~~ECOLOGICAL~~

~~COMPARATIVE~~ STUDIES ON SEEDLING GROWTH OF TEMPERATE AND TROPICAL TREES

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by

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SUMMARY

The investigations here reported were designed to study the comparative physiological characteristics of *Quercus robur*, *Betula pendula* seedlings as influenced by aspects of soil and light environments. A comparative soil type experiment using a tropical fast-growing tree (*Terminalia ivorensis*) in addition to the temperate trees was also possible.

The investigations involved four main experiments:-

(i) The effects of nitrogen and phosphorus deficiencies in the seedling growth of *Quercus robur* and *Betula pendula*.

(ii) The effects of soil volume variation on the seedling growth of *Q. robur* and *B. pendula*.

(iii) The effects of soil type on the seedling growth of *Q. robur*, *B. pendula* and *T. ivorensis*.

(iv) The effects of shade and fertilizer on the seedling growth of *Q. robur* and *B. pendula*.

These experiments were set up to explore the limiting factors responsible for failure of natural regeneration. The first experiment involved using an artificial growing medium (peralite) fed with different types of culture solutions for the growth of the seedlings. The role of nitrogen, phosphorus, and complete absence of nutrients on seedlings was examined. *Q. robur* was more sensitive to nitrogen deficiency than to that of phosphorus. *Q. robur* seedlings performed similarly in absence of phosphorus and in complete presence of nutrients. *B. pendula* seedlings on the other hand were seriously affected by the deficiency of both elements and phosphorus seemed more important than nitrogen to *B. pendula* seedling growth.

Chemical analyses showed evidence of nitrogen deficiency in both species. In *Q. robur* phosphorus did not show any marked inbalance. *B. pendula* seedlings in a number of treatments were too small for any detailed analysis. The chemical analyses also confirmed the acorn as a main source of nutrient supply of young seedlings of *Q. robur*. Dry matter yield of *Q. robur* was not affected by soil volume variation, while *B. pendula* seedlings had growth performances almost proportional to the soil volume available. An attempt to distinguish the separate effects of mechanical impendance and aeration gave no clear-cut result.

The soil type experiment was designed to investigate the role of soil factors on the seedling growth of *Q. robur*, *B. pendula* and *T. ivorensis*. Only *B. pendula* seemed able to grow (even though slowly) on a calcareous soil, *Q. robur* did not produce new shoots at all, while a number of *T. ivorensis* seedlings died on this calcareous soil. The growth of all seedlings on two other soil types (acidic) was relatively poor. These soils were generally poor in major soil nutrients especially nitrogen, phosphorus and potassium. The fourth soil type from under a rich mixture of *B. pendula* and *Q. robur* trees produced good growth of seedlings generally. The soil was rich in the major soil elements. The analysis of plant growth showed that the three species were affected by ontogenetic drift.

B. pendula had the highest relative growth rates in all soil types, and *Q. robur* the least. Due to the nature of the different soils, the relative growth rates of the seedlings were markedly affected. On the calcareous soil, *Q. robur* and *T. ivorensis* showed no dry weight increase after transplanting. On the soil type IV the species had high growth rates which fell with time.

These results indicate that soil factors may affect the distribution of Q. robur and B. pendula, although other factors were also thought to interact with soil nutrients.

The effects of shade and fertilizer on the seedling growth of Q. robur and B. pendula was investigated by growing these seedlings in shaded enclosures providing 30%, 10% and 5% approximately of total daylight. The soil condition on which the seedlings were growing was also varied by growing some seedlings in ordinary garden soil and others in garden soil mixed with a level of John Innes fertilizer. While all the seedlings of Q. robur in 5% light survived but without further growth, all the B. pendula seedlings in 5% light died within one month. The best growth for both species was in 30% light. Q. robur was not influenced by the fertilizer treatment. The fertilizer addition was significant to the B. pendula seedling only in the 30% light and only towards the end of the season. The fertilizer effect was also thought to have increased the susceptibility of B. pendula seedlings to fungal attack in the 5% light. B. pendula showed adaptation to shading by increasing specific leaf area.

The experiment on various degrees of shading on B. pendula seedlings previously grown in 100% daylight helped to clarify some points about this species under shade. The results of the specific leaf area values increasing with shade confirms the fact that B. pendula might probably withstand some shading if for example it was able to put up some growth under a temporarily open canopy. The results also indicate the fact that B. pendula would respond favourably to fertilizer application at this seedling stage, if the light condition is adequate. The performance of B. pendula seedlings in 25% and 85% daylight were quite comparable.

In conclusion, it was believed that light was the major important factor of the environment (apart from biotic factors) affecting natural regeneration of Q. robur and B. pendula seedlings in British semi-natural forests, except in certain types of soils, for example on certain calcareous soils. Further studies on these seedlings especially in relation to their herbaceous competitors was recommended.

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CHAPTER I

GENERAL INTRODUCTION

GENERAL INTRODUCTION

A. General Historical Review

Man has been associated with the forest from very early times by dwelling in it, hunting for food and making medicine from the forest organisms. Wilde (1946) reported that early man made observations on the relationship that existed between the soil and forest vegetation.

The increase in knowledge in science from the early times brought about a more systematic study of the forest, especially from the edaphic view point. As food had been more important to mankind than wood production, it was agriculture rather than forestry that a relationship between chemical factors and productivity was first diagnosed (Earl of Dundonald, 1795; and Darwin, 1800). However a more general relationship between the soil and silviculture had earlier been appreciated (Bacon, 1627; Evelyn, 1674; Carlovit, 1713; Duhamel, 1760; Hartig, 1791).

The beginning of the 19th Century saw further integrated studies being done between chemistry, agriculture and forestry, including those of Cotta (1809), Hundeshagen (1830), and Schantz (1823). Grebe, a German forester, probably started the physiological-ecological approach to forestry. He was quoted by Cotta in 1844 as follows:- "As silvicultural horizons widen, the importance of environmental conditions becomes more pronounced. It appears clearly to the foresters that the form of forest management is determined by a number of physical influences related to topography, geology, type of soil and climate." Pfeil (1860) was another German with similar thoughts with Grebe.

Historical reviews of Wilde 1947; Goodall and Gregory 1947; and Gardiner 1968, were consulted for details of older works which have not been seen by me. Lamb and Ntima (1971) was similarly consulted for T. ivorensis

Both workers contributed greatly to new ideas of forestry practice at this period.

The beginning of the twentieth century marked an era of intensive research in forest soils and tree growth. This enabled foresters to begin integration of soil science and silviculture. Russian workers including Glinka (1908) and Gedroiz (1912) made valuable contributions at this stage.

Related observations on plant environmental requirements, made by such ecologists as Sukachev (1913) of Russia and Cajander (1909) of Finland, led foresters to classify sites on a botanical basis.

About this same period (1890-1919) the Americans were also working towards the goal of forestry management based on ecological principles. Workers in the American field included Merriam (1898), Cowles (1899), Hilgand (1906), Bownran (1911), Bray (1915), Clements (1916) and Toumey (1916).

Plant nutrition studies have been going on since the time of Liebig (1840). Such investigations involved the addition of artificial fertilizers to crop soils in the field with observation of the resultant effects on plant performance. Other workers at this stage included Lawes and Gilbert (1895). Errors due to different sites and the seasonal factors were not considered so that general inferences were difficult to make. Furthermore, this method of determining plant fertilizer requirement was expensive. This field trial method is still applicable today, but usually in conjunction with pot or water culture methods (Goodall and Gregory, 1946).

The pot culture method was developed to reduce costs and is more controllable. Workers who first used the pot method included Mitscherlich (1925), Stewart (1932), Behrens (1935), Gilbert and Pember (1935), Capo (1938), and Fernes and Trumble (1943).

The pot methods also have various disadvantages including the indirect application of their results to general field conditions. Gerlach (1926), Schuster and Stephenson (1940) and Goodall and Gregory (1947). Nevertheless, the pot methods make it possible to study single effects of the soil environment whereas in the field the complex interactions are difficult to sort out. As already stated, a combination of methods is most effective in determining such factors as plant nutrient requirements.

Nutritional studies in plants were necessary when it became clear that due to soil nutrient deficiencies, plant growth was abnormal. Such deficiencies (called diagnostic symptoms) were recognised in many plants by such workers as Jones (1929), Piper (1940), and Wallace (1943). The symptoms included various disturbances of growth especially abnormalities in form and colour of leaves. Many workers have given evidence of the difficulty of interpreting deficiency symptoms in plants in relation to soil elements and plant growth. Chapman et al (1939), Chapman and Brown (1941, 1941a, 1942), Wallace (1943), Drosdoff and Kenworthy (1944), Goodall and Gregory, (1947). Consequently deficiency symptoms have limited applications in nutritional studies.

Attempts were also made to solve fertilizer requirement problems by simply analysing soil samples before applying fertilizers. A relationship between soils and plants had been established Wilde (1946). The methods of soil analysis however frequently produced results without any correlations between soil chemical compositions and plant growth, Hall and Plymen (1902). There was at this time a temporary decline in soil chemistry studies, attention was now moving to soil physics (Wilde 1947).

Soil chemistry with improved methods of analysis available soon played a major part in plant nutrition studies. Prominent workers who applied such methods in tree studies included Samson (1912), Nemec and Kvapil (1925), Asltonen (1925), Hartmann (1925), Wherry (1927), Frank (1927) and Wilde (1934). Such studies included the classification of plants into two main groups, those preferring acidic and those of basic sites. They were also able to relate other soil conditions as low availability of nutrients to these groups wherever appropriate. Magistad (1925), Wilde (1947).

Pioneers in chemical plant analysis as an index of available nutrient supplies were Liebig (1840), Weinhold (1862, 1864), Hellriegel (1867), Heinrich (1882) and Helmkampf (1892). Various parts of the plant were analysed and conflicting views were held about what part of the plant showed the most correct relationship to the soil condition. Most of the studies were in food crops. Atterberg (1886, 1887, 1887a, 1887b, 1888a, 1889 and 1901) used sand culture and field methods on oat. Goodall and Gregory (1947) reviewed the use of plant analysis, especially of leaves for assessment of plant nutritional status. In addition to soil analyses, investigation of the chemical composition of plants was essential in determining their nutritional requirements.

The various site factors affecting tree growth include the following (i) Climate including radiation, air temperature, rainfall, relative humidity and wind; (ii) Topography including physiography, aspect and slope(iii) Soil-texture, structure, pH, ground water, mineral nutrient status and temperature; (iv) Biotic factors associated plants, animals above and below soil.

The complexity of these interacting factors as they affect tree growth involve various methods of studying.

For instance the trees themselves show various characteristics due to the site quality. Since the site is a dynamic ecosystem with many interacting parts, the best estimates are those of the important factors of the ecosystem Spurr and Barnes (1973).

In this work the aim was to consider the adaptations of two temperate trees, Betula pendula Roth. and Quercus robur L. to particular environmental conditions. The two trees, sometimes (but not always) associated together, are widespread in semi-natural woodlands in Britain. Q. robur is the more important species economically and historically. A fast-growing tropical Nigerian rain forest tree was also selected for comparative studies.

B. Review of literature on Quercus robur, Betula pendula and Terminalia ivorensis

Q. robur a member of the family Fagaceae is a native tree of Britain, belongs to a large genus of shrubs and trees distributed throughout the temperate regions of the northern hemisphere. It is sometimes called the Common Oak or pedunculate oak. It is the characteristic dominant tree of clay and loam soils in most parts of England. It is also dominant or co-dominant with Q. petraea on the damper acid sands. Q. petraea is the common species in Wales, Ireland and the West of Scotland (Clapham, Tutin and Warburg, 1952; Jones, 1959). Q. robur grows up to 30-40m in height and is a deciduous woodland tree.

B. pendula Roth. (B. verrucosa Ehrh.) * is another British nature tree, it is commonly called Silver Birch, and it grows to 25m on lighter soils. It colonizes healthlands, and forming woods there as a successional stage to mainly Q. petraea.

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* The nomenclature of British plants in the thesis follows Clapham, Tutin and Warburg-that is Flora of the British Isles.

It is more common than B. pubescens in dryer conditions of South England. It is also distributed in many parts of the temperate northern hemisphere. Clapham et al describe it as rare on chalk. Like Q. robur, B. pendula (a member of the Betulaceae) is a deciduous tree.

Terminalia ivorensis A. Chev belongs to the family Combretaceae. It is being used in timber plantations by tropical silviculturists. T. ivorensis is native to tropical Latin America as well as tropical West Africa. In Nigeria, it is widely distributed but not common. Lamb and Ntima (1971). It is also a deciduous tree, and grows up to 45m.

Betula spp. are also generally treated as the Quercus spp are in Britain. Neither species of Betula is used in plantations and are part of the small percentage of semi-natural woodland left in Britain. Betula spp are sometimes used ornamentally. Terminalia ivorensis is a major Nigerian export tree, but many forests in which it occurs naturally now have very low productivities generally. Bamgbala and Oguntala (1973).

Salisbury (1916) perhaps was the first to make a detailed investigation involving studies of aerial and soil factors in relation to the distribution of Quercus robur and other associated species in Hertfordshire woods. He took measurements of temperature, rainfall and humidity and he also obtained information on soil acidity, water content and humus status. Finally he distinguished between the light phase and the shade phase before associating species societies to these factors of the environment. This was obviously a stage beyond the general observation type of study which prevailed before his time.

Yet these studies did not deal much with seedling performance of the Q. robur trees as influenced by the environmental factors analysed.

Secondly, the biotic factors operating in woodland regeneration were not considered, Watt (1919) dealt with the failure of natural regeneration in British oakwoods. He attempted to follow the route of the acorns (fruits) from the time of falling in autumn to seedling germination and establishment stages. Prolific production of acorns and germination of numerous seedlings were followed by the disappearance of these seedlings in later seasons. Watt investigated the roles of animals, parasites leaf defoliators light and other factors, on the fate of the acorns and seedlings. This indeed was the first experimental ecological approach to studying the regeneration of British oakwoods. In his conclusion, he stressed the major role of animals in destroying acorns, and pointed out that certain seed beds in dry oakwoods were unfavourable for acorn germination. Finally, he associated fatal effects of fungi on oak seedlings with diminishing light supply. Watt has indicated the suitability of certain soil types to favourable seedling germination and he has identified the light factor as a major condition for seedling establishment, even with the relatively simple experiments carried out.

Between 1919 and 1939, very little progress was made in determining the failures of natural regeneration in British oak woods. This view was confirmed by Tansley (1939) who remarked that "The intensity of light required under different conditions for the vigorous growth of oak seedlings has never been exactly determined; but it is certain that the oak is a 'light demander' through all stages of its life-history, and that seedlings flourish best in the open or in the lightest of shades."

Until Saxon times, most of Britain was covered by forest, with Q. robur as an important, often dominant, species. Felling of oak has probably exceeded re-establishment ever since Roman times. Tansley reported 6.4% and 3.1% oakwood cover for Hertfordshire and Essex respectively, while Streeter (1973) quotes 8% as the total woodland cover for Britain, only about 13% of the woodland area being oak. Fast-growing conifers predominate in timber plantation areas, and oakwoods are maintained principally for their amenity value and for conservation purposes.

In 1954, Fairbairn attempted quantifying the relative shade-casting properties of different types of forest and of individual oak trees. He used photo-electric cells and obtained percentages of shades in relations to total day light. His conclusion was that Q. petraea casts more shade than Q. robur; this may have ecological importance, especially in relation with seedling regeneration, although Fairbairn did not deal with this aspect.

The first detailed review of Quercus species in Britain is that of Jones (1959). Jones dealt mainly with the taxonomy, morphology and general ecology of the genus raising a number of points relevant to this work. Q. robur he says prefers more basic soils, rich in mineral nutrients, combined with a tolerance of water-logging. He states that Quercus leaves decay faster than those of Betula in relation to soils, he concludes that "there has been very little experimental study of the relation between soils and growth."

On the influence of density of planting or natural occurrence on the height performance of Quercus sp., Jones made the following statement:

"It is notorious that the height attained by Quercus depends greatly on its density and on the species with which it is mixed; given plenty of space, the tree spreads rather than grows in height. Conspicuous though this phenomenon is, it is difficult to find figures to demonstrate it."

The effect is usually presumed to be connected with shading, but this hypothesis does not appear to have been critically tested for large trees.

In relation to light requirement, Jones did not quantify the need of Q. robur, but referred to "sufficient light" or "moderate shade" or "abundant light". Obviously there is need to determine the actual light requirement, for better silvicultural management. Jones however pointed out that "The general character of the field-layer is determined not only by the soil but to an even greater extent by the desity of canopy, amount of litter and the silvicultural treatment." This inference on shade and nutrient uptake poses yet another challenge for experimental work. Mihovic (1952) quoted by Jones believes that the mycorrhizal fungi are carried by the acorns. If this is correct, then the possible advantages are to assist the young seedlings in nutrient uptake especially at the early stage.

Finally, Jones believes that in a thicket of Rosa, Crataegus and Betula, Quercus saplings show remarkable ability to struggle upwards and frequently regenerate when gaps arise in the woods. Thus it behaves like a pioneer when occasion demands. While Q. robur regenerates more freely in open speces, Q. petraea does so in moderate canopy. Mention was also made of animal and pathogen effect on acorns and young seedlings, although no experimental evidence was reported.

Studies on the physiological ecology of Quercus species have been prominent in the period since 1960. Ovington and Macrae (1960) investigated the roles of shade and soil type on the seedling growth of Q. petraea. They concluded that shade was more effective than soil type in controlling seedling growth, and considered that relative insensitivity to soil type was an effect of acorn reserve. It is desirable to explore further the different roles of shade and soil type. Jones (1959) has pointed out the possible interaction of shade and soil on plant growth; the role of the acorn needs fuller study in relation to the shade-soil effects.

Jarvis (1963), studying acorn size effects on Q. petraea seedling growth, observed that the relative growth rates of the seedlings were independent of size and origin of acorn, but that the size of the seedlings at harvest was linearly related to the acorn size and that the cotyledons were exhausted in one season's growth. Jarvis (1964) went further in his studies of Q. petraea. Using growth analysis methods, he observed that Q. petraea has shade adaptability similar to that described of other shade plants. Compensation point for this species was between 2 - 6% daylight. Shaw (1968) performed a quantitative study of the role of biotic factors in the failure of germination of acorns. He claimed that up to 99% of the acorns are destroyed annually soon after falling in autumn, by various predators, mainly rabbits. Those that escaped predation were those covered by litter and were able to germinate in the following spring. This experiment shows clearly that control of acorn predation or, at least, efficient management of seedling development is vital to the regeneration and maintenance of Quercus woodlands. This emphasizes the need for further studies of other aspects of the environment especially light and soils as they affect the natural regeneration of the species.

Newnham and Carlisle (1969) performed perhaps the most detailed nutritional studies on the Quercus species. Using mainly sand-culture technique, they found the optimum nitrogen and phosphorus requirements of the species. The work also involved plant chemical analysis. The studies confirmed the view of Jones (1959) that Q. petraea and Q. robur tend to grow on different sites. Newnham and Carlisle observed that Q. robur is more tolerant of low nitrogen supply than Q. petraea.

The results indicated nutrient deficiencies at certain culture concentrations, and this was confirmed by soil culture experiments, yet the actual role of the acorns was not explored. Milles (1972) sowed Q. robur acorns on bared ground and followed the establishment procedure on an English heath. He confirms Shaw's (1968) view of acorn predation by rabbits. In his conclusion he did not believe that the seedling stage was necessarily more critical than other stages.

Tansley (1939) dealt with the distribution of birch Betula pendula and B. pubescens as native British trees. Tansley considered birch and pine woods together because according to him they have closely similar requirements and considered them both as climatic climax species in the conditions of the uplands of northern Britain. He further stated that "Birch gives way to pine in direct competition on soils favourable to both, but maintains itself better (though making very poor growth) under generally adverse conditions of soil and climate." Apparently the reference of birch and pine as climatic climaxes must be related to soil types as well. He also recognized an oak-birch-heath situation which he claimed is maintained by perpetual human influence.

Jones (1959) also confirmed the association of Quercus spp. and Betula spp. on nutrient deficient soils, where Jones claimed that Betula behaves as a pioneer after felling or fire. Unfortunately there are no experimental evidence to justify this claim as far as Betula in the British Isles are concerned. The rarity of birch on calcareous soils was also reported by Jones. In Scotland, birch is the commonest natural woodland type remaining especially in the highlands Kinnaird (1970). Here (in Scotland) McVean (1964) claimed that the taxonomic situation is difficult and imperfectly known. He also recognized distribution of the birches along soil type lines.

The failure of natural regeneration of birch woods has been reported by the U.K. Nature Conservancy, Kinnaird (1970). Ovington and Madgwick (1959) had earlier stated that natural regeneration of birch in Britain was unreliable, hence the tree was rarely used by British foresters. They stated also that the approach has changed to growing birches as plantation trees (commonly with pines) rather than depending entirely on natural regeneration. About the same time Nature Conservancy workers at Merlewood were studying the effects of site factors on a mixture of Quercus petraea, Pinus sylvestris and Betula pendula. (U.K. Nature Conservancy Report 1958). It was observed that B. pendula had, when growing in natural sands, higher nutrient-uptake and productivity rates than P. sylvestris in plantations at the initial state, but that this phenomenon was not maintained when the canopy closed. The pine productivity then became greater than that of birch, suggesting that Briches are intolerant of shade.

The degree of intolerance needs quantitative study. Ovington and Madgwick (1959), believed that once woodland conditions are created in the plantations, natural regeneration may be of increased importance. By studying the rate of dry matter production of birch natural woodlands, they obtained figures which proved that up to a certain age birch natural woodlands were more productive than pine plantations, (Pinus sylvestris). They observed that natural stands tend to attain maximum site utilization, with dry matter production exceeding that of plantations. The necessities with regard to birch are (i) an adequate supply of viable fruits and (ii) suitable site conditions. Birches produce more than enough fruits annually and it is more likely that site conditions are the real limiting factors for good establishment of birch woods. Consequently, studies into site factor (climatic and edaphic) preferences are needed for a basis of better birch forest management. The stoppage of growth increment with age may have to do with root restriction of the birch trees, this again needs some experimental explanation.

Site factors in forestry include both the aerial and subterranean factors. Wilde (1946). Light as a major factor in affecting Birch distribution in British woods has long been recognized Tansley (1939). McVean (1964) stated that in Scotish birch woods, root competition as well as light reduction are among factors hindering regeneration. Grime (1966) classified Q. robur as shade-tolerant and Betula lenta as shade-intolerant. In an initially heavily stocked natural woods of birch, Ovington and Madgwick (1959) noted that 50% mortality occurs every ten years, death causing reduction in stocking density till a few trees become dominant.

Often the role of the different factors could not be separated. Experiments on B. pendula were planned to investigate some of these factors individually (others controlled as much as possible). The interaction of light and nutrients was also studied to some extent.

It has been claimed that in some conditions birch promotes the growth of other species. Cotta (1817) thought that the role of birch was to provide shade for beech, while Pfeil (1860) suggested mixed planting of birch, pine and beech. Conflicting views (van Fiscloach, 1892) on the merits of birch were also held at this period. Birch has also been described as improving the quality of soils for forestry (Gardiner, 1969). Dimberley (1951, 1952a and b, 1953) claims that birch roots are superior to those of pine in penetrating and exploiting the subsoil. Podsolisation and general soil deterioration may follow establishment of conifers, as has been observed by Kennedy (personal communication) in Picea sitchensis planations in Wales; birch may be capable of reversing these soil changes. The U.K. Nature Conservancy in its 1958 report, while studying the role of birch in regard to soil fertility stated that "the maintenance of soil fertility is important in forestry as well as in agriculture. It is important to select tree species for afforestation that will conserve the soil and improve its fertility."

Ovington and Madgwick (1959) observed that birch stands (natural woods) return up to 50% of nutrient uptake annually in terms of leaf fall. This, in conjuction with rapid decay of birch litter, promotes a high rate of nutrient cycling in birch woodlands.

Terminalia species are reported to be distributed throughout the tropical and subtropical region of the world (Royen 1964). The two major species in Nigeria are T. superba and T. ivorensis, in various localities throughout the rainforest (Griffths, 1959 and Keay et al 1960). T. ivorensis is well distributed in sites with rainfall of above 50" (1270 mm) p.a. and cannot withstand drought. It also prefers low altitudes 2000-4000ft. (610-1219m), although it fares badly in valley bottoms Lamb and Ntima 1971).
T. ivorensis is a good coloniser of abandoned farmlands, Richards (1952) in a general description of the West African rainforest described Terminalia sp. as "a common forest storey tree," i.e. an emergent in the upper storey of the forest. T. ivorensis grows best in sandy loams of Western Nigeria, though it prefers lateric loams in Sierra Leone and clay loams in Tanzania Willan (1966). The unsuitable sites as far edaphic factors are concerned include water-logged clays, dry sands and grassland areas Lamb and Ntima (1971). There are unfortunately no experimental data to describe the response of T. ivorensis in relation to soil factors. Jones (1969), quoted by Lamb and Ntima (1971) stated that "Thre is an evidence in the Pra-Annum Forest Reserve in Ghana, of wide scale mortality in a plantation planted in 1933 using Taungya technique. (silviculture combined with crop growth between young trees) - Originally Cedrela and Terminalia were mixed but the Cedrela was poisoned in 1963. An increment plot revealed no growth of the Terminalia between 1958 and 1962, when trees started to die. By 1966 nearly all the T. ivorensis were dead." Lamb and Ntima remarked that "this site may have been unsuitable for the species." This is a reason why detailed site studies (edaphic and climatic) in relation to the growth patterns of these trees are important to the successful culture of Terminalia.

The natural regeneration of T. ivorensis (and of all natural rainforest woodland trees) in Nigeria is very poor Bamgbala and Oguntala (1973). In an attempt to promote the natural regenerations of various rain forests in Nigeria, a system of removing unwanted trees and climbers in order to create more gaps in the canopy (called the Tropical Shelterwood System) was started about 30 years ago. Although this method proved successful in Malaysia, in Nigeria, it promoted the growth of weeds and climbers in the gaps, which the desired species could not grow through. Lowe (1971) personal communications. Jones (1969) stated that light seems to be important for the growth of T. ivorensis. Lamb and Ntima (1971) claim that the natural regeneration of T. ivorensis is fairly good especially in areas with ample overhead light or in cleared areas. This view is supported by the fact that the artificial regeneration of this species is good, i.e. growth in 100% light. The optimum light regime for the growth of T. ivorensis is still required, especially as these workers also stated that shade is applied to young seedlings (but removed as soon as possible). Thus the seedling stage obviously does not respond favourably to total daylight.

Although the planting of T. ivorensis has been going on in Nigeria since 1928,(Mackay, 1953 ; Lowe 1965), very little is known about its growth characteristics from an experimental view point. Wadsworth and Lawton (1968) pointed out the scarcity of information on growth rates of herbaceous and woody tropical plants.

Damptey (1964) found the growth pattern of T. ivorensis to take the form of short "bursts" followed by slower growth. He also observed that T. ivorensis responds unfavourably to short day periods (11 hours) and cool nights 20°C. Longman (1969) from a grafting experiment confirmed Damptey's findings that even mature trees also respond to factors of daylength and temperature. Under nursery condtions, Jones (1969) recorded 25-50% germination for T. ivorensis

Okali (1971) in Ghana performed an analysis of grwoth of four tropical forest tree seedlings (including T. ivorensis and Helianthus annuus) with the view of ascertaining whether woody plants in the tropics have a lower assimilation rate than herbaceous plants. He found that the three species, Chlorophora excelsa, Musanga cecrepioides and Terminalia ivorensis had lower net assimilation rates than Helianthus annuus and also that among the woody species T. ivorensis had the highest relative growth rates. The plants were grown in full daylight.

In another complementary experiment using the same species as above Okali (1972) using the growth analysis techniques, found no great disparity between the woody plants and Helianthus in adaptation to light since both require high light intensities for maximum growth, he concluded. Okali suggested that T. ivorensis behaves as a pioneerspecies. This also confirms the observations of Jones (1969) and Lamb and Ntima (1971). Up to 98% of Nigerian forests belong to the natural forest zone, that is plantation forests produce only about 2% of present Nigerian forest needs. Yet it is now clear that the system of promoting natural regeneration or in some places line planting still leaves the forest stocking of desirable species low. It appears that conditions for optimum growth must be created within the forests. It is also likely that biotic factors (especially animals feeding on tree fruits) might be other factors influencing failure of natural regeneration. The edaphic factors and light requirements similarly require additional studies.

Lundegardh (1931) also emphasised the importance of studying tree juvenile forms, and pointed out that while physiological characteristics play an important part in the survival of plants, little is known of the physiological features of many species. Quantitative study of the physiology of plants in relation to environmental variation now forms an important part of experimental ecology. Thus there is sufficient justification for studying aspects of seedling growth in trees when considering factors affecting their success in various conditions.

The factors influencing the natural regeneration of _Q. robur_ and _B. pendula_ in the British Isles might not be dissimilar in principle to those affecting _T. ivorensis_ and other trees in Nigeria and elsewhere. A comparative study of the temperate tree seedlings with the tropical _T. ivorensis_ might reveal similarities or otherwise between the species, and this could give clues to the failure of their natural regeneration in their respective habitats.

The observations and experiments already reviewed in relation to the chosen species indicate that studies of adaptation to extreme edaphic and shade factors seem the most urgent problems in ecological studies on these species. A series of experiments to test the responses of seedlings to these factors were designed and carried out. The experiments dealt with growth in simplified environments, on the principle that in such conditions it should be easier to identify the responses of plants to the environmental features which were deliberately varied.

C. Aims and scope of the present study

In sequence of procedure, the following experiments were carried out:-

(i) The effects of nitrogen and phosphorus deficiencies on the seedling growth of Q. robur and B. pendula.

(ii) (a) The effects of soil volume variation on the seedling growth of Q. robur and B. pendula.

  (b) The effects of pot enclosure on the seedling growth of B. pendula.

(iii) The effects of soil types on the seedling growth of Q. robur, B. pendula and T. ivorensis.

(iv) (a) The effects of shade and fertilizer on the seedling growth of Q. robur and B. pendula.

  (b) The effects of shade and fertilizer on the seedling growth of B. pendula previously grown in 100% daylight.

The aim of these experiments was to explore the roles of certain components of the aerial and soil environment, as they influence the growth and distribution of these seedlings; with the view of obtaining some explanations to their natural regeneration problems.

The roles of individual ions, the influence of limiting soil space (volume) and soil type variations were conceived as factors of the soil environment worthy of being studied in relation to the growth of these seedlings.

Light (or shade) was considered as an important factor of the environment studied in relation to nutrient uptake of the Q. robur and B. pendula seedlings.

The investigations here reported were carried out under greenhouse conditions.

The use of greenhouse conditions had practical advantages, in promoting rapid growth, and in allowing some control of the aerial environment. Great caution is however essential in applying conclusions from greenhouse work to field conditions.

CHAPTER II

METHODS OF SOIL AND PLANT ANALYSIS USED IN THIS WORK

Preparation and Methods of Soil and Plant Analysis used in this work

Preparation of Soil Sample
(For all determinations in the work unless otherwise stated.)

The soils used in this work were collected and stored in polythene bags prior to their use. The soils were thoroughly mixed and a sample portion was taken after the removal of big stones, undecomposed plant and animal debris.

The big lumps were broken up and the soil was air-dried for three days. Humus mats and soil clods were crushed in a mortar, the soil was then sifted through a 2 mm. mesh diameter brass sieve which retained stones and gravel. These were weighed and the "fine earth" material was also weighed to give approximate percentage values for soil particle-size composition. The "fine earth" samples were then labelled and stored in small polythene bags.

Determination of the Hydrogen Ion Concentration

A sample sieved, air-dried soil was mixed with aerated distilled water in the ratio of 10gm. soil : 50ml. water and shaken for 50 seconds.

The soil/water mixture was placed near the glass electrode for about 15 minutes to attain a constant temperature with the equipment. The pH was later read directly.

Determination of Percentage Loss on Ignition

The soil samples were oven-dried at 80°C for 12 hours, and weighed. They were then transferred into a muffle furnace. (see Piper 1942). The temperature was raised to 450°C, and maintained at this temperature for about 30 minutes. The samples were later cooled in a desiccator and weighed to obtain the weight due to loss on ignition.

Determination of Exchangeable Hydrogen

A sample of air-dried and sieved soil was suspended in normal ammonium acetate at pH 7.0. The 1:10 mixture was allowed to stand for 1 hour with occasional shaking, after which the pH was determined on the mixture.

The method just described follows that of Brown, (1947) and Schollenberger and Simon, (1945) up to this point. In order to obtain the values of milliequivalents of exchangeable hydrogen Brown read off his values from a curve produced by plotting pH values of ammonium acetate leachates against a series of milliequivalents obtained by titration.

In this work to obtain the milliequivalents from the pH values, the following procedure was employed. N/10 HCL was added at intervals to a known volume of ammonium acetate (the same volume used for the soil samples). The pH change observed was plotted against the increase in volume of the N/10 HCL (see Fig. II-1) For every 1ml. N/10 HCL applied, it was assumed that the milliequivalents exchangeable hydrogen was 0.1. Thus exchangeable hydrogen values of the soil samples were read directly from this curve. The values obtained from this method agreed well with those read from Brown's curve or calculated from the equation derived from it by Jackson (1958).

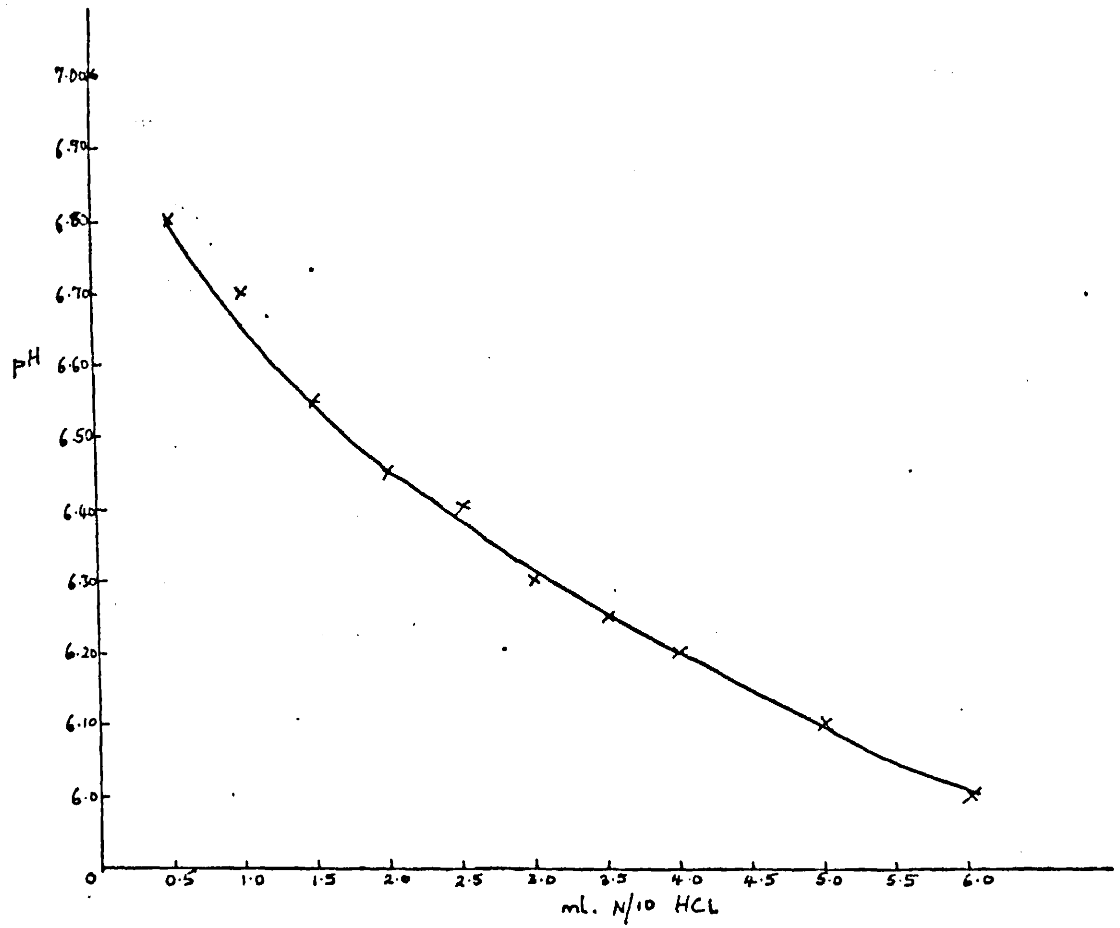


Fig. II-1 Curve produced for the determination of soil exchangeable hydrogen. See Chapter II for details.

The Determination of Exchangeable Bases

A suspension of soil sample in normal acetic acid was shaken intermittently for 1 hour. The pH of the suspension was determined by means of a glass electrode. This method was also based on Brown's up to this point.

Brown obtained a curve from which he read his values, by plotting the pH of normal acetic acid - soil mixtures against the bases found by analysis of ammonium acetate leachates of a series of soils.

In this determination, the pH changes of normal acetic acid to which N/10 NaOH was added at intervals was recorded. The pH values were plotted against increase in volume of N/10 NaOH to obtain a curve from which the milliequivalents of the soil samples were obtained directly. This was possible because of the assumption that for every ml. of N/10 NaOH added, there was a corresponding value of 0.1 milliequivalent.

Again the values of exchangeable bases obtained by this adaptation agreed well with those obtained from Brown's curve, or from the equation derived therefrom by Jackson.

This adaptation has the advantage of a greater pH range (2.3 - 3.5) for milliequivalents determination compared with Brown's of pH 2.30 to 2.90.

The Determination of Sodium and Potassium

(Flame Photmeter method)

Leaching with Normal Ammonium Acetate at pH7

The method of leaching used to extract available cations from the soil was an adaptation of that of Schollenberger and Simon (1945).

