex interdependence between the parameters investigated. This indicated that selection against one undesirable trait, for example forking, may also eliminate another,

for example the formation of multiple stems.

(d) Apical dominance.

(1) The percentage bud activity was maximal at about four weeks after decapitation. Thereafter the activity declined as the uppermost shoots exerted dominance over lower members. This 4-week value was considered to be a measure of the strength of apical dominance and varied between clones. Graphical analysis of the trends in bud activity enabled several other parameters to be obtained.

(2) A regression analysis of the trends in bud activity provided a measure of rate at which dominance became reasserted (the reassertion slope). It was postulated that this slope was a measure of apical control. The intercept of fitted lines between the early part of bud activity and the later part (phase of reassertion of dominance) provided another parameter, which was called the potential bud activity. (Chapter 8).

(3) The correlation between bud activity at 4 weeks and the branching habit (total number of branches) in the field at 4-years in the same clones revealed a good correlation (r 2 +0.76).

(4) On the basis of this, clones were ranked according to their branching habit. This showing clones with high apical dominance (low number of branchers) and those with low apical dominance (high number of brancher). A 15 % gain in improvement of branching habit was estimated to result from a selection of 50 % based on ranking for apical dominance and branching habit. (Chapter 8).

(e) Other studies of clonal variation

(1) Seedling populations from the wet (high forest) zone grew faster, and produced less branches (higher apical dominance) than those from the dry (savannah) zone both before and after decapitation. Between both full-sib populations and the above seedlots, the presence of active cotyledonary buds was identified in some seedlings. These later produced more branches than in those without this characteristic (Chapter 9).

(2) An examination was made of the performance of certain progenies and clones over three sites within the natural range of the species in Nigeria. There was substantial variation between progenies and clones within and between sites in the parameters examined. Some clones were ranked consistently high at all three test sites (Chapter 10).

(3) In juvenile clonal plants the maximum photosynthetic rate was reached at around 765 $\mu E\ m^{-2}\ s^{-1}$, irrespective of clone. Rates of photosynthesis, varied significantly between clones on both leaf area and leaf dry weight basis. Respiration rates and the resistances to Carbon dioxide ($r_s CO_2$ and $r_m CO_2$) and H_2O ($r_s H_2O$) were also different between these clones. However no relationships existed between the parameters examined and the field performance of the corresponding clones at 4 years. (Chapter 11).

Triplochiton scleroxylon K. shum; has a wide geographic range over most of the countries in the Moist tropical forests of West and Central Africa.

It is out-breeding (Howland and Bowen 1977; Leakey *et al* 1981), and thus populations are heterogenous. As demonstrated in this thesis, clones are highly variable, even when they originate from the seame seedlot.

This characteristic is a very valuable one in the present case with *T. scleroxylon* and in other forest species of this nature as selection for improvement from individual clonal characteristics can result in substantial gains and improvement of stock for commercial plantations.

The relationship between the physiological process of apical dominance and branching in the field reported in this thesis, is an added tool for improvement at an early stage, as superior clones can be selected more quickly. As also demonstrated, this can result in further gains as far as branching habit, yield and form of trees is concerned. Furthermore, as Johnson (1976) and many others have pointed out, economic yields from plantations exceed those of natural forests andmoreover that plantation may help to alleviate the pressure on the natural genepool remaining, as the demand for tropical hardwood products increase in the world market.

The presence of active cotyledonary buds in young seedlings and the higher branching in these plants, whether half-sib or full-sibs, whose parents had earlier been noted to produce this characteristic, probably points to the fact that when seedlings are produced for vegetative multiplication, those with active cotyledonary nodes

should be discarded thereby eliminating potential gross deformities.

The performances of clones at different sites however, is vital to the success of an improvement programme, a broadly stable clone being more useful than a site-specific clone. The variation in the performances of clones over the 3 test-sites has shown that some clones display greater stability than others. That some clones are tolerant of extreme environmental stress is demonstrated in the water stress experiment, where clone 8047 produced smaller leaves, following decapitation, at high water stress and hence did not display the extreme vulnerability to water stress. This clone is probably broadly stable in relation to water regime, and might grow well at any site within the natural range. On the other hand the production of strong basal branches by most clones at Afaka Station in northern Nigeria, probably indicates a real climatic limit for the production of merchantable bole.

Although there was no relationship between the rate of photosynthesis and clonal performances in the field, it is possible that by breeding, 'elite' clones with desirable form characteristics could be crossed with those with high rates of photosynthesis thereby producing even better planting stock.