The extractant solution used was normal ammonium acetate at pH 7. A 1:10 soil sample and N ammonium acetate mixture was shaken for a few minutes and then allowed to stand overnight. Filtering was done with Whatman No. 42 filter paper.

Samples were analysed using an EEL flame photometer and their concentrations obtained from standard curves produced for sodium and potassium. The standard solutions were made up in N. ammonium acetate. The concentration values obtained were later converted to milliequivalents per 100 gm soil.

An attempt was made to read the values of concentration of calcuim and magnesium from this ammonium acetate leachate, using the EEL flame photometer. This was not possible because of the difficulty in suppressing the actions of the interfering ions. Consequently the titration method was used as discussed elsewhere.

Estimation for total calcium and magnesium

The sodium carbonate fusion as a method of liquefying the soil samples was used in preference to the hydrogen fluoride method because of the less risks involved in the former.

This fusion method (after Jackson 1958) involved igniting samples of dry soil sodium carbonate with a Meker burner flame, till the mixture (soil - sodium carbonate) was liquefied.

The thinly spread paste was later dissolved in water, for the estimation for calcium and magnesium. One of the difficulties encountered in this determination was the presence of interfering ions Piper (1950), Jackson (1958), Heald (1965), Hesse (1971) such as reffous iron, manganese and phosphate. Reagents such as cyanide and hydroxylammonium chloride have been used to suppress or render in active interfering ions. Heald (1965) used standard EDTA in excess to remove phosphete interference. The ammonium hydroxide - bromine separation method Jackson (1958) was found most suitable. This separation was carried out before titrating with versene (EDTA). For calcium determination, murexide was used as indicator: magnesium determination was carried out on the same sample after the destruction of the Murexide indicator with bromine water. The solution was titrated further with versene, using Eriochrome Black T as indicator. Calcium and magnesium concentrations in the soil samples were then calculated. The details see Jackson (1958).

Estimation of available phosphorus

Soil phosphorus can be considered as non-available, potentially available and immediately available phosphorus. Plants are believed to take up inorganic phosphorus from the soil solution in the form of orthophosphate (Hesse, 1971).

Of all the methods mentioned in the literature for the extraction of available phosphorus (there is no one method that can be called ideal, it all depends on the kind of soil being investigated and the aims of the determinations) the method chosen was the sodium bicarbonate extraction method. Olsen et al (1954), found a high correlation between sodium bicarbonate extractable phosphorus and uptake of phosphorus by plants.

A mixture of soil sample, activated charcoal and sodium bicarbonate at pH 8.5 was shaken intermittently for 30 minutes, then filtered with Whatman No. 42 filter paper. The colorimetric method was used to estimate for phosphate in solution.

The chlorostannous acid reductant method in hydrochloric acid was used for the soil samples, whereas the chlorostannous reductant method in sulphuric acid was considered suitable for the range of plant samples. All samples were read at 660nm. transmission on the Beckman spectrophotometer. Standard curves were produced from solutions made with the extraction solutions in the soil and plant samples respectively. For details of methods see Jackson (1958) and Hesse (1971).

The sodium bicarbonate solution was prepared freshly each time a batch of determination was to be made. The stannous chloride was stored in a device that prevented contract with air and new solution was prepared at monthly intervals. The temperature was kept at 20-25°C during the determinations. These devices reduced possible sources of variation in the analytical results. See Hesse (1971).

Digestion of Plant Samples for Sodium, Potassium and Phosphorus determination

The plants parts analysed in this work include leaf, stem and root of Q. robur and B. pendula. The acorns of Q. robur were also analysed as stated in the nutrient deficiency experiment Chapter III.

The plant parts, oven dried at 80°C for 48 hours were cooled in a desiccator prior to weighing for digestion.

The digestion method used was the wet digestion type after Piper (1942) and Jackson (1958). The ratio of the digesting acids, Perchloric acid (sp. gr. 1.54) (Sulphuric acid 98%) and nitric acid (sp. g. 1.42) used was 1 : 2 : 2 respectively. For samples over 5 mg., 5 ml. of acid mixture was used. When very small samples less than 5 mg. were being digested the volumes of acids used were proportionally reduced.

The EEL flame photometer was used to read luminousity values for sodium and potassium concentrations in the samples. The standard solutions included a known volume of the mixed digesting acids.

The solution obtained from this digestion was also used for the phosphorus determination as reported elsewhere.

Nitrogen Determination

The principle involved in this determination is the estimation of nitrogen that is convertible from soil and plant samples into gaseous ammonia by a combination of several processes. The gaseous ammonia is then absorbed by an acid and estimated by a titration method. This is the basis of a Kjeldhal - Conway micro-method for the determination of nitrogen.

The method is mainly in two parts (i) the digestion and (ii) the micro-diffusion (Conway, 1947).

(i) The Kjeldhal digestion

Various workers have discussed the main difficulties that must be considered for a successful digestion. These include (i) the type of nitrogenous matter involved as it affects the speed and completeness of digestion (Steward & Durzan 1965). Other factors which affect the rate of digestion and the completeness of digestion discussed in the analytical literature include the digesting temperature and the kind and amount of catalysts. (Conway, 1947; Jackson, 1958). The completeness of the recovery of nitrogen has also been evaluated. The following method was used to digest soils and plant samples used in this work.

1gm. soil sample was digested in a Kjeldhal 30 ml. flask using 5 ml. conc. sulphuric acid, Plant samples which had been dried for 48 hours were digested using a minimium of 2.5 ml. conc. sulphuric acid for samples below 5 mg. and 5 ml. of conc. sulphuric acid for samples 5 mg. or over. By appropriate manipulation of the amount of sulphuric acid in digestion and the final volume to which the digest was diluted, it was possible to estimate nitrogen content of plant samples as small as 5 mg.

The Kjeldhal catalyst tablet was used. Digestion was complete in both soil and plant samples in about 4 hours of digestion following a method similar to Jackson (1958).

(ii) The micro-diffusion

The micro-diffusion technique for estimating the ammonia nitrogen is basically a Conway (1947) adaptation. Boric acid containing bromcresol green and methyl red mixed indicator was used to absorb the ammonia gas liberated from the sample with the help of 40% sodium hydroxide, 0.02N hydrochloric acid was used in the titration of the boric acid. The volume of Hydrochloric acid required for the blank neutralization was deducted from each sample titration.

Every ml. 0.02N Hydrochloric acid used was equivalent to 280ug. nitrogen in the plant or soil aliquot taken. The percentage of easily mineralisable nitrogen in the original soil or plant sample was later calculated. See Conway (1947).

Determination of dry weight of plants

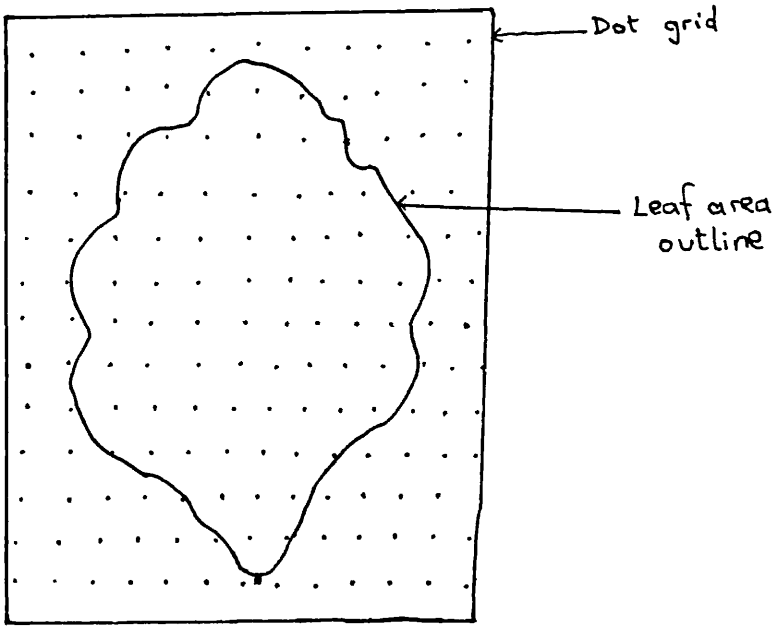
Each plant was washed first in tap water, later with distilled water. It was mopped with tissue paper, then the various organs were separated. The plant parts were allowed to air-dry for about five hours (this prevented plant parts from sticking to drying bottles). The plant parts were then dried in a fan oven at 80°C for 48 hours. The dry weights were then obtained.

Measurement of leaf area

Following the recommendation of Shaw (personal communiation) 'dot grids' were used. These consisted of small dots marked out in square pattern on sheets of transparent plastic. When a grid was laid out over a leaf outline, the leaf area could be related to the dot density and the number of dots enclosed. By selection from a range of grids with different dot densities (see Fig.II-2) rapid area measurements of reasonable precision were possible, even when leaf sizes varied widely.

Leaf Area Measurement

Fig. II-2



Plant growth analysis methods

For calculation of the quantities used in the analysis of plant growth, the formulae quoted by Evans (1972) were used.

(i) Mean relative growth rate

$$\bar{r} = \frac{\ln W_2 - \ln W_1}{T_2 - T_1}$$

where $\bar{r}$ is the mean relative growth rate over the period between the first and the second harvest

W_1 is plant dry weight at first harvest

W_2 is plant dry weight at second harvest

$T_2 - T_1$ is the interval between first and second harvests.

(ii) Mean unit leaf rate

$$\bar{E} = \frac{2(W_2 - W_1)}{(LA_2 + LA_1)\,(T_2 - T_1)}$$

where: $\bar{E}$ is the mean unit leaf rate over the period between the first and the second harvest

LA_1 is the leaf area at the time of the first harvest

LA_2 is the leaf area at the time of the second harvest

This formula for unit leaf rate was used mainly on grounds of ease of computation. In general, the precision of the experimental data was insufficient to allow critical examination of the assumptions used in deriving the various alternative unit leaf rate formulae.

CHAPTER III

THE EFFECTS OF NITROGEN AND PHOSPHORUS DEFICIENCIES ON SEEDLING GROWTHS OF *QUERCUS ROBUR* L. AND *BETULA PENDULA* ROTH.

INTRODUCTION

Quercus robur L. and Betula pendula Roth. are climatic and edaphic climax and sub-climax species of the British Isles respectively, (Tansley 1939, 1944). Many workers have reported the failure of these species to regenerate generally (Watt 1919; Tansley, 1939; Jones, 1957; Milles, 1972). Rabbits have been observed by these workers to be the main predators on Q. robur acorns and seedlings. There have been no such observations on B. pendula seedlings. The B. pendula fruits are very small (3-5mg). Extreme shade has also been described as cause of failure to germinate and establish their seedlings by both species, especially for B. pendula (Milles, 1972). It has also been observed that many soils (woodland and heath) on which these trees grow have been getting lower in terms of mineral element composition. Phosphorus is the element reported to be the most deficient. (Newnham and Carlisle 1969)

Very few nutrional experiments have been performed using B. pendula and Q. robur. Both Newnham and Carlisle (1969) and Ingestad (1957 and 1970) have attempted to determine the optimum nutritional requirements of Q. robur and B. pendula seedlings respectively. Newnham and Carlisle found that phosphorus did not have as great an effect on dry weight yield as did nitrogen on Q. robur seedlings, even though the soil on which the parent tree was growing was deficient in phosphorus. These authors did not, however explore the possible role of the Q. robur fruit (acorn) as a main source of nutrient supply, especially at this early stage of the plant development.

Ingestad (1957) noted that birch, *B. pendula* (in Sweden) had higher requirements for nitrogen than for phosphorus or indeed any other major element. Can the same hold true for *B. pendula* in the British Isles?

The work to be described was planned to investigate how *Q. robur* and *B. pendula* would respond when grown on media lacking nitrogen or phosphorus. Secondly, it was desirable to know how both species would behave in a solution that had no nutrients at all (distilled water). Here it was supposed the acorn effect could be studied.

Methods and Materials

The *Q. robur* fruits used in this experiment were collected in October, 1971 from Wimbledon Common, South of London, and the *B. pendula* fruits from Codicote Heath. Under the conditions used, *Q. robur* germinated in about 30 days, and *B. pendula* in about 14 days. The germination of the *Q. robur* fruits was thus started two weeks ahead of the *B. pendula* fruits.

The fruits were first germinated in trays filled with peralite*, distilled water being applied till the start of the experiment. Seedlings were selected for uniformity. The *Q. robur* seedlings were 7-10 cm. in height and the *B. pendula* 1 cm. when they were transplanted into polystyrene pots, of 150 ml. volume filled with peralite, on the 25th of December, 1971.

One *Q. robur* seedling was put into each pot while about three *B. pendula* seedlings were used. Later on in the experiment the *B. pendula* seedlings were reduced to one. All the *Q. robur* seedlings survived the transplant process, but a few *B. pendula* seedlings had to be replaced.

Experimental Design

The design of this experiment was a single completely randomized block with four replicates. The positions of the seedlings of all treatments were randomized at monthly intervals during the experiment.

The potted plants were put on benches in the green-house heated to raise the temperature to 70-80°F (21-27°C) maximum. No artificial lighting was used.

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* British Gypsum Co. Ltd.

The Nutrient Solution

The nutrient solutions used in this work were based on that of Hewitt (1952). The recipe is shown in Table III.1.

The complete or the control solution differed from (i) the minus nitrogen solution by the replacement of KNO_3 and $Ca(NO_3)_2$ by K_2SO_4 and $CaCl_2$ respectively; (ii) the minus phosphorus solution by the presence of K_2SO_4 in the minus phosphorus instead of $Ca_2(H_2PO_4)_2$. Distilled water was the fourth treatment. The solutions were stored in the dark in large bottles. There was no visible microbial growth. At monthly intervals new culture solutions were prepared.

Application of Nutrient Solutions

The nutrient solution was applied from the surface 25cc per pot per day. Because of the smallness of the pots used in this work and also the great susceptibility to dryness of the peralite (the supporting growth medium), the volume was increased to 50ml. The rate of drying became erratic as it was influenced very much by the weather. The daily supply of nutrients was abandoned after about two months of experimentation and solution was applied when the pots appeared dry. Equal volumes of solution were applied to all pots.

At the end of each week the peralite was washed with distilled water and the nutrient solution application continued. This procedure kept the pH at 5.1-5.3, and removed much of the green algal growthwhich was very common in pots being supplied with the complete nutrient solution.

TABLE III-1

The Composition of the Culture Solutions

Salt	Concentration mg/100 ml	Milli-equiv / litre
KNO_3 / K_2SO_4*	202 / 80.7*	2 / 1*
$Ca(NO_3)_2$/$CaCl_2$* (Anhydrous)	328 / 111*	4 / 2*
$Ca_2(H_2PO_4)_2$ / K_2SO_4 ***	154.5 / 87**	4 / 1*
$MgSO_4 \cdot 7H_2O$	184	1.5
Ferric citrate(Fe^{+++})	49	0.6
$MnSO_4 \cdot 4H_2O$	223	0.002
$CuSO_4 \cdot 5H_2O$	2.5	0.002
$ZnSO_4 \cdot 7H_2O$	58	0.002
H_3BO_3	186	0.03***
Na_2MoO_4	0.35	0.0002

---

* K_2SO_4 and $CaCl_2$ used in the minus nitrogen solution in place of KNO_3 and $Ca\ (NO_3)_2$ respectively.

** K_2SO_4 used in the minus phosphorus solition instead of $Ca_2(H_2PO_4)_2$

*** In milli-mols / litre

Ordinary distilled water was used as the fourth treatment.

Observation on Experimental Plants

The heights of the plants and the stem diameters 1cm. above the peralite level were measured at monthly intervals.

The first harvest was taken on the 31st of May, 1972, the second followed in another month. For harvest procedure see Methods and Materials in chapter II.

Deficiency Symptoms and General Morphology

The effect of the experimental treatments were first observed in the B. pendula seedlings many of which died soon after transplant in treatments lacking phosphorus. There was no such problem with the Q. robur seedlings except that apical dormancy was first broken in the control (complete nutrient solution) the others following a few days later. (Q. robur grows in "flushes").

Comparatively, the treatment effect were more apparent in the B. pendula seedlings than in the Q. robur. Generally, the B. pendula seedlings growing in the minues nitrogen, minus phosphorus and water only solutions were dwarfed, compared with the control. The shoots were thin, leaves small and without lustre.

The Q. robur seedlings survived for a longer period than B. pendula before showing any deficiency symptoms. Apart from the smaller growth of Q. robur seedling in the minus nitrogen and water only solutions compared with the control and the minus phosphorus, the only diagnostic symptoms of mineral deficiency was the progressive development in the minus nitrogen and water only treatments of pale greenish, yellowish and necrotic leaves; symptoms similar to those associated with nitrogen deficiency as described by Wallace (1943). There were no purplish or bluish tints to indicate a phosphorus deficiency in either the minus phosphorus or the water only treatments.

The observed symptoms in *Q. robur* started after about two months of experimentation. The *B. pendula* seedlings showed symptoms of both nitrogen and phosphorus deficiencies. Pale, greenish to yellowish for nitrogen and purplish or bronze tints for phosphorus deficiency, occurred in the minus nitrogen and minus phosphorus treatments respectively. The water only treatment in *B. pendula* simply gave a necrotic situation in the leaves, no other colour was developed that could be associated with a particular deficiency. The symptoms began within one month of the start of the experiment in the *B. pendula* seedlings.

A number of seedlings in the minus phosphorus and water only solutions died before the completion of the experiment, while the *Q. robur* seedlings survived the four treatments. The detrimental effects of mineral deficiencies on the root growth was observed mainly in the *B. pendula* seedlings.

Apart from the control, all the other samples developed very poor roots, the poorest were in the minus phosphorus and water only treatments. The roots being extremely thin and fibrous. The roots of the *Q. robur* seedlings in the minus nitrogen and water only were long and slender, the others were normal.

Fig.III-1 The height growth of *Q. robur* seedlings in four types of nutrient solutions (Mean values of 4 replicates)

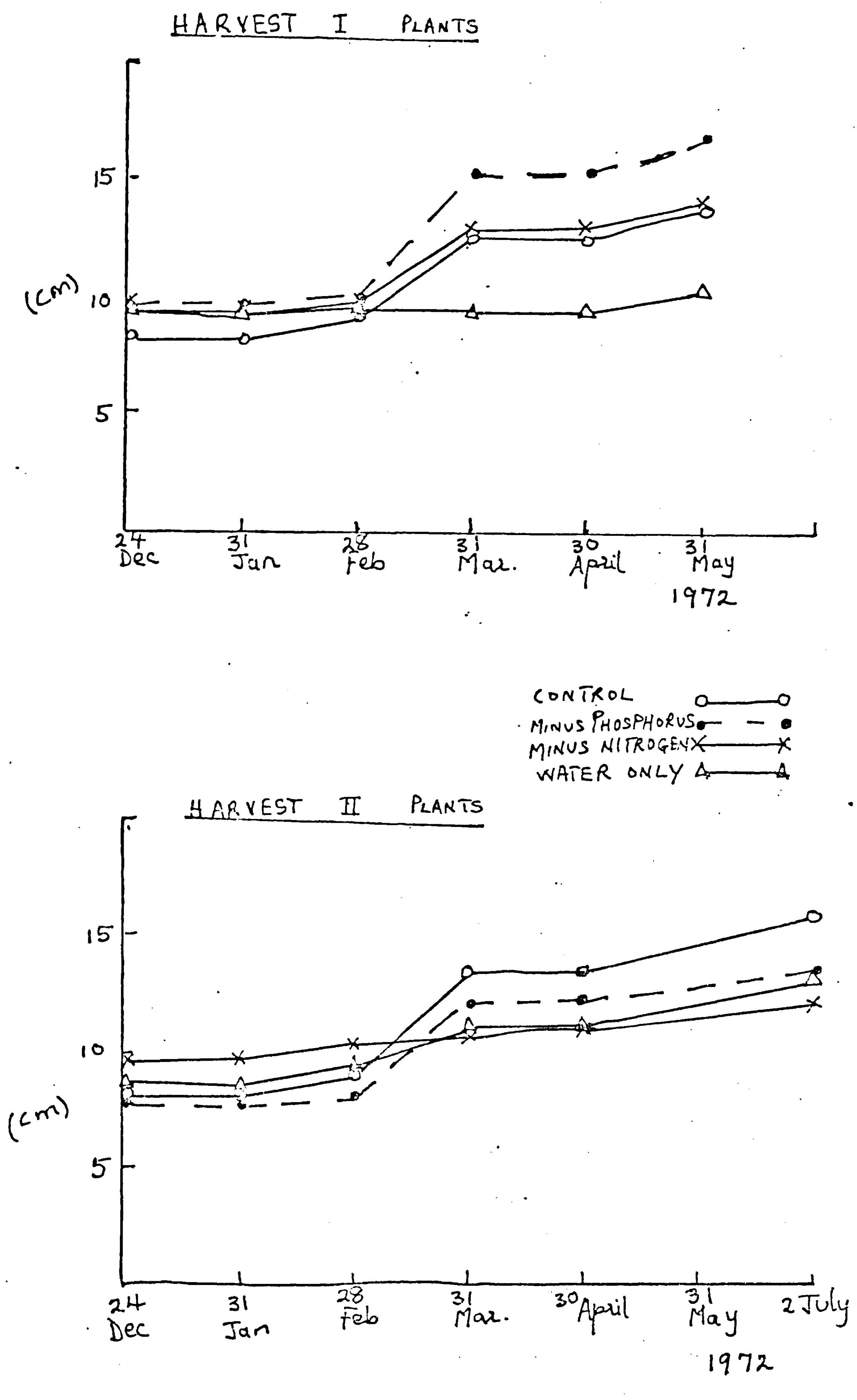
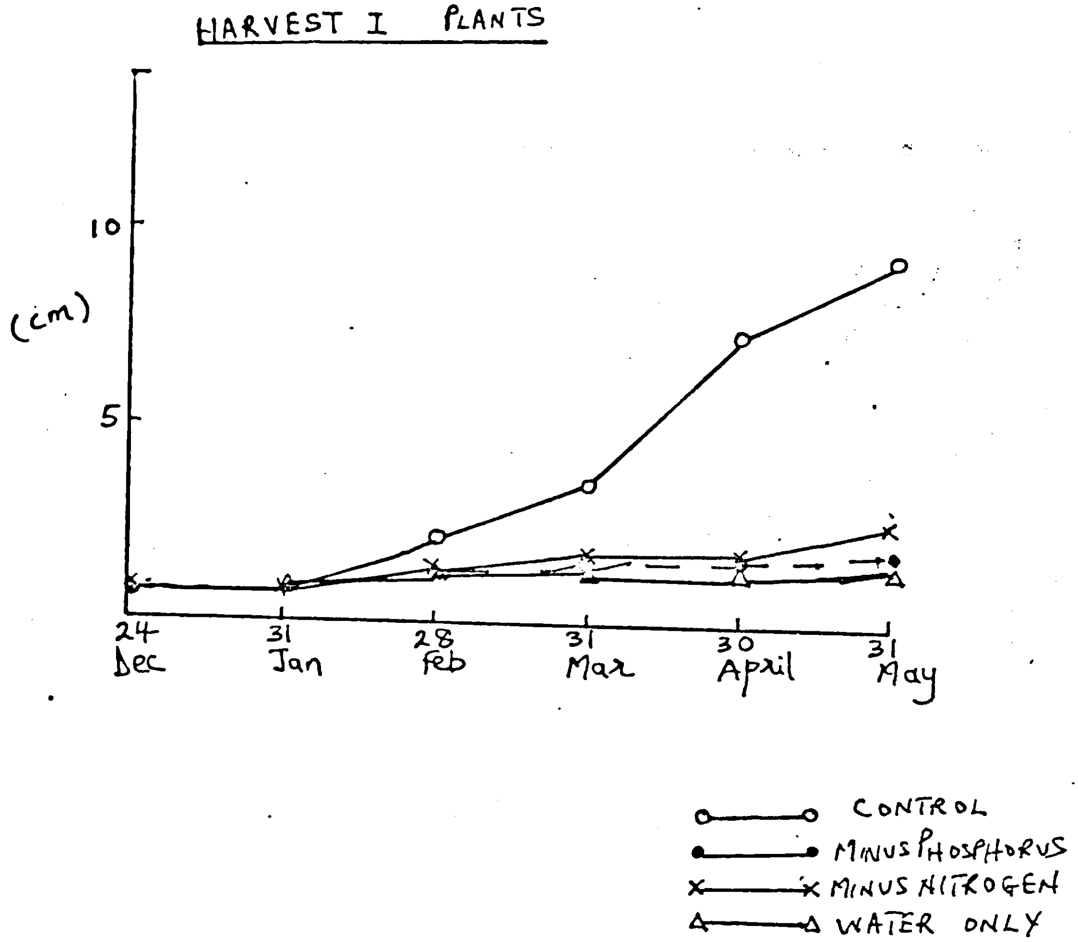


Fig. III-2 The height growth of B. pendula seedlings in four types of nutrient solutions (Mean values of 4 replicates)



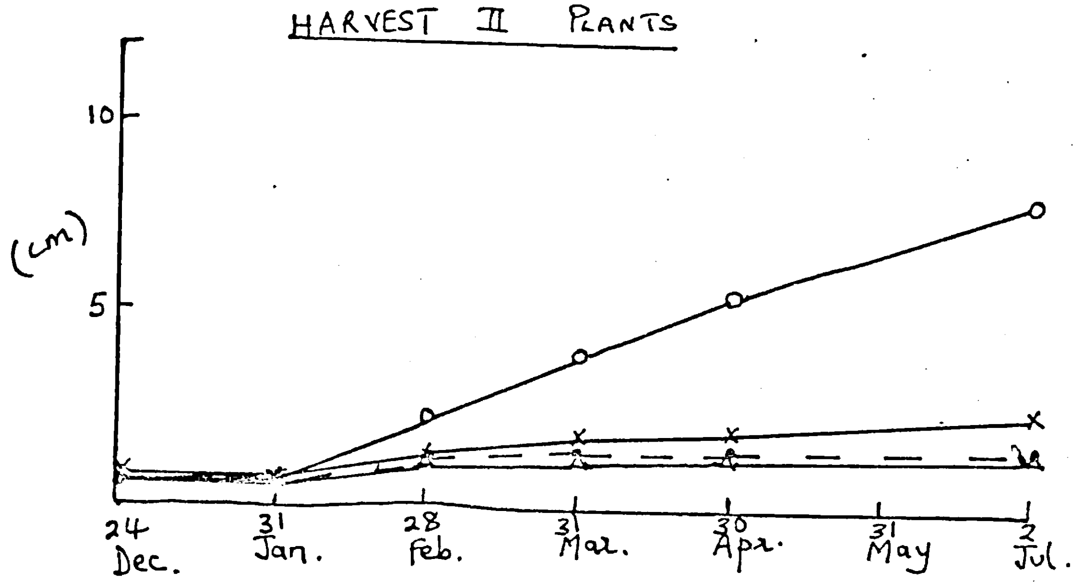
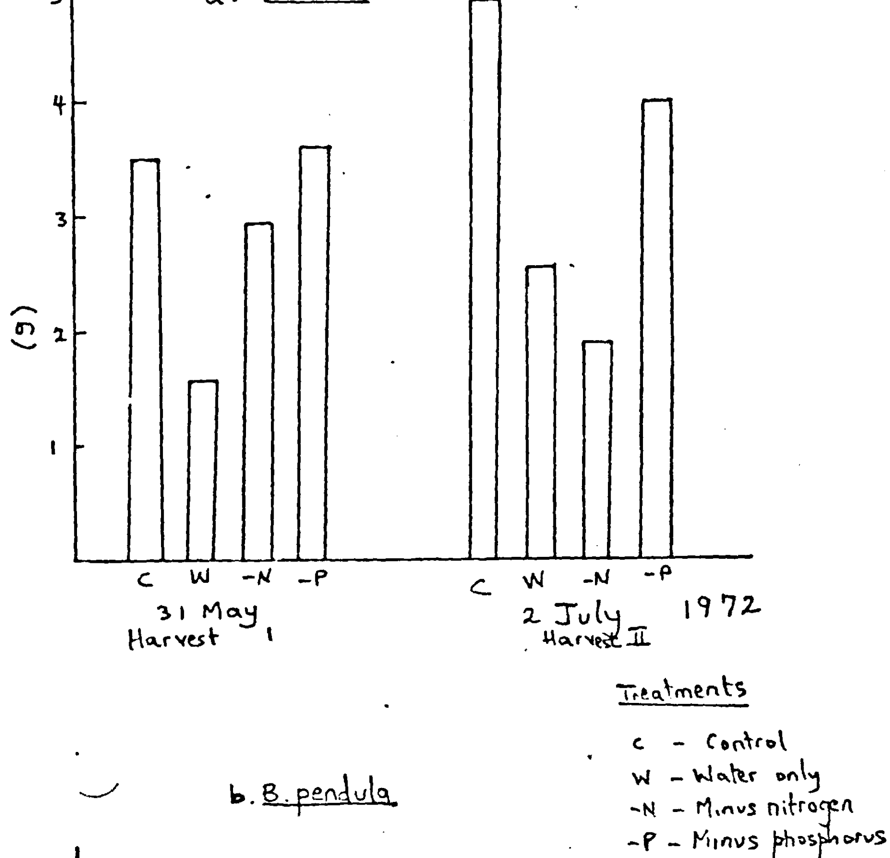
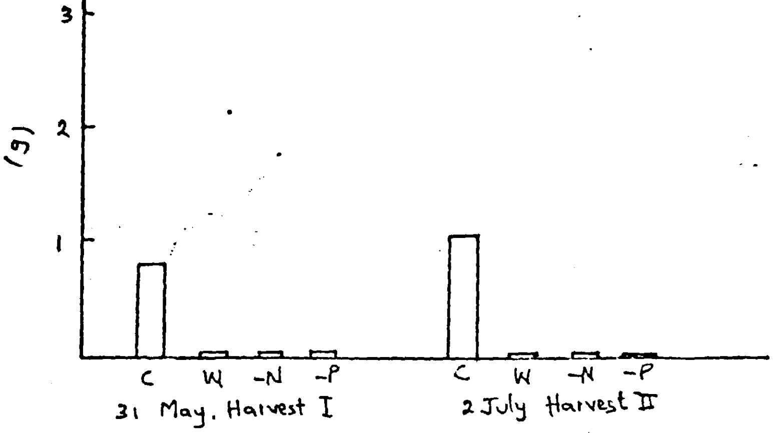


Fig III-3 Dry weight yields (total) of *Q. robur* and *B. pendula* grown in four types of solutions. (Mean values of four replicates)

a. *Q. robur*



b. *B. pendula*



Plant Heights and Dry Weights

(a) Heights (Figs. III 1 & 2) indicate the rate of shoot growth in height in both the Q. robur and the B. pendula seedlings. In both species, active growth started between February and March, in all treatments except the minus nitrogen, minus phosphorus and water only in B. pendula. The two species, as the graphs show, have different growth patterns. The Q. robur seedlings grew in "flushes" while the B. pendula seedlings grew more or less continuously, rather than periodically. The two species differed widely in their responses to the treatments. In Q. robur there was no consistent relationship of height and treatment, though it did appear that a rather high proportion of the water only seedlings failed to make a spring growth flush. In B. pendula, however, there were great treatment effects. In Table III-3, from the height values it can be seen that by the time of harvest the control seedlings had heights about four times as great as the other treatments. The minus nitrogen, minus phosphorus and water only seedlings also differed from each other in height, though the differences were much smaller than those involving the control seedlings.

(b) Dry Weight

(i) General The data for plant dry weight were examined statistically using analysis of variance. Tables III-6 and III-7 summarise the variance ratio values obtained. The significant values in the analyses for harvest II were greater than the corresponding values for harvest I. This shows that the effects of nutrient deficiencies in both species became stronger in the time between the harvests.

TABLE III-2

The effects of nitrogen and phosphorus deficiencies on the heights and dry weighhs of *Q. robur* seedlings
(Mean values of 4 replicates)

HARVEST I 31 May 1972

Treatment	Control	Water Only	Minus Nitrogen	Minus phosphorus
Height (cm)	13.80 (±5.03)	10.20 (± 0.94)	13.90 (± 2.65)	16.80 (± 5.21)
Total plant dry weight (g)	3.56	1.77	2.90	3.63
Leaf dry weight (g)	0.67	0.19	0.40	0.64
Stem dry weight (g)	0.66	0.24	0.53	0.68
Root dry weight (g)	2.23	1.34	1.97	2.31
Fruit left-over (g)	0.68	0.49	0.46	0.56
HARVEST II 30 June 1972				
Height (cm)	15.75 (± 5.76)	13.00 (± 2.18)	11.75 (± 0.43)	13.25 (± 6.05)
Total plant dry weight (g)	4.97	2.64	1.97	4.10
Leaf dry weight (g)	0.71	0.38	0.23	0.51
Stem dry weight	0.81	0.47	0.32	0.61
Root dry weight (g)	3.45	1.79	1.42	2.98
Fruit left-over (g)	0.46	0.51	0.53	0.45

For analysis of variance see Tables III-6 + 7.

Figures in parenthesis indicate standard error values.

Table III-3

The effects of nitrogen and phosphorus deficiencies on the heights and dry weights of B. pendula seedlings
(Mean values of 4 replicates)

HARVEST I 31 May 1972

Treatment	Control	Water Only	Minus Nitrogen	Minus Phosphorus
Height (cm)	9.25 (± 1.55)	1.00 (0)	2.25 (± 0.02)	1.50 (± 0.06
Total plant dry weight (g)	0.7879	0.0049	0.0426	0.0069
Leaf dry weight (g)	0.3559	0.0013	0.0170	0.0020
Stem dry weight (g)	0.1472	0.0013	0.0062	0.0018
Root dry weight (g)	0.2848	0.0023	0.0194	0.0029
HARVEST II 30 June 1972				
Height (cm)	7.62 (± 2.57)	1.32 (± 0.03)	2.07 (± 0.13)	1.25 (± 0.03)
Total plant dry weight (g)	1.0501	0.0027	0.0324	0.0053
Leaf dry weight (g)	0.4284	0.0011	0.0111	0.0018
Stem dry weight (g)	0.1929	0.0008	0.0058	0.0016
Root dry weight (g)	0.4288	0.0008	0.0155	0.0019

For analysis of variance see Tables III 6 & 7.

Figures in parenthesis indicate standard error values.

Table III-4

The effects of nitrogen and phosphorus deficiencies on the plant part ratios and growth rates of B. pendula seedlings
(Mean values of four replicates)

Treatment	Control	Water Only	Minus Nitrogen	Minus Phosphorus
HARVEST I 31 May 1972				
Leaf Weight Ratio	0.45	0.27	0.40	0.32
Root/Shoot Ratio	0.59	0.89	0.78	0.73
HARVEST II 30 June 1972				
Leaf weight Ratio	0.41	0.41	0.34	0.34
Root/Shoot Ratio	0.69	0.42	0.94	0.56
Growth rates between hearvests				
Absolute Growth Rate (g) per week	0.065	-0.0005	-0.0034	-0.0004
Relative Growth Rate (per week)	0.072	-0.15	-0.068	-0.19

TABLE III-5

The effects of nitrogen and phosphorus deficiencies on the plant part ratios and growth rates of Q. robur seedlings.
(Mean values of four replicates)

Treatment	Control	Water Only	Minus Nitrogen	Minus Phosphorus
HARVEST I 31 May 1972				
Leaf Weight ratio	0.16	0.084	0.12	0.15
Root/Shoot Ratio	1.69	3.11	2.11	1.75
HARVEST II 30 June 1972				
Leaf Weight Ratio	0.13	0.12	0.092	0.11
Root/Shoot Ratio	2.27	2.10	2.58	2.66
Growth rates between harvests				
Absolute Growth Rate g per week	0.35	0.22	-0.24	0.12
Relative growth Rate per week	0.082	0.10	-0.095	0.03

Interpretation of Statistical Analyses

Analyses of variance were performed to test the statistical significance of the effects arising from the species (S) and from other treatments (T). Levels of significance were found from the appropriate variance ratio tests.

Throughout this work, statistical analyses are presented in a way similar to Table III - 6.

The variance ratio values for Species (S), Treatment (T_1), Species X Treatment (S X T_1) and Replicate (R_1) are derived from the analysis of the data from the whole experiment. The degrees of freedom of these variables are as follows:

S	1
T_1	3
S X T_1	3
R_1	3
Residual error	21
Total	31

The variance ratio values for Treatment (T_2) and Replicate (R_2) are derived from the analysis of the data from *Q. robur* only, and have degrees of freedom as follows:

T_2	3
R_2	3
Residual error	9
Total	15

Similarly, values for treatment (T_3) and Replicate (R_3) refer to the analysis of the data from *B. pendula*.

Table III - 6 and other tables of variance ratio values show "Replicate" variables corresponding to the blocks of a randomised block design. The experiment described in Chapter III was set up in a completely randomised design, so the "Replicate" variances do not differ from the corresponding Residual error variances.

TABLE III-6

Variance ratio values from the analysis of variance of plant dry weight results of Q. robur & B. pendula seedlings grown in four types of solutions (Complete, minus phosphorus, minus nitrogen and water only)

HARVEST I 31 May 1972

Variables	Total Plant Dry Weight	Leaf	Stem	Root	Seed
Species (S)	150.00***	29.25***	30.20***	189.13***	
Treatment (T_1) (Q. robur & B. pendula)	4.75**	6.25**	2.40 NS	3.46 NS	
Treatment (T_2) (Q. robur)	3.32 NS	3.33 NS	2.1 NS	3.04 NS	0.36NS
Treatment (T_3) (B. pendula)	60.00***	152.5***	26.0***	26.00***	
Species X Treatment (S X T_1)	2.16 NS	1.75 NS	1.2 NS	2.13 NS	
Replicate (R_1) (Q. robur & B. pendula)	0.21 NS	0.5 NS	0.4 NS	0.07 NS	
Replicate (R_2) (Q. robur)	0.20 NS	0.5 NS	0.5 NS	0.12 NS	0.54 NS
Replicate (R_3) (B. pendula)	1.10 NS	1.62 NS	1.00 NS	1.0 NS	

NS Not Significant

* Significant at 5% probability level

** Significant at 1% probability level

*** Significant at 0.1% probability level.

TABLE III-7

Variance ratio value from the analysis of variance of plant dry weight results of Q. robur and B. pendula seedlings grown in four types of solutions. Complete, minus phosphorus, minus nitrogen and water only.

HARVEST II 30 June 1972

Variables	Total Plant Dry Weight	Leaf	Stem	Root	Seed
Species (S)	380.66***	64.13***	37.16***	12.59**	
Treatment (T_1) (Q. robur & B. pendula)	17.00**	20.73***	30.3***	5.10**	
Treatment (T_2) (Q. robur)	9.49**	5.33*	5.6*	11.47**	0.72NS
Treatment (T_3) (B. pendula)	538.50***	898.50***	120.66***	81.36***	
Species X Treatment (S X T_1)	4.67*	0.20NS	2.0 NS	2.40 NS	
Replicate (R_1) (Q. robur & B. pendula)	0.93 NS	0.80 NS	0.5 NS.	0.36 NS	
Replicate (R_2) (Q. robur)	0.96 NS	0.66 NS	0.50 NS	1.21 NS	1.27 NS
Replicate (R_3) (B. pendula)	1.75***	1.50 NS	1.00 NS	0.95 NS	

NS Not Significant
* Significant at 5% probability level
** Significant at 1% probability level
*** Significant at 0.1% probability level.

Precise interpretation of the variance ratio values is prevented by heterogeneity of variance, especially in the case of B. pendula, where very wide differences in dry weights were found.

(ii) Growth in complete nutrient solution

Both species produced substantial dry weights in the control treatment. Over the period between the first and second harvests, the mean absolute growth rate of B. pendula was much less than that of Q. robur. On the other hand, the relative growth rates of B. pendula seedlings over the period between the harvests were greater than those of Q. robur.

The distribution of dry matter in the species was very different. Q. robur had relatively very heavy roots (root/shoot ratios 1.7 - 3.1) while the ratios in B. pendula were 0.6 - 0.9. The leaf weight ratios of B. pendula were about three times those of Q. robur, and this would be expected to give higher relative growth rates in B. pendula.

(iii) Growth in distilled water only

In these conditions, B. pendula showed lower dry weights than in any other treatment; the weights were less than 1% of the controls. The B. pendula seedlings supplied with water only gave lower dry weight values at the second harvest than at the first. Necrosis had started, abscission of the leaves had set in and the plants were already dying. There were no such severe effects amongst the Q. robur seedlings in any of the treatments.

This indicates that the acorn reserves allow survival for a considerable period even in complete absence of nutrients. The mean dry weight of Q. robur seedlings in this treatment was higher at the second harvest than at the first, but the averages were not precise enough to show definitely that the seedlings were still able to carry on dry matter production.

The analyses of variance showed no significant connection between treatment and the dry weight of the fruit left over. The fairly wide variations which occurred presumably followed from random variations in the original acorn weights.

(iv) Nitrogen deficiency effect

In both the Q. robur and the B. pendula seedlings, minus nitrogen treatments gave considerably lower yields in total, leaf, stem and root dry weights than those in the control treatments. The absence of nitrogen depressed the values of dry weights in all the plant parts. In Q. robur, the minus nitrogen seedlings had dry weights about the same as the water only ones, while in B. pendula, the mean dry weights of minus nitrogen plants were at least six times those of the water only treatment.

(v) Phosphorus deficiency effect

In absence of phosphorus, Q. robur showed no appreciable difference in dry weight from the control at the first harvest. At the second harvest, the mean dry weight was rather less than that of the control, but still well above the values for water only and minus nitrogen.

In *B. pendula*, the minus phosphorus seedlings had much lower dry weights than the minus nitrogen ones; they showed values more comparable with the water only treatment. As in the other nutrient deficient treatments, *B. pendula* gave lower dry weights in the second harvest, and showed signs that the plants would not have lived much longer.

TABLE III-8

Chemical Analysis of Q. robur seedlings grown in four types of nutrient solution and harvested twice

(a) Nitrogen % of Dry Weight

Treatment	Total* Plant	Leaf	Stem	Root	Acorn Left Over
Harvest I 31 May 1972					
Control	1.01	2.01	1.06	0.76	Not Determined
Water Only	0.89	1.40	0.76	0.87	
Minus Nitrogen	0.67	1.22	0.63	0.59	
Minus Phosphorus	0.97	1.80	0.80	0.78	
Harvest II 30 June 1972					
Control	0.82	2.45	0.81	0.64	1.31
Water Only	0.61	1.43	0.52	0.48	0.48
Minus Nitrogen	0.60	1.75	0.35	0.49	0.44
Minus Phosphorus	0.81	2.45	0.95	0.48	0.56

(b) Phosphorus % Dry Weight

Teatment	Total* Plant	Leaf	Stem	Root	Acorn Left Over
Harvest I 31 May 1972					
Control	0.32	0.33	0.32	0.32	Not Determined
Water Only	0.29	0.15	0.15	0.34	
Minus Nitrogen	0.29	0.25	0.32	0.48	
Minus Phosphorus	0.26	0.20	0.21	0.30	
Harvest II 30 June 1972					
Control	0.32	0.41	0.33	0.27	0.39
Water Only	0.26	0.32	0.22	0.26	0.38
Minus Nitrogen	0.41	0.36	0.29	0.45	0.47
Minus Phosphorus	0.24	0.35	0.28	0.21	0.42

* These values are for the total plant excluding the acorn.

For analysis of variance see Tables III - 11 & 12

Table III-8 (contd.)

(c) Potassium % of Dry Weight

Treatment	Total * Plant	Leaf	Stem	Root	Acorn Left Over
HARVEST I 31 May 1972					
Control	0.60	1.11	0.33	0.53	
Water Only	0.84	2.41	0.45	0.71	
Minus Nitrogen	0.89	1.23	0.43	0.80	
Minus Phosphorus	0.72	1.25	0.37	0.65	
HARVEST II 30 June 1972					
Control	0.66	1.13	0.41	0.62	1.07
Water Only	0.69	1.67	0.53	0.64	1.83
Minus Nitrogen	0.80	1.73	0.51	0.80	1.12
Minus Phosphorus	0.73	1.47	0.47	0.65	1.45

(d) Sodium % of Dry Weight

Treatment	Total Plant	Leaf	Stem	Root	Acorn Left Over
HARVEST I 31 May 1972					
Control	0.25	0.17	0.19	0.30	
Water Only	0.27	0.31	0.27	0.28	
Minus nitrogen	0.22	0.19	0.19	0.29	
Minus Phosphorus	0.22	0.19	0.21	0.24	
HARVEST II 31 June 1972					
Control	0.37	0.61	0.51	0.30	5.37
Water Only	0.34 036 ?	0.30	0.68	0.27	6.13
Minus Nitrogen	3.50	0.35	0.56	11.85	4.31
Minus Phosphorus	0.27	0.32	0.30	0.29	4.81

* These values are for the total plant excluding the acorns.

Table III-9

Chemical Analysis of B. pendula seedlings grown in four types of nutrient solution and harvested twice. Samples in minus phosphorus and water only solutions were too small for any chemical analysis
Values represent means of 4 replicates

(a) Nitrogen % of Dry Weight

Treatment	Total Plant	Leaf	Stem	Root
HARVEST I 31 May 1972				
Control	0.98	1.22 (± 0.01)	0.65 (±0.001)	0.78 (±0.0002)
Minus Nitrogen	0.49 (± 0.007)	0.32 (± 0.0001)	0.30 (± 0.0001)	0.69 (± 0.0003)
HARVEST II 30 June 1972				
Minus Nitrogen	NOT DETERMINED			

(b) Phosphorus % of Dry Weight

Treatment	Total Plant	Leaf	Stem	Root
HARVEST I 31 May 1972				
Control	0.08	0.14 (± 0.00011)	0.08 (±0.00001)	0.14 (± 0.0003)
HARVEST II 30 June 1972				
Control	0.09	0.07 (± 0.00001)	0.07 (± 0.00001)	0.12 (± 0.00001)
Minus Nitrogen	0.06	0.03 (± 0.0001)	0.05 (±0.0001)	0.08 (±0.0001)

Figures in parenthesis indicate standard error values.

Table III-9(contd.)

Chemical Analysis of B. pendula seedlings grown in four types of nutrient solution and harvested twice. Samples in minus phosphorus and water only solutions were too small for any chemical analysis
Values represent means of 4 replicates

(c) Potassium % of Dry Weight

Treatment	Total Plant	Leaf	Stem	Root
HARVEST I 31 May 1972				
Control	1.10	1.12 (± 0.0002)	0.86 (±0.001)	1.15 (±0.003)
Minus Nitrogen	0.07	0.07 (±0.0001)	0.08 (±0.00001)	0.10 (± 0.0002)
HARVEST II 30 June 1972				
Control	0.90	0.87 (± 0.001)	0.65 (± 0.002)	1.07 (± 0.002)
Minus Nitrogen	0.09	0.08 (± 0.0001)	0.04 (±0.0001)	0.14 (± 0.002)

(d) Sodium % of Dry Weight

Treatment	Total Plant	Leaf	Stem	Root
HARVEST I 31 May 1972				
Control	0.44	0.48 (± 0.002)	0.34 (±0.0003)	0.46 (± 0.0011)
Minus Nitrogen	0.13	0.08 (± 0.0004)	0.24 (±0.0003)	0.14 (± 0.0010)
HARVEST II 30 June 1972				
Control	0.33	0.41 (±0.004)	0.24 (±0.002)	0.30 (±0.001)
Minus Nitrogen	0.05	0.05 (±0.0001)	0.05 (±0.0002)	0.05 (±0.0003)

Figures in parenthesis indicate standard error values.

TABLE III-10

Chemical Analysis of Acorn left over

PERCENTAGE DRY WEIGHT

ELEMENT	FRESH SEED	CONTROL	WATER	-N	-P
		TREATMENT			
% NITROGEN	2.62	1.31	0.48	0.44	0.56
% PHOSPHORUS	0.61	0.39	0.38	0.47	0.42
% POTASSIUM	2.94	1.07	1.83	1.12	1.45
% SODIUM	6.58	5.37	6.13	4.31	4.81

For analysis of variance see Table III - 12

TABLE III-11

F Values in the analysis of variance of plant mineral content in *Q. robur* seedlings

VARIABLES		Total Plant	Plant Part Leaf	 Stem	 Root	Harvest I Seed
Nitrogen	Treatment	2.15	3.25	1.09	0.55	Not
	Replicate	0.91	0.50	3.00	0.88	Determined
Phosphorus	Treatment	3.31	6.02*	4.80*	1.42	
	Replicate	1.16	2.00	3.33	1.03	
Potassium	Treatment	6.00*	10.30**	1.20	2.22	
	Replicate	0.17	0.84	1.10	0.50	
Sodium	Treatment	2.40	0.37	3.11	0.14	
	Replicate	1.44	0.26	1.52	1.16	

NS	Not Significant
*	Significant at 5% probability level
**	Significant at 1% probability level
***	Significant at 0.1% probability level.

TABLE III-12

Variance ratio and values from the analysis of variance of *Q. robur* seedlings analysed chemically.

			Plant Part			Harvest II
Variables		Total	Leaf	Stem	Root	Seed
Nitrogen	Treatment	7.80**	8.08**	3.75	0.74	4.71*
	Replicate	2.23	1.25	1.62	1.94	1.50
Phosphorus	Treatment	2.35	0.58	0.93	0.32	3.72
	Replicate	2.23	2.13	1.15	0.21	0.44
Potassium	Treatment	8.63**	5.01*	1.00	6.08*	0.72
	Replicate	8.58**	7.48**	0.59	2.36	0.75
Sodium	Treatment	2.69	7.40**	0.95	2.84	4.84*
	Replicate	0.95	0.53	0.25	1.01	0.01

NS	Not Significant
*	Significant at 5% Probability Level
**	Significant at 1% Probability Level
***	Significant at 0.1% Probability Level

Plant Nitrogen Content

The results of the plant analysis for nitrogen (% values) are presented in table III-8a for the *Q. robur* samples. The minus nitrogen seedlings had the lowest concentration of nitrogen at the first harvest, 0.67% compared with 0.89 - 1.01% (Total Plant) in the other treatments. The control samples had the highest values, with the values for minus phosphorus being fairly comparable to the control values. The leaf values for *Q. robur* were generally higher than those from other plant parts in all treatments, although again the minus nitrogen samples had comparatively low values, the control and minus phosphorus values were higher than those of others. The root samples in *Q. robur* had higher values than the stem in all treatments except the water only treatment.

The *B. pendula* control values for percentage nitrogen (Table III-9) were lower than those of the *Q. robur* at the first harvest, the leaf showed the highest values compared with other plant parts. The minus nitrogen seedlings of *B. pendula* had still lower percentages of nitrogen, without high leaf values.

The *Q. robur* values at the second harvest were increased slightly in the control, minus phosphorus, and in the minus nitrogen as well. Generally the minus nitrogen and especially the water only samples had fairly low nitrogen in comparison with the other treatments. The leaf samples showed higher values generally than other parts. The trend shown in the total plant values was observed in the plant parts i.e. the control with the highest values followed by the minus phosphorus, the minus nitrogen and water only with the least values.

The root samples, except in the minus nitrogen had the lowest values, of the plant parts.

The B. pendula seedlings could not be analysed for nitrogen at the second harvest. The chemical analysis of the acorns showed that, there had been some depletion of nitrogen by all the seedlings. The minus phosphorus seedlings had acorns with the lowest percent nitrogen compared with the unused acorns, the control seedlings had acorns with about 50% of original nitrogen concentration, while the other treatments had about 20% (Table III-19). Since the acorn weights were reduced during seedling growth, the amounts of nitrogen removed from the acorn must have been quite great.

Plant Sodium Content

The percentage sodium in total plant dry weight for many treatments seemed comparable, among the Q. robur seedlings at the first harvest. (0.22% - 0.27%) (Table III-8d). The B. pendula values were generally higher than the Q. robur in the control samples at the first harvest. The B. pendula total plant percent sodium was 0.13% in minus nitrogen seedlings and 0.44% control. While the B. pendula control leaf percent sodium value was fairly high, (0.48%), the minus nitrogen values were fairly low, about 0.08%.

At the second harvest, the Q. robur seedlings had increases in their percentage sodium concentrations generally. The sudden increases in these values were mainly in the leaf and stem in both samples (Table).

The minus phosphorus *Q. robur* seedlings showed very little increase in their sodium content between the two harvests. The high total plant percent sodium in the *Q. robur* minus nitrogen seedlings came about from the increase in the root values. The cause of this increase could not be ascertained but the variation between replicates was very high in this case. The analysis of the acorns left over gave generally high sodium values (4.31 - 6.13%) in comparison with the unused acorn of 6.58% sodium (Table III - 10). The percent sodium in *B. pendula* seedlings decreased generally at the second harvest with fairly low sodium content generally.

The acorn analysis (Table III-10) indicates that the control and minus nitrogen *Q. robur* had the lowest values for percentage potassium and the water only the highest. In all treatments however, the values were much lower than that of the fresh acorns, suggesting that the seed reserve is an important source of potassium for the seedling of *Q. robur*.

Plant Potassium Content

The percentage potassium values in the water only of *Q. robur* seedlings were generally higher than those in the other treatments (Table III-8c).The lowest values were in the control (*Q. robur* seedlings) followed by the minus phosphorus seedlings. The control and minus phosphorus seedlings had higher dry weights than the minus nitrogen and water only seedlings (Table III-2). Thus the low potassium concentrations may not mean that potassium uptake had been reduced. The leaf in all treatments had the highest values for percentage potassium, the stem had the lowest values. (The acorns left over at the first harvest were not analysed).

In *B. pendula*, the control had much higher percentage potassium than the minus nitrogen, it was the reverse of *Q. robur*. The potassium content in *Q. robur* at the first harvest ranged from 0.60% control, to 0.89% (minus nitrogen) total plant potassium, the water only and minus phosphorus values coming in between (Table III-8c).The *B. pendula* control value was 1.10% and the minus nitrogen value 0.07% (Harvest I).

At the second harvest, the potassium content in the water only (*Q. robur* seedlings) had decreased while the values in other treatments increased over the first harvest values, 30 days earlier. Despite this the water only and minus nitrogen samples still had higher potassium percentage values in the leaves than the control and minus phosphorus samples. The *Q. robur* range this time was 0.69% in the water only to 0.80 minus nitrogen (total plant).

The *B. pendula* control samples had slightly lower percentage potassium at the second harvest than at the first (total plant) (Table) . The *B. pendula* value at this harvest was also higher than the *Q. robur* control values. The *B. pendula* percentage potassium values (total plant) increased in the minus nitrogen seedlings between the first and second harvests. The root contributed most to this increase.

Plant Phosphorus Content

The results of the phosphorus analysis of the *Q. robur* and *B. pendula* seedlings are presented in Tables III-8 and III-9. For *Q. robur* Table III-8b, the total plant percentage phosphorus did not show any marked variation as a result of the treatments.

The values ranged from 0.26% minus phosphorus to 0.32% control at the first harvest. When the plant parts are considered, it appears that the root phosphorus content was higher than in other parts. The only exceptions are the control seedlings with fairly similar values for percent phosphorus 0.32 - 0.33%. The water only and minus nitrogen root phosphorus values were about double leaf values. The leaf and stem percent values were fairly comparable in all treatments among the Q. robur seedlings. Phosphorus at the time of this harvest was not limiting growth. Because of their small size, B. pendula seedlings grown in absence of phosphorus could not be analysed. However, even with phosphorus in the culture solution, the B. pendula samples at the first harvest were fairly low when compared with the Q. robur values, the low B. pendula values were also expressed in the plant parts with the stem having the lowest values. The minus nitrogen samples for B. pendula could not be analysed at this harvest.

At the second harvest, after 1 month, the Q. robur values did not show any great variation from the first harvest values as far as the total plant phosphorus percentage was concerned. Only the minus nitrogen seedlings showed any high increase in the value of percentage phosphorus. This movement of phosphorus from the root to other parts of the plant, increased their relative values of the leaves, but left the total plant concentrations more or less unchanged. Thus the Q. robur leaves in particular had higher percentage phosphorus values generally compared with the first harvest.

The B. pendula total plant percent phosphorus was relatively low.

The *Q. robur* acorn analysis (Table III-10) shows that while the acorns from seedlings had lower values than the ungerminated acorns, the treatments did not appear to affect the amount of phosphorus left over in the acorns. For instance the control and water only percentage phosphorus values in the acorns were fairly similar.

DISCUSSION

Dry Weight

It has been reported that *Q. robur* fruit reserve serves the young seedling for over a year before soil effects could be apparent (Jones, 1959).

In greenhouse works however, seedlings put on growth rapidly compared with natural conditions. Thus these results must be considered in terms of the more favourable conditions existing in the greenhouse, which obviously affect not only mineral element uptake but other aspects of plant growth.

The results of this experiment show that the acorn indeed serves as the main source of nutrient supply up to the first harvest, for *Q. robur*. There were no statistically significant effects of variation on the plant growth (dry weight yields) of *Q. robur* seedlings at the first harvest. Thus the acorn reserve buffered the seedlings against the inadequacies of nutrient balance in the minus phosphorus, minus nitrogen and water only treatment solutions. See TableIII-6. Had this experiment been terminated here, the impression would have been that *Q. robur* was not responsive to mineral deficiencies at this stage of its development.

The results of the second harvest TableIII-2and Fig.III-3show that the effects of the treatment were statistically significant on *Q. robur* seedlings only 30 days after the first harvest. *Q. robur* grows in "flushes" and the harvest II height values were not generally higher than those of the first harvest (TableIII-2). The increases in dry weights of stem and root parts of control and minus phosphorus treatments brought about the better performances at this harvest. As dry weight yields from photosynthesis depend on balanced mineral nutrition in the plant, it is safe to assume that *Q. robur* seedlings inthe control and minus phosphorus utilized the nutrients available to produce higher yields. In other words, Q. robur seedlings became dependent for nutrients on the treatment solutions (rather than the acorn reserve) between the first and second harvests. This point also illustrates the fact that time of harvest and conditions of growth should be clearly stated in plant nutrition results, this point is often missed by many workers.

The results of Q. robur seedling growth in this work confirm those of Newnham and Carlisle (1969) who reported Q. robur as being unsusceptible to phosphorus deficiency at this seedling stage. They also reported Q. robur dominant in natural soils deficient in phosphorus. The suggestion is that Q. robur has "adapted" itself to a situation of phosphorus deficiency. This characteristic helps the seedling through the acorn which is sufficiently rich in phosphorus to enable the young seedling to produce a substantial root and shoot system without absorbing additional phosphorus. It is clear that this situation cannot continue for long as the phosphorus supply in the fruit in the course of time becomes exhausted and the cotyledons are unable to supply further nutrients, as was observed in this work. The water only treatments indicate this condition, here Q. robur seedlings had the least dry weights at the end of the experiment.

The behaviour of Q. robur in nitrogen deficient solutions as given in this work (dry weights) are also consistent with the results of Newnham and Carlisle (1969). The dry weight yields were lower than those of the control and minus phosphorus, but higher than those of water only.

It is also reported that Q. robur soils are generally not deficient in available nitrogen (Peterken and Lloyd, 1967; Newnham and Carlisle, 1969).

Thus the deficiency response by Q. robur seedlings in the minus nitrogen solutions in this experiment relates to the natural distribution of the species. That is the tree is not adapted to a nitrogen deficient solution and thus gives relatively severe deficiency symptoms when exposed to such a situation as reported in this work.

The general pattern of dry matter distribution in relation to the treatments as indicated by the root-shoot ratios indicates that at this seedling stage, root growth was more important than shoot. The generally increased root/shoot ratios at the second harvest illustrates this point. See Table III-4 . The effects of treatment on Q. robur acorn reserves left at the end of harvests I and II did not show any significant variation (Table III-6) The growth responses of B. pendula seedlings in the four types of culture solutions were quite clear from the beginning, an apparent effect of low amount of nutrient reserve in the rather small fruits. As already reported B. pendula was greatly responsive to a phosphorus deficient solution. The treatment effects produced highly significant F values in the analysis of variance of dry weights, both in the first and second harvests. This is a contrast to the Q. robur situation as the latter was more or less unresponsive to phosphorus deficiency during the period of this experiment. Thus it may be expected that in the field both species may not be present together on a phosphorus deficient soil type. Jones (1959) has in fact observed associations of Q. robur and Betula spp. on nutrient rich soils whereas Betula spp. are associated with Q. petraea on nutrient deficient soils.

The actual nutrient concentrations were not given. It can only be assumed that probably phosphorus was not seriously deficient in these soils where Q. petraea and Betula spp. are associated. Observations were unfortunately not made on the Q. robur and B. pendula seedlings during this experiment as to whether or not mycorrhiza were developed under the experimental conditions available. Thus in making references to natural conditions, caution must be exercised as both species were observed by the writer to have mycorrhizal associations in the field.

The results of this experiment clearly indicate that B. pendula is more sensitive to phosphorus deficiency than to that of nitrogen. This is a contrast to the findings of Ingestad (1957) who stated that B. verrucosa (Ehrh) (synonymous with B. pendula was more affected by nitrogen than by phosphorus deficiency. The results of this experiment also show that B. pendula has very restricted growth in the absence of nitrogen, so do not conflict with the views of Tamm and Hesselman, quoted by Ingestad (1957) that "birch" was nitrogen requiring. In Britain Binns (1966) working on current fertilizer research with the Forestry Commission, stated that phosphorus is the nutrient most frequently found limiting to tree growth in the forest. This agrees with earlier views expressed on phosphorus. Other workers have observed nitrogen limiting to other trees e.g. Scots pine on peat. (Brown et al, 1966). These workers indicated that poor aeration impaired nitrogen uptake in this peat condition. In view of the above evidence, it is unlikely that either Q. robur or B. pendula would establish on such soils.

Plant Elemental Composition

Many workers have found correlations between plant yields and plant elemental composition. (Chapman, 1962; Ferwerda, 1961 and Broeshart et al, 1957). Although no correlation tests were done on the results, yet the relationship between plant yield and major elemental composition seems apparent in this work. The relationship observed involved two major characteristics:
(i) The "need" of the plant and (ii) the behaviour of the elements concerned generally.

The results of the plant analysis and the plant dry matter productions show that while both *Q. robur* and *B. pendula* responded to nitrogen and phosphorus deficiencies the relative differences on their responses depended on their varied requirement. For instance the high concentrations of nutrients in the cotyledons of *Q. robur* (Table III-19) obviously prevented any immediate response to these deficiencies by the growing seedlings. On the other hand the response of *B. pendula* without any such nutrient reserves was apparent within days. That the acorn could not serve the *Q. robur* seedlings with adequate amount of nutrients for too long is shown by the differences in the state of the nutrients between the first and the second harvests. The relatively low concentrations of nitrogen in most parts of water only and minus nitrogen growing seedling together with restricted dry matter production, indicate the levels at which plant nitrogen content limits growth.

Broeshart and Ferwerda (1957) have objected to the method of comparing the chemical composition of samples taken at different (or sometimes) unknown periods, because of variations due to sampling and to seasonal effects. The variation in the elemental composition of the *Q. robur* and *B. pendula* seedlings within a period of two months confirms this view.

It is possible to compare the values from this experiment with certain others obtained in literature corresponding to deficiency symptoms, on the assumption that this exercise is relative and not absolute. The leaf percentage nitrogen for Q. robur and B. pendula seedlings grown in water only and minus nitrogen were below those associated with deficiency symptoms by Newnham and Carlisle (1969). They found chlorosis and loss of older leaves in plants of Q. robur with mean leaf nitrogen concentrations of 1.84 - 1.99%. In the current experiment, seedlings of comparable age with those used by Newnham and Carlisle had leaf nitrogen concentrations of 1.40 - 1.43% when grown on water only and 1.22 - 1.75% when grown on minus nitrogen solution. While Newnham and Carlisle gave 14 p.p.m. of nitrogen to their seedlings, the seedlings in the current experiment had no nitrogen. The seedlings which had nitrogen provided showed leaf nitrogen of 1.80 - 2.01% at the first harvest and 2.45% at the second harvest. These values compare with 2.6% associated by Newnham and Carlisle with maximum growth. The absence of nitrogen or phosphorus did not appear to have had much effect on the potassium content of the Q. robur seedlings, but on the other hand the absence of nitrogen in the medium seemed to have affected adversely the potassium uptake of B. pendula seedlings. Possibly the acorn effect was significant in preventing "imbalance" in the potassium uptake. The sodium content of Q. robur seedlings seemed to be increasing with time irrespective of treatment while the converse was true for B. pendula even in the control. The behaviour of sodium in plants is also not yet clearly understood and the accumulation of sodium in the Q. robur is an example.

Nitrogen and phosphorus have constituent and functional roles in plants, while potassium and sodium are mainly functional. (Wilde, 1946). The deficiency of phosphorus is easily overlooked, while that of nitrogen and potassium are readily observed.

These experiments have been useful in bringing out the single factors of these elements as they affect the growth of the tree seedlings. Yet the results must be interpreted with caution as elements do not usually behave singly. Secondly, the mycorrhizal relationship (not examined at all in this work) could be crucial to nutrient uptake in the field. The production of ectotrophic mycorrhiza in many tree seedlings associated with nutrient uptake has been identified by a number of workers. (Richards, 1968; Fowells and Krauss, 1959 and Hewitt, 1966). Such relationships between roots, fungi and nutrients are still not clearly defined, but it is of potential importance in the nutritional studies of most forest trees including conifers.

CHAPTER IV

THE EFFECTS OF SOIL VOLUME ON SEEDLING GROWTH AND NUTRIENT UPTAKE OF *Q. ROBUR* L. AND *B. PENDULA* ROTH.

INTRODUCTION

The previous experiment on nitrogen and phosphorus deficiency explored the role of two individual major soil nutrients in the growth of *Q. robur* and *B. pendula*. It must however be remembered that even when these elements are present in sufficient amount in the soil, other factors might prevent their uptake and subsequent utilization by the plants. Such factors include reduced soil volume for free root growth and development. This kind of situation may be brought about by a number of ecological conditions like soil shallowness, waterlogging and density effect of other trees. Three important limiting factors thus arise (i) mechanical impedance, (ii) poor aeration and (iii) restricted water (and thus nutrient) availability (Eavis, 1972). Jones,(1959) observed that the height attained by *Q. robur* depends greatly on its density and on the species with which it is mixed. It would be interesting to study the mechanisms which limit this plant under dense conditions.

Tansley (1944) described *B. pendula* as a pioneer species which prepares the soil for more exacting species like *Q. robur* which he termed a successor. Thus in the natural afforestation process, *Q. robur* might be expected to colonise birch-dominated woodland. There are no reports known to the author which describe the growth patterns of these species during this period of succession.

In this work, it is hypothesized that such growth effects might be apparent even at the seedling stage, when encouraged by such treatments as soil volume variation.

Larsen and Sutton (1963) by using phosphorus P^{32} studied the effect of soil volume on the absorption of phosphorus by rye grass and on the determination of labile soil phosphorus. They found that the uptake of phosphorus followed the same pattern as the yield of dry matter. There was however no explanation given of the situation in which small pots had lower dry plant weights though they contained more labile phosphorus.

Hoyle (1971) observed that it is not only physical conditions that inhibit birch (B. allenghaniensis) growth; calcium and nitrogen deficiencies as well as aluminium toxicity retarded both primary root growth and shoot development.

In view of this, it was necessary in this work to minimize a number of environmental factors by (i) using soil samples fertilized with a constant level of John Innes mixture to reduce such effects as Hoyle described; (ii) watering the pots uniformly and regularly from the top, to ensure adequate water and aeration (Eavis, 1972; Warnaars and Eavis, 1972); (iii) ensuring a bulk density similar for all treatments ; (iv) growing the plants under uniform conditions in the green house. Thus of all the methods available for studying the effect of varying amounts of nutrient uptake, the one chosen was by grading the pot sizes from which Q. robur and B. pendula might draw nutrients. Nutrient uptake was determined by soil analysis methods, with plant analysis where found appropriate.

From the point of view of the forester, who may wish to start seedling trees in pots, it is desirable to use pots of a size which combines good seedling growth with economy of potting soil and other materials. It was hoped that this experiment would yield some guidance on the factors to be considered in pot size selection.

Materials and Methods

Seed germination

On 24 February, 1972 several acorns (3-4 g in wight, from a single tree on Clapham Common Heath, London) were planted in peralite and watered with tap water only.

On 3 March, 1972, B. pendula seeds from Codicote Heath were planted also in peralite and also watered with tap water only.

On 7 and 8 April, 1972 the seedlings of Q. robur and B. pendula were transplanted into three sizes of black polythene pots.

It took the Q. robur acorns up to 21 days to germinate; on the other hand, B. pendula commenced germination after 8 days. Transplanting had to wait till enough seedlings (as uniform in size as possible) for the experiment were obtained.

The Pots used in this Experiment

Table IV-1 gives the details of the pots used in this experiment.

Pot size Denotation	Height Overall (cm)	Diameter Top inside (cm)	Weight of Soil g/pot	Soil Weight Ratio
Small	8	9.5	275	1
Medium	11	11	550	2
Large	12	13	825	3

Each pot had four holes (6mm in diameter) at the bottom for drainage. The pots were put on plastic trays to prevent solution loss through the holes. Pots of the same size were put together on trays. Further details of pot arrangements will be described later (See Experimental design)

The Green House Conditions

This experiment was performed in an electrically-heated glasshouse, the minimum temperature of which was 60°F (15.6°C) and maximum 110°F (43.3°C) During hot weather it was not always possible to control the maximum temperature even with the windows opened. This caused some leaves of B. pendula to be prematurely shed.

There was no additional light to that provided by daylight within the greenhouse. In mid-summer, the green-house was shaded with a green net to reduce the temperature within. This seemed effective. The experimental plants were first placed on benches in the greenhouse, but were later put on the floor to increase the headroom.

The Experimental Design

The design of this experiment employed randomised blocks. Each species in a particular pot size was regarded as one treatment. There were four replicates for each treatment. Six harvests were planned to commence as soon as the plants had established themselves in the pots. In actual fact, when the harvests were started, the plants had started wintering - shedding their leaves and developing dormant buds. An attempt to induce continued growth by increasing photoperiod failed.

The small plastic trays containing each batch of experimental pots were put together in sets on a large plastic tray, i.e. one large plastic tray held three small plastic trays carrying the small, medium and large pot treatments.

There were four large trays in all, one for each replicate. The positions of the small trays within the large ones were varied periodically.

Further details of soil used in this work

The soil samples were collected in the departmental botanic garden and a constant level of standard John Innes Fertilizer was mixed with it. The fertilizer composition was:

2 parts of Nitrogen	(hoof and horn)
2 parts of Phosphorus	(superphosphate of lime)
1 part of Patash	(sulphate of potash)

Fertilizer was mixed with the soil at a rate of $4\frac{3}{4}$ ounces of the fertilizer to each bushel of soil.

The soil mixture was:

medium loam	2 parts
peat	1 part
coarse sand	1 part.

Table IV-2

The composition of the soil in the pots after the addition of a constant level of John Innes fertilizer (Mean values of three replicates)

Mechanical Composition		
% Coarse Soil	39.34	(± 0.45)
% Fine soil	60.66	(± 0.45)
pH	6.88	(± 0.0015)
Exchangeable hydrogen (mEq/100g soil)	2.00	(0.0)
Exchangeable bases (mEq/100g soil)	16.80	(±0.62)
% Loss on ignition	9.03	(± 0.39)
Extractable phosphorus mg/100g soil	1.45	(± 0.004)
% Nitrogen	0.12	(0.0)
Available potassium mEq/100g soil	1.74	(± 0.005)
Available sodium mEq/100g soil	2.26	(± 0.003)
Total Calcium mEq/100g soil	5.66	(± 0.28)
Total magnesium mEq/100g soil	3.99	(± 0.13)

Figures in parenthesis indicate standard error values.

For soil analysis methods see Chapter II.

HARVESTING

Harvesting was started on 16 October, 1972 and continued subsequently at two weeks interval till 27th December, 1972. Plant height and stem diameter at 1 cm above soil surface were recorded from the beginning of this experiment at 1 month intervals and also during the harvests (now at two week intervals). In addition during harvests root length (maximum, not aggregate) was measured for every plant. Each plant was segmented into leaves, stems and roots (with residue of acorns in the case of the oak seedlings). For the details of the dry weight determination see Chapter II. The soil samples left in each pot were stored and analysed chemically as soon as possible for the following:-

(1) pH
(2) Exchangeable hydrogen
(3) Exchangeable bases
*(4) Percentage loss on ignition
(5) Nitrogen
*(6) Calcium
*(7) Magnesium
(8) Available Potassium
(9) Available Sodium
(10) Available Phosphorus

* Determined only at the beginning of the experiment.

It was also decided to analyse the various plant parts for nitrogen to see the relationship between the nitrogen left in the pots and that taken up in plant growth.

It was easy to wash off the soil from the roots of the Q. robur seedlings in all treatments.

The pattern of growth of the B. pendula seedling roots was completely different from that of the Q. robur seedlings. The tendency was to produce large numbers of branching roots with the main or tap root being relatively inconspicuous.

The large and medium pots produced seedlings with the greatest mass of roots; it was difficult to wash off the soil from them. Conversely, the roots of B. pendula in the small pots were small, long and thin, mainly fibrous, and easy to wash.

The harvesting of the seedlings were started on 16 October 1972; at this time wintering (leaf abscission) had started. B. pendula began abscission and dormancy first, Q. robur followed gradually about a month later. Both species seemed to have behaved fairly similarly as far as abscission and dormancy was concerned and no effect due to pot size variation was noticeable in either species.

RESULTS

GENERAL MORPHOLOGY

Shoot Growth

It was difficult to observe any apparent effect of soil volume variation on the general growth of the Q. robur seedlings, even after 9 months of plant growth. The only noticeable thing was that Q. robur seedlings growing in the large and medium pot sizes produced branches on their main stem, whereas the seedlings in the small pot sizes simply grew uniformly tall without branches.

The B. pendula seedlings on the other hand showed a different pattern of growth. It was obvious that the seedlings in the large and medium pots performed better (thick stems, many branches and medium to large leaves) than the seedlings in the small pots. The B. pendula seedlings in the small pots had generally and relatively a poorer growth. The leaves were small; the main stem thin and very litter branched. It appeared that the B. pendula seedlings in the large and medium pots were doing better than the Q. robur seedlings.

Root Growth

This trend of general growth pattern just described was observed on the roots when washed. The Q. robur seedlings in all pot sizes had a greater bulk of roots than the B. pendula. The Q. robur seedlings in both large and medium pots had larger and more uniformly thick tap roots and more lateral roots than the seedlings in the small pots. However the main roots of the Q. robur seedlings in the small pots were much thicker than those in the other treatments; the roots did not attempt to extend themselves, rather they grew 'inwards' culminating in the production of a single thick root system, with very few branches.

Table IV-3

The effect of soil volume on height and dry weight yields of *Quercus robur* (Mean values of 4 replicates and 6 harvests)

	Pot Size		
	Large	Medium	Small
Plant height (cm)	27.25 (± 0.27)	24.36 (± 0.64)	32.30 (± 1.47)
Total plant dry weight (g)	11.71	10.50	10.46
Leaf (g)	1.71	1.57	1.33
Stem (g)	2.53	2.15	2.52
Root (g)	7.02	6.31	6.15
Fruit left over (g)	0.45	0.47	0.46
Root/Shoot Ratio	1.66	1.70	1.58
Leaf weight ratio	0.15	0.15	0.13

For analysis of variance see Table IV-5

Figures in parenthesis indicate standar error values.