Further work on the variability of *T. scleroxylon* clones include the following:

1. Effects of various hormones on apical dominance in *T. scleroxylon*; to shed more light on the mechanism of correlative inhibition generally and in particular *T. scleroxylon*.
2. Effects of apical dominance on wood characteristics; to find out whether selection based on the intensity of apical dominance for form and yield is compatable with the production of good quality timber.
3. Further investigations into the phenomenon of active cotyledonary buds just after germination. Further crosses between plants with this characteristic will help to elucidate the genetic basis of this interesting but undesirable feature.
4. The estimation of genetic parameters, and further estimations of selection gains at different selection intensities will be valuable in the justification of the improvement of this species at the early stages using the indirect method reported in the present work.
5. An important corollary to this work will be the development of an early selection method for pest and disease resistance.

Finally, great attention should now be given to the planning and selection of clones with desirable branching characteristics which will produce well formed trees of high economic potential for inclusion in large planting programmes.

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APPENDIX 1

Specimen assessment sheet used for recording field measurements. (Chapters 6, 7 and 10).

ASSESSMENT OF:..... OBSERVER: .....

Species: Triplochiton Expt. No..... Date of Treatment
Date of Assessment
Ident. No..... Time since Treatment
Details of measurement made: Assessment No.

Line number																							
Plant number																							
Height (m)																							
No. of stems, incl. main																							
Multistem 1, height																							
" 2, "																							
" 1, diam. at 10cm																							
" 2, diam. at 10cm																							
Main stem diameter at 10cm																							
" " " 130cm																							
Height to lowest living branch																							
Syllepticity (0 - 5)																							
Total branches present																							
No. of branches 0 - 1.3m																							
" " scars "																							
No. of branches 1.3-2.3m																							
" " scars "																							
" " branches 2.3-3.3m																							
" " scars "																							
" " branches 3.3 - 4.3m																							
" " scars "																							
" " branches 4.3 -5.3m																							
" " scars "																							
" " branches 5.3 -6.3m																							
" " scars "																							
" " branches 6.3 - 7.3m																							
" " scars "																							
" " branches 7.3-8.3m																							
" " scars "																							
" " branches 8.3-9.3m																							
" " scars "																							
" " branches 9.3-10.3m																							
" " scars "																							
No. of true forks																							
Height to fork 1																							
Are forks annual ?																							
No. of attempted forks																							
Are attempted forks annual?																							
No. of heavy branches																							
Are heavy branches annual ?																							
Subjective form (0 - 10)																							
Subjective vigour (0 - 10)																							
Zonocerus ?																							
Termites ?																							
Adventitious shoots?																							
Rot ?																							
Fire (1 - 3)																							
Comments																							

APPENDIX 2.

Program for calculating clonal means and standard errors for the Gambari Field data. (Chapter 6).

```
      COMMAND:LIST(OYE)
      C     PROGRAM TO FIND CLONAL MEANS OF THE GAMBARI       DATA
                  DIMENSION SS(46),AMS(46)
                  DIMENSION  JCLONE(26),A(50,500),SUM(50),AMEAN(50)
           1,SUMSQ(50),SQSUM(50),SE(50),SD(50)
            DATA JCLONE /017507,017502,017505,017506,017508,017510,016601,
           1016608,017710,014409,014401,014407,013709,014404,017501,
           2022401,022411,022508,014212,014210,013903,013909,
           3014405,014505,016103,026104/

              COUNT=0
        102 FORMAT(1H1,' CLONE',F10.0,' NUMBER OF TREES=',F10.0)
        103 FORMAT(' MEANS ARE AS FOLLOWS')
        104 FORMAT(' HEIGHT=          ',3F10.4)
        105 FORMAT(' STEM NUMBER=     ',3F10.4)
        106 FORMAT(' MSTEM 1 HEIGHT ',3F10.4)
        107 FORMAT(' MSTEM 2 HEIGHT ',3F10.4)
        108 FORMAT(' MSTEM 1 DIAM,10',3F10.4)
        109 FORMAT(' MSTEM 2 DIAM,10',3F10.4)
        110 FORMAT(' MSTEM 0 DIAM,10',3F10.4)
        111 FORMAT(' MSTEM 0 DIAM130',3F10.4)
        112 FORMAT(' H LOWEST LIVE B',3F10.4)
        113 FORMAT(' SYLLEPTICITY   ',3F10.4)
        114 FORMAT(' TOTAL BRANCHES ',3F10.4)
        115 FORMAT(' BRANCHES 0-1.3M',3F10.4)
        116 FORMAT(' SCARS    0-1.3M',3F10.4)
        117 FORMAT(' BRANCH 1.3-2.3M',3F10.4)
        118 FORMAT(' SCARS  1.3-2.3M',3F10.4)
        119 FORMAT(' BRANCH 2.3-3.3M',3F10.4)
        120 FORMAT(' SCARS  2.3-3.3M',3F10.4)
        121 FORMAT(' BRANCH 3.3-4.3M',3F10.4)
        122 FORMAT(' SCARS  3.3-4.3M',3F10.4)
        123 FORMAT(' BRANCH 4.3-5.3M',3F10.4)
        124 FORMAT(' SCARS  4.3-5.3M',3F10.4)
        125 FORMAT(' BRANCH 5.3-6.3M',3F10.4)
        126 FORMAT(' SCARS  5.3-6.3M',3F10.4)
        127 FORMAT(' BRANCH 6.3-7.3M',3F10.4)
        128 FORMAT(' SCARS  6.3-7.3M',3F10.4)
        129 FORMAT(' BRANCH 7.3-8.3M',3F10.4)
        130 FORMAT(' SCARS  7.3-8.3M',3F10.4)
        131 FORMAT(' BRANCH 8.3-9.3M',3F10.4)
        132 FORMAT(' SCARS  8.3-9.3M',3F10.4)
        133 FORMAT(' BRANCH 9.3-0.3M',3F10.4)
        134 FORMAT(' SCARS  9.3-0.3M',3F10.4)
        135 FORMAT(' NO TRUE FORKS  ',3F10.4)
        136 FORMAT(' H TO FORK1     ',3F10.4)
        137 FORMAT(' FORKS ANNUAL?  ',3F10.4)
        138 FORMAT(' ATTEMPTED FORKS',3F10.4)
        139 FORMAT(' ATT.FORKS ANN? ',3F10.4)
        140 FORMAT(' HEAVY BR. NO.  ',3F10.4)
        141 FORMAT(' HEAVY BR. ANN? ',3F10.4)
        142 FORMAT(' SUBJ FORM SCORE',3F10.4)
        143 FORMAT(' SUBJ VIGOUR    ',3F10.4)
        144 FORMAT(' ZONOCERUS?     ',3F10.4)
        145 FORMAT(' TERMITES?      ',3F10.4)
        146 FORMAT(' ADVENTITIOUS?  ',3F10.4)
        147 FORMAT(' ROT?           ',3F10.4)
        148 FORMAT(' FIRE?          ',3F10.4)
             DO 7 II=2,46
           SUMSQ(II)=0
           SQSUM(II)=0
      7         SUM(II)=0
            READ(5,99)J
      99          FORMAT(I3)
           DO 1 I=1,J
           READ(5,100)(A(K,I),K=1,36)

         1 READ(5,101)(A(K,I),K=37,46)
           DO 3 IZ=1,26
           COMP=FLOAT(JCLONE(IZ))
             WRITE(6,150)COMP
      150    FORMAT(1H ,F12.3)
              DO 2 I=1,J
           TEST=A(1,I)

            IF(TEST.NE.COMP)GO TO 2
           COUNT=COUNT+1.0
           DO 4 II=2,46
           SQ=A(II,I)**2
```

CONTD.