Table IV-4

The effect of soil volume on height and dry weight yields of B. pendula seedlings. (Mean values of 4 replicates and 6 harvests)

	Pot Size		
	Large	Medium	Small
Plant height (cm)	66.05 (±0.96)	68.55 (±1.15)	48.55 (±0.58)
Total plant dry weight (g)	13.30	12.69	5.81
Leaf (g)	2.20	2.24	0.91
Stem (g)	5.87	5.78	2.58
Root (g)	5.23	4.67	2.32
Root/Shoot ratio	0.64	0.58	0.65
Leaf weight ratio	0.17	0.18	0.16

For analysis of variance see Table IV-5

Figures in parenthesis indicate standard error values.

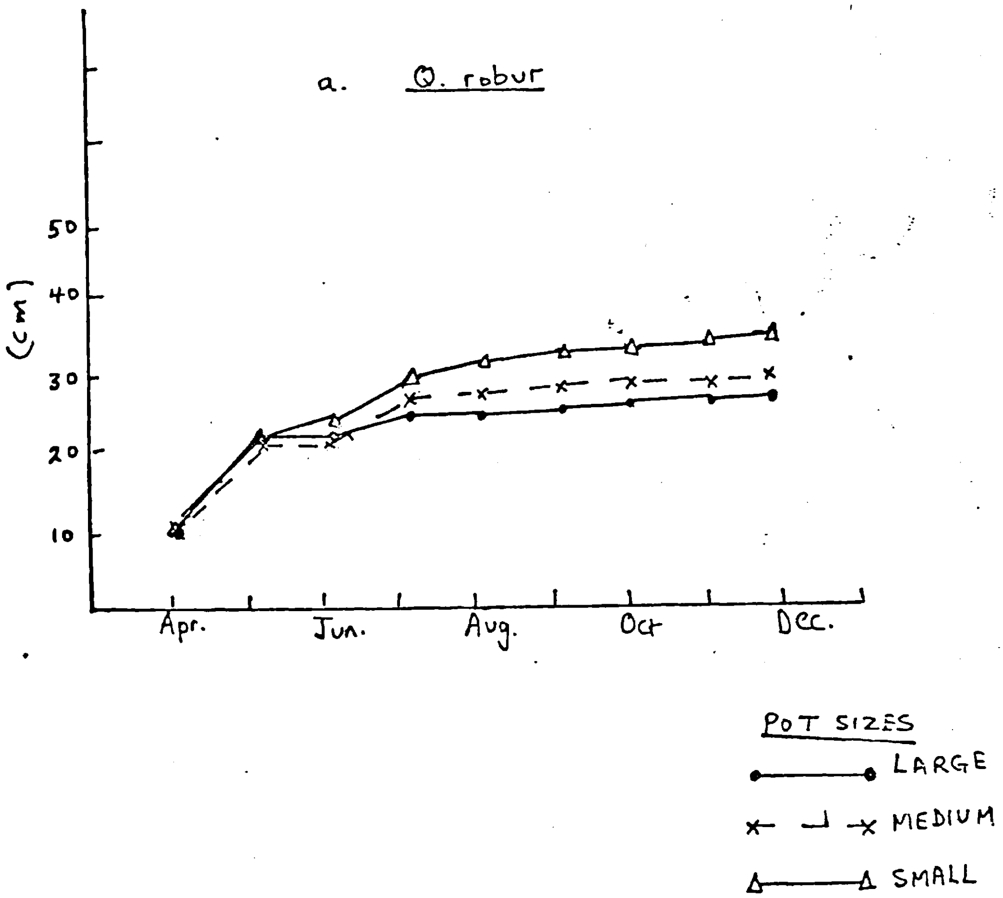
TABLE IV-5

Variance Ratio (F) values in the analysis of variance of plant dry matter production as a result of soil volume variation treatments (A summary of 6 harvests and 4 replicates)

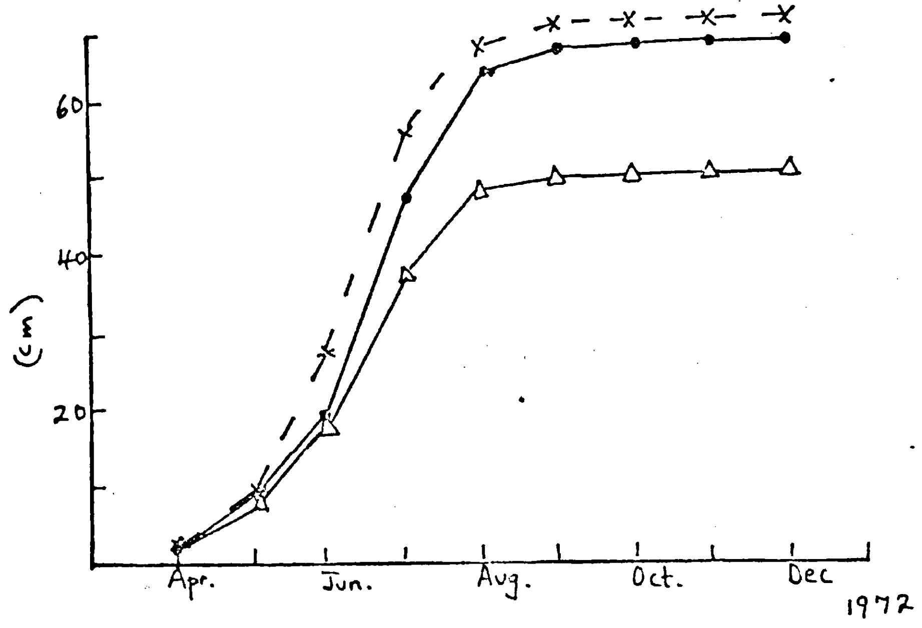
	PLANT PARTS			
Variables	Total Plant Dry Weight	Leaf	Stem	Root
Species (s)	0.17 NS	0.78 NS	25.19***	28.19***
Treatment (T$_1$) (*Q. robur* & *B. pendula*)	8.35**	5.42*	5.47*	5.89*
Treatment (T$_2$) (Q. robur)	0.72 NS	0.17 NS	0.83 NS	1.11 NS
Treatment (T$_3$) (*B. pendula*)	31.50**	34.73**	19.27*	41.26***
S X T$_1$	6.43**	4.65*	4.54*	2.37 NS
Replicate (R$_1$) (*Q. robur* & *B. pendula*)	0.79 NS	0.35 NS	0.60 NS	1.90 NS
Replicate (R$_2$) (*Q. robur*)	0.90 NS	0.19 NS	1.27 NS	2.57 NS
Replicate (R$_3$) (*B. pendula*)	1.00 NS	1.01 NS	0.56 NS	2.86 NS

NS	Not Significant
*	Significant at 5% probability level
**	Significant at 1% probability level
***	Significant at 0.1% probability level.

Fig.IV-1 The effect of soil volume variation on the height growth of *Q. robur* and B. pendula seedlings (Mean values of 4 replicates)



b. B. pendula



Height

In both species, shoot growth started between April and May 1972. In *B. pendula*, growth appeared to be continuous, the rates differing in accordance with the pot treatment, while in *Q. robur*, growth in height proceeded in an intermittent manner 'flushes'. The first flush was in May and produced growth with short internodes; the second growth flush in July had longer internodes than the first. An unsuccessful attempt was made to induce further flushing during the harvest period by exposing the plants to additional light from a mercury vapour source.

Fig .IV-1 and Tables IV-3/4 show the general trends in the height performance of both species. *B. pendula* seedlings grew taller than *Q. robur* seedlings generally, the results in tables showing that *B. pendula* seedlings, in both large and medium pots were more than double the height of the tallest *Q. robur* seedlings.

Large and medium pots gave similar heights in *B. pendula*, but the small pots had seedlings which were conspicuously shorter. In *Q. robur*, on the other hand, the greatest mean heights were found in the seedlings growing in the small pots.

Plant Dry Weight yields

Total Plant dry weight

In Fig .IV-2 the total plant dry weight values are graphed out. As the harvests were done at the end of the growing season, it was not possible to measure the effect of soil volume variation on the rate of dry matter production. Thus variations between harvests in these results can only be regarded as due to sampling error.

Table IV-6 The effect os soil volume on soil/plant ratio values of *Q. robur* and *B. pendula* seedlings

(a) *Q. robur*

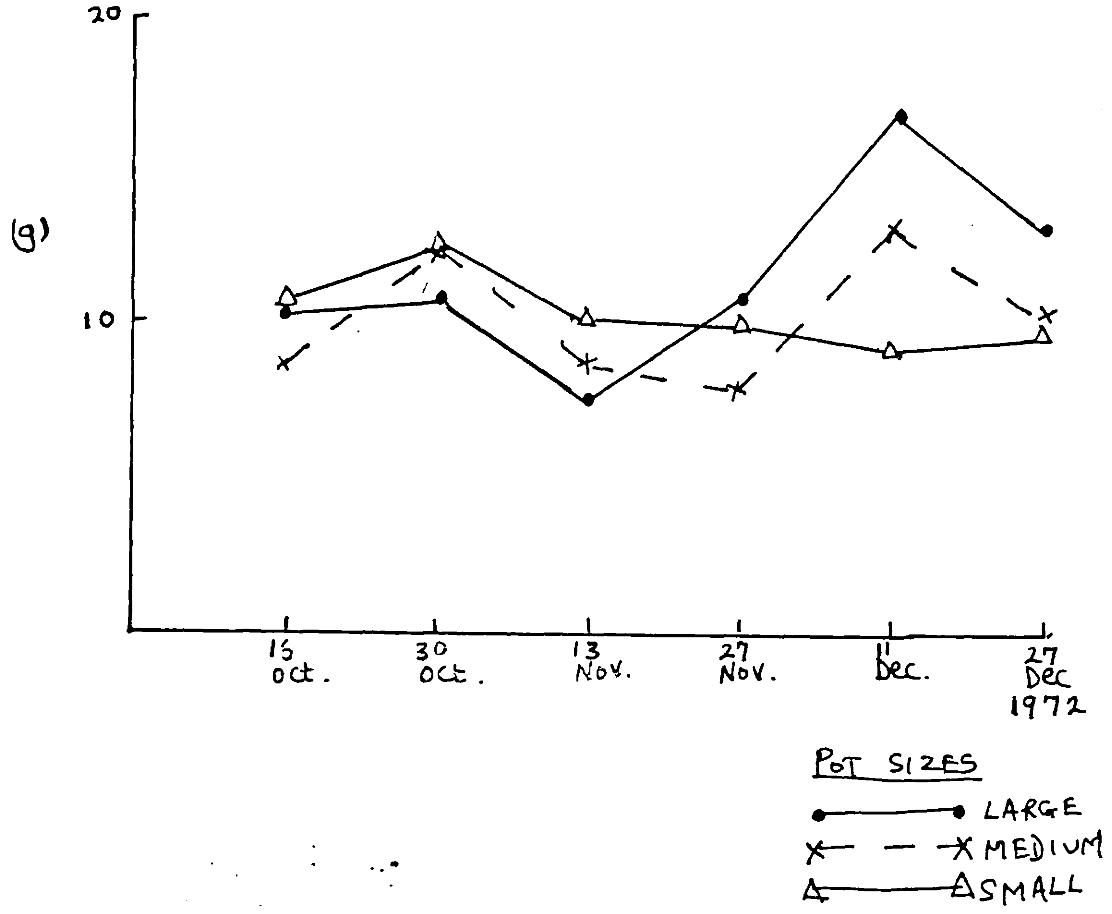
Pot Size	Large	Medium	Small
Soil Weight (g)	825	550	275
Soil Weight Ratio	3	2	1
Mean Total Plant Dry Weight (g)	11.71	10.49	10.46
Plant Ratio	1.1	1.0	1.0
Plant Weight per unit soil weight (g per g)	0.014	0.019	0.038

(b) *B. pendula*

Pot Size	Large	Medium	Small
Soil Weight (g)	825	550	275
Soil Weight Ratio	3	2	1
Mean Total Plant Dry Weight (g)	13.29	12.69	5.81
Plant Ratio	2.2	2.1	1.0
Plant weight per unit soil weight (g per g)	0.016	0.023	0.021

Fig. IV-2
The effect of soil volume variation on the total plant dry matter production of Q. robur and B. pendula seedlings
(Mean values of 4 replicates)

a. Q. robur



b. B. pendula

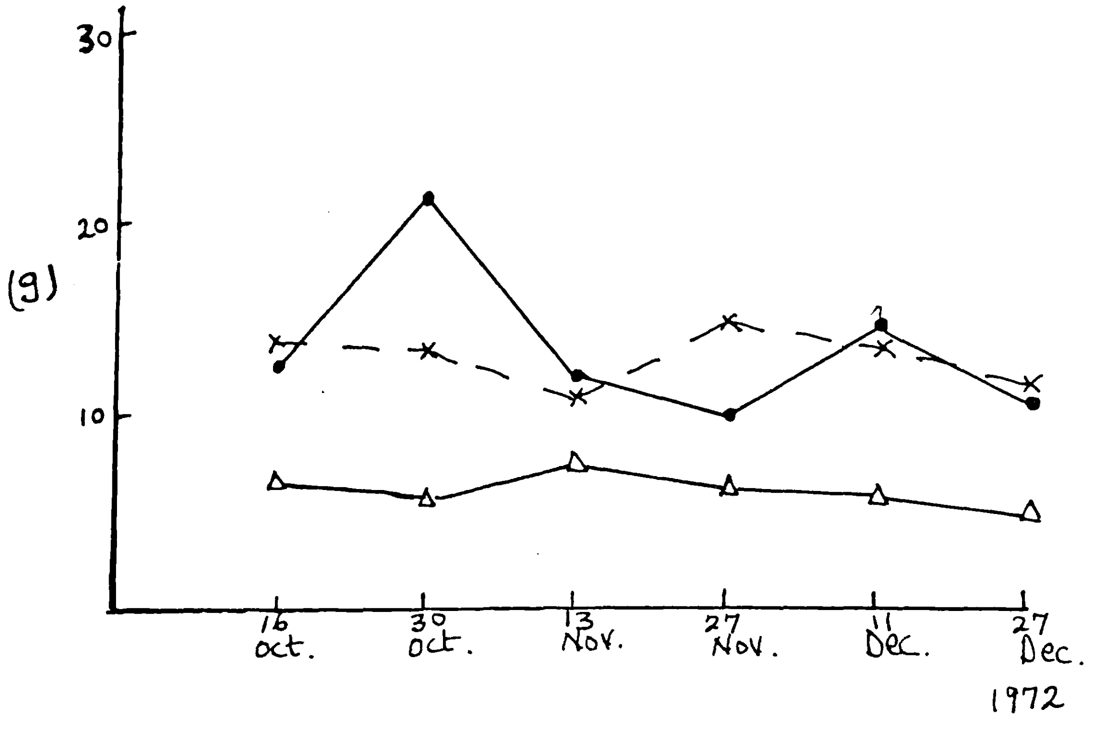
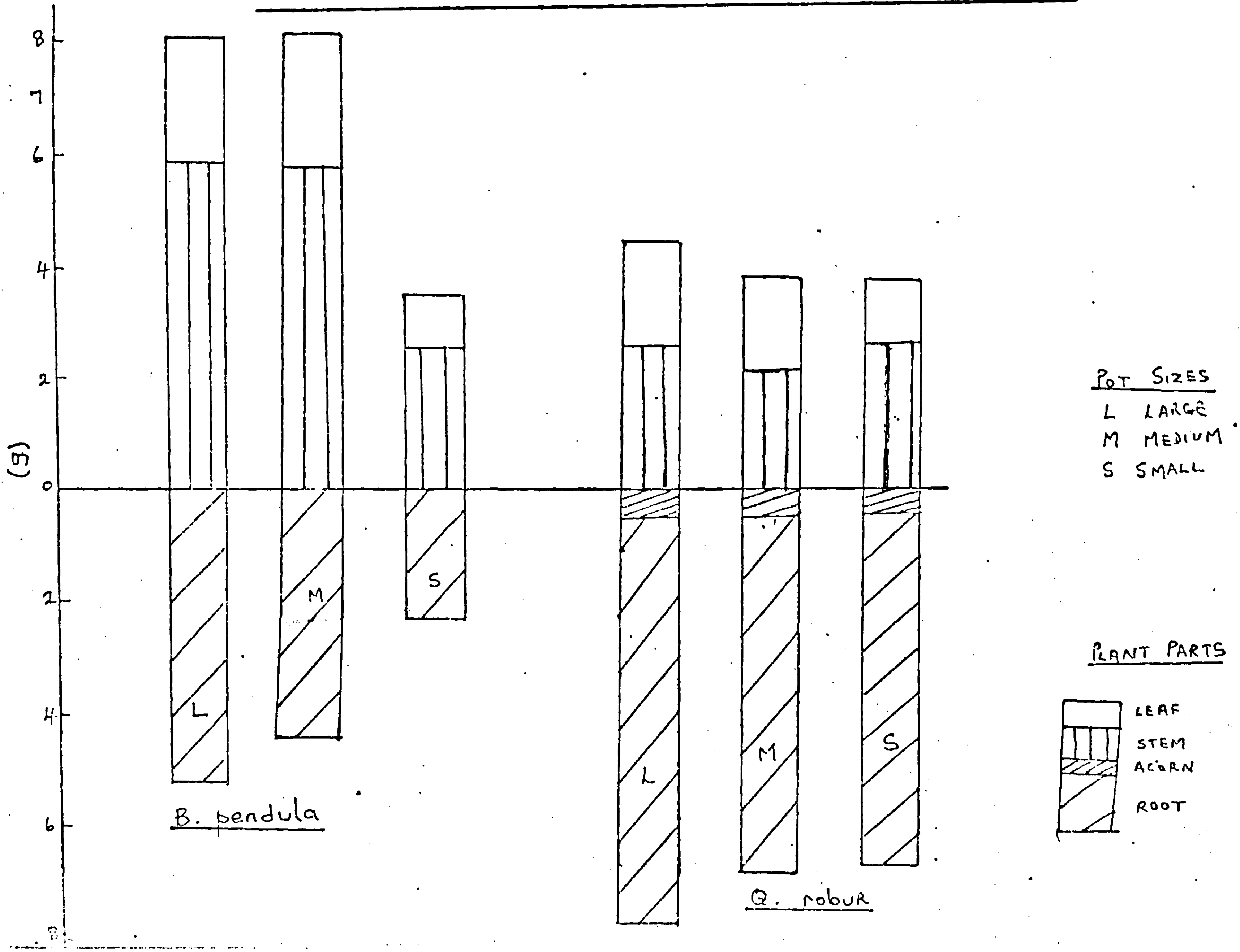


Fig. IV-3 The effects of pot sizes on the plant dry matter distribution of _Q. robur_ and _B. pendula_ seedlings. (Mean values of 24 replicates)



The patterns of dry matter production are illustrated in Fig.IV-2 and Tables IV-3,4. In Fig.IV-2a, the intertwining of the lines indicate the relatively little effect of soil volume variation on Q. robur seedling growth. For analysis of variance see Table IV-5 .

In B. pendula a contrasting situation exists. Fig.IV-2b shows that the least total plant dry matter production was in the small pots. Again the effects of the large and medium pot sizes are relatively small. Only in Table IV-4 that the effects of the pot sizes as far as the large and medium pots are concerned can be ascertained clearly. Even then the large and medium pot size values are quite comparable.

Plant dry matter distribution

Q. robur and B. pendula were morphologically different types of plants as Fig.IV-3 indicates. For Q. robur more than 50% of the plant dry matter was in the roots. It was the reverse in B. pendula, the latter producing more shoot than root. Table and Fig.IV-3 show that there was no effect of treatment on the acorns left over in the Q. robur seedlings. It was in the leaves and roots that Q. robur seedlings grown in large pots produced more dry matter than in the other pots. Otherwise the results in the three treatments are quite comparable (Tables IV-3,4).

In B. pendula there were small yields as far as the roots, stems and leaves were concerned in the seedlings in small pots. The highest values for root dry weights (5.23 g) were in large pots and it was mainly in the root yields (0.55g above the medium pot size values) that the overall gain in total dry weight of 0.61 g in the large pots was obtained over the medium pot seedlings.

The effect of plant growth on soil mineral composition in the three pot sizes (Mean values of 4 replicates and 6 harvests)

(a) Hydrogen ion concentration, pH

The pH values of soil samples in all treatments increased considerably when compared with the unused soil sample at the beginning of the experiment. Fig .IV-4 and TablesIV-7 & 8.

The effect of harvest on the pH values was not considered important, as the plants had started dormancy at the time of first harvest. This also applies to all other soil conditions to be described later.

The effect of the pot sizes on the soil pH values seems to be important in both the Q. robur and B. pendula samples. The lowest pH values were obtained in the large pots, the highest in the small, the medium coming in between.

The pH values in B. pendula pots were generally higher than those in Q. robur pots irrespective of treatment. Thus the soil samples became more basic (chemically) rather than acidic as a result of the growth of the roots of the experimental seedlings, in the pots.

(b) Exchangeable hydrogen

The exchangeable hydrogen in the unused soil sample was 2.0 m.eq/100 g soil. At the time of harvesting the exchangeable hydrogen in all treatments was zero. It should be noted, however that the original exchangeable hydrogen available at the beginning of the experiment was low (2.0m eq/100g Soil) due to the John Innes fertilizers employed.

Table IV-7
A summary of the mineral composition of the soil in which Q. robur was grown in three pot sizes, large, medium and small
(Mean values of 24 pots)

	* Soil unused at the beginning of the experiment	Pot Sizes		
		Large	Medium	Small
pH	6.88	7.24	7.25	7.44
** Exchangeable Hydrogen	2.0	0	0	0
** Exchangeable Bases	16.80	34.91	32.64	33.82
** Cation Exchange Capacity	18.50	34.91	32.64	33.82
** Sodium	2.26	1.69	1.36	2.06
** Potassium	1.74	2.01	1.85	1.79
Nitrogen	0.12	0.19	0.20	0.22
Phosphorus m eq/g soil	2.82	3.47	3.38	3.31

* Mean of three replicates only

** Values in m eq/100g soil.

For analysis of variance see Table IV - 9

Table IV-8

A summary of the mineral composition of the soil in which *B. pendula* was grown in three pot sizes, large, medium and small (Mean values of 24 pots)

	* Soil unused at the beginning of the experiment	Pot Sizes		
		Large	Medium	Small
pH	6.88	7.34	7.48	7.52
** Exchangeable Hydrogen	2.0	0	0	0
**Exchangeable Bases	16.80	35.73	34.87	37.27
** Cation Exchange Capacity	18.80	35.73	34.87	37.27
** Sodium	2.26	1.80	2.25	2.21
** Potassium	1.74	1.86	1.83	1.72
Nitrogen %	0.12	0.18	0.20	0.22
Phosphorus m eq./g soil	2.82	3.59	3.53	3.69

* Mean of three replicates only

** Values in m eq/100g soil.

For analysis of variance see Table IV - 9

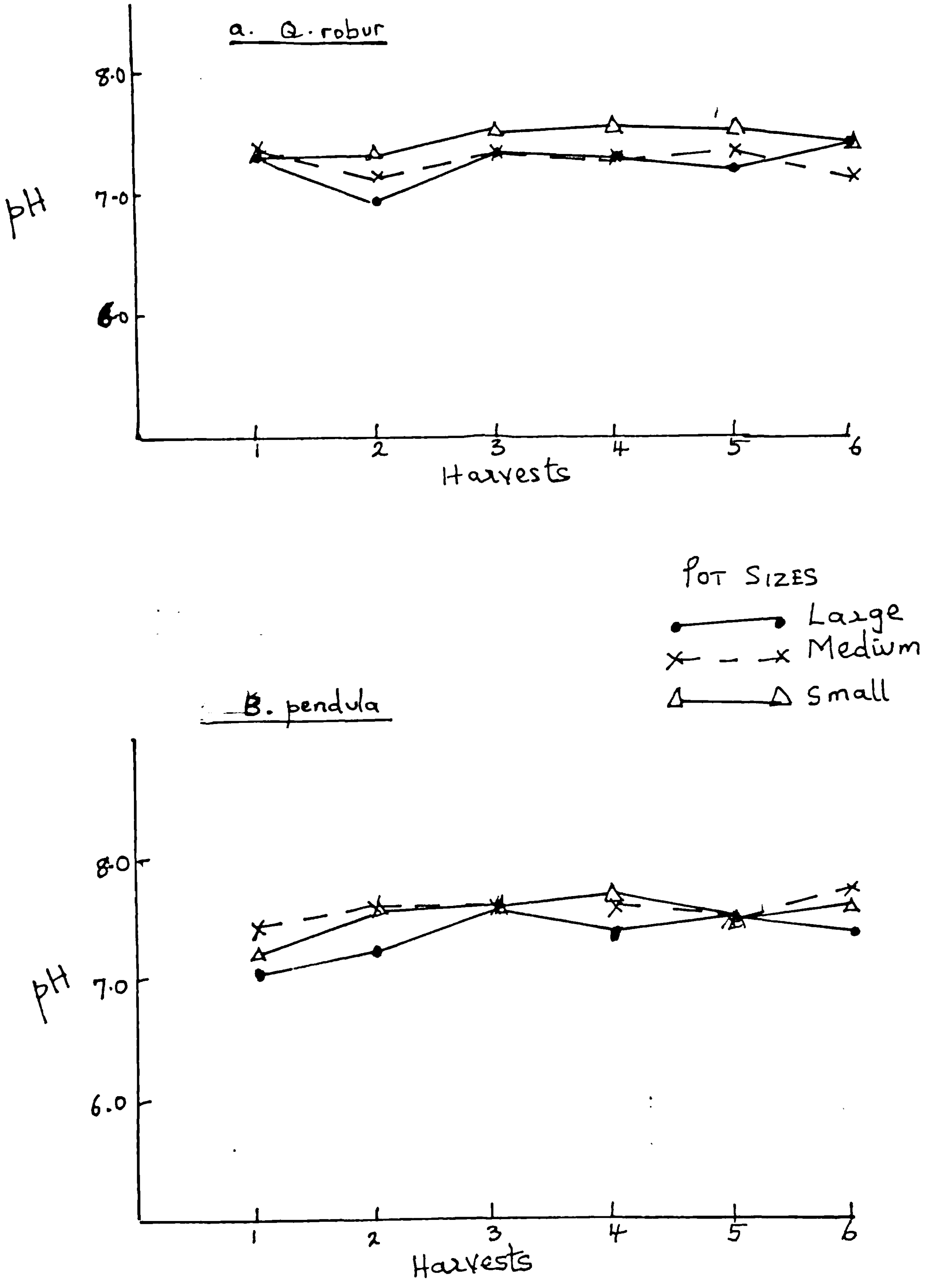
TABLE IV-9

Variance Ratio (F) values in the analysis of variance of soil analysis in three pot sizes in which Q. robur and B. pendula were grown (A summary of 6 harvests and 4 replicates)

Variables	pH	Exchangeable			Soil Properties	
		Bases	Sodium	Potassium	Mineral Nitrogen	Available Phosphorus
Species (s)	15.21^{**}	2.30 NS	14.29^{**}	0.69 NS	1.48 NS	5.00^{*}
Treatment (T_1) (Q. robur & B. pendula)	10.78	1.00 NS	5.62^{*}	1.23 NS	7.40^{**}	0.33
Treatment (T_2) (Q. robur)	52.70^{***}	3.39 NS	30.62^{***}	2.40 NS	3.70 NS	0.17 NS
Treatment (T_3) (B.pendula)	11.15^{**}	1.30 NS	11.61^{**}	2.44 NS	29.20^{***}	1.36 NS
S X T_1	2.02 NS	0.53 NS	6.19^{*}	0.10 NS	0.33 NS	0.16 NS
Replicate (R_1) (Q. robur & B. pendula)	0.94 NS	0.05 NS	1.85 NS	0.01 NS	0.18 NS	1.66 NS
Replicate(R_2) (Q. robur)	8.50^{*}	0.22 NS	1.25 NS	0.77 NS	0.41 NS	4.17 NS
Replicate(R_3) (B.pendula)	0.18 NS	0.16 NS	5.71^{*}	0.87 NS	0.60 NS	2.52 NS

NS Not Significant
* Significant at 5% Probability level.
** " " 1% " "
*** " " 0.1% " "

FIG. IV-4
Hydrogen Ion Concentration (pH) values of soil samples in three pot sizes in which *Q. robur* and *B. pendula* seedlings were grown (Mean values of 4 replicates) Harvests 1 - 6, 16 October to 27 December at two week intervals.



(c) Exchangeable bases

The exchangeable bases determined at harvest time were more than double their original values at the beginning of the experiment. See Tables IV-7&8. This phenomenon was observed in all pots of both species. It was not possible to determine when the values rose. The *B. pendula* values were higher than those of *Q. robur* generally. The small pots of *B. pendula* had the highest values of exchangeable bases 37.27 meq/100 g soil, those of the large and medium pots of this species were quite comparable, 35.73 and 34.87 meq/100g soil respectively. The *Q. robur* soils of all treatments are quite comparable large pot 34.91, medium pot 32.64 and small pot 33.82 meq/100 g soil respectively.

(d) Cation Exchange Capacity

These values are obtained by adding the exchangeable hydrogen and exchangeable bases values together. Since the results of the exchangeable hydrogen determination were zero at harvest time in all treatments, the cation exchange capacity values of the soils are the same as those obtained for the exchangeable bases. Thus what was stated earlier for exchangeable bases for the two species investigated in the three pots is equally true for cation exchange capacities of these soils.

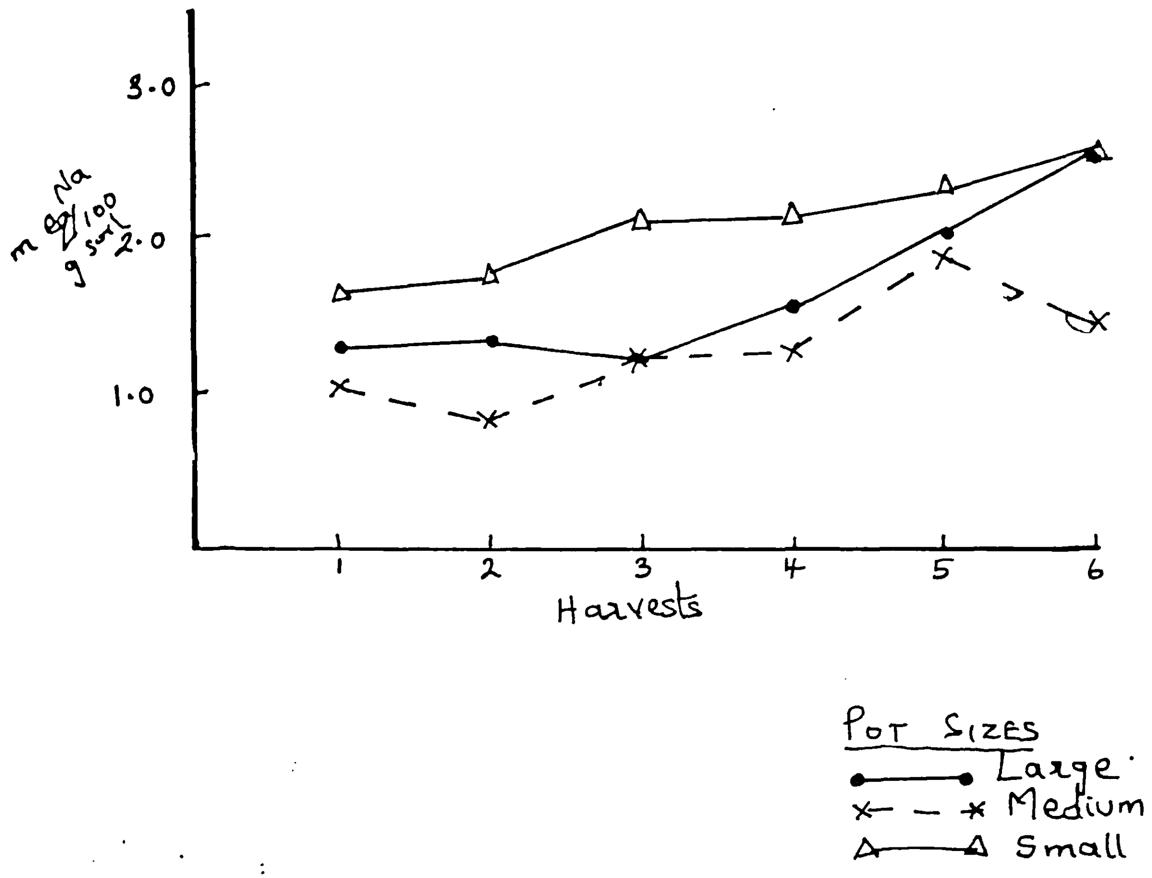
It is worthy of note that as the exchangeable hydrogen in the soil decreased to zero, the exchangeable bases increased. Tables IV-7+8.

(e) Exchangeable Sodium

For the exchangeable values of sodium in the soil samples see Tables IV-7+8 and Fig. IV-5.

Fig. IV-5
Sodium concentration values of soil samples and three pot sizes in which Q. robur and B. pendula seedlings were grown (Mean values of 4 replicates) Harvests 1-6, 16 Oct. - 27 Dec. at two week intervals

a. Q. robur



b. B. pendula

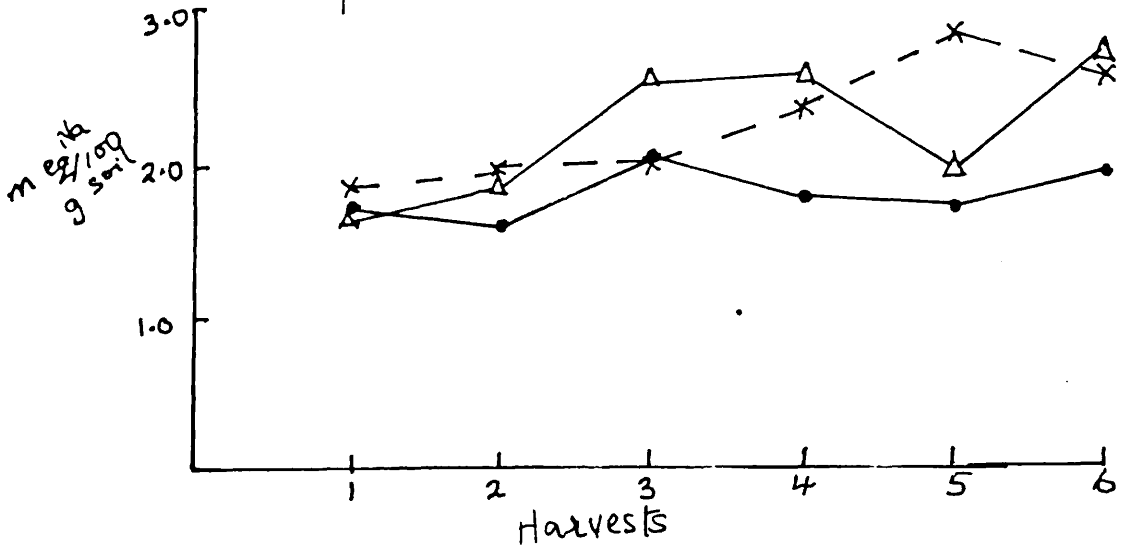
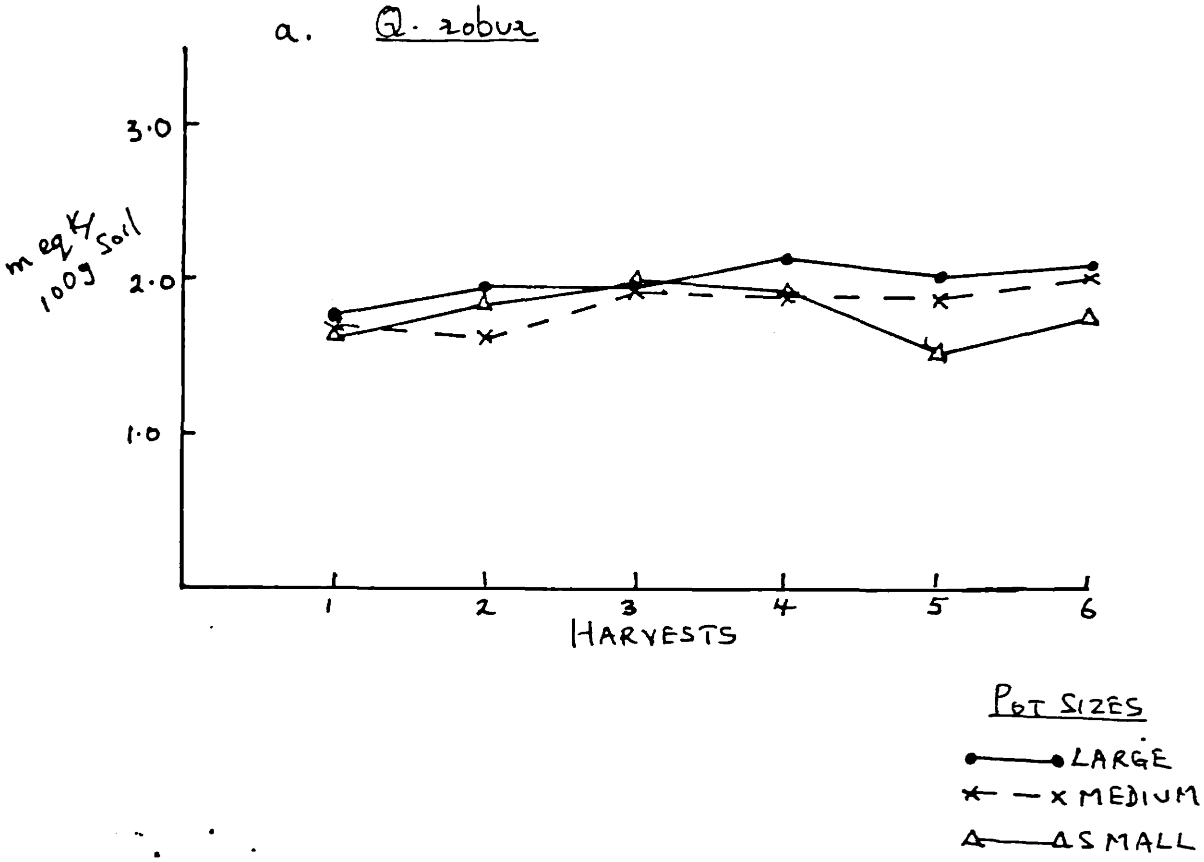
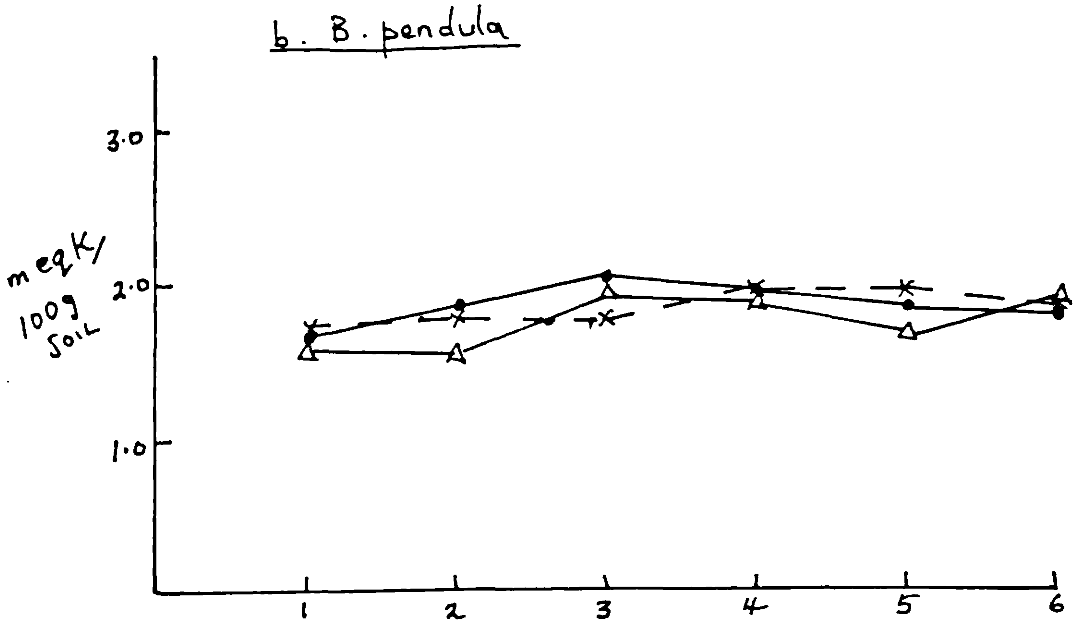


Fig IV-6
Potassium concentration values of soil samples in three pot sizes in which Q. robur and B. pendula seedlings were grown (Mean values of 4 replicates) Harvest 1-6,
16 October to 27 December at two week intervals


a. Q. robur


b. B. pendula

The exchangeable sodium values at harvesting were generally slightly lower than the original values of the unused soils. The lowest values were obtained in the large pots of both *Q. robur* and *B. pendula* samples, and the medium pots of *Q. robur*. The *Q. robur* values were generally lower than those of *B. pendula* i.e. a greater uptake of sodium from the soils by *Q. robur* seedlings. There was relatively little uptake of sodium by the *B. pendula* seedlings from the pots especially from the medium pot size and to some extent the small pots.