CONTD.

```
      SUMSQ(II)=SUMSQ(II)+SQ
         SUM(II)=SUM(II)+A(II,I)
        AMEAN(II)=SUM(II)/COUNT
      SQSUM(II)=SUM(II)**2
      SS(II)=SUMSQ(II)-(SQSUM(II)/COUNT)
             IF(COUNT.EQ.1)COUNT=1.00001
             AMS(II)=SS(II)/(COUNT-1)
      SD(II)=SQRT(AMS(II))
4      SE(II)=SD(II)/(SQRT(COUNT))
2      CONTINUE
        IF(COUNT.LT.0.5)GO TO 97

      WRITE(6,102)COMP,COUNT
      COUNT=0.0
      WRITE(6,103)
      WRITE(6,104)AMEAN(2),SD(2),SE(2)
      WRITE(6,105)AMEAN(3),SD(3),SE(3)
      WRITE(6,106)AMEAN(4),SD(4),SE(4)
      WRITE(6,107)AMEAN(5),SD(5),SE(5)
      WRITE(6,108)AMEAN(6),SD(6),SE(6)
      WRITE(6,109)AMEAN(7),SD(7),SE(7)
      WRITE(6,110)AMEAN(8),SD(8),SE(8)
      WRITE(6,111)AMEAN(9),SD(9),SE(9)
      WRITE(6,112)AMEAN(10),SD(10),SE(10)
      WRITE(6,113)AMEAN(11),SD(11),SE(11)
      WRITE(6,114)AMEAN(12),SD(12),SE(12)
      WRITE(6,115)AMEAN(13),SD(13),SE(13)
      WRITE(6,116)AMEAN(14),SD(14),SE(14)
      WRITE(6,117)AMEAN(15),SD(15),SE(15)
      WRITE(6,118)AMEAN(16),SD(16),SE(16)
      WRITE(6,119)AMEAN(17),SD(17),SE(17)
      WRITE(6,120)AMEAN(18),SD(18),SE(18)
      WRITE(6,121)AMEAN(19),SD(19),SE(19)
      WRITE(6,122)AMEAN(20),SD(20),SE(20)
      WRITE(6,123)AMEAN(21),SD(21),SE(21)
      WRITE(6,124)AMEAN(22),SD(22),SE(22)
      WRITE(6,125)AMEAN(23),SD(23),SE(23)
      WRITE(6,126)AMEAN(24),SD(24),SE(24)
      WRITE(6,127)AMEAN(25),SD(25),SE(25)
      WRITE(6,128)AMEAN(26),SD(26),SE(26)
      WRITE(6,129)AMEAN(27),SD(27),SE(27)
      WRITE(6,130)AMEAN(28),SD(28),SE(28)
      WRITE(6,131)AMEAN(29),SD(29),SE(29)
      WRITE(6,132)AMEAN(30),SD(30),SE(30)
      WRITE(6,133)AMEAN(31),SD(31),SE(31)
      WRITE(6,134)AMEAN(32),SD(32),SE(32)
      WRITE(6,135)AMEAN(33),SD(33),SE(33)
      WRITE(6,136)AMEAN(34),SD(34),SE(34)
      WRITE(6,137)AMEAN(35),SD(35),SE(35)
      WRITE(6,138)AMEAN(36),SD(36),SE(36)
      WRITE(6,139)AMEAN(37),SD(37),SE(37)
      WRITE(6,140)AMEAN(38),SD(38),SE(38)
      WRITE(6,141)AMEAN(39),SD(39),SE(39)
      WRITE(6,142)AMEAN(40),SD(40),SE(40)
      WRITE(6,143)AMEAN(41),SD(41),SE(41)
      WRITE(6,144)AMEAN(42),SD(42),SE(42)
      WRITE(6,145)AMEAN(43),SD(43),SE(43)
      WRITE(6,146)AMEAN(44),SD(44),SE(44)
      WRITE(6,147)AMEAN(45),SD(45),SE(45)
      WRITE(6,148)AMEAN(46),SD(46),SE(46)
97        CONTINUE
      DO 6 II=2,46
      SUMSQ(II)=0
      SQSUM(II)=0
      SUM(II)=0
    6 AMEAN(II)=0

    3 CONTINUE
      STOP
  100 FORMAT(F6.0,F3.0,F1.0,6(F3.0),F2.0,F1.0,23(F2.0),F1.0,F2.0)
  101 FORMAT(F1.0,F2.0,8F1.0)
      END
```

APPENDIX 3.

Program for calculating means and standard errors of branch characteristics from Gambari field experiment. (Chapter 7).

```
Command:LIST(IBAZ)
C       PROGRAM TO FIND CLONAL MEANS OF THE IB DATA
          REAL*8 ITEMNAME
        DIMENSION JCLONE(21),COUNT(21),ZCLONE(10,6,21,5),ACLONE(6,71,5),

       1 ITEMNAME(6),ASTAT(6),ERROR(21,6,5)
        DIMENSION AMEAN(21,6,5),QCLONE(71)
        DATA ITEMNAME/'BRANCHHT','LENGTH B','NODE NO ','DIAM BR ',
       1'ANGLE   ','SECONDBR'/
        DATA JCLONE /017710,017507,017510,014409,014405,017502,017505,
       1017506,
       1 017508,013709,014404,014407,016601,014401,014502,013903,014212,
       1022411,
       1 017708,014201,013705/
        DO 50 K=1,21
        COUNT(K)=0
        DO 50 IT=1,6
        DO 50 J=1,5
        AMEAN(K,IT,J)=0
        ERROR(K,IT,J)=0
         ACLONE(IT,K,J)=0
        DO 50 I=1,10
          ZCLONE(I,IT,K,J)=0
50          CONTINUE
        DO 1 I=1,71
        READ(5,100),QCLONE(I),((ACLONE(IT,I,J),J=1,5),IT=1,5)
        READ(5,102)(ACLONE(6,I,J),J=1,5)
1       CONTINUE
  100 FORMAT(I6,5F3.0,5F3.0,5F3.0,5F3.1,5F2.0)
  102 FORMAT(5F2.0)
        DO 2 K=1,21
        DO 2 I=1,71
        ITEST=QCLONE(I)
        KTEST=JCLONE(K)
        IF(ITEST.NE.KTEST)GO TO 2
        IF(ITEST.EQ.KTEST)COUNT(K)=COUNT(K)+1
        IREP=COUNT(K)
        DO 3 J=1,5
          DO 3 IT=1,6
      3 ZCLONE(IREP,IT,K,J)=ACLONE(IT,I,J)
2       CONTINUE
        DO 4 K=1,21
        DO 4 IT=1,6
        DO 4 J=1,5
        IREP=COUNT(K)
        DO 5 IIREP=1,IREP
        ASTAT(IIREP)=ZCLONE(IIREP,IT,K,J)
      5 AMEAN(K,IT,J)=AMEAN(K,IT,J)+ZCLONE(IIREP,IT,K,J)
        AN=COUNT(K)
            CALL STAT(AN,ASTAT,SE)
        ERROR(K,IT,J)=SE
      4 AMEAN(K,IT,J)=AMEAN(K,IT,J)/COUNT(K)
C     C NOW PRINT THE ANSWERS
        WRITE(6,104)
        DO 6 K=1,21
        DO 6 IT=1,6
        DO 6 J=1,5

         WRITE(6,103)JCLONE(K),ITEMNAME(IT),J,AMEAN(K,IT,J),ERROR(K,IT,J)
      6 CONTINUE

    104 FORMAT(1H1,'CLONE','   ITEM ','POSITION','   MEAN   ','STANDARD ER
       1ROR')
    103 FORMAT(1H ,I6,A8,I8,2F10.5)
        STOP
        END
        SUBROUTINE STAT (BN,BSTAT,SERR)
        DIMENSION BSTAT (10)

        SUMSQ=0
          SUM=0
        IENT=IFIX(BN)
        DO 1 I=1,IENT
      1 SUM=SUM+ BSTAT(I)
        SUM=SUM/BN
        DO 22 I=1,IENT
        DIFF=SUM-BSTAT(I)
        IF(DIFF.LT.0)DIFF=(-1)*DIFF
     22 SUMSQ=SUMSQ+(DIFF**2)
          IF(BN.EQ.1)BN=2
        AMS=SUMSQ/(BN-1)
        SD=SQRT(AMS)
        SERR=SD/(SQRT(BN))
        RETURN
        END
```