The sodium values of *Q. robur* in the small and large pots tended to increase during the last two harvests, these values were comparable to the original values of sodium at the beginning of the experiment; on the other hand the values in the medium pots were decreasing. The role of harvesting on the uptake of sodium by *Q. robur* seedlings was not apparent.

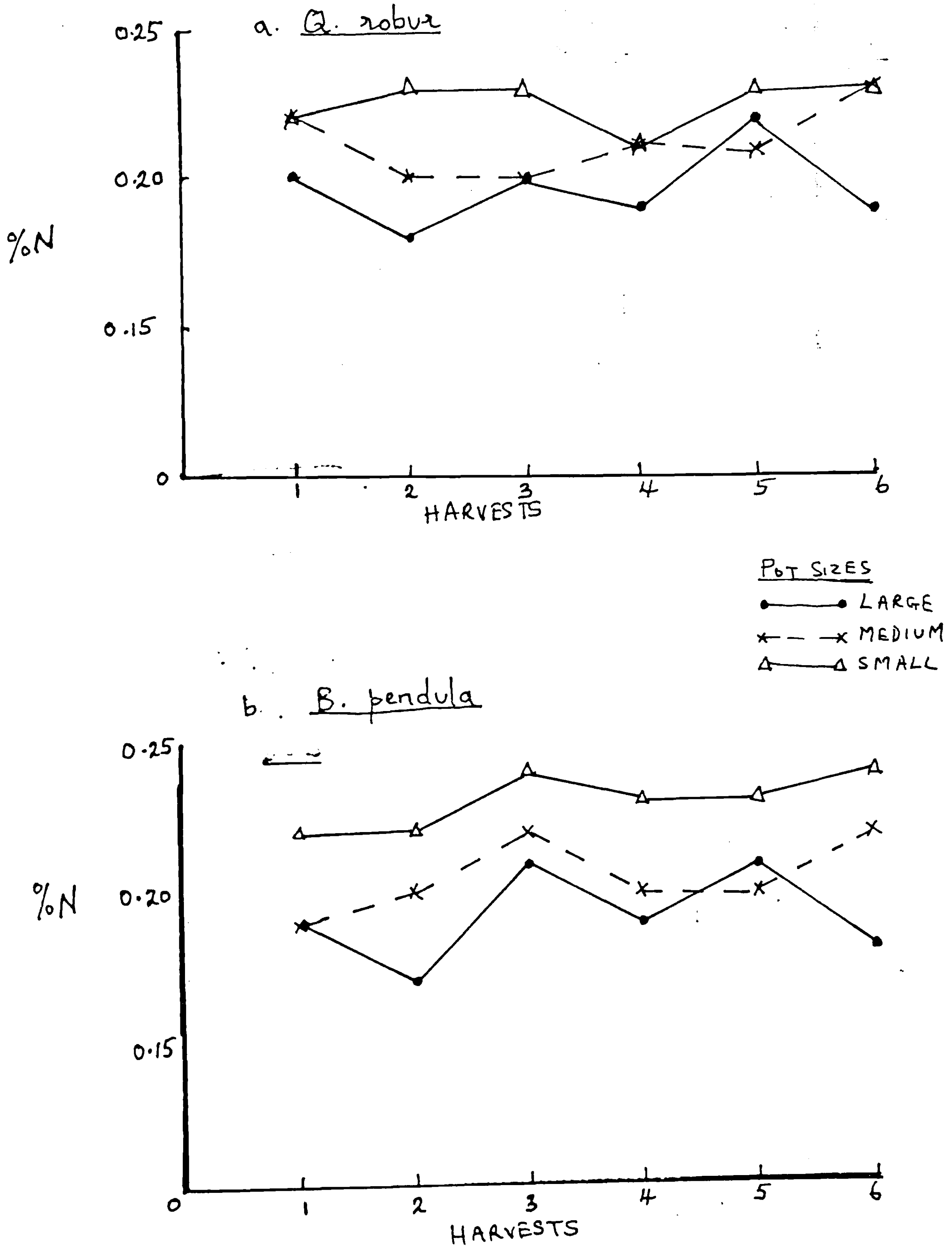
In the *B. pendula* species see Fig.IV-5b the sodium m eq values in medium and small pots were sometime higher than the original values at the beginning of the experiment, but on the whole (as the means of all harvests indicate in TableIV-8), the sodium uptake in the medium and small pots were low. Thus sodium uptake was greater by *Q. robur* than *B. pendula* in all pots.

(f) Exchangeable potassium

Potassium is one of the exchangeable bases and the rate of its uptake as influenced by the three pots was not quite apparent. There was generally higher exchangeable potassium values at harvest than at the beginning of the experiment. The only exception was in the small pot size of *B. pendula* which had a lower value 1.72m eq/100g compared with 1.74m eq/100g at the beginning of the experiment.

Fig. IV-7

Percentage Nitrogen values of soil samples in three pot sizes in which Q. robur and B. pendula seedlings were grown (Mean values of 4 replicates) Harvests 1-6, 16 October to 27 December at two week intervals.



See Tables IV-7,8 and Fig .IV-6. The highest potassium values were obtained in the large pots of Q. robur seedlings 2.01m eq (1.74 m eq original values). On the whole the Q. robur values of all treatments were slightly higher than those of B. pendula i.e. the Q. robur seedlings initiated a greater potassium exchange activity than B. pendula seedlings. In both species the highest potassium values were in the large pots, then the medium pots and the least values were in the small pots.

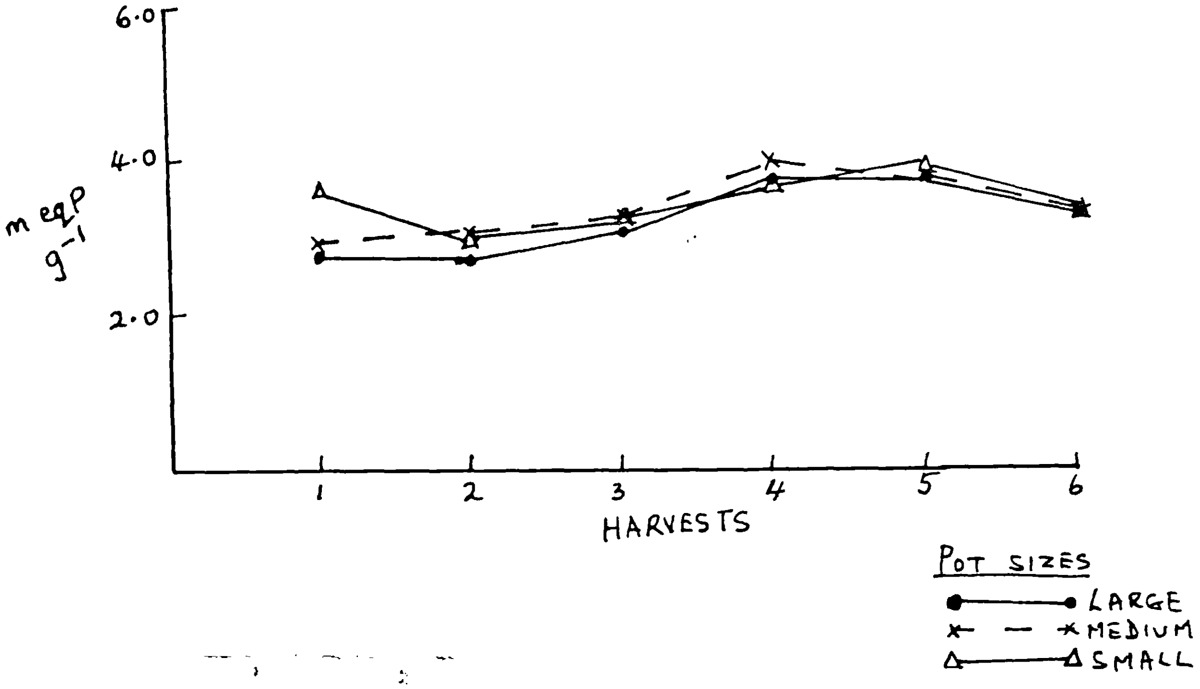
(g) Mineralisable Nitrogen

The percentage nitrogen values at the end of the experiment were higher than at the beginning. The overall mean values of percentage nitrogen present in all harvests were virtually the same for both Q. robur and B. pendula species (see Tables IV-7,9). The slight difference was in the large pots 0.18% for B. pendula and 0.19% for Q. robur, the other values for medium and small pots were exactly the same for both species.

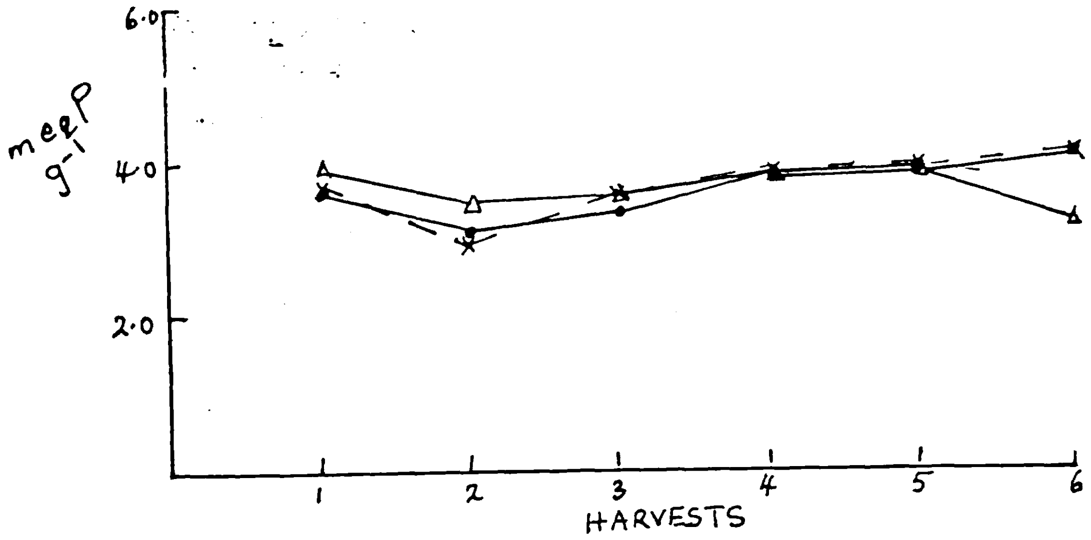
The highest nitrogen values were in the small pots 0.22% (showing the least amount of nitrogen uptake) the medium pots were next with 0.20% nitrogen, the large pots with the least i.e. with the greatest amount of nitrogen uptake. In B. pendula the large and medium pot nitrogen values were fairly comparable but the small pots had generally higher nitrogen concentrations than the other pots in all harvests. In Q. robur seedlings (Fig.IV-7) the differences between the values of the pot sizes in all harvests were less consistent.

Fig' IV-8

Phosphorus concentration values of soil samples in three pot sizes in which Q. robur and B. pendula seedlings were grown (Mean values of 4 replicates) Harvests 1 - 6, 16 October to 27 December at two week intervals.



b. Betula pendula



Available phosphorus

The effects of pot size variation and seedling growth in these were not apparent on the values of available phosphorus determined at the harvesting. See Tables IV 7, 8 and Fig. IV 8. There was generally a greater amount of available phosphorus at the time of harvest than at the beginning of the experiment. *Q. robur* pots had slightly lower amounts of available phosphorus than *B. pendula*. The large pots of *Q. robur* had the highest amounts 3.47 m eq/g the medium pot size had 3.38 m eq/g and the small pots 3.31 m eq. Thus *Q. robur* seedlings removed more phosphorus from the soils than *B. pendula*. With *B. pendula* the relationship between pot size variation and phosphorus uptake was not quite clear. The smallest pots contained the highest amount of phosphorus 3.69 m eq/g soil, the large pots had 3.59 m eq, and the medium had the least 3.53 m eq.

Plant Nitrogen (% Dry Weight)

The Q. robur and B. pendula seedlings were grown in the three pot sizes were analysed chemically for mineralisable nitrogen. Only the first harvest (of six harvests) seedlings were analysed.

The results are given in TableIV-10. Generally, the Q. robur seedlings showed slightly higher percentage nitrogen values.

Total Plant % Nitrogen

In both species the large and medium pot sizes had seedlings with higher nitrogen values, than those of small pot sizes. The values of the large and medium pots were comparable in Q. robur (1.38% large and 1.42% medium); B. pendula medium and small pots had similar values.

The values from small pots in both species were also comparable 1.00% Q. robur and 1.05% B. pendula.

Plant parts and percentage nitrogen

A similar pattern just described for total plant(%)nitrogen was also observed in the leaf(%)nitrogen. The values for the medium and large pot sizes in both species ranged from 2.27 - 2.41. The small pot size values were slightly lower than in the other pots, with values of 1.85 - 2.03%. The B. pendula small pot seedlings had the lowest values for leaf(%)nitrogen.

TABLE IV-10

Nitrogen content (% dry weight) of Q. robur and B. pendula seedlings grown in three pot sizes. (mean values of 4 replicates)

(a) Q. robur

HARVEST I

Pot Size	Total Plant	Leaf	Stem	Root	Fruit left over
Large	1.38	2.27	1.21	1.22	1.43
Medium	1.42	2.41	1.15	1.26	1.12
Small	1.00	2.03	0.73	1.05	1.40

(b) B. pendula

Pot Size	Total Plant	Leaf	Stem	Root
Large	1.25	2.38	0.84	1.23
Medium	1.11	2.31	1.05	1.26
Small	1.05	1.85	0.84	0.98

For analysis of variance see Table IV - 11

TABLE IV-11

Variance Ratio Values from the analysis of variance of *Q. robur* and *B. pendula* plant percentage nitrogen analysis

Sources of Variation	Total Plant	Plant Parts		
		Leaf	Stem	Root
Species (S)	0.22 NS	0.03 NS	0.77 NS	0 NS
Treatment(T_1) (*Q. robur* & *B. pendula*)	2.30 NS	0.76 NS	1.75 NS	0.93 NS
Treatment (T_2) (*Q. robur*)	2.87 NS	1.66 NS	13.0**	0.50 NS
Treatment (T_3) (*B. pendula*)	4.24 NS	2.06 NS	1.20 NS	3.69 NS
Species X Treatment (S X T_1)	0.009 NS	0.07 NS	0.87 NS	0.05 NS
Replicate (R_1) (*Q. robur* & *B. pendula*)	0.57 NS	0.36 NS	0.41 NS	0.46 NS
Replicate (R_2) (*Q. robur*)	0.43 NS	1.11 NS	4.5 NS	0.50 NS
Replicate (R_3) (*B. pendula*)	2.84 NS	2.62 NS	0.50 NS	1.33 NS

NS Not Significant

* Significant at 5% probability level

** Significant at 1% probability level

*** Significant at 0.1% probability level.

The *Q. robur* values were higher than the *B. pendula* values in large and medium pots as far as the stem percentage nitrogen was concerned. (TableIV-10). The *Q. robur* samples ranged from 0.73 - 1.21 and the *B. pendula* values 0.84 - 1.05.

The root samples had values for percentage nitrogen slightly lower than those of the stem in both species; the range for *Q. robur* was 1.05 - 1.26% and *B. pendula* 0.98 - 1.26.

In both species the samll pots had lower values compared with the other pot sizes.

THE EFFECTS OF SOIL VOLUME AND POT ENCLOSURE ON THE SEEDLING GROWTH OF B. PENDULA

Introduction and Methods

The results obtained from the growth of Q. robur and B. pendula seedlings in three pot sizes have indicated that while Q. robur was relatively unresponsive to pot size variation, growth of B. pendula was very much influenced by soil volume variation. The chemical analysis of soil samples from pots in which these seedlings had been growing did not indicate that nutrients were limiting the growth of the B. pendula seedlings. Two possible causes of restricted growth were mechanical impedance (due to restricted pot size) and aeration, as factors operating upon the roots of the seedlings.

Accordingly, an experiment was planned to investigate the role of aeration (pot enclosure) on the growth of the B. pendula seedlings. Two pot sizes, medium and small (see page 39) were used. The medium pot contained twice the weight of soil in the small pot. B. pendula seedlings from the same source as the ones for the major experiment (page 39) were used. Three uniformly germinating seedlings were transplanted into the pots, the seedlings being very small. Later the pots were thinned to one seedling each. There were four replicates for each treatment. Later each set of medium and small pots was divided into two groups. In one group each pot was enclosed in a transparent polythene bag tied with a wire twisted round the stem of the seedling; whenever necessary the bag was opened to water the soil. In the other group the pots were simply left open. The covered pots naturally did not require as much watering as the uncovered because there was very little direct evaporation from the soil. The experiment was carried out in the greenhouse.

The first harvesting was performed on the 17 May after about 6 weeks of seedling growth, when the effects of pot size was beginning to show. It was at this time that covers were fitted to the first group. Thereafter two other harvestings were made at two week intervals.

RESULTS

General Observations

The effects of pot size were as usual quite conspicuous on the general growth of the seedlings, the seedlings in the small pots being generally smaller than those in the medium pots. So far as the main treatment was concerned, the younger leaves of many seedlings in the enclosed pots were pale greenish and the older ones yellowish. This was more noticeable in small-pot seedlings. There was one dead seedling in the first harvest amongst the small-pot seedlings. The seedling collapsed and appeared somewhat diseased. The cause was probably severe waterlogging which was not detected soon enough. Generally, however it was difficult to observe major differences in plant growth as a result of the pots being enclosed or not.

Height

There was a continuous shoot production by seedlings in the medium pots, whether enclosed or not; but seedlings in the small pots showed fairly little increase in height compared with the situation when the treatment began (See Table IV-12)

Dry Weights

The dry weights of the seedlings taken at the time of enclosure showed that even at this stage, the medium-pot seedlings had dry weights especially in the leaf and stem about double those of the small-pot seedlings.

TABLE IV-12

The effects of soil volume and pot enclosure on the seedling growth of B. pendula
(Mean values of 4 replicates)

RESULTS

Height and Plant dry weights

(a) At commencement of treatment (enclosure in polythene)
17 May 1974

Pot size	Height (cm)	Total Plant Dry Weight	Leaf (g)	Stem	Root
Medium	6.0 (± 0.93)	0.12 (±0.001)	0.017 (± 0.0005)	0.02 (±0.0001)	0.03 (±0.0001)
Small	5.05 (± 0.71)	0.07 (±0.0004)	0.04 (±0.0001)	0.01 (±0.002)	0.02 (±0.00003)
Control Pots 31 May 1974					
Medium	8.55 (± 2.50)	0.30 (±0.002)	0.17 (±0.002)	0.06 (±0.0003)	0.07 (±0.0001)
Small	5.17 (± 0.19)	0.13 (±0.0005)	0.07 (± 0.0001)	0.03 (±0.00002)	0.04* (±0.0001)
Enclosed Pots 31 May 1974					
Medium	7.87 (± 1.62)	0.28 (±0.002)	0.16 (±0.001)	0.07 (±0.0002)	0.05 (±0.0003)
Small	5.06 (± 1.00)	0.14 (± 0.0009)	0.08 (± 0.0003)	0.03 (±0.0001)	0.03 (±0.0002)
Control Pots 14 June 1974					
Medium	10.62 (± 4.75)	0.60 (± 0.019)	0.32 (±0.0002)	0.14 (±0.0008)	0.14 (±0.0023)
Small	6.75 (± 2.00)	0.23 (± 0.004)	0.12 (± 0.0014)	0.05 (±0.0002)	0.06 (±0.0012)
Enclosed Pots 14 June 1974					
Medium	11.50 (± 5.00)	0.47 (±0.	0.23 (±0.0046)	0.11 (±0.0013)	0.13 (±0.0017)
Small	6.10 (± 1.99)	0.26 (±0.0001)	0.13 (±0.0004)	0.06 (±0.0001)	0.07 (±0.0001)

Figures in parenthesis indicate standard error values.

After two weeks of treatment the total dry weights from medium pots were about double those from small pots, whether enclosed or control; compare the figures 0.30g and 0.13g for controls, 0.28g and 0.14g for treated pots respectively. Prima facie, at this harvest there was no evident effect of the enclosure treatment on the dry matter production. As observed in the major experiment (page 97), the shoot dry weights were higher than the root values in all treatments. It was also clear that at this harvest in all cases the dry weights had at least doubled compared with the initial values two weeks earlier. After a further two weeks (14 June), this pattern of doubling of dry weights had become irregular. It was only in the control plants in medium pots that this rate of increase had been sustained, the total dry weight having risen in the fortnight from 0.30g to 0.60g. There was a greater shoot (especially leaf) production in the medium pot controls than in the others; but in the case of the roots this was not so. The results for the small pots control and enclosed were less definite.

Thus on the present evidence the effect of enclosure seems small, to what extent enclosure constricts the oxygen supply is problematical. Clearly the matter needs further investigation.

DISCUSSION

The result just described indicated that *Q. robur* and *B. pendula* respond differently to soil volume restrictions even though both tree species sometime live together as for example in an "Oak - birch heath" (Tansley, 1939 and Jones, 1957).

The tendency of *Quercus* species to grow to considerable heights when in dense stands have been observed by Jones (1957). The results of this experiment (Fig.IV-1a) recall this observation, i.e. *Q. robur* in the smallest pots grew tallest. This behaviour was not observed in *B. pendula*. The *Q. robur* seedlings in the other pot sizes were producing branches - a situation commonly observed when trees are grown in isolation rather than in close associations. Thus, the ability of many trees to achieve great heights in close stands may be partly associated with a response to a restricted soil volume. The fact that *B. pendula* behaved differently emphasizes the fact that general rules about tree-spacing in forestry management must be regarded with caution.

The growth rates of trees are commonly measured by foresters in terms of rate of height increase and rate of volume production. (Wareing, 1966). The results of this work suggest that the tallest tree may not necessarily be the tree with the greatest dry matter production. In fact *Q. robur* samples in the largest pots had the greatest dry weights but the smallest heights. This difference was not however statistically significant. Consequently the use of height as a measure of tree growth needs to be used with caution.

The growth in dry weight of *B. pendula* seedlings was almost proportional to the amount of soil volume available; i.e. the bigger the pot size the greater the dry weights.

This variation in *B. pendula* growth in various pot sizes was highly significant statistically. This was not the case with *Q. robur* however.

The different patterns of root behaviour by both species have already been described (Results). The strategy of dry matter distribution by the different species needs some discussion. *Q. robur* has a higher root/shoot ratio than *B. pendula*, yet was able to withstand root restriction better than the latter. Thus the types of root system of the different species responded differently to the soil volume conditions. For instance the dry weights of the roots of *B. pendula* seedlings in the small pots were significantly lower than in the larger pots (See TableIV-5). This was not the case in *Q. robur*. The *Q. robur* seedlings were on the other hand able to produce roots fairly normally in the small pots. The same phenomenon holds true for other plant parts i.e. leaf and stems. (TablesIV-3+4pages96+97). Stem parts contained generally the greatest dry weights in *B. pendula*, the leaves the least. In all these parts the treatment effects were apparent. In view of the above it is suggested that the difference in response of the two species to pot size variation is a characteristic one. Thus they stand to behave differently in the field when soil volume becomes restricted by, for example, the high density of a homogeneous or a mixed stand.

Many workers have observed that birches generally are sub-climax species to oaks in many sites (Wilde, 1946; Tansley, 1919; and Jones, 1959). The results from this investigation suggest that inability of *B. pendula* to adapt to soil volume restriction is a possible mechanism of its exclusion from a site by *Q. robur* in the natural succession of plants.

Mechanisms or causes of responses to soil volume restriction

Hoyle (1971) observed that *B. alleghaniensis* develops a shallow root system in podzol soils, as a result of subsoil nutrient conditions. This could not be the reason why *B. pendula* developed poor roots in this experiment as a uniform soil type was used (see methods). Thus nutrient availability was expected to be fairly adequate for the seedlings, and deficiency would not be expected to be the cause of restricted growth.

The results of the chemical analysis of the soil samples left in the pots at the end of the experiment (TablesIV-7.8) showed that the elements analysed for showed some adequacy of nutrient availability in all the pots. The fairly similar amounts of nutrients left in the pots (TablesIV-7.8) indicate that both species removed nutrients from the different pots at comparable rates in most cases. This is inspite of the fruit reserve of *Q. robur* samples (which had fairly similar acorn dry weights at the end of the experiment in the three pots). This also shows that *B. pendula* is a more"vigorous" plant in mineral uptake from soils especially when ample root space is available.

Most of the elements for which the soils were analysed showed higher concentrations in the soil in which plants had grown than in the'unused' soil. This was probably caused by slow release of nutrients from the fertilizer applied to the soil. Potassium and nitrogen behaved fairly similarly in soils of both species. Phosphorus, however was taken up differently i.e. the *Q. robur* values were fairly higher than the *B. pendula's* generally. (TablesIV-7.8)

This suggests that chemical changes took place in the soil, according to the characteristics of the elements and the requirements of the different seedlings under the experimental conditions. Lowe (1973, personal communications) said that the John Innes compost used in this work sometimes behaves "irregularly" as far as elemental composition is concerned. Nevertheless the results of this experiment showed that the growths of the seedlings in the pots had some effects on the soils' composition, not due to chance. Consistently high nitrogen levels were found in small pots in which <u>B. pendula</u> had been grown. Assuming that soil nitrogen determined by the Kjeldahl method is related to the availability of nitrogen to roots, this indicates that low nitrogen availability could not have been the cause of restricted growth in <u>B. pendula</u>. The behaviour of other elements could not easily be associated with the general patterns of plant growth. The results of phosphorus content in <u>B. pendula</u> soils are similar to those obtained by Larsen and Sutton (1963) on rye grass. Phosphorus is one of the elements in the "available form" in the soil. Such elements are said to be always in equilibrium in the soil solution. Steward (1963) suggested that plant growth in such soils could disturb the balance, causing the removal of the "available" element but the "lost" element is soon replaced by an exchange action from the solid phase of the soil. From this theory, it could be deduced that variation from this role was probably due to the fact that in the smaller pots <u>B. pendula</u> could not take up the available phosphorus at a normal rate because sufficient amounts of roots were not available, but with <u>Q. robur</u> the reverse was the case.

The results discussed so far indicate that soil elements as such did not limit plant growth in the small pots of either species. Thus the other possible causes of poor root growth and hence plant performance in B. pendula were either due to mechanical indedance or lack of adequate aeration or both. Warnaars and Eavis (1972) distinguished between "aeration effects and "mechanical indedance" as they influence the growth of pea (Pisum sativum)

From all the evidence available it is clear that Q. robur did not show any poor growth due to small size of the pots; B. pendula evidently responded poorly in root production or general plant growth, because the root growth was impeded by the physical conditions created by the small pots and was not able to "adapt" to this condition as Q. robur did. As stated earlier, the B. pendula seedlings show some indication of restriction of growth in the medium pot sizes. (TableIV-4) shows that plant dry weight per unit soil weight was very similar in both small and medium pots, indicating that volume available may directly limit root growth.

The possible role of aeration in this phenomenon had to be separately investigated to determine its influence alone or in combination with restricted volume for the B. pendula seedlings.

The effects of pot enclosure

The results (Table IV-12) of this supplementary experiment confirm the earlier results of B. pendula being limited in growth by mechanical impedence as created by the small pots, in which the seedlings were growing. The effects of pot enclosure was not apparent on the seedling growth in terms of dry matter production.

Warnaars and Eavis contended that sandy soils with less than 25% gas filled pore space were most affected by poor aeration. It was not possible to measure the oxygen content of the experimental soil which was mainly a loamy type of soil. Thus the direct relationship between aeration and root for plant growth could not be ascertained. Moreover, it was not possible to enclose the pots completely and possible entrance of air through the wire knotted polythene bags must be envisaged. Secondly air-renewal was possible during water supply to the pots. Thus this experiment does not help to verify the role of poor aeration on the growth of the *B. pendula* seedlings. A more controlled experiment is therefore needed.

CHAPTER V

THE EFFECTS OF SOIL TYPES ON THE SEEDLING GROWTH OF *Q. ROBUR*, *B. PENDULA* AND *T. IVORENSIS*

INTRODUCTION

There is a necessity to conserve Q. robur species or an oakwoodland ecosystem. Up to 70 - 75% of Britain used to be a woodland (with Q. robur as a dominant species). Today only 8% of Britain is woodland. 13% of British woodland today is Quercus spp. and only 1% of this is protected by the Forestry Commission (Tansley, 1919; Jones, 1959; Streeter, 1973). Up to 99% of acorns (fruits of Quercus spp.) are lost annually in various forms, in a number of sites (Watt, 1919; Shaw, 1968).

The scarcity of Quercus seedlings and saplings in many oakwoodlands has also been reported. Ovington and Macrae (1960). This scarcity has been attributed to such effects as grazing, defoliation, extreme shade, and inadequate soil and climatic conditions (Watt, 1919; Jones, 1959; Shaw, 1968; Newnham and Carlisle, 1969; Milles Gradwell, 1973; Steele 1973). Kinnaird (1974) examined the relationship between soil conditions and the behaviour of naturally-established Betula seedlings at sites in Scotland.

Little further information is available on the state of natural regeneration of B. pendula seedlings, except in a general comparison with other species especially Quercus spp. In view of the fact that the Quercus spp. regenerates at a slower rate than expected, the Forestery Commission in Britain are planting Quercus seedlings and also restocking derelict woodlands with nursery germinated Quercus seedlings. The present trend of Quercus conservation is to encourage the trees in "good" areas and to create new forests by planting nursery seedlings.

This involves the search for good sites for a better woodland management. (Penistan, 1973). Ovington and Macrae (1960) observed that "if natural regeneration is to be encouraged, information is needed on the effects of site conditions on Quercus spp. seedlings growth".

The aim of the work described was to investigate whether soil factors might be instrumental in preventing or retarding natural regeneration of Q. robur and B. pendula in British conditions. Harper et al (1965) have pointed out the difficulty in measuring the micro-environment of a particular site, and only green-house work has been successful, they stated.

In this work soil samples were taken from four sites in which Q. robur and B. pendula were (i) completely absent (Site I) (ii) sparsely present (Sites II and III, Q. robur more abundant here than B. pendula) and (iii) both abundantly present (Site IV, B. pendula being more abundant.)

The soils were analysed physically (rough) and chemically for major elements. The experiment was carried out between May and September, 1973 in the period of normal active growth for all species (See Experiments I & II for Q. robur and B. pendula). Observations were made on a few seedlings of T. ivorensis for over 1 year in the green-house before using them experimentally and they were found to grow continuously in long day-lengths and when well watered.

Methods and Materials

Location and Description of Sites

All the four sites investigated lie within an area between Hitchin and Welwyn Garden city. Welwyn Garden city is about 34 km. (22 miles) north of London. The sites are located in the middle of South-East England, and were selected to represent a range of soil types.

SITE I

Grid reference TL 173242 is about ⅓km. west of Preston. It has an elevation of 120m (400 ft). The underlying rock is cretaceous chalk. The soil is very calcareous, giving a greyish colour; it crumbles easily and there was evidence of earthworm activities. A very thin layer of litter was present. This site was apparently a mixed plantation, with no *Q. robur* and *B. pendula* trees or seedlings. *Fagus sylvatica* (Beech) with some chlorotic leaves, *Acer pseudoplatanus* and *Larix decidua* (Larch) were the dominant trees. Other trees present in lower numbers were *Ulmus glabra* (Elm), *Picea sitchensis* (sitka spruce) *Aesculus hippocastanum* (Horse chestnut) and *Fraxinus excelsior* (Ash). These trees formed a canopy about 12m (40 ft.) in height. The only shrubs present, were *Thelycrania sanguinea* and *Sambucus nigra*.

The ground flora (rather sparse) consisted of the following species: *Urtica dioica* *Mercurialis perennis* *Arum maculatum* *Acer pseudoplatanus* seedlings were abundant. A few woody climbers were also present, *Clematis vitalba* and *Hedera helix*.

SITE II

This site and site III (to be described later) were in the Codicote Heath about ½ km. from Codicote. The same grid reference TL 209184 is applicable for both sites. Site II has an elevation of 100m (330 ft.) on a small hill and was separated from site III by a road. The underlying rock is the same for both sites - glacial gravel over upper chalk. Site II had a lot of gravel and pebbles near the surface.

The main trees though sparsely present were *Q. robur* (probably planted) and *B. pendula* forming an incomplete canopy. There was no under-storey; the ground flora included *Acer pseudoplatanus* seedlings, some of which were dying back. The main species of the ground vegetation were *Deschampsia flexuosa*, *Holcus mollis* *Pteridium aquilinum* and *Rubus fruticosus*. The mosses *Polytrichum* sp. and *Mnium* sp. were fairly common. *B. pendula* seedlings were present in patches of mineral soils. No *Q. robur* seedlings were observed.

SITE III

This site had the same grid reference TL 209184 with II but was located on the floor of a small valley at an elevation of 90m (300 ft.) There was however no evidence of flooding effect on this site. The sub-soil was clayey.

Q. robur though sparsely present was the dominant tree, but a few *B. pendula* trees were also present. A few *Fagus sylvatica* (Beech) trees *Acer pseudoplatanus* (Sycamore) and *castanea sativa* (sweet chestnut) trees were also present.

The herb layer was sparse, the main species were Luzula pilosa. Endymion non-scriptus (Bluebell) (seasoning), Mercurialis percunis . The common fern was Pteridium aquilinum. The only woody climber present was Hedera helix (Ivy)

SITE IV

Grid reference TL 225144. The site is in Sherrardspark Wood and it stretches adjacent to Welwyn Garden City in a north-east direction. The underlying rock was Reading, Beds. The elevation of this site was 110m (350 ft.). The top soil was about 10cm rich in humus mixed with gravel. The sub-soil was a greyish mixture of clay, gravel and pebbles. B. pendula was abundantly present and Q. robur was rather sparse, both forming a thick canopy not higher than 15m (50ft.)

A few Fagus sylvatica (sapling stage). Carpinus betulus and Populus tremula shrubs were present. The herb layer was mainly of Endymion non-scriptus, Teucrium scondonia and Luzulapilosa, with Galium saxatile Hypericum pulchrum. Juncus conglomeratus Deschampsia flexuosa and Rumex acetosella in less shaded areas. The only climber observed was Lonicera periclymenum. B. pendula seedlings and saplings were fairly common especially in the less shady parts. Q. robur seedlings (though few) were also observed.