APPENDIX 4

Program for analyses of correlation between juvenile (glasshouse) and mature (field) data of *T. scleroxylon*. (Chapter 8).

```
Command:LIST(MCORR2)
C 'MCORR2' CALCULATES A MATRIX OF CORRELATION COEFFICIENTS BETWEEN 'V'
C VARIABLES (V<OR=22), ALL VARIABLES HAVING THE SAME NUMBER OF CASES,
C 'C' (C<OR=32). ANY CASE = 0 IS NOT USED IN THE CALCULATION OF
C CORRELATION COEFFICIENTS. COEFFICIENTS SIGNIFICANT AT THE 5% LEVEL
C ARE UNDERLINED WITH ASTERISKS.
C
C HOW TO USE 'MCORR2':
C THE PROGRAM READS A FREE-FORMAT DATA FILE ARRANGED SO THAT THE LIST
C OF CASE VALUES FOR EACH VARIABLE OCCUPIES 1 COLUMN OF A 2-DIMENSIONAL
C MATRIX.
C
C TO SET LINE-PRINTER TO 132 CHARACTERS PER LINE OUTPUT:
C PRESS 'CONTROL' & 'SHIFT' KEYS SIMULTANEOUSLY, HOLD, THEN PRESS 'A'.
C RELEASE 'CONTROL' & 'SHIFT',TYPE 'W' 1 SPACE '132', PRESS
C 'RETURN'.
C
C TO RUN PROGRAM TYPE:
C
C     FORTE(MCORR2,OBJ)    WHERE OBJ = OBJECT FILENAME
C     DEFINE(4,INPUT)      WHERE INPUT = DATA FILENAME
C     RUN(OBJ)
C
      CHARACTER*5 SIG(22,22)
      INTEGER C,V,CT,N
      REAL*4 A(22,22),B(22,22),R(22,22),NX,SX,SX2,SXY,SY,SY2,R1,R2,SER,R
     *R,T(30)
      DATA A/484*0./,B/484*0./,R/484*0./,SIG/484*'     '/
      DATA T(1)/12.706/,T(2)/4.303/,T(3)/3.182/,T(4)/2.776/,T(5)/2.571/
      DATA T(6)/2.447/,T(7)/2.365/,T(8)/2.306/,T(9)/2.262/,T(10)/2.228/
      DATA T(11)/2.201/,T(12)/2.179/,T(13)/2.160/,T(14)/2.145/
      DATA T(15)/2.131/,T(16)/2.120/,T(17)/2.110/,T(18)/2.101/
      DATA T(19)/2.093/,T(20)/2.086/,T(21)/2.080/,T(22)/2.074/
      DATA T(23)/2.069/,T(24)/2.064/,T(25)/2.060/,T(26)/2.056/
      DATA T(27)/2.052/,T(28)/2.048/,T(29)/2.045/,T(30)/2.042/
      WRITE(6,603)
  603 FORMAT(' ','ENTER NUMBER OF VARIABLES')
      READ*,V
      WRITE(6,604)
  604 FORMAT(' ','ENTER NUMBER OF CASES')
      READ*,C
      DO1 I=1,C
    1 READ(4,*)(A(I,J),J=1,V)
      DO11 I=1,C
      DO11 J=1,V
   11 B(I,J)=A(I,J)
      DO2 J=1,V
      DO2 K=1,V
      NX=C*1.
      CT=C
      SX=0.
      SX2=0.
      SXY=0.
      SY=0.
      SY2=0.
      DO3 I=1,C
      IF((A(I,J).GT.0.).AND.(B(I,K).GT.0.))GOTO5
      NX=NX-1.
      CT=CT-1
      GOTO3
    5 SX=SX+A(I,J)
      SY=SY+B(I,K)
      SXY=SXY+A(I,J)*B(I,K)
      SX2=SX2+A(I,J)**2
      SY2=SY2+B(I,K)**2
    3 CONTINUE
      R1=SXY-SX*SY/NX
      R2=(SX2-SX**2/NX)*(SY2-SY**2/NX)
      R(J,K)=R1/SQRT(R2)
      IF(R(J,K).LE.0.999999)GOTO6
      SIG(J,K)='*****'
      GOTO2
    6 SER=SQRT((1-R(J,K)**2)/(NX-2))
      RR=R(J,K)/SER
      IF((RR.GT.T(CT-2)).OR.(RR.LT.(-T(CT-2))))SIG(J,K)='*****'
      IF((RR.LE.T(CT-2)).AND.(RR.GE.(-T(CT-2))))SIG(J,K)='     '
    2 CONTINUE
      DO4 I=2,V
      N=I-1
      WRITE(6,601)(R(I,J),J=1,N)
  601 FORMAT(' ',22(1X,F5.2))
      WRITE(6,602)(SIG(I,J),J=1,N)
  602 FORMAT(' ',22(1X,A5))
    4 WRITE(6,605)
  605 FORMAT(' ')
      STOP
      END
```