Plant germination and transplant

The Q. robur fruits were collected from a tree growing near a park in Staplehurst, Kent, England.
The B. pendula fruits were from the same batch obtained from Codicote heath used in the deficiency and soil volume experiments already described; the Terminalia ivorensis fruits were from Akure Forest Reserve, Nigeria. The fruits were collected from a single tree each to reduce variability. Under the conditions used the Q. robur fruits germinated in about 30 days and B. pendula fruits within 14 days. The T. ivorensis fruits took up to 2 months to germinate, even then scratching of the fruit coat was done as a form of pre-treatment to promote germination. This proved successful, but insufficient T. ivorensis seedlings were available at the time of transplant of the three species being investigated. Consequently, only 3 harvests were done on the T. ivorensis seedlings, while Q. robur and B. pendula had 4 harvests each. The germination procedures were carried out in the hot greenhouse.

On 9 May, 1973, the three species were transplanted into the different four soil types from peralite where they had been receiving only tap water. No heating was provided, but to reduce excessive heating on very hot days, the greenhouse was covered with green nets as the B. pendula and T. ivorensis seedlings wilted temporarily. The windows were well opened. The minimum temperature was not lower than 60°F; (15.6°C) it was not possible to control the maximum temperature. The floor was constantly kept wet, to keep the greenhouse reasonably humid.

The Experimental Design

The experimental design was a completely randomized type, with four treatments (soil types I, II, III and IV) four replicates and four harvests for Q. robur and B. pendula. Three harvests only were possible for T. ivorensis.

The medium (11 x 11)cm pot size (see the results of the soil volume experiment) was used. Each pot contained one seedling. Watering with tap water was done from the top. It was necessary to replace a few B. pendula seedlings of soil type III.

On 28 June, 1973 after 50 days of growth in the soil types, the first harvest was performed as described in Chapter II. Tables V-1a & b give the details of the soil properties).

TABLE V-1a.

Chemical data of the soils from 5-15cm depth from the sites. Mean values of 3 samples. (Figures in parenthesis indicate standard error values)

	SITES	
	I	II
Colour	Greyish with white tints of CaC^{O3}	Light brown
Mechanical Analysis Rough Estimate	Coarse soil 58.54% Fine soil 41.46%	33.12% 66.88%
pH	7.95 (± 0.001)	4.78 (±0.0003)
* Exchangeable hydrogen	-	16 (0)
* Exchangeable bases	Not determined	4.80 (± 2.55)
* Cation exchange capacity	" "	20.80
* Exchangeable sodium	0.40 (±0.001)	0.31 (± 0.003)
* Exchangeable potassium	0.58 (±0.0002)	0.65 (± 0.0002)
* Total Calcium	149.6 (±0.51)	8.12 (± 0.0018)
* Total magnesium	11.38 (± 0.0018)	4.72 (± 0.0018)
% Nitrogen	0.40 (± 0.0005)	0.40 (0)
% Loss on ignition	14.07 (±0.15)	15.75 (±0.08)
Available phosphorus ppm	88 (± 0.7)	66 (± 1.20)

* Values in meq/100g Soil

TABLEV-16.

Chemical data of the soils from 5-15cm depth from the sites. Mean values of 3 samples. Figures in parenthesis indicate standard error values.

		SITES	
		III	IV
Colour		Light-brown	Brownish-black
Mechanical analysis	Coarse Soil	24.83%	48.27%
Rough estimate	Fine soil	75.1%	51.73%
pH		4.20(0)	4.30 (± 0.0010)
* Exchangeable hydrogen		9.33 (±0.001)	26.66 (± 0.002)
* Exchangeable bases		6.20 (±2.62)	11.60 (±2.80)
* Cation exchange capacity		15.53	38.26
* Exchanageable sodium		0.28 (± 0.0001)	0.47 (±0.0001)
* Exchangeable potassium		0.49 (± 0.0001)	1.17 (± 0.0001)
* Total calcium		3.20 (0)	7.32 (0)
* Total magnesium		4.60 (0)	4.36 (± 0.0018)
% Nitrogen		0.23 (±0.0001)	1.05 (± 0.0010)
% Loss on ignition		8.89 (± 0.04)	44.83 (± 1.75)
Available phosphorus ppm		68 (± 1.55)	164 (± 0.06)

* Values in meq/100g soil

A summary of the soil nutrient conditions

The chemical analysis performed on the soil samples from the various sites indicated that there were major differences in the relative amounts of nutrients present. (TableV-1). Sites II - IV were acid soils and the only basic soil was from site I. Despite the fact that the acidic soil types had fairly comparable pH values (pH range 4.20 - 4.78) they differed greatly in their relative abundance of a number of nutrients. For instance, the soil type IV had the highest values for exchangeable hydrogen and exchangeable bases, with values about double those in soil types I & II.

The soil type I being a calcareous soil had zero values for exchangeable hydrogen, but the exchangeable bases could not be determined as there was a great deal of carbon dioxide evolution.

For the following observations (i)% Loss on ignition, (ii) soil percentage nitrogen (iii) exchangeable sodium, (iv) Exchangeable potassium and (v) total calcium, a clear pattern of nutrient concentrations was observed in all soil types. Soil type IV had the highest values generally, and soil type III, the lowest the other two types coming in between. The high value of 44.83 percentage loss on ignition for soil type IV is conspicuous, so also the high total calcium values for soil type I.

It appears all the soil samples except soil type IV had low values, generally for nitrogen, potassium and phosphorus, three major soil nutrients. All the samples including soil type IV with the exception of soil type I had low magnesium values.

Soil type II had the lowest values for available phosphorus 66.ppm . those for soil type I - III were also low in comparison with the soil type IV. Thus generally there were major differences in the concentrations of the nutrients present in the soil types in which <u>Q. robur</u>, <u>B. pendula</u> and <u>T. ivorensis</u> were grown.

RESULTS

Visual Observations

The fact that the variation of the soil type was having a great influence on the growth of all seedlings were quite apparent visually. See PlatesV-1-8). The most affected seedlings as far as visual observations were concerned were the <u>T. ivorensis</u> seedlings. It was with these seedlings that the coloration due to mineral excesses or deficiencies were most obvious, although the other species showed growth forms corresponding to the soil situations.

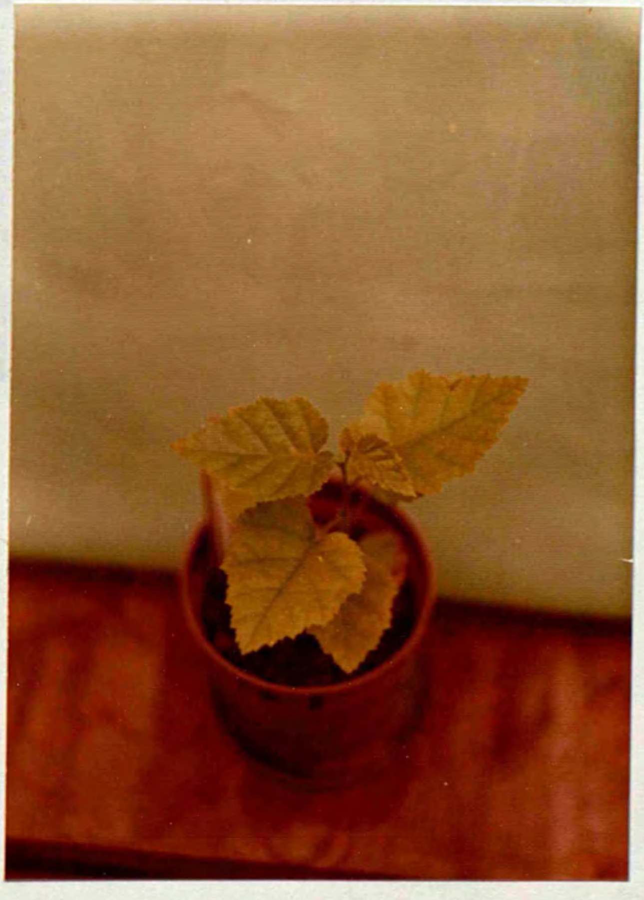
Plates show the effect of high calcium carbonate concentration on the growth of all the species. All the seedlings in the calcareous soil of site I had bleached or yellowish leaves. <u>T. ivorensis</u> appeared the most affected. <u>T. ivorensis</u> seedling leaves turned from light yellowish to brownish and eventually necrosis and abscission occurred. No leaf abscission was observed in the other species. A few <u>T. ivorensis</u> seedlings died after two and a half months of relatively little growth. The signs shown were those associated with lime-induced chlorisis.

<u>Q. robur</u> seedlings performed reasonably well in soil types II and III, except that the leaves were pale and there were very few flushes compared with seedlings growing in soil type IV soils.

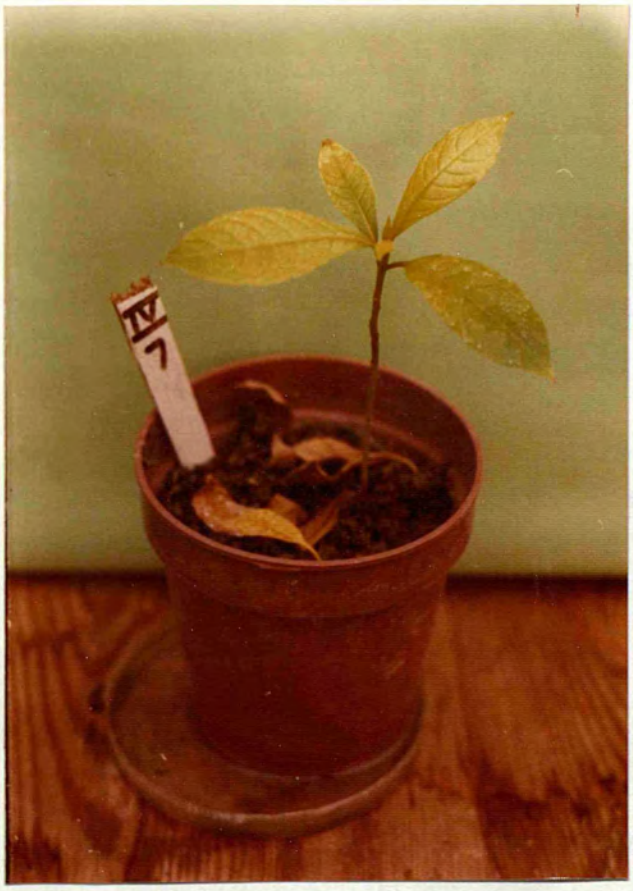
Plates V - 1, 2 & 3 Q. robur, B. pendula and T. ivorensis seedlings in calcareous soil type I respectively. Q. robur seedlings developed no new shoot in this soil type, B. pendula overcame the chlorotic conditions, the leaves becoming greenish later. Growth however was generally relatively poor. Most T. ivorensis seedlings died in soil type I within three months.

V- 1

V- 2



V - 3



Plates V-4 & 5. *T. ivorensis* seedlings in soil types II & III, with the leaves turning purplish starting from the tips, becoming reddish later and premature abscission eventually resulting. N.P.K. generally low in these soils.

Ⅴ - 4

Ⅴ - 5

Plates V - 6, 7 & 8 *Q. robur*, *B. pendula* and *T. ivorensis* seedlings in soil types I, II, III & IV (from left to right) respectively. Note the similar pattern of response by the species in the various soils.

V - 6

V - 7

V-8

The growth of B. pendula seedlings appeared normal, no deficiency symptoms of any sort, except that the plants were slower growing than those in soil type IV, B. pendula seedlings in soil type III showed the greatest edaphic effects. The seedlings were dwarfed, many leaves were necrotic with brown marginal scorching, possibly a result of potassium deficiency. Soil types II & III soils produced a variety of leaf colorations in T. ivorensis seedlings. The leaves within one month of growth soon developed intervenal and marginal purple tints, developing inwards gradually. Later the purple colouration turned reddish and abscission ultimately resulted.

Some leaves of T. ivorensis on these sites simply turned yellowish. These symptoms were probably of phosphorus and nitrogen deficiencies respectively (Wallace, 1943). Soil Types II and III appeared to have influenced these seedlings equally.

All the species performed well in soil type IV, the Q. robur produced up to three flushes within three months. No deficiency symptoms of any sort were shown by Q. robur or by B. pendula.

The leaves of T. ivorensis were well expended in soil type IV (see Plate 7-8) although a few old leaves developed purplish and yellowish colours, especially when the greenhouse became very hot, and there was some premature abscission, perhaps related to low humidity.

Table V-2

The effects of soil types on the Q. robur seedling height (cm) and total plant dry weights (g)(Mean values of 4 replicates)

	Height				Dry Weight			
Soil Type	I	II	III	IV	I	II	III	IV
Harvests								
A								
30 June	20.7	21.6	23.5	28.8	4.93	4.25	4.85	4.17
	(±30.62)	(±16.56)	(±24.0)	(±19.94)				
B								
31 July	15.8	26.0	28.5	48.8	5.01	6.78	6.56	8.91
	(±11.7)	(±25.0)	(±23.1)	(±22.5)				
C								
31 Aug.	19.5	21.1	18.8	36.2	6.69	9.03	7.46	11.10
	(±16.31)	(±2.50)	(±0.94)	(±32.0)				
D								
30 Sept.	15.7	31.5	20.6	37.2	5.86	10.90	8.12	16.56
1973	(±2.15)	(±7.62)	(±3.84)	(±75.0)				

Figures in parenthesis indicate standard error values

For analysis of variance see Table V-5.

TABLE V-3

The effects of soil types on the *B. pendula* seedling height (cm) and total plant dry weights (g) (Mean values of 4 replicates)

	Height				Dry weight			
Soil Type	I	II	III	IV	I	II	III	IV
Harvests								
30 June	2.2	3.4	1.2	15.4	0.0083	0.0147	0.0025	0.29
	(± 0.10)	(±0.14)	(±0.47)	(±1.72)				
31 July	4.5	11.5	1.5	46.1	0.055	0.25	0.0092	3.64
	(± 0.73)	(± 1.0)	(±0.006)	(±10.10)				
31 Aug.	10.1	21.5	7.8	55.5	0.42	0.76	0.15	7.22
	(± 3.50)	(± 5.62)	(±2.4)	(±5.62)				
30 Sept.	10.2	31.1	8.5	58.5	0.79	2.90	0.73	9.60
	(± 1.62)	(± 7.11)	(±4.11)	(±6.91)				

For analysis of variance see Table V-5.

Figures in parenthesis indidate standard error values.

Table V-4

The effect of soil types on the T. ivorensis seedling height (cm) and total plant dry weight (g). (Mean values of 4 replicates)

	Height				Dry weight			
Soil Type	I	II	III	IV	I	II	III	IV
Harvests								
A								
30 June	8.7 (± 1.0)	9.0 (±0.10)	9.0 (±0.38)	12.1 (±5.1)	0.36	0.38	0.37	0.78
B								
31 July		NOT	DETERMINED					
C								
31 August	9.2 (±0.96)	13.8 (±2.46)	15.1 (±4.55)	24.0 (±1.81)	0.49	1.59	1.32	6.08
D								
30 Sept.	9.8 (±2.0)	14.5 (± 1.97)	15.4 (±6.0)	31.3 (±5.01)	0.38	1.90	1.58	9.64

For analysis of variance see Table V-5.

Figures in parenthesis indicate standard error values

TABLE V-5

Variance ratio values in the analysis of variance of *Q. robur*, *B. pendula* and *T. ivorensis* (a) total plant dry matter yields of seedings grown *in four soil types (T)*

HARVESTS /-

TABLE I

VARIABLES	A	C	D
Species (s)	132.14***	26.89***	81.25***
Treatments (T_1) (All Species)	0.02 NS	10.25*	70.37***
Treatments (T_2) (*Q. robur*)	1.11 NS	2.60 NS	50.70***
Treatments (T_3) (*B. pendula*)	469.0***	239.84***	60.58***
Treatments (T_4) (*T. ivorensis*)	6.39*	18.57***	65.18***
S X T_1	0.55 NS	0.39 NS	0.87 NS
Replicate (R_1) (All species)	0.32 NS	0.07 NS	0.67 NS
Replicate (R_2) (*Q. robur*)	1.73 NS	0.73 NS	0.23 NS
Replicate (R_3) (*B. pendula*)	1.05 NS	1.52 NS	0.91 NS
Replicate(R_4) (*T. ivorensis*)	1.69 NS	1.61 NS	1.09 NS

/-	Harvest B not analysed statistically.
NS	Not Significant
*	Significant at 5% Probability Level
**	Significant at 1% Probability Level
***	Significant at 0.1% Probability Level

Fig.V-1 Height of *Q. robur*, *B. pendula* and *T. ivorensis* seedlings grown in soil types I, II, III, IV and harvested four times. (Mean values of four replicates)

Fig.

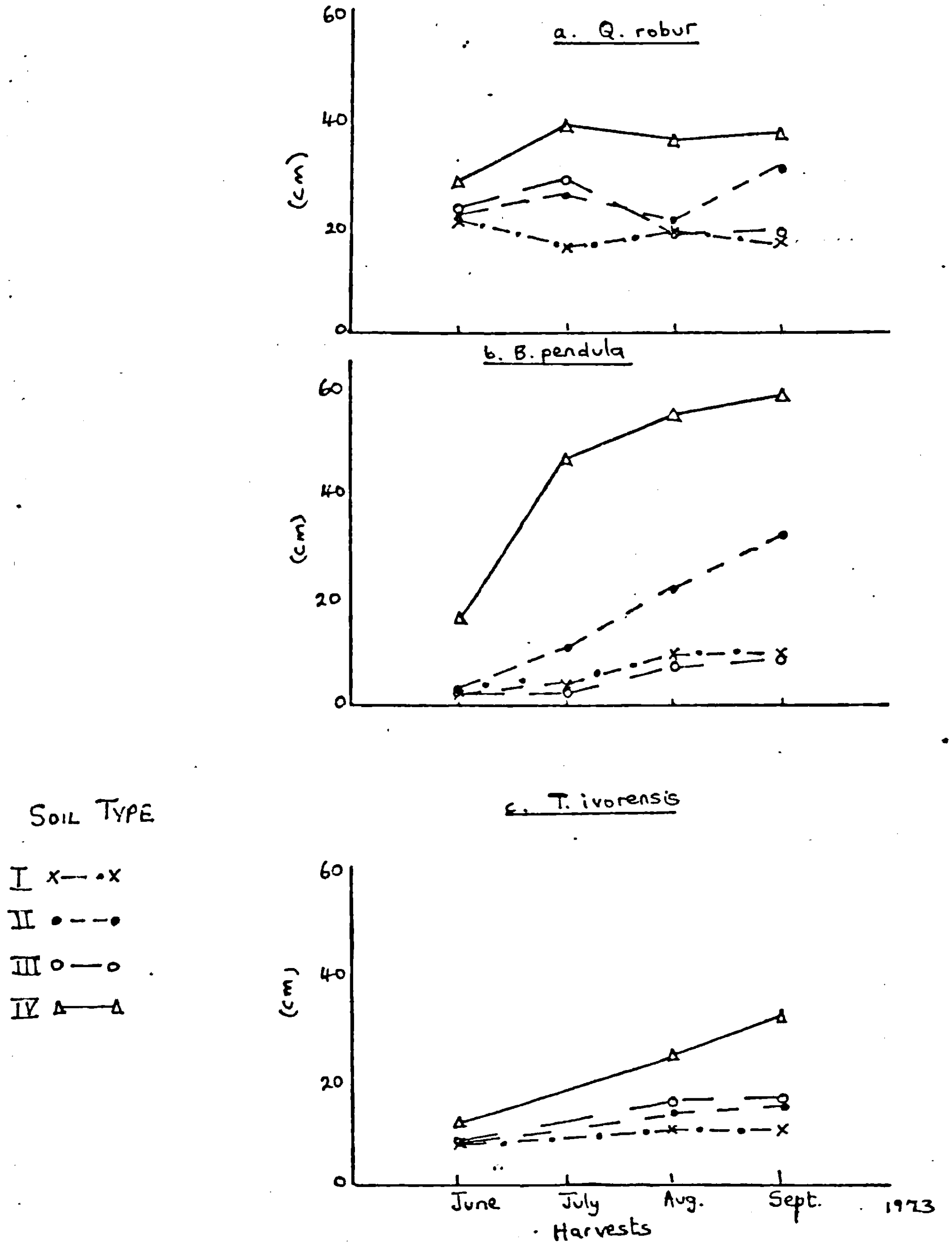
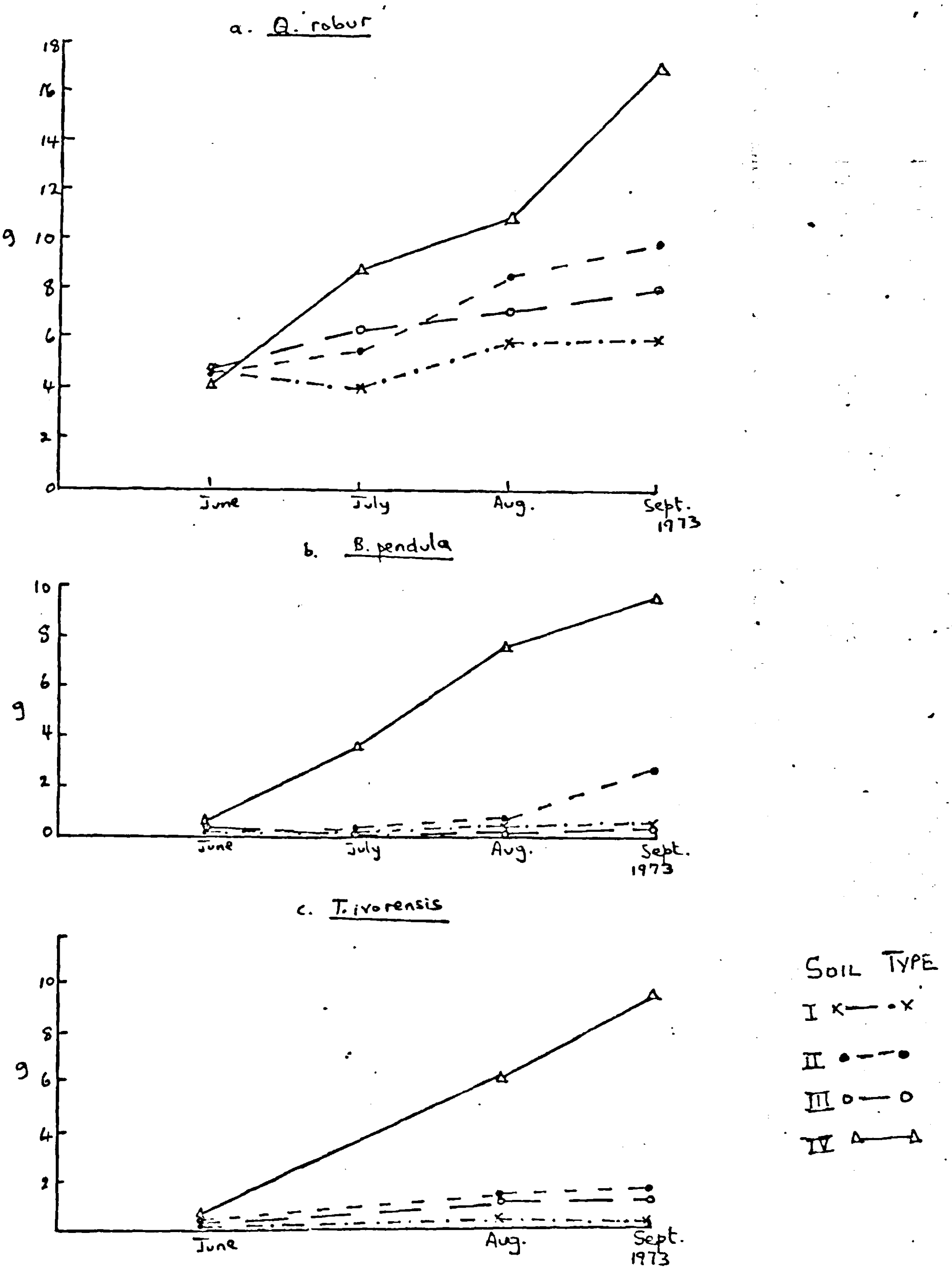


Fig.V-2 Total plant dry weight values of Q. robur, B. pendula and T. ivorensis seedlings grown in soil types I, II, III IV and harvested four times.
(Mean values of four replicates)

Fig.V-2



The effects of soil type on root growth

When the roots were examined, all the species developed rather poor roots in soil type I. It was easy to wash off soils from all roots. The most poorly developed roots were those of the *T. ivorensis*. The roots of *B. pendula* seedlings were the poorest in soil type III, thin and long. All species developed fairly good roots in soil type II, the best roots were produced by *Q. robur* seedlings.

Height and dry weight yields

Tables V-2-4 and Figs. V-1+2 show the trends of growth performances of all species as far as heights and dry weights are concerned. *B. pendula* were the fastest growing trees (shoot elongation) reaching a maximum of 58.5cm in soil type IV (Table V-3). There was no evidence of shoot elongation by either *Q. robur* or *T. ivorensis* in soil type I (Figs V-1+2).

It was in July, between the first and second harvests that *Q. robur* and *B. pendula* grew most. The *T. ivorensis* shoot production appeared most steady when all species were examined in soil type II. There was no evidence of dormancy setting in with the *T. ivorensis* seedlings. (Note the curves in Figs V-1+2. It is however interesting to note that *B. pendula* in soil type III seemed to be growing uniformly, without the effect of dormancy setting in yet. (For explanation see discussion).

Q. robur gave the highest yields on all soil types. (Regarding the acorn effect, see discussion).

Soil type I gave the lowest dry weight yields for all species except perhaps B. pendula which had comparable yields on soil type III. On soil type I, T. ivorensis had the lowest total dry weight values in the last harvest, and a number of seedlings died. Highest yields of all species were in soil type IV, Q. robur, T. ivorensis and B. pendula yielded 16.56g, 9.64g, and 9.61g respectively. These are quite comparable but when the initial seed weights (approximately 1 - 1.5g in Q. robur, 0.2g in T. ivorensis and05g in B. pendula) are considered, the relative growth performance of B. pendula could be better appreciated.

TABLE V-6.

The effects of soil types on seedling growth of *Q. robur.* Plant dry matter distribution (g).
Mean of 4 replicates

	SOIL TYPE			
	I	II	III	IV
Leaf (g)				
Harvests				
30 June	0.68	1.03	1.06	1.13
31 July	0.62	1.12	1.45	2.09
31 August	0.99	1.32	1.15	2.16
30 Sept	0.52	1.51	0.84	2.24
Stem (g)				
Harvests				
30 June	0.95	0.82	1.00	0.76
31 July	0.75	1.18	1.50	1.88
31 August	1.04	1.71	1.57	2.36
30 Sept	0.85	2.31	1.55	3.51
***Root (g)**				
Harvests				
30 June	3.30	3.64	4.66	4.49
31 July	2.40	3.48	6.00	7.08
31 August	2.79	3.61	4.74	5.73
30 Sept	2.28	4.93	6.58	10.81

* Includes values for fruit left-over.

For analysis of variance see Tables V-9-11.

Table V-7.

The effects of soil types on seedling growth of B. pendula.
Plant dry matter distribution (g) Mean values of 4 replicates

	SOIL		TYPE	
	I	II	III	IV
Leaf				
Harvests				
30 June	0.0037	0.0091	0.0009	0.18
31 July	0.0327	0.14	0.0040	1.79
31 August	0.19	0.39	0.09	2.60
30 September	0.17	0.90	0.17	2.45
Stem				
Harvests				
30 June	0.0015	0.0027	0.0007	0.0645
31 July	0.0115	0.0561	0.0029	1.12
31 August	0.08	0.19	0.03	2.68
30 September	0.45	0.73	0.36	3.66
Root				
Harvests				
30 June	0.0031	0.0029	0.0009	0.0451
31 July	0.0108	0.0486	0.0023	0.73
31 August	0.15	0.18	0.03	1.94
30 September	0.17	1.27	0.20	3.49

For analysis of variance see Tables V-9-11.

TABLE V - 8

The effects of soil types on seedling growth of *T. ivorensis*. Plant dry matter distribution (g) (Mean values of 4 replicates)

	Soil Type			
Leaf	I	II	III	IV
Harvests				
30 June	0.13	0.20	0.19	0.47
31 August	0.23	0.57	0.58	2.89
30 September	0.15	0.78	0.72	4.38
Stem				
Harvests				
30 June	0.08	0.07	0.08	0.11
31 August	0.09	0.25	0.30	1.34
30 September	0.07	0.30	0.37	2.42
Root				
Harvests				
30 June	0.15	0.11	0.10	0.20
31 August	0.17	0.37	0.44	1.85
30 September	0.14	0.72	0.49	2.84

For analysis of variance see Tables V-9-11

TABLE V-9. Leaf Dry weights Variance Ratio Values

Variables	HARVESTS A	C	D
Species (s)	47.37***	2.17 NS	3.23 NS
Treatments (T_1) (All Species)	2.50 NS	18.15***	43.16***
Treatments(T_2) (*Q. robur*)	1.77 NS	4.19*	19.00***
Treatments(T_3) (*B. pendula*)	134.00***	190.33***	66.28***
Treatments (T_4) (T. ivorensis)	15.33***	33.44***	149.70***
S X T1	0.50 NS	1.09 NS	4.09**
Replicate (R_1) (All species)	0.05 NS	0.04 NS	0.13 NS
Replicate (R_2) (*Q. robur*)	0.35 NS	0.80 NS	1.84 NS
Replicate (R_3) (*B. pendula*)	1.00 NS	1.33 NS	1.29 NS
Replicate (R_4) (T. ivorensis)	1.33 NS	1.66 NS	1.90 NS

NS	Not Significant
*	Significant at 5% Probability Level
**	Significant at 1% Probability Level
***	Significant at 0.1% Probability Level.

Harvest B not analysed statistically.

TABLE V-10. Stem Dry Weights Variance Ratio Values

Variables	*HARVESTS		
	A	C	D
Species (S)	4.11*	7.74***	10.68***
Treatments (T_1) (All Species)	0.10NS	12.51***	31.59***
Treatments(T_2) (*Q. robur*)	0.44 NS	2.22 NS	13.65**
Treatments(T_3) (*B. pendula*)	131.66***	166.75***	36.36***
Treatments (T_4) (T. ivorensis)	1.15 NS	22.24***	78.83***
S X T1	0.26 NS	1.25 NS	1.29 NS
Replicate (R_1) (All Species)	0.16 NS	0.09 NS	1.03 NS
Replicate (R_2) (*Q. robur*)	0.44 NS	0.40 NS	0.94 NS
Replicate (R_3) (*B. pendula*)	1.33 NS	1.25 NS	0.60 NS
Replicate (R_4) (*T. ivorensis*)	1.80 NS	1.63 NS	2.83 NS

NS	Not Significant
*	Significant at 5% Probability Level
**	Significant at 1% Probability Level
***	Significant at 0.1% Probability Level.

Harvest B not analysed statistically.

TABLE V-11.

Root Dry Weights Variance ratio values

Variables	HARVESTS A	C	D
Species (S)	87.47***	96.53***	230.37***
Treatments (T_1) (All Species)	0.45 NS	6.38**	48.12 **
Treatments (T_2) (*Q. robur*)	1.76 NS	2.00 NS	49.76***
Treatment (T_3) (*B. pendula*)	43.25***	67.00***	69.57***
Treatments (T_4) (*T. ivorensis*)	2.00 NS	9.15**	13.13**
S X T_1	0.58 NS	0.39 NS	3.59*
Replicate (R_1) (All Species)	0.27 NS	0.84 NS	0.22 NS
Replicate (R_2) (*Q. robur*)	1.11 NS	1.16 NS	0.35 NS
Replicate (R_3) (*B. pendula*)	1.33 NS	1.20 NS	1.70 NS
Replicate (R_4) (*T. ivorensis*)	1.77 NS	1.76 NS	0.18 NS

NS Not Significant

* Significant at 5% probability level

** Significant at 1% probability level

*** Significant at 0.1% probability level.

Fig. V-3 The effects of soil type (I, II, III, & IV) on the plant dry matter distribution of Q. robur seedlings. (Mean values of 4 replicates)

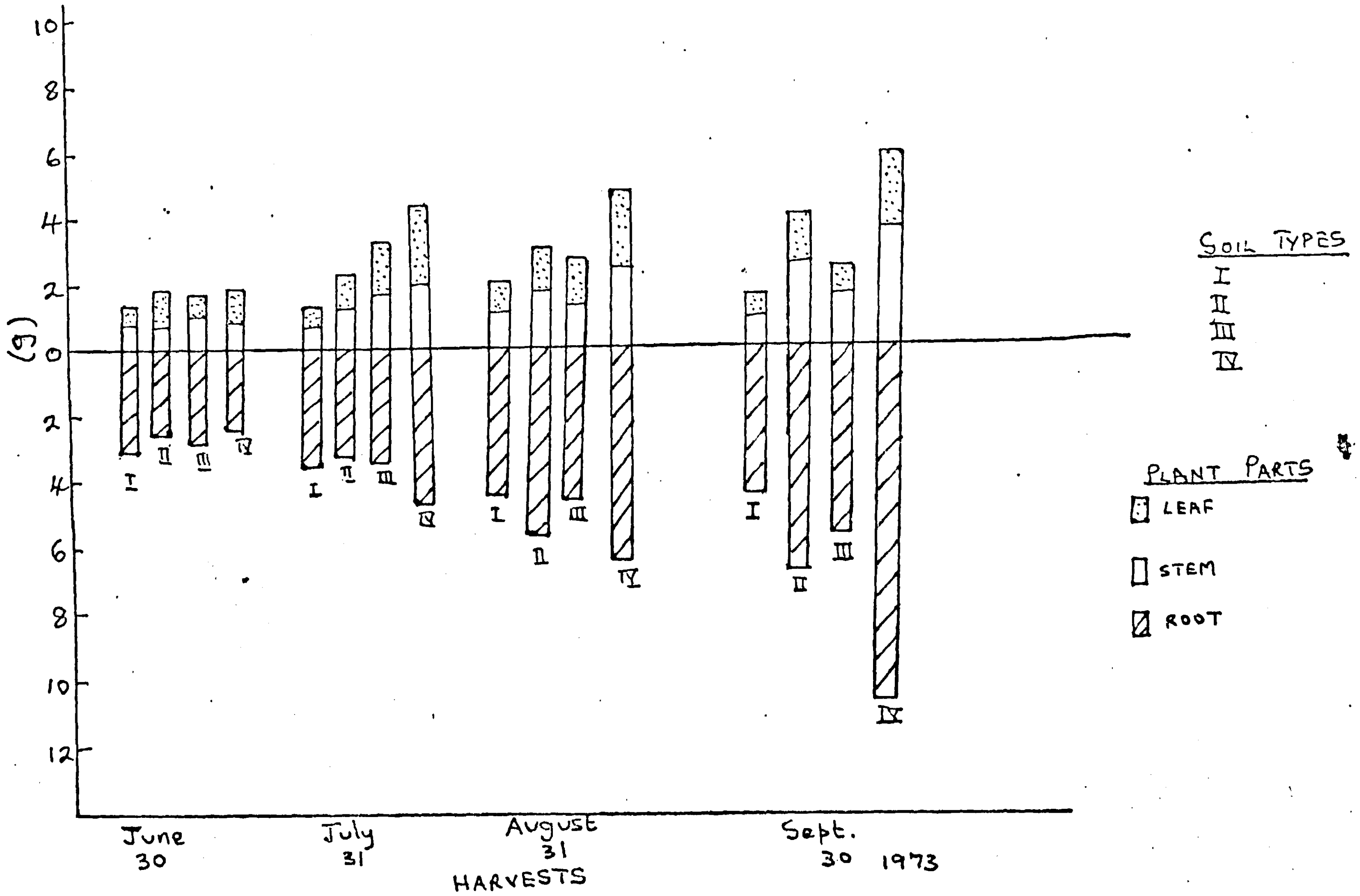


Fig.IV-4 The effects of soil type (I, II, III, IV) on the plant dry matter distribution of B. pendula seedlings. (Mean values of 4 replicates)

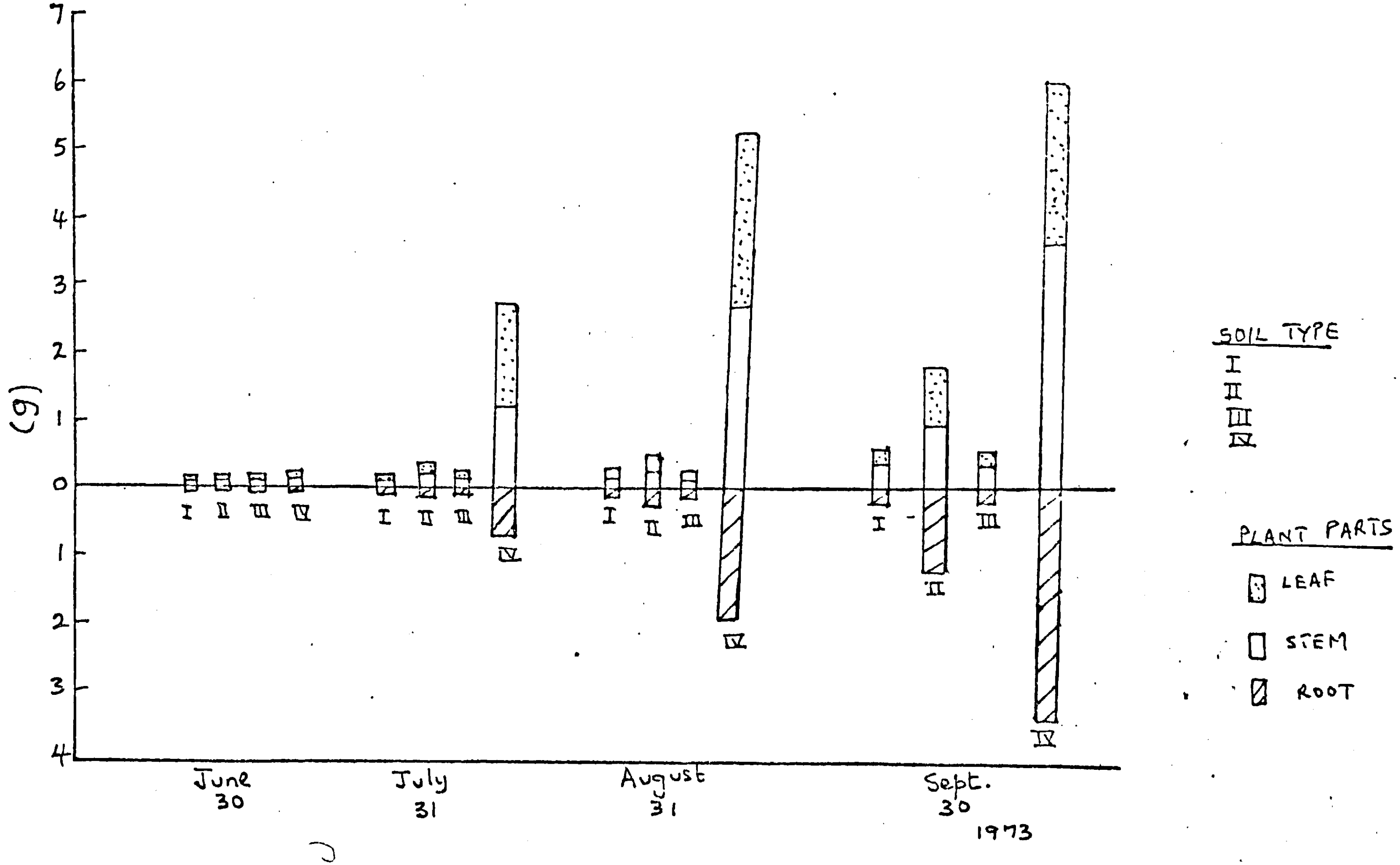
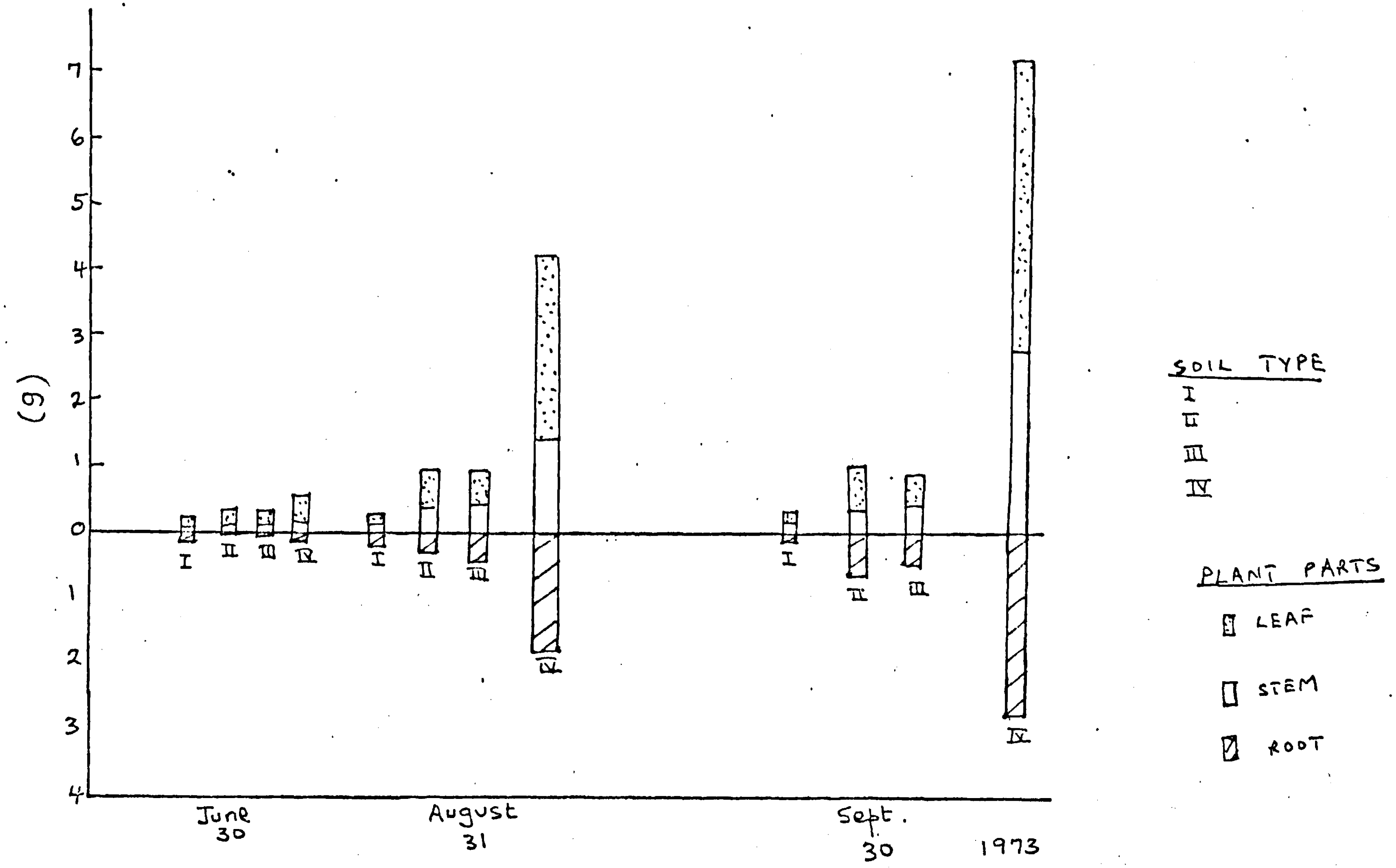


Fig.V-5

The effects of soil type (I, II, III, & IV) on the plant dry matter distribution of T. ivorensis seedlings.
(Mean values of 4 replicates).