APPENDIX 5

Program for calculating data from progeny-clone/site interaction experiment. (Chapter 10).

```
Command:LIST(IBAZ)
C       PROGRAM TO FIND CLONAL MEANS OF THE IB DATA
          REAL*8 ITEMNAME
        DIMENSION JCLONE(21),COUNT(21),ZCLONE(10,6,21,5),ACLONE(6,71,5),

       1 ITEMNAME(6),ASTAT(6),ERROR(21,6,5)
        DIMENSION AMEAN(21,6,5),QCLONE(71)
        DATA ITEMNAME/'BRANCHHT','LENGTH B','NODE NO ','DIAM BR ',
       1'ANGLE   ','SECONDBR'/
        DATA JCLONE /017710,017507,017510,014409,014405,017502,017505,
       1017506,
       1 017508,013709,014404,014407,016601,014401,014502,013903,014212,
       1022411,
       1 017708,014201,013705/
        DO 50 K=1,21
        COUNT(K)=0
        DO 50 IT=1,6
        DO 50 J=1,5
        AMEAN(K,IT,J)=0
        ERROR(K,IT,J)=0
         ACLONE(IT,K,J)=0
        DO 50 I=1,10
          ZCLONE(I,IT,K,J)=0
50          CONTINUE
        DO 1 I=1,71
        READ(5,100),QCLONE(I),((ACLONE(IT,I,J),J=1,5),IT=1,5)
        READ(5,102)(ACLONE(6,I,J),J=1,5)
1       CONTINUE
  100 FORMAT(I6,5F3.0,5F3.0,5F3.0,5F3.1,5F2.0)
  102 FORMAT(5F2.0)
        DO 2 K=1,21
        DO 2 I=1,71
        ITEST=QCLONE(I)
        KTEST=JCLONE(K)
        IF(ITEST.NE.KTEST)GO TO 2
        IF(ITEST.EQ.KTEST)COUNT(K)=COUNT(K)+1
        IREP=COUNT(K)
        DO 3 J=1,5
          DO 3 IT=1,6
      3 ZCLONE(IREP,IT,K,J)=ACLONE(IT,I,J)
2       CONTINUE
        DO 4 K=1,21
        DO 4 IT=1,6
        DO 4 J=1,5
        IREP=COUNT(K)
        DO 5 IIREP=1,IREP
        ASTAT(IIREP)=ZCLONE(IIREP,IT,K,J)
      5 AMEAN(K,IT,J)=AMEAN(K,IT,J)+ZCLONE(IIREP,IT,K,J)
        AN=COUNT(K)
            CALL STAT(AN,ASTAT,SE)
        ERROR(K,IT,J)=SE
      4 AMEAN(K,IT,J)=AMEAN(K,IT,J)/COUNT(K)
C       C NOW PRINT THE ANSWERS
        WRITE(6,104)
        DO 6 K=1,21
        DO 6 IT=1,6
        DO 6 J=1,5

         WRITE(6,103)JCLONE(K),ITEMNAME(IT),J,AMEAN(K,IT,J),ERROR(K,IT,J)
      6 CONTINUE

  104 FORMAT(1H1,'CLONE',' ITEM ','POSITION',' MEAN ','STANDARD ER
     1ROR')
  103 FORMAT(1H ,I6,A8,I8,2F10.5)
        STOP
        END
        SUBROUTINE STAT (BN,BSTAT,SERR)
        DIMENSION BSTAT (10)

        SUMSQ=0
          SUM=0
        IENT=IFIX(BN)
        DO 1 I=1,IENT
      1 SUM=SUM+ BSTAT(I)
        SUM=SUM/BN
        DO 22 I=1,IENT
        DIFF=SUM-BSTAT(I)
        IF(DIFF.LT.0)DIFF=(-1)*DIFF
     22 SUMSQ=SUMSQ+(DIFF**2)
          IF(BN.EQ.1)BN=2
        AMS=SUMSQ/(BN-1)
        SD=SQRT(AMS)
        SERR=SD/(SQRT(BN))
        RETURN
        END
```

APPENDIX 6

This appendix should be read in conjunction with Chapter 11.

Water vapour calibration

Calibration for the water vapour equipment, 880 model DPM was done using a WG 600 water vapour generator (ADC). This equipment was designed to produce a series of known concentrations of water vapour from a supply of dry air at a pressure of 1.4 bar.

The linear least square regression was performed for the electrical output of the dew point meter against the dew point of the calibration air over the range of 14 to 27 ^{o}C dew point.

The relationship between DPT and the electrical output gave $r = 0.998$.

Calibration of IRGA

To accurately determine the rate of photosynthesis, it is important to establish the zero point and the sensitivity of the IRGA, as the CO_2 differences being measured are very small. To enable fast and accurate calibration, the 'tube length' technique of Parkinson and Legg (1971) was used (see Sestak *et al* 1971 for detail explanation).

APPENDIX 7.