Plant dry matter distribution

TableV-6-8 & FigsV-3-5 indicate the differences between *Q. robur* and *B. pendula* and *T. ivorensis* as far as dry matter distribution within the plant is concerned. Evidently, *Q. robur* produced more root than shoot whereas *B. pendula* and *T. ivorensis* produced more shoot than root. *B. pendula* however in general produces more stem than leaf. In *T. ivorensis* the leaves contribute most to the total dry weight. It was in the last harvest that the pattern of distribution of dry matter in all soil types and for all species became most apparent.

It is however interesting to note that in *Q. robur*, there was relatively little increase in shoot production between harvests, yet the root production progressed steadily in accordance with the type of soil.

In *B. pendula* and *T. ivorensis*, all plant parts developed steadily in a proportion indicating the manner of distribution of dry matter in each species. TableV-7,8 & Figs. V-4,5.

Relative Growth Rates

The mean relative growth rate values for the three species are given in Tables V-12 & 13. The relative growth rate values express the proportional rates of increase in dry weight. Thus the relative growth rate is an important measure of the plant growth performance. *B. pendula* showed the highest relative growth rate values in all soil types when compared with other species followed by *T. ivorensis*. *Q. robur* had the least values. The various values evidently showed differences due to soil type as well as seasonal trend or age. Soil type I especially, and soil type III showed the lowest relative growth rate values in all species, whereas soil type IV had the highest values generally. Seedlings of *Q. robur* followed this general pattern of relative growth rates on different soil types. The relative value of relative growth rate on soil type I for the harvest interval C -D indicated the adverse effect of this soil type on the growth of *Q. robur*. The relative growth rate values were low in the last harvest interval.

In comparison with *Q. robur* even in its best soil type soil type IV (range 0.04 - 0.17 gg^{-1} wk^{-1}. *B. pendula* showed high relative growth rate values generally even in soil type I where it had the lowest values 0.02 - 0.41 gg^{-1} wk^{-1}. Despite these high relative growth rate values, *B. pendula* had values differing between soil types and between harvests not conforming to any particular pattern.

For instance in soil type I, *B. pendula* had relative growth rate values fairly high between June and August $0.41-0.46gg^{-1}wk^{-1}$, but these values fell drastically in the period August-September to $0.02gg^{-1}wk^{-1}$. Soil type II however showed *B. pendula* with a high relative growth rate in June - July, $0.41gg^{-1}wk^{-1}$ but fell later to $0.26gg^{-1}wk^{-1}$ and rose again slightly in August - September to $0.30ggwk^{-1}$. On the other hand, soil type III showed *B. pendula* with a very high relative growth rate of $0.64gg^{-1}wk^{-1}$ in July - August, while in other periods the rate was $0.25gg^{-1}wk^{-1}$. In soil type IV, the situation was different from the others in that *B. pendula* had a very high growth rate to start with $0.56gg^{-1}wk^{-1}$ which kept falling as the season progressed.

Generally, *B. pendula* had higher relative growth rates in soil types II and III than in either soil type I or IV.

T. ivorensis, like *Q. robur*, had fairly low relative growth rates in all soil types when compared with *B. pendula*. In soil type I, the value was very low in June-August and in September a negative growth rate of $0.08gg^{-1}wk^{-1}$ occurred. The relative growth rate values for *T. ivorensis* in soil types II and III were fairly similar; low in June - August and very low in August - September especially in soil type III with $0.0005gg^{-1}wk^{-1}$.

It was in soil type IV that *T. ivorensis* has its highest relative growth rate values $0.23gg^{-1}wk^{-1}$ in June - August, this value fell about 50% in August - September.

Table V-12.

Observations on Q. robur and B. pendula seedlings grown in four soil types I, II, III and IV and harvested four times A, B, C. D, June, July, August and September, 1973 respectively (Mean values of 4 replicates)

	Unit Leaf Rate $g/dm^{2}\ wk^{-1}$			Relative Growth Rate $ggwk^{-1}$		
Soil Type	A - B	B - C	C - D	A - B	B - C	C - D
I	0.02	0.17	-0.02	0.004	0.04	-0.006
II	0.01	0.29	0.18	0.04	0.09	0.04
III	0.04	0.06	0.10	0.06	0.02	0.03
IV	0.32	0.10	0.27	0.17	0.04	0.09
B. pendula						
I	0.10	0.21	0.01	0.41	0.46	0.02
II	0.08	0.10	0.21	0.41	0.26	0.30
III	0.15	0.17	0.16	0.25	0.64	0.25
IV	0.24	0.12	0.05	0.56	0.16	0.13

TABLE V- 13

Observations on T. ivorensis seedlings grown in four soil types I, II, III & IV and harvested four times (A, B, C & D) June, July, August and September, 1973

Soil Type	Unit Leaf Rate (d$\bar{m}^2$ g^{-1})		Relative Growth Rate (ggwk^{-1})	
I	A - C	C - D	A - C	C - D
II	0.04	-0.05	0.04	-0.08
II	0.13	0.12	0.13	0.07
III	0.14	0.006	0.14	0.005
IV	0.18	0.12	0.23	0.11

The relative growth rate may be analysed into components (Evans 1972). In this work it seemed appropriate to divide the relative growth rate into three components: unit leaf rate, leaf weight ratio and specific leaf area. Study of the components helps to show which features of the plant influence its growth most strongly.

Unit Leaf Rate

This measure of growth (the rate of dry matter increase per unit leaf area, sometimes called net assimilation rate) in a major component of relative growth rate. The values from June 30 to September 30 are given in TablesV-12+13. Ther were marked differences amongst the species and also between soil types and times of harvest as these figures indicate. Generally, the soil type I showed seedlings with the lowest unit leaf rates and soil type IV with the highest values in all species.

Q. robur in soil types I and II showed unit leaf rate values rising from 0.02 and 0.01$gdm^{-2}wk^{-1}$ to 0.17 and 0.29$gdm^{-2}wk^{-1}$ respectively, then became negative (-.02) in soil type I a possible sign of oncoming death; and 0.18$gdm^{-2}wk^{-1}$ in soil type III in August - September. Although, the soil type II values for Q. robur were higher than those of soil type I, they however showed a similar seasonal trend. It was only in soil type III that the unit leaf rate values increased though in small proportions as the season advanced. Q. robur unit leaf rate values of soil type IV seedlings were high 0.32$gdm^{-2}wk^{-1}$ in June-July period, fell off to about $\frac{1}{2}$ this value in July - August and rose to nearly the original value 0.27$gdm^{-2}wk^{-1}$ in August - September.

There was no indication of any constant or unchanging leaf rate values in *Q. robur* result of the soil type differences or to seasonal trend. There were no negative unit leaf rate values in *B. pendula* though the values of soil type I were the lowest in this species, the values here rose and then fell sharply (Table V-12).

Soil type II *B. pendula* seedlings, had fairly steady unit leaf rate values in June - August, but the values were increased in August - September (rather than decrease as it happened in other soil types) to a value about double the original values. The soil type III unit leaf rate values for *B. pendula* were fairly constant throughout this experiment, but in soil type IV, the high values in June - July of 0.24gdm^{-2}wk^{-1} fell off progressively in about 50% proportions, (0.24 -0.12 - 0.05gdm^{-2}wk^{-1}) in the later harvest intervals.

T. ivorensis seedlings in soil type I had the lowest unit leaf rates in this experiment. Soil type II values were fairly constant (June - August 0.13gdm^{-2}wk^{-1}; and August - September 0.12gdm $^{-2}$wk^{-1}). Soil type III had high unit leaf rate value in June - August period, but this fell off very rapidly to 0.0006gdm^{-2} wk-1 soil type IV showed a similar high trend at the beginning, but fell off comparatively slightly from 0.18 to 0.12gdm^{-2}wk^{-1}. Thus the general trend as far as unit leaf rates in all species and of all treatments were concerned was towards a decrease rather than increase as the season progressed.

Table V - 14

Observation on Q. robur seedlings grown in four soil types (I, II, III, IV) and harvested four times (A. B, C, D) June, July, August, & September, 1973

(Mean Values of 4b replicates)

SOIL TYPES	LEAF AREA (dm^2)				SPECIFIC LEAF AREA (dm^2/g)				LEAF WEIGHT RATIO			
1.	A	B	C	D	A	B	C	D	A	B	C	D
1.	1.44	1.09	1.62	1.09	2.11	1.77	1.65	2.10	0.14	0.10	0.14	0.09
2.	2.09	2.14	2.48	2.89	2.03	1.92	1.88	1.92	0.23	0.10	0.15	0.14
3.	2.24	2.58	2.00	2.06	2.11	1.78	1.35	2.45	0.21	0.22	0.16	0.10
4.	2.28	4.12	5.03	4.27	2.02	1.98	2.33	1.90	0.27	0.23	0.19	0.13

TABLE V-15.

Observations on B. pendula seedlings grown in four soil types (I, II, III & IV) and harvested four times (A, B, C, & D) June, July, August and September, 1973. (Mean values of 4 replicates)

SOIL TYPES	LEAF AREA (dm^2)				SPECIFIC LEAF AREA (dm^2/g)			
	A	B	C	D	A	B	C	D
I	0.03	0.17	0.81	0.69	0.30	5.02	4.26	1.69
II	0.05	0.62	1.66	2.86	5.77	4.44	4.25	1.65
III	0.006	0.01	0.38	0.53	7.00	3.15	4.00	6.32
IV	0.93	5.57	7.87	7.06	5.19	3.11	3.03	3.28

No harvest II was taken for T. ivorensis . T. ivorensis seedlings in soil type IV produced fairly high values of leaf area according to the age of the seedlings; 1.01 dm^2 in June, 5.31 dm^2 in August and 8.07 dm^2 in September producing a steady increase throughout the season (fig V-6).

When the three species were considered together, all produced their maximum leaf area values in soil type IV. Q. robur had the lowest maximum value of 5.03 dm^2 in August, followed by B. pendula with 7.87 dm^2 in August as well, but T. ivorensis had 8.07 dm^2 as its highest value during this experiment in September at the time of the last harvest.

Specific Leaf Area

The three species investigated responded differently from the leaf area results just given in respect to their specific leaf area values i.e. the area of leaf per unit of leaf dry weight. The clear pattern of differences as caused by the different soil types on leaf area values were not observed in the specific leaf area values, although the species behaved differently according to their stage of development. (Tables V-14-16).

Q. robur seedlings in all soil types had values of specific leaf area fluctuating between 1.35 and 2.45 $dm^2\ g^{-1}$ throughout the experiment. There was no effect due to harvest on Q. robur seedling specific leaf area values in any soil type. Q. robur if anything, seemed to have been little influenced by soil type as far as the specific leaf area values were concerned, i.e. the Q. robur specific leaf area values was fairly constant irrespective of treatment or time of harvest.

Table V-16.

Observations on T.ivorensis seedlings grown in four soil types (I, II, III, IV) and harvested four times (A, B, C, D) June, July, August and September, 1973 (Mean values of four replicates)

SOIL TYPES	LEAF AREAS (dm^2)				SPECIFIC LEAF AREA dm^2/g			
	A	B	C	D	A	B	C	D
1.	0.26	-	0.47	0.29	2.01	-	2.05	1.92
2.	0.41	-	0.99	1.49	2.04	-	1.77	1.91
3.	0.38	-	1.13	1.07	2.09	-	1.95	1.49
4.	1.01	-	5.31	8.07	2.15	-	1.84	1.84

TABLE V - 17

Leaf weight ratio values of Q. robur, B. pendula and T. ivorensis seedlings grown in four soil types I, II, III & IV and harvested four times(A, B, C, & D) June, July, August and September, 1973 (Mean values of 4 replicates)

Q. robur

Soil Type	HARVESTS			
	A	B	C	D
I	0.14	0.10	0.14	0.09
II	0.23	0.19	0.15	0.14
III	0.21	0.22	0.16	0.10
IV	0.27	0.23	0.19	0.13

B. pendula

Soil Type				
I	0.45	0.62	0.46	0.37
II	0.65	0.58	0.51	0.31
III	0.30	0.43	0.56	0.35
IV	0.50	0.44	0.33	0.26

T. ivorensis

Soil Type				
I	0.39	-	0.46	0.45
II	0.51	-	0.48	0.42
III	0.51	-	0.44	0.52
IV	0.61	-	0.48	0.45

TABLE V-13.

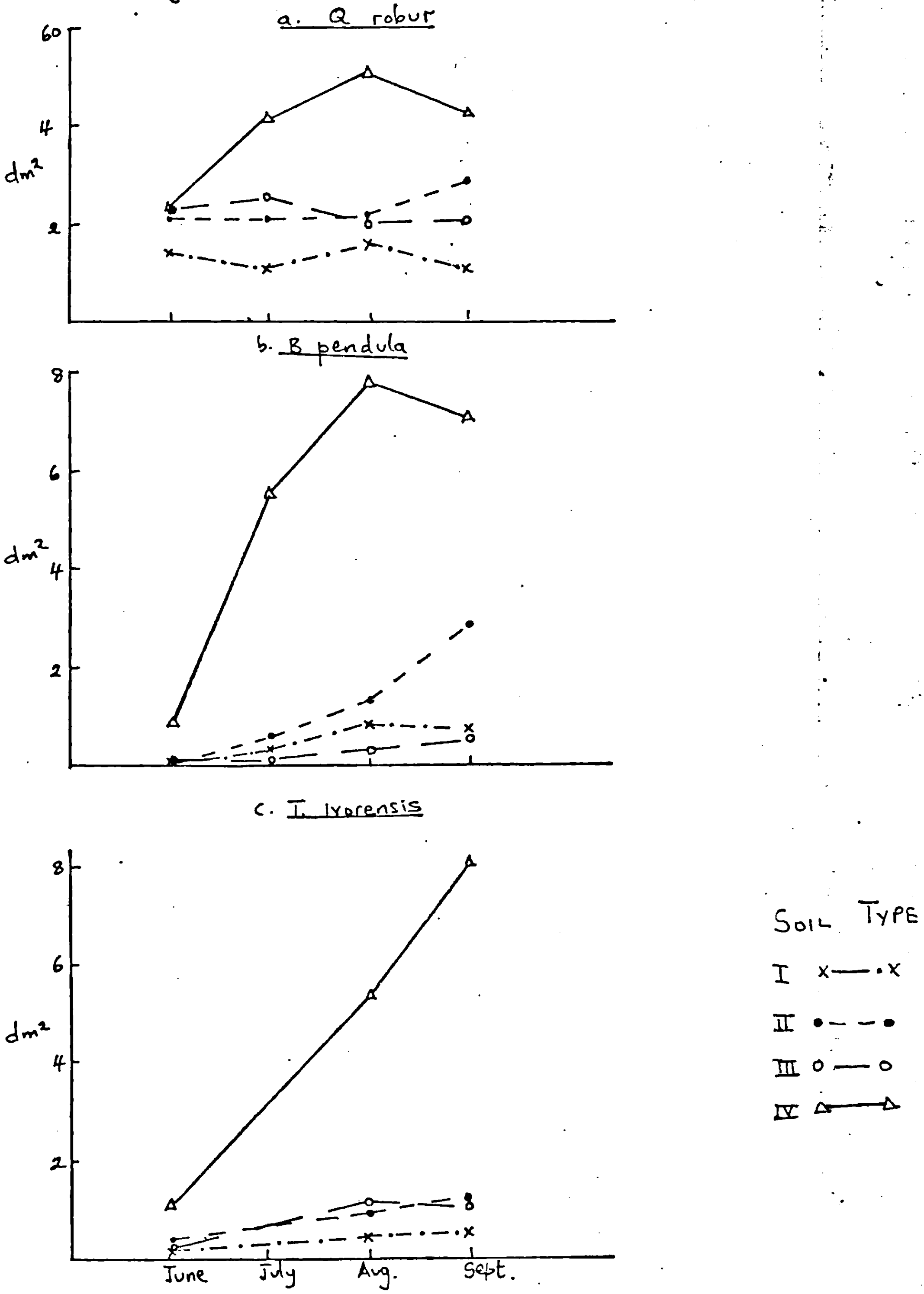
Leaf Area Variance Ratio Values

Variables	HARVESTS		
	A	C	D
Species (S)	35.12***	2.96NS	0.12 NS
Treatments (T_1) (All species)	3.56*	67.23**	58.72***
Treatments (T_2) (*Q. robur*)	1.29 NS	18.23***	12.43 **
Treatments (T_3) (*B. pendula*)	205.0***	326.60***	53.94***
Treatments (T_4) (*T. ivorensis*)	1.66 NS	77.15 ***	186.87***
S X T_1	0.53 NS	4.14**	5.62***
Replicate (R_1) (All Species)	0.21 NS	0.05 NS	0.54 NS
Replicate (R_2) (*Q. robur*)	0.44 NS	0.44 NS	0.96 NS
Replicate (R_3) (*B. pendula*)	1.25 NS	0.20 NS	3.79 NS
Replicate (R_4) (*T. ivorensis*)	1.33 NS	0.57 NS	3.12 NS

NS	Not Significant
*	Significant at 5% probability level
**	Significant at 1% probability level
***	Significant at 0.1% probability level.

Fig.V-6 Leaf Area values of Q. robur, B. pendula and T. ivorensis seedlings grown in soil types I, II, III, IV and harvested four times. (Mean values of four replicates)

Fig. V-6



Leaf Area

The effects of soil type on leaf production and expansion are given in tables V-14-16. The three species *Q. robur*, *B. pendula* and *T. ivorensis* showed marked differences in leaf area values as caused by the different soil types on which they were grown. Soil type IV produced the highest leaf area values in all species, followed by soil type II while soil type I and III produced the plants with the lowest leaf area values. In soil type I, *Q. robur* seedlings showed no increase in leaf area since the first leaves after germination were produced. The leaf area values ranged from 1.09 dm^2 to 1.63 dm^2. The same observation was equally true for *Q. robur* in soil type III, the values ranging from 2.00 dm^2 to 2.58 dm^2, those values though higher than those in soil type I did not show any increase between harvests. (*Q. robur* produces only one or two flushes of leaves in a growing season.) Thus soil types I and III did not allow either leaf production or expansion.

Q. robur seedlings showed a progressive increase in leaf area in both soil types II and IV, though the values climbed more steeply in site IV, reaching a maximum in August. In Soil Type II *Q. robur* seedlings had leaf area values ranging from 2.09 to 2.89 dm^2. In soil type IV, *Q. robur* values ranged from 2.28 to 5.03 dm^2.

B. pendula with very small leaves at the time of germination, was more greatly influenced by soil type as far as leaf area production was concerned, than *Q. robur*.

All *B. pendula* seedlings showed increases in leaf area values at least between June and August, before winter effects started to count in September.

The seedlings in the four soil types differed in their rate of leaf area expansion. Soil type III was the poorest site for B. pendula with the highest value in September only 0.53 dm^2. Soil type I had low values for B. pendula with the highest leaf area values of 0.81 dm^2 in August falling to 0.69 dm^2 in September.

Soil type II leaf area values for B. pendula, though low compared with soil type IV; showed a progressive increase throughout the season, the values ranged from 0.05 in June to 2.86 dm^2 in September, a steady increase throughout the season.

B. pendula in soil type IV showed a great increase in leaf area during July from 0.93 dm^2 to 5.57 dm^2, about a 600% increase. There was a further increase in leaf area by B. pendula in August and the value fell from 7.87 dm^2 at the end of August slightly to 7.06 dm^2 at the end of September, a result of winter conditions, possibly related to day length.

Terminalia ivorensis (a tropical tree) had a patternof leaf area expansion similar to that of B. pendula except that with T. ivorensis leaf area expansion seemed to have continued steadily especially in the soil type IV which was the best soil for all species. Obviously, T. ivorensis was not experiencing any winter effects, being perhaps unaffected by day length changes. In soil type I, T. ivorensis had very low leaf area values, in June, it was 0.26 dm^2, rose to 0.47 dm^2 in August, and fell to 0.29 dm^2 in September when the plants in this soil type were dying. T. ivorensis behaved fairly similarly in soil types II and III with fairly comparable values at all harvests (Range 0.38 - 2.09 dm^2).

B. pendula was different from *Q. robur* and *T. ivorensis* in that there was a trend with *B. pendula* specific leaf area values to decrease with time with very few exceptions, especially soil type III (See TableV-15).

The highest specific leaf area values in *B. pendula* were in the first harvest (June) for all treatments, with soil type I having the highest of 8.30 dm^2 g^{-1} followed by soil type II next with 5.77 dm^2 g^{-1} and soil type IV with 5.19 dm^2 g^{-1} the lowest at this harvest. In soil types I & II these values fell steadily to 1.69 dm^2 g^{-1} and 1.65 dm^2 g^{-1} respectively. However, soil type III had values which kept fluctuating in rather erractic manners as the experiment progressed. Soil ty;e IV had specific leaf area values fairly comparable at these harvests range 3.11 to 3.28 dm^2 g^{-1}.

T. ivorensis had fairly low specific leaf area values, compared with *B. pendula*; the values were similar to those of *Q. robur* . The range of specific leaf area values for *T. ivorensis* was from 1.49 dm^2 g^{-1} to 2.15 dm^2 g^{-1}, showing very little fluctuations due to soil type effects or harvest. The highest specific leaf area values were those of the first harvest, with the exception of soil type I with the highest value in July, the second harvest.

Comparatively, only *B. pendula* showed the most marked effects the soil type and time of harvest on the specific leaf area values, with the relatively high values at the beginning of the experiment, which generally fell towards the end of the experiment. For *Q. robur* and *T. ivorensis* it appeared the specific leaf area values were fairly constant during the growth of the seedlings in the different soil types.

Leaf Weight Ratio

The results of the leaf weight ratio obtained from the three experimental plants are shown in table V-17. The relatively higher leaf weight ratio values of B. pendula and T. ivorensis that those of Q. robur seedlings indicate the characteristic natures of the different plants in respect of the role the leaves play in total dry matter production. The effects due to the soil types as well as seasonal trend seemed to have produced marked effects on the leaf weight ratios in all the seedlings.

Q. robur seedlings (with the lowest leaf weight ratio of the three species) had the highest leaf weight ratio in the soil type IV of the first harvest (June), 0.27, the lowest values generally were in soil type I which fluctuated between 0.10 and 0.14 in June - August and fell to 0.09 in September; generally a low range of leaf weight ratios throughout the experiment. The other three soil types had a fairly similar trend as the leaf weight ratio values decreased steadily from a range 0.21 to 0.27 in June to 0.90 - 0.14 in September.

Thus in soil types II - IV, Q. robur leaf weight ratios were fairly comparable. B. pendula seedlings in soil types I & III had leaf weight ratios which rose at first and later fell as the season progressed, but site II and IV had leaf weight ratio values, high in June, but fell steadily through July, August and September. Soil type II values were generally higher than those of soil type IV. (TableV-17). The ratios in September in both cases were about half those in June, at the first harvest.

T. ivorensis had leaf weight ratios higher than those of B. pendula or indeed Q. robur, but the general pattern of distribution was similar to that of B. pendula. For instance as in B. pendula, in soil type I the leaf weight ratio rose from 0.39 to 0.46 and fell slightly to 0.45 in September.

With soil type III however, the leaf weight ratios fluctuated in the experiment. In soil types II and IV, however, the pattern observed in B. pendula or in Q. robur to a less extent was also observed i.e. high leaf weight ratios in June(0.61 soil type IV and 0.51 soil type II) which fell progressively to 0.42 and 0.45 in September respectively. It must be noted however that though the leaf weight ratio in T. ivorensis fell as the experiment progressed, the fall was not as great as those of B. pendula or Q. robur in which the values fell to about 50% at the last harvest. In T. ivorensis the fall was about 20-25%.

DISCUSSION

It is clear from the results that the soil types produced obvious effects on the seedling performances of the three different species of trees being investigated.

The species behaved fairly similarly on most sites e.g. developing chlorotic leaves in soil type I, and all seedlings generally performing well in soil type IV. The differences were mainly in terms of degree of responses to the soil types. For instance, while all species developed chlorotic leaves in soil type I, Q. robur failed to renew growth after the initial germination performance, but all seedlings remained alive throughout the experiments. B. pendula in soil type I, though it developed chlorotic leaves, showed continued growth (small in comparison with other soil types) throughout the period of this experiment i.e. through a growing season. T. ivorensis on the other hand developed chlorotic leaves like the other species, but a number of deaths occurred within two months of the experiments. The chemical analysis of soil type I (TableV-1) indicates that calcium, mainly calcium carbonate, was chiefly abundant in great excess when compared with other elements. Studies concerned with the growth responses of plants on calcareous soils show reduced growth associated with chlorisis in some species (Grime, 1966; Rorison, 1967).

From this investigation, the chemical conditions associated with calcium carbonate abundance responsible for the apparent intolerance and susceptibility of T. ivorensis seedlings in calcareous soils, of site I were not fully investigated.

T. ivorensis has never been reported on calcareous soils; (Lamb and Ntima 1971) describe the plant as growing best in various types of loams. There is no record of any observations of performances on calcareous soils, and the results of this experiment suggest that it would not be profitable to attempt to establish T. ivorensis on calcareous soils.

Q. robur, though with chlorotic symptoms, seemed to be tolerant of the calcareous condition. The leaves and the stems showed no relative increases in dry matter production, (there was an apical dormancy situation throughout), there were however some increases in root dry weights from 3.30 g in June to a maximum of 4.66g in August. Thus it appeared there was no root dormancy. The relationship between calcareous soil conditions and apical dormancy of Q. robur seedlings in the soil type I is not clear. Q. robur has been reported on a number of limestone soils especially carboniferous limestones (Jones, 1959; Newnham and Carlisle, 1969). These soils have supported oak-ash woodlands for centuries, but Newnham and Carlisle associate poor natural regeneration with phosphorus deficiency on these limestone soils. They do not state any values for the calcium carbonate content of the soils they used, but surface soils over hard limestones in N.W. England are often not calcareous. Thus for Q. robur the mere abundance of calcium in soil type I was not the only cause of apical dormancy, though, it brought about the chlorotic symptoms. In relation to soil type IV, soil type I was particularly low in nitrogen phosphorus and potassium, while other soil conditions (apart from calcium, but including physical composition) seemed adequate (Table V-1).

It is possible that the high calcium content in relation to the low amounts of the three major plant elements N P K brought about the growth conditions, but the chlorotic leaf condition can be caused by lack of iron. The acorns (fruit of Q. robur) from this experiment were not analysed, even though the effect of the acorn would have been favourable rather than otherwise to the young seedlings.

B. pendula seemed to be the plant most adapted to the conditions of soil type I. The seedlings after an initial slow start, soon showed some form of steady growth especially between July and August. The leaves which were clearly yellowish in the first month became greenish yellow towards the end of the experiment in August - September. This phenomenon also coincides with increases in dry weights. Therefore, B. pendula appeared to have adapted itself in soil type I. Gardiner (1966) reviewed the literature on the reputation of birch for soil improvement. Birch with pine and larch (in Switzerland) have been recommended in pioneer forest practice (Kasthoffer, and Gehret, in Gardiner 1966) While there are no experimental data available to the author on the growth performances of B. pendula on calcareous soils, the evidence from these experiments indicate that if all other conditions remained equal B. pendula could establish itself on the soil type I.

The pH of the soil from site I was 7.95. While the relationship between mineral contents and soil pH is yet unclear Hackett (1967) further work is needed (including plant analysis) for explaining the performances of these temperate and tropical tree seedlings on this calcareous soil.

The other soil types in which the seedlings were grown were acidic, varying greatly in the relative abundance of the major elements analysed, the soil type III, being the most acidic - pH 4.20. This is quite comparable with soil type IV, pH value of 4.30, (Jones, 1959) has associated Q. robur predominance with a soil pH range of 4.9 - 5.4. Soil types II and III though adjecent to one another were quite different in chemical composition, soil type II was richer in all elements analysed (except in available phosphorus) than soil type III. Soil type II was particularly richer than soil type III in the following: exchangeable hydrogen, exchangeable calcium, and potassium, nitrogen and organic matter. The better performances generally of all species in the soil type II than in soil types I and III indicate the importance of these elements in the growth responses of these seedlings. As no plant analysis was done, it was impossible to relate plant growth directly to soil nutrient conditions, in this experiment. An earlier experiment (Experiment I) has however shown clearly the possibility of depressed or abnormal growths by Q. robur and B. pendula in nutrient deficient cultures. Since tap water was used for watering the pots, the pH and calcium availability of the soils during the experiment is certain. Tap water contains considerable amounts of calcium, so that calcium deficiency is not likely to have limited growth in this experiment.

It has been observed (Binns, 1966) that single elements e.g. phosphorus could be limiting to tree growth in many British soils. It is possible that the absence of seedling of Q. robur and sparse presence of B. pendula on soil types II and III could be explained partly by the poor nutrient situation especially in soil type III.

T. ivorensis showed symptoms of deficiency similar to those of potassium and phosphorus deficiency, and T. ivorensis did poorer relatively on soil type II and III than the other temperate species. Thus, the tropical tree seedling did not show any form of plasticity in response to the varied soil types I - III, i.e. T. ivorensis showed its inability to grow properly in poor soils generally. It only performed reasonably well in soil type IV(a humus type of soil).

Soil type IV was particularly rich in exchangeable hydrogen, bases, nitrogen and percentage loss on ignition, but the phosphorus content was merely adequate. It was here that all seedlings produced their highest dry weights. There is therefore an evidence of relationship between soil chemical composition and general plant performances, though the mechanism of inter-relationship needs further studies. However, the following relationships from the data is suggested:

Soil Type	I	II	III	IV
Soil nitrogen	medium	medium	low	high
Soil phosphorus	medium	medium	medium	high
Soil potassium	low	medium	low	high
Plant dry weight				
Q. robur	low	medium	medium	high
B. pendula	low	medium	low	high
T. ivorensis	low	low	low	high

The growth analysis was very informative in describing the ontogenetic drifts within the different species. Evans (1972) stated that problems of changing structure and function affect all plant parts. The studies showed clearly the organic rather than inorganic changes constantly going on in the plant as a whole. The aim was to examine the relationship between soil properties and plant growth forms. Growth analysis studies also link soil effects with rate of photosynehesis.

The relative growth rate values show B. pendula as the fastest growing plant of the three examined (highest relative growth rate values in all soil types). The negative values by T. ivorensis and Q. robur in soil type I emphasize their general poor performances in this soil type. The B. pendula results confirm the observations of Jones (1959); Gardiner, (1966) T. ivorensis is a fast-growing tropical tree, the results from this experiment show clearly that soil conditions could make the tree a slow growing plant on the contrary or make it totally absent from any particular habitat. The low relative growth rate values for Q. robur even in soil type IV, confirms the observations of many workers that Q. robur is relatively a slow growing plant, the poorer values in other soil types especially soil type I also indicates the importance of soil conditions as it affects general plant performances.

The striking result from Table V-12 is the fact that B. pendula despite the initial low "capital" (fruit reserve) had the highest mean relative growth rate values in all soil types, i.e. all the species had different relative growth rates, with Q. robur with the slowest rate.

What is the ecological significance of the relationship between species, soil nature and growth rates? The limitations of this experiment must first be pointed out. (i) This was a greenhouse study and the plants were experiencing conditions that are unnatural (ii) A progressive analysis of the soils in which the plants were growing would have been useful in correlating rate of soil nutrient availability and plant growth rates (iii) Plant analysis to monitor nutrient utilization would similarly have been useful. The pot size was not considered limiting as the same "medium" size obtained from the soil volume experiment which gave yields of about 13g dry weight in B. pendula.

However, the following suggestions were made in relation to the ecological significance of the soil types. In soil type IV all the seedlings rapidly utilized available nutrients during the first few months and thus had high relative growth rates then. But as this was a pot experiment, the amount of nutrients available was restricted and thus the growth rates by all species began to slow down.

The quantity of nutrients readily available, the rate of replacement and the genetic composition of the different speices were the main causes of the different growth rates and total dry matter production by the three species studied.

Grime (1966) stated that in cleared productive sites, species with prolific seed production and with an efficient dispersal mechanism and also equipped with high relative growth rates, have better chances of colonizing such sites. He cited Betula populifolia and Ailanthus altissima as examples. The results of the soil type experiment indicate that B. pendula fits this description of a pioneer species quite well. T. ivorensis has also been described as exhibiting pioneer characteristics (Lamb and Ntima, 1971). The high relative growth rates in soil type IV suggest that a good soil i.e. with high nutrient balance is one of the preconditions for such good growth. Q. robur, although relatively slower growing than the other two species, the results of growth in soil type IV also suggests that this species has some fast growth characteristics as well, thus on occasions could behave as a pioneer species. Shaw (personal communications 1974) also shares this view. However, the initial relative growth rates of Q. robur on soil type IV are much lower than those of B. pendula for the same harvest interval.