(a)

```
          LIST(H2OFLUX)
           DIMENSION DP(3),A(3)
          REAL MV1,MV2
10          READ(5,*)MV1,MV2,ALT,AL
           DP(1)=1.6454*MV1-36.7255
            DP(2)=1.6454*MV2-36.7255
          DP(3)=ALT
C          TENTENS EQUATION, THEN FIX UNITS TO CGS
          DO1 I=1,3
          A(I)=0.61078*10**(7.5*DP(I)/(237.3+DP(I)))
          A(I)=A(I)*10

1         A(I)=A(I)*0.76E-6
          DELTA=A(2)-A(1)
          E=(DELTA*0.907023*7000)/(60*AL)
           R=(A(3)-A(2))/E
            AK=1/R
          WRITE(6,101)DP(1),DP(2),ALT,E,R,AK
          GOTO10
101       FORMAT(' '3(F6.3,' '),F12.9,2F6.3)
          STOP
          END
```

(b)

```
HOST: 2972
User:EBFR13
Pass:
LOGGED ON
SS 2.03
11/05/81 17.43.41  Users=37  Fsys=10
See ALERT re next release of the Subsystem.

Group Holder : EBFR28    Funds left :  928.00

Command:LIST(CO2FLUX)
1         READ(5,*)Z,C,R,A,W
            CALIB=Z-C
                 RR=Z-R
          PPM=(RR/CALIB)*17.49
          RATE=(PPM*0.22915)/A
          RATEW=(PPM*0.22915)/W
          WRITE(6,100)Z,C,R,A,W,RATE,RATEW
          GOTO1
100       FORMAT(' ',7F10.5)
          STOP
          END

Command:
```

Computer Program for calculating (a) Water vapour conductance and leaf resistance, based on mean leaf area, (b) CO_2 flux based on leaf area and leaf dry weight basis.

Appendix 8.

```
FILE *CALIB880*
C   A PROGRAM FOR CALIBRATION OF THE 880 DEWPOINT METERS, USING
C   THE ADC WATER VAPOUR GENERATOR (WG600). DATA SHOULD BE IN A FORM:-
C   01_02_03_04_CRYSTT_DPM
C   WHERE 01 ETC. IS THE VALVE POSITION; 0 FOR OFF, VALVE NO. FOR ON,
C   DPM-DEWPOINT METER VOLTAGE.
C   OUTPUT IS ON CHANNEL SIX AND CAN BE FED TO APPLE WITH MINIMAL EDITING
      REAL*8 DATE,TIME
      DIMENSION PERC(30),DPM(30),DPT(30),01(30),02(30),
     *03(30),04(30),CDPT(30),E(30),EC(30),CRYSTT(30)
      J=0.0
      DO 1 I=1,30
      READ(5,*,END=1)01(I),02(I),03(I),04(I),CRYSTT(I),DPM(I)
      J=J+1
    1 CONTINUE
      DO 2 I=1,J
      PERC(I)=0.0
      IF(01(I).NE.0.0.AND.01(I).NE.1.0)WRITE(6,400)
      IF(03(I).NE.0.0.AND.03(I).NE.3.0)WRITE(6,400)
      IF(04(I).NE.0.0.AND.04(I).NE.4.0)WRITE(6,400)
      IF(02(I).NE.0.0.AND.02(I).NE.2.0)WRITE(6,400)
      IF(01(I).EQ.1)PERC(I)=.102
      IF(02(I).EQ.2)PERC(I)=PERC(I)+.1820
      IF(03(I).EQ.3)PERC(I)=PERC(I)+.288
      IF(04(I).EQ.4)PERC(I)=PERC(I)+.428
      CDPT(I)=((CRYSTT(I)*1.135)-11.68)
    2 CONTINUE
      CALL VAP(CDPT,EC,J)
      CALL HDATE(DATE)
      CALL CTIME(TIME)
      WRITE(6,100)TIME,DATE
      DO 3 I=1,J
      E(I)=EC(I)*PERC(I)*1/(1-(EC(I)*(1-PERC(I))/101.325))
      A=(LOG10(E(I)/.61078))/7.5
      DPT(I)=(237.3*A)/(1-A)
      WRITE(6,200)DPT(I),DPM(I),E(I)
    3 CONTINUE
      WRITE(6,300)
  100 FORMAT(1H ,/,' WATER VAPOUR CALIBRATION FOR 880 USING WG600',/,
     *' ',45('*'),//,' PROGRAM RUN AT- ',A8,' , DATE- ',A8,//,
     *1H ,' DEWPT(C)     DPM(MV)    VAPP(KPA)')
  200 FORMAT(3F10.4)
  300 FORMAT(1H ,3('-1 '))
  400 FORMAT(1H ,'****** ERROR IN VALVE DATA ******')
      STOP
      END
```