It is dangerous to draw conclusions or inferences from results of soil type experiments to explain tree seedling regeneration or succession in forest sites. Obviously the pressures of the environment acting on species selection or survival must be complex. Many workers have indicated that light plays a major role in natural selection Hughes (1966) and Coombe (1966). Thus further work on the influence of light (or shade) on nutrient uptake and plant growth seemed inevitable, before any firm conclusions on the seedling behaviour of Q. robur and B. pendula in natural sites could be reached.

CHAPTER VI

THE EFFECTS OF SHADE AND FERTILIZER ON THE SEEDLING GROWTHS OF *Q. ROBUR* AND *B. PENDULA*

INTRODUCTION

In an attempt to investigate the role of various aspects of the environment on the causes of failure of natural regeneration in Q. robur and B. pendula seedlings the following experiments have been carried out. The effects of (i) two major soil nutrients nitrogen and phosphorus (ii) soil volume variation (iii) soil type variation on the growth of these seedlings.

Other factors of the environment important to these plants and indeed all plants include biotic and climatic. The role of animals in the natural regeneration of these Q. robur fruits and seedlings have been clearly elucidated. (Salisbury, 1916; Tansley, 1919; Watt, 1919; Jones, 1959; and Shaw, 1966).

Climatic factors influencing the growth of these species have received very little attention. Of all the climatic factors; light, rainfall, temperature, wind gaseous composition and variation etc. perhaps light is the most important single factor affecting plant growth and distribution generally.

The importance of light as it affects various components of relative growth rate of a number of woody species has been studied. Coffea species have a well developed shade tolerance (Huxley, in Murray and Nichols, 1966). Quercus petraea is a moderately shade tolerant species, (Jarvis, 1964). There is no detailed study available to the author of Q. robur and B. pendula species in their relationship with light, only general inferences such as Q. robur being shade tolerant, and Betula spp. being intolerant (Tansley, 1919; Jones, 1959; Salisbury, 1916; Grime, 1966). There was therefore a necessity to quantify the degree of tolerance or intolerance of these species.

Poor light intensity has been described as a precursor of plant susceptibility to other harzards such as fungal attack (Grime, 1966). It was considered desirable to determine the susceptibility of Q. robur and B. pendula seedlings to the low light intensities which normally occur in many British woodlands. There are two light phases in British deciduous woods during a particular growing season. (i) The light phase from the spring (percentage total light 30 to 60% of that in the open) and (ii) the shade phase mid-May to autumn, light 0.2% to 5% (Salisbury, 1916; Tansley, 1919; Blackman and Rutter, 1946; Coombe, 1966)

The inability of seedlings in shade to survive has been associated with fungal attack (Vaartaja, 1952 and 1962); similarly infection has been reported to be increased by shading. (Grime and Jeffrey, 1965).

Watt (1919) observed that uncontrolled tree felling in an oak-Hornbeam wood in Hertfordshire allowed much light to reach herbaceous plants, so that such plants as Pteriduim aquilinum and Deschampsia flexuosa effectively cut off light and encouraged fungal (mildew) activity, eventually killing the Quercus seedlings and producing an oak-birch-heath vegetation.

In view of the above observations, an attempt was made to investigate the growth responses of Q. robur and B. pendula seedlings in low light intensities in order to establish the minimum amount of light required for survival.

As light conditions have been observed to be related to the nutrient requirements of trees (Wilde, 1946); it was considered desirable in this work to consider the interaction of light and fertilizers on the seedling survival and growth of Q. robur and B. pendula

Methods and Materials

Seed germination and transplant

Q. robur and *B. pendula* fruits were germinated in peralite, fed with tap water only. The seedlings, which had been germinating under (approx.) 30 per cent day light were tranplanted into pots on the 7 June, 1973.

Soil Conditions

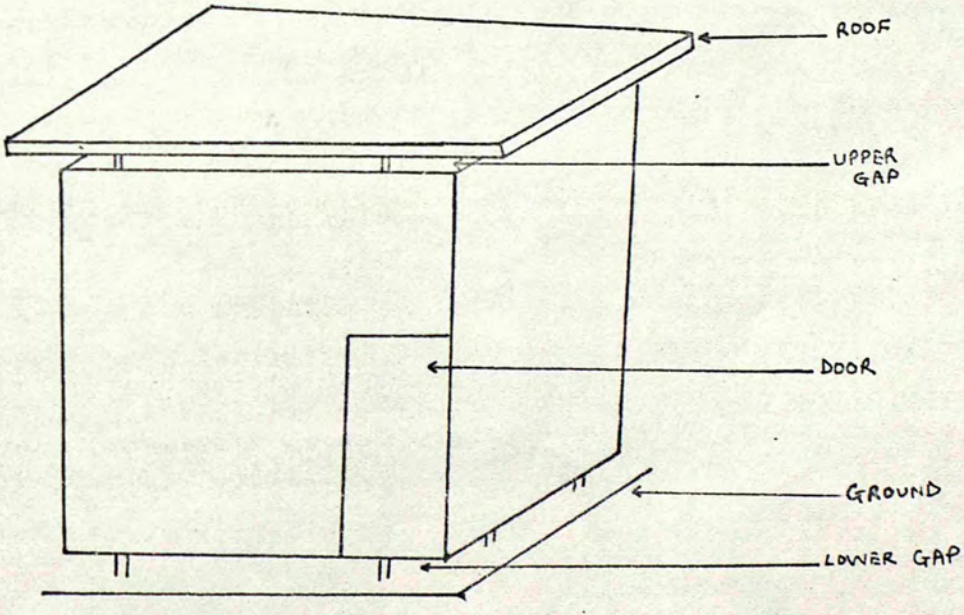
A soil sample obtained from the college garden was divided into two parts: one part was mixed with one level of John Innes fertilizer, the other half was used unfertilized. Thus providing two soil type conditions, fertilized (F) and unfertilized (No F)

The Cubes

Three cubes were constructed to provide shade at 30 per cent, 10 per cent and 5 percent approximately respectively (Plate VI-1 , and Fig.VI-1). The wooden cubes were covered with various layers of green polythene to provide the required shading conditions. The polythene sheet was of the non-clear type. Though it was green in colour, examination with a spectrophotometer suggested that its light transmission raised little with wavelength in the visible range. A gap 6in (15cm) wide was provided at the top and at the bottom of each cube to allow a free passage of air (see Fig.VI-1). The details of the cubes environment during the experimental period is given in Table .

Plate VI-1 The picture of the cubes used to provide the shading intensities for the tree seedlings being studied in this experiment.

Fig. VI-1. A Diagram of one of the cubes indicating the provision made for air flow. (Upper and lower gaps)



Thus these seedlings were grown in cubes covered with green polythene sheets to provide approximately 30%, 10% and 5% light (per cent of total day light) and in two types of soil (i) the ordinary garden soil (ii) the garden soil mixed with one level of John Innes fertilizer. The experiment was carried out in the summer months of 1973.

Climatic conditions within the cubes

Temperature

The temperature fluctuations during the experimental period within the 30%, 10% and 5% light cubes are presented in tableVI-1 and Fig.VI-2The 30% cube was the hottest during rhe day and the coldes at night. Conversely the 5% cube had the lowest temperature readings during the day and highest at night.

The meximum temperature range in all cubes was 70°-89°F (21.1-31°C) and the minimum range was 45°-61°F (7.2-15°C)during the experimental period. The daily mean temperature values indicate the fact that there was little variation in the temperature condition within the cubes of the three light intensities. The differences between the maximum and minimum temperature values within the cubes could not be regarded as great.

On the whole, June, July and especially August had high temperatures and it was not until September that the temperature began to fall.

Humidity

The relative humidity values are given in Table and shown in Fig.VI-2. Again, the cubes differed very slightly in the amount of water vapourwithin them during this experiment. Humidity values ranged from 67.42% August, 5% cube and 86.30% October 30% cube.

Table VI-1

The Temperature data within the shade cubes in which Q. robur and B. pendula seedlings were grown

Month		Temperature °F		
1973		Maximum	Minimum	Mean
	1.	86.0 (30.0)	52.6 (11.66)	69.3 (20.5)
June	2.	86.0 (30.0)	50.7 (10.55)	68.1 (20.1)
	3.	80.8 (27.22)	56.7 (13.9)	68.7 (20.5)
	1.	87.9 (31.66)	51.0 (10.55)	69.5 (21.11)
July	2.	83.1 (28.33)	51.6 (11.11)	67.3 (19.44)
	3.	79.9 (26.66)	61.7 (15.55)	70.8 (21.55)
	1.	89.4 (31.66)	49.4 (9.33)	69.4 (20.5)
August	2.	86.0 (30.0)	53.1 (11.66)	69.5 (21.11)
	3.	85.4 (29.40)	60.3 (15.55)	72.8 (22.77)
	1.	81.3 (28.33)	47.8 (9.44)	64.5 (18.33)
September	2.	79.6 (26.66)	49.0 (9.44)	64.3 (17.77)
	3.	72.7 (22.77)	48.4 (8.88)	60.5 (16.11)
	1.	74.5 (23.88)	45.0 (7.22)	59.8 (15.55)
* October	2.	73.0 (22.77)	46.0 (7.77)	59.8 (15.55)
	3.	70.0 (21.11)	48.4 (8.88)	59.2 (15.00)

1	30% Light
2	10% Light
3	5% Light
*	Mean values for 1 week only.

Figures in parenthesis indicate °C values.

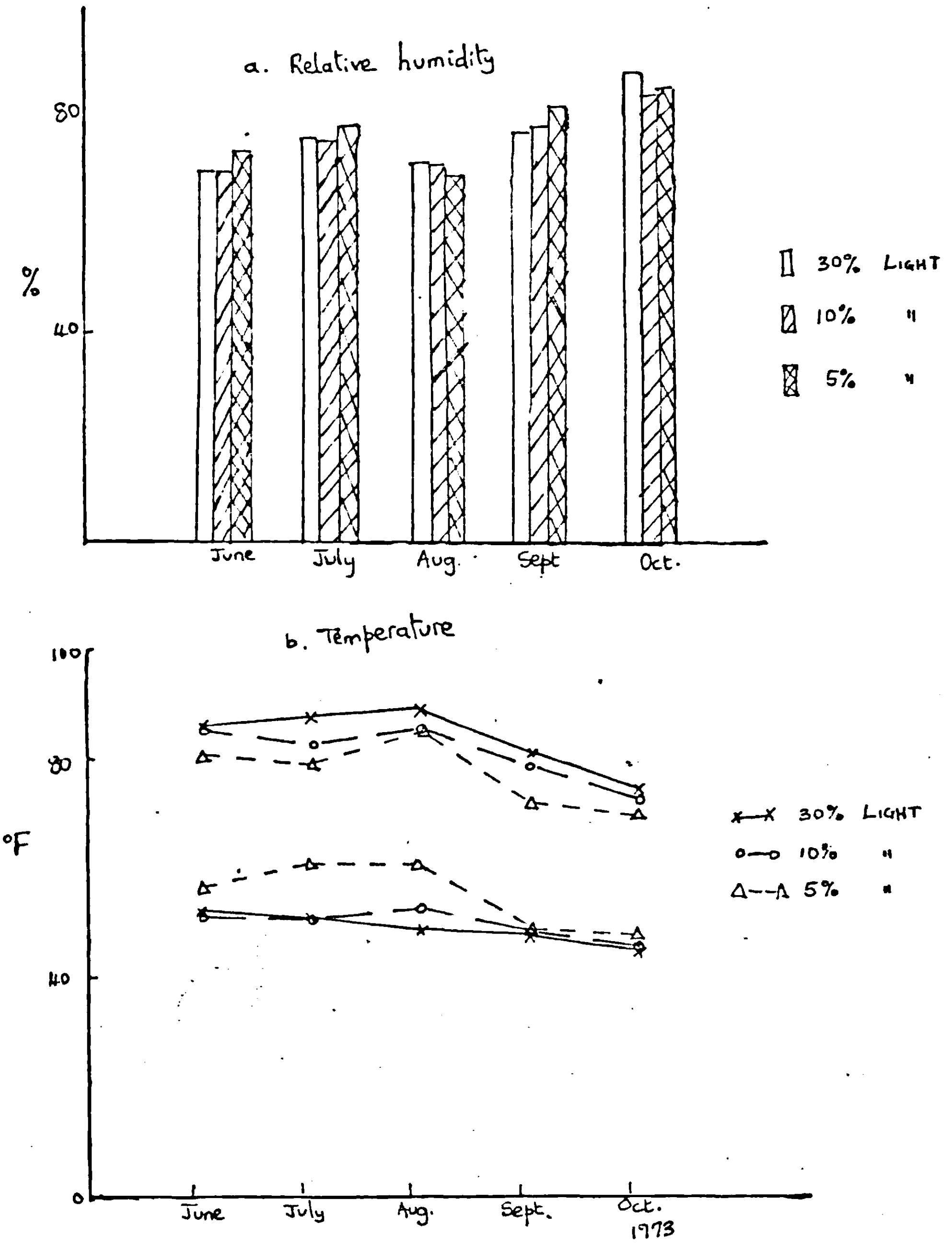
Table VI-2

The percentage relative humidity values within the shade cubes in which Q. robur and B. pendula seedlings were grown

Month (1973)	Light	Relative Humidity (Percentage)
June	30%	68.26
	10%	69.26
	5%	71.41
July	30%	74.04
	10%	73.65
	5%	76.43
August	30%	69.50
	10%	69.20
	5%	67.42
September	30%	74.78
	10%	75.87
	5%	79.84
* October	30%	86.30
	10%	82.70
	5%	83.0

* Mean values for 1 week only.

Fig.VI-2 Relative humidity and temperature values of 30%, 10% and 5% growth cubes for *Q. robur* and *B. pendula* seedlings. (Mean values of four replicates)



It is worthy of note that there is a relationship between temperature and humidity generally within the cubes when it was hot the relative himidity was fairly low (June, July and August), but when the autumn cold was setting in the relative humidity was increasing. The pots within the cubes required less frequent watering from September.

The fairly similar climatic conditions within the cubes indicate the effect of the gaps left at the bottom and upper part of the cubes, (see Fig.VI·2) to facilitate a continuous flow of air within the cubes.

Thus, generally the various layers of polythene producing the 30%, 10% and 5% light intensities affected slightly the maximum and minimum temperatures, but left the main temperature and relative humidity fairly similar, within the cubes. The cubes had to be cleaned once a week as they were continuously covered by black soot. The cubes were placed on a site where the effect of mutual shading by the cubes, or shading due to other nearby objects was minimal.

Experimental Design and Layout

The experimental design was a factorial one as follows:
Two plant species, three light regimes, two soil type conditions, four replicates and four harvests.
The Q. robur and B. pendula seedlings were randomized within each cube. The floor of each cube was covered with a polythene sheet, and the seedling pots were put on a layer of gravel spread on the sheet, thus eliminating contaminating effects of underlying soil.

The seedlings were watered with tap water from the top once daily. Over 50 per cent of the B. pendula seedlings were dead within one week of transplant in the 5 per cent cube. As they died, they were replaced until it was clear that cause of of death was not as a result of the transplant operation, but due to the low light intensity available. Percentage death determination was later started.

Harvesting

The first harvest was carried out on the 31 July, 54 days after transplant, 3 other harvests were carried out at 21 days interval. At each harvest, the following were determined: (i) plant height, (ii) plant part dry weight i.e. leaf, stem and root, and (iii) leaf area. For details of the harvest procedure see Chapter II.

THE EFFECTS OF TREATMENTS ON PLANT SURVIVAL

There was 100 per cent survival of the Q. robur seedlings in all treatments. The leaves of the seedlings in the 5% light regime were however, becoming necrotic from the 48th day, although no abscission was observed. Some leaves also turned yellowish but there were no deaths at all.

Table gives the survival values of the B. pendula seedlings. Although there were replacemtns of dead seedlings in both the 5% and 10% treatments throughout the first month of experimentation, it became clear later that the B. pendula seedlings could not survive in the 5% cube for up to 1 month.

The compensation point for B. pendula therefore appeared to lie between 5% and 10% light regimes.

There was no observable effect of fertilizer presence or absence in preventing or bringing about the deaths of the B. pendula seedlings. The variation in survival values between the fertilized and non-fertilized soil in the 10% cube was probably connected with fungal attack. Of course, there was no fertilizer effect on the Q. robur seedling survival as there were no deaths at all.

Survival Values

Q. robur had 100% survival in all treatments i.e. at 5%, 10% and 30% light, with or without fertilizer in the soil.

Table VI-3

B. pendula results, Number of plants surviving, 4 plants per treatment were planted at the beginning of the experiment.

Soil Status	Light Regime	HARVESTS			
		July 31	August 21	September 12	October 4
NO FERTILIZER	30%	4	4	4	4
	10%	4	3	4	4
	5%	4	0	0	0
FERTILIZER	30%	4	4	4	4
	10%	4	4	1	1
	5%	4	0	0	0

HEIGHT AND DRY WEIGHT YIELDS

(a) Height In FiguresVI-3&4,the height and dry weight yields are presented. Within the period of this experiment, there was no evidence of shoot development by Q. robur seedlings growing in the 5% light regime. Compare the figures from the beginning of the first harvest to the last. (TableIV-7& FigIV3&4). No effect of fertilizer could be substantiated either. Some 10% light Q. robur seedlings broke dormancy once (not more thqn once) i.e. produced a "flush" of shoot, others remained dormant throughout. Thus Q. robur seedlings in 10% light, grew rather taller (generally) than those in 5%. The seedlings in 10% light, with fertilizer grew taller than those in 10% light, no fertilizer, The same trend was observed in seedlings growing in 30% light, though the fertilizer effect on height growth seems more apparent. Table and Fig. . The B. pendula seedlings in 30% light, with fertilizer grew tallest, reaching a maximum of 19.85cm in September, generally a better performance than seedlings in the same light regime, but without fertilizer. The better performance of seedlings in 30% light than those in 10% light is quite evident even though the B. pendula seedlings in the 10% light regime were *etiolated Fig VI-3.

The 5% light seedlings because of their high mortality are not considered. On the whole, Q. robur seedlings were taller than B. pendula probably the effect of food reserves in the Q. robur acorns.

B. pendula seedlings in both 10% and 30% light, but without fertilizer started leaf abscission (wintering) earlier than those in other treatments. This did not happen in Q. robur seedlings.

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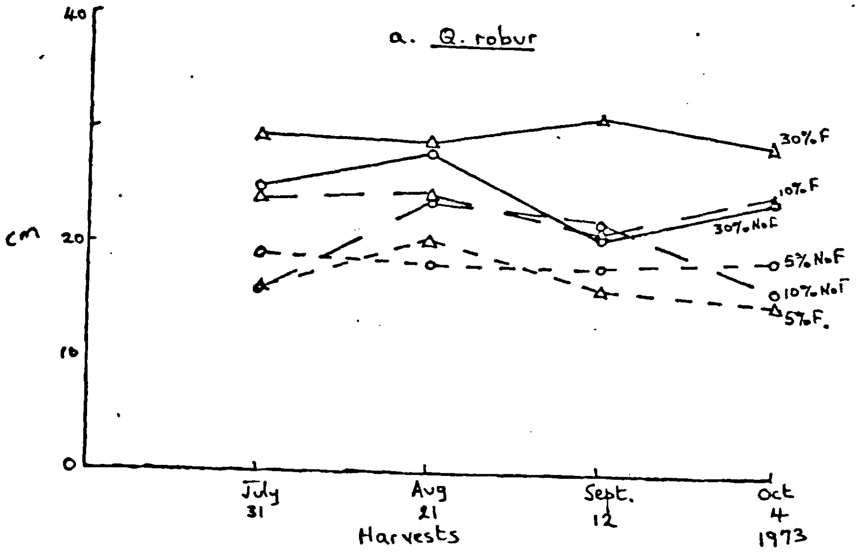
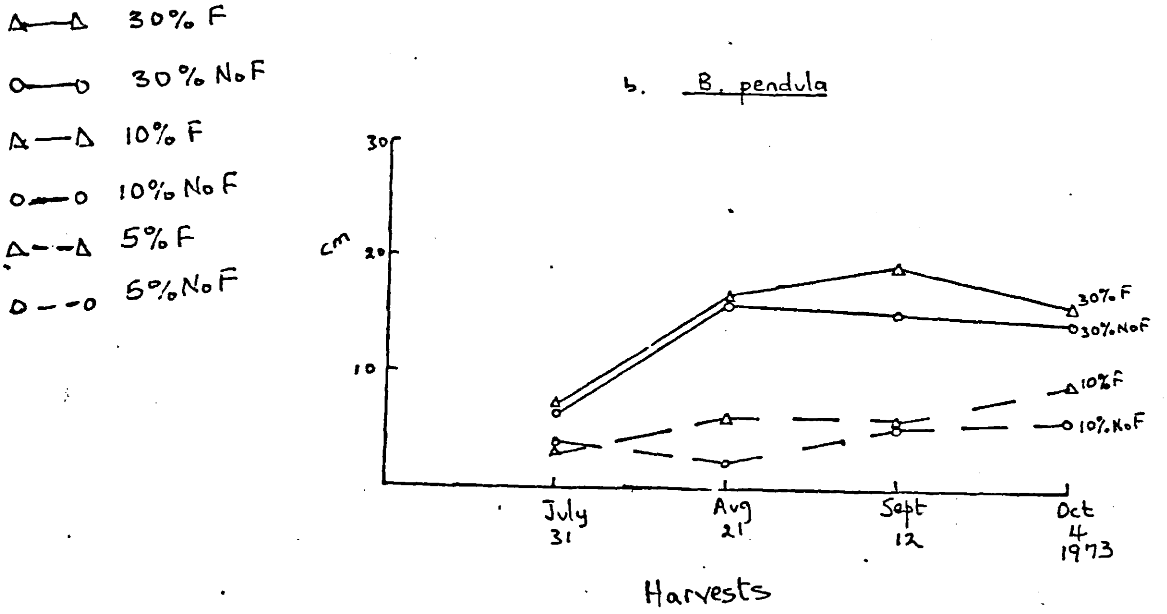
* The term 'etiolated' here refers to excessive stem elongation only, and does not imply absence of chlrophyll.

Fig.VI-3 Height values of *Q. robur* and *B. pendula* seedlings grown in 30%, 10% and 5% light, with (F) and without (No F) fertilizer. (Mean values of four replicates)

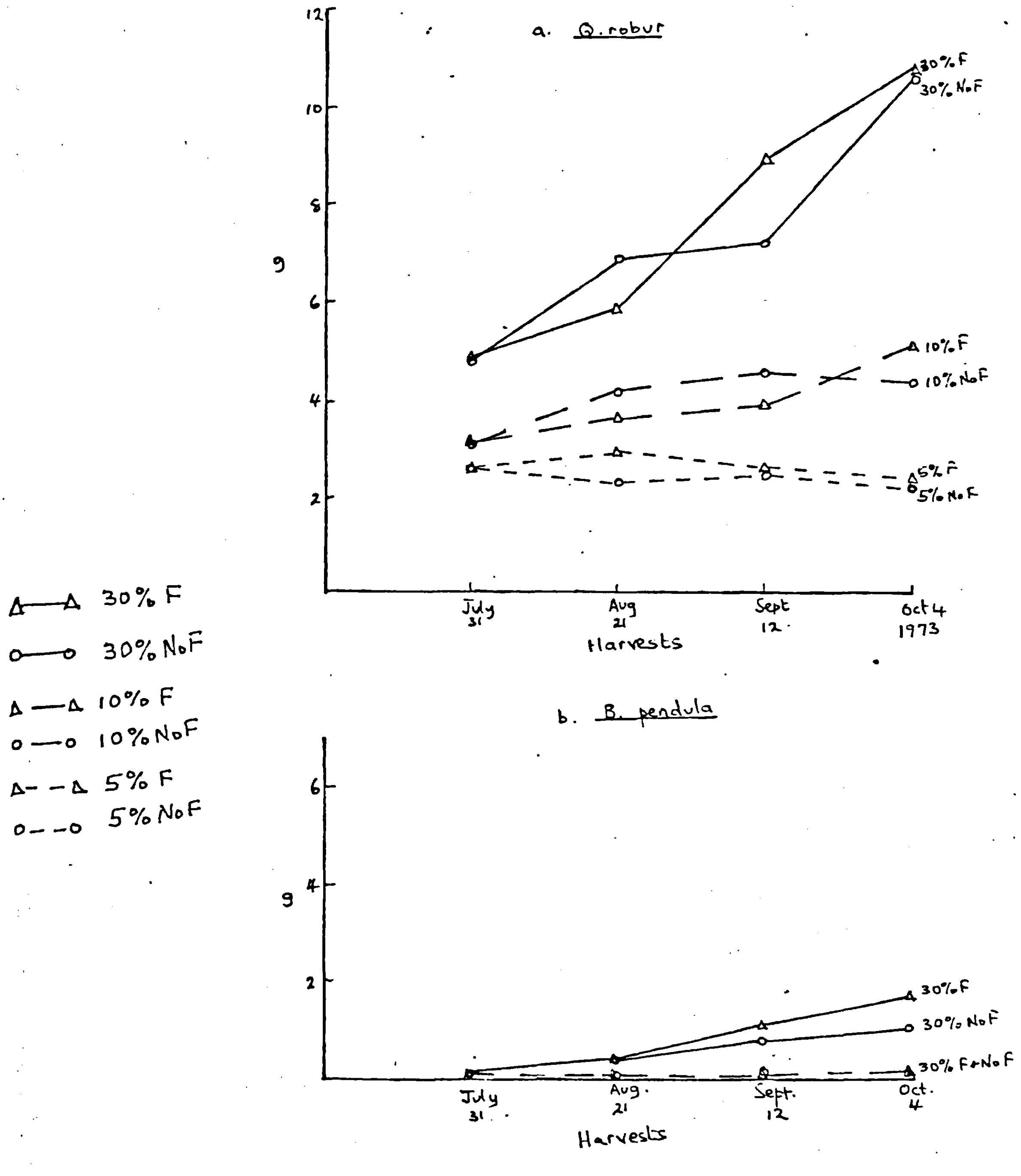


a. Q. robur



b. B. pendula

Fig.VI-4 Total plant dry weight values of Q. robur and B. pendula seedlings grown in 30%, 10% and 5% light, with (F) and without (No F) fertilizer. (Mean values of four replicates)



Plates VI-2 & 3 B. pendula & Q. robur seedlings grown in 30%, 10% and 5% light with (F) and without (No F) fertilizer.

Note: all the B. pendula seedlings died within one month in 5% light.

VI - 2

VI - 3

Table VI-4

The effects of shade and fertilizer on the total plant dry matter production of Q.robur seedlings (g) Mean values of 4 replicates

Soil Status	Light %	HARVESTS July 31	August 21	September 12	October 4 1974
NO	30	4.62	6.97	7.36	10.56
Fertilizer	10	3.05	4.13	5.04	4.32
	5	2.60	2.73	2.50	2.90
With	30	4.75	6.03	8.96	10.82
	10	3.10	3.56	3.98	5.02
Fertilizer	5	2.50	2.96	3.09	2.30

For analysis of variance see Table VI - 6

TABLE VI-5
The effects of shade and fertilizer on the total plant dry matter production of B. pendula seedlings (g)

SOIL STATUS	LIGHT %	HARVESTS			
		July 31	August 21	September 12	October 4 1974
No Fertilizer	30	0.0437 (±0.004)	0.4489 (±0.02)	0.8877 (±0.08)	1.0365 (±0.21)
	10	0.0057 (±0.004)	0.0067 (±0.0005)	0.0200 (±0.004)	0.0446 (±0.005)
	5	0.0017 (±0.0003)	-	-	-
With Fertilizer	30	0.0743 (±0.004)	0.4507 (±0.01)	1.1131 (±0.07)	1.7772 (±0.11)
	10	0.0051 (±0.001)	0.0078 (±0.002)	0.0235 (±0.001)	0.0912 (±0.004)
	5	0.0019 (±0.0002)	-	-	-

Figures in parenthesis indicate standard error values.

TABLE VI-6

Variance ratio values in the analysis of variance of Q. robur total plant dry matter production of seedlings grown in (T) 30%, 10%, 5% light and with (F) or without fertilizer (No F)
(MEAN VALUES OF 4 REPLICATES)

	HARVESTS			
Variables	I	II	III	IV
Fertilizer (F) effect	0.01 NS	1.69 NS	0.20 NS	0.004 NS
Treatment (T_1) (No F)	7.66^{**}	17.83^{***}	19.79^{***}	7.05^{*}
Treatment (T_3) (F)	12.44^{**}	26.27^{**}	24.81^{**}	30.26^{***}
F X T_1	0.01 NS	0.44 NS	1.12 NS	0.04 NS
Replicate (R_1) (No F & F)	0.21 NS	0.03 NS	0.61 NS	0.20 NS
Replicate (R_2) (No F)	0.05 NS	0.79	1.42 NS	0.94 NS
Replicate (R_3)	1.41 NS	0.93 NS	0.95 NS	0.96 NS

NS	Not Significant
*	Significant at 5% probability level
**	Significant at 1% probability level
***	Significant at 0.1% probability level.

Dry Weight Yields

Total plant dry matter production

The effect of shade was definitely more important than that of fertilizer. The fertilizer effect seems unimportant (See analysis of variance). Although the dry weight yields in all treatments did not correspond to the light ratios, yet the shade effects are quite apparent. There was no evidence of increase in dry matter production by Q. robur seedlings in 5% light, throughout this experiment, suggesting that, in the conditions of this experiment, 5% daylight is close to the compensation point of Q. robur.

The effects of both shade and fertilizer were more obvious in B. pendula seedlings than in Q. robur (Table VI-5 and Fig. VI-5); the shade effect evidently more important e.g. 1.0363g total dry weight 30% light, no fertilizer and 0.091g 10% light with fertilizer respectively.

The effect of fertilizer seemed important only in the last harvest when dormancy was starting (shorter day lengths and lower temperatures See Fig. VI-4). The dry matter production in B. pendula in 30% light with fertilizer seemed continuous, 1.7772g harvest IV compared with 1.0363g in the same light regime without fertilizer. The fertilizer effect seemed apparent only at this stage of development.

The Q. robur seedlings had higher yields in all treatments than B. pendula seedlings, again probably the acorn effect (See discussions).

Table VI-7

The effects of shade and fertilizer on the distribution of plant dry matter of *Q. robur* seedlings (g)

Mean values of 4 replicates

Soil Status	Light %	Leaf July 31	Leaf Aug 21	Leaf Sept 12	Leaf Oct 4	Stem July 31	Stem Aug 21	Stem Sept 12	Stem Oct 4	Root* July 31	Root* Aug 21	Root* Sept 12	Root* Oct 4
		HARVESTS (1973)											
	30	1.20	1.29	1.00	1.39	0.96	1.68	1.59	2.02	2.48	4.00	4.77	7.15
No fertilizer	10	0.48	0.71	0.86	0.53	0.63	0.92	1.18	0.71	1.94	2.50	3.00	3.08
	5	0.54	0.51	0.49	0.43	0.51	0.44	0.41	0.53	1.55	1.78	1.60	1.94
	30	1.27	1.04	1.95	1.88	0.92	1.65	2.01	2.40	2.56	3.34	5.00	6.54
	10	0.56	0.48	0.74	0.73	0.67	0.80	0.84	1.21	1.87	2.28	2.40	3.08
	5	0.54	0.57	0.49	0.37	0.44	0.50	0.40	0.37	1.52	1.89	1.80	1.56

* - Includes values of left-over acorn (fruit)

For analysis of variance see Tables VI-9-11

Table VI-8
The effects of shade and fertilizer on plant dry matter distribution of <u>B. pendula</u> seedlings (g) (Mean values of 4 replicates) (except as stated in foot notes)

Soil Status	Light	Leaf				Stem				Root			
		HARVESTS											
	%	Jul 31	Aug 21	Setp 12	Oct 4	Jul 31	Aug 21	Sept 12	Oct 4	Jul 31	Aug 21	Sept 12	Oct 4 (1973)
NO Fertilizer	30	0.0257	0.2431	0.3719	0.2797	0.0123	0.1230	0.2594	0.3527	0.0057	0.0828	0.2564	0.4039
	10	0.0029	0.0089[+]	0.0110	0.0162	0.0018	0.0017[+]	0.0079	0.0186	0.0010	0.0011[+]	0.0024	0.0098
	5	0.0006	—	—(')	—	0.0007	—	—	—	0.0004	—	—	—
With Fertilizer	30	0.0456	0.2351	0.5078	0.5184	0.0177	0.1357	0.3164	0.5513	0.0110	0.0799	0.2889	0.7075
	10	0.0025	0.0088	0.0141[*]	0.0378	0.0018	0.0027	0.0049[*]	0.0412[*]	0.0008	0.0013	0.0045[*]	0.0122[*]
	5	0.0007	—	—	—	0.0007	—	—	—	0.0005	—	—	—

* One plant surviving

(') dead

\+ 3 plants surviving

Table VI-9 Variance ratio values in the analysis of variance of *Q. robur* leaf dry matter production of seedlings grown in (T) 30%, 10%, 5% light with (F) or without (No F) fertilizer

Mean of 4 replicates

Variables	HARVESTS			
	I	II	III	IV
Fertilizer (F) effect	0.12 NS	0.92 NS	0.94 NS	0.39 NS
Treatment (T_1) (No F & F)	10.13**	7.46*	4.06*	5.07*
Treatment (T_2) (No F)	10.15*	14.50**	3.50 NS	5.55*
Treatment (T_3) (F)	22.63**	12.33**	8.00*	12.45**
F X T_1 (Fertilizer X Shading)	0.03 NS	0.46 NS	1.36 NS	0.22 NS
Replicate (R_1) (No F & F)	0.16 NS	0.15 NS	0.60 NS	0.31 NS
Replicate (R_2) (No F)	0.38 NS	2.50 NS	1.24 NS	1.15 NS
Replicate (R_3)	1.01 NS	0.33 NS	1.42 NS	0.76 NS

NS	Not significant
*	Significant at 5% Probability Level
**	Significant at 1% Probability Level
***	Significant at 0.1% Probability Level.

TABLE VI-10

Variance ratio values in the analysis of variance of Q. robur stem dry matter production of seedlings grown in (T) 30%, 10%, 5% light, with (F) or without (No F) Fertilizer

	HAVERSTS			
Variables	I	II	III	IV
Fertilizer (F) (effect)	0.05 NS	0.33 NS	0.007 NS	0.26 NS
Treatment (T_1) (No F & F)	9.60**	9.79**	9.67**	4.40
Treatment (T_2) (No F)	4.40 NS	11.15**	23.83**	6.16*
Treatment (T_3) (F)	30.06***	21.25**	9.71*	7.70*
F X T_1 (Fertilizer and Shading)	0.08 NS	0.24 NS	0.70 NS	0.16 NS
Replicate (R_1) (No F & F)	1.20 NS	0.12 NS	0.85 NS	0.38 NS
Replicate (R_2) (No F)	0.54 NS	0.67 NS	2.82 NS	1.11 NS
Replicate (R_3) (F)	4.94 NS	0.14 NS	0.78 NS	1.35 NS

NS Not Significant
* Significant at 5% probability level
** Significant at 1% probability level
*** Significant at 0.1% probability level

TABLE VI-11

Variance ratio values in the analysis of variance of <u>Q. robur</u> root (including acorn left over) dry matter production of seedlings grown in (T) 30%, 10%, 5% light with F or without (No F) fertilizer

Variables	HARVESTS I	 II	 III	 IV
Fertilizer (F) effect	0.0004 NS	1.05 NS	0.02 NS	0.06 NS
Treatment (T_1) (No F & F)	4.04*	17.75***	31.70***	5.94*
Treatment (T_2) (F)	5.43*	19.14**	30.60***	7.16*
Treatment (T_3) (F)	5.60*	22.50**	42.92***	23.63**
F X T_1 (Fertilizer X Shading)	0.02 NS	0.99 NS	0.65 NS	0.02 NS
Replicate (R_1) (No F & F)	0.46 NS	0.30 NS	0.53 NS	0.13 NS
Replicate (R_2) (No F)	0.56 NS	0.03 NS	0.96 NS	0.85 NS
Replicate(R_3) (F)	1.30 NS	2.20 NS	0.40 NS	1.72 NS

NS Not Significant
* Significant at 5% probability level
** Significant at 1% probability level
*** Significant at 0.1% probability level

Table VI-12

Variance ratio values in the analysis of variance of Q. robur shoot/root ratios of seedlings grown in (T) 30%, 10%, 5% with (F) or without (No F) fertilizer

Variables	I	II	III	IV
Fertilizer (F) effect	0.02 NS	0.01 NS	0.21 NS	1.14 NS
Treatment (T_1) (No F & F)	1.74 NS	0.41 NS	1.25 NS	0.07 NS
Treatment (T_2) (No F)	2.32 NS	0.54 NS	2.00 NS	2.82 NS
Treatment (T_3) (F)	2.80 NS	3.70 NS	2.47 NS	0.77 NS
F X T_1	0.06 NS	0.19 BS	0.99 NS	0.42 NS
Replicate (R_1) (No F & F)	1.62 NS	0.16 NS	2.66 NS	0.42 NS
Replicate (R_2) (No F)	2.05 NS	0.84 NS	2.81 NS	2.49 NS
Replicate (R_3) (F)	3.33 NS	1.01 NS	3.66 NS	1.30 NS

NS	Not Significant
*	Significant at 5% probability level
**	Significant at 1% probability level
***	Significant at 0.1% probability level

Fig. VI-5 Plant Dry Matter Distribution of *Q. robur* seedlings grown in 30%, 10% and 5% light with and without fertilizer.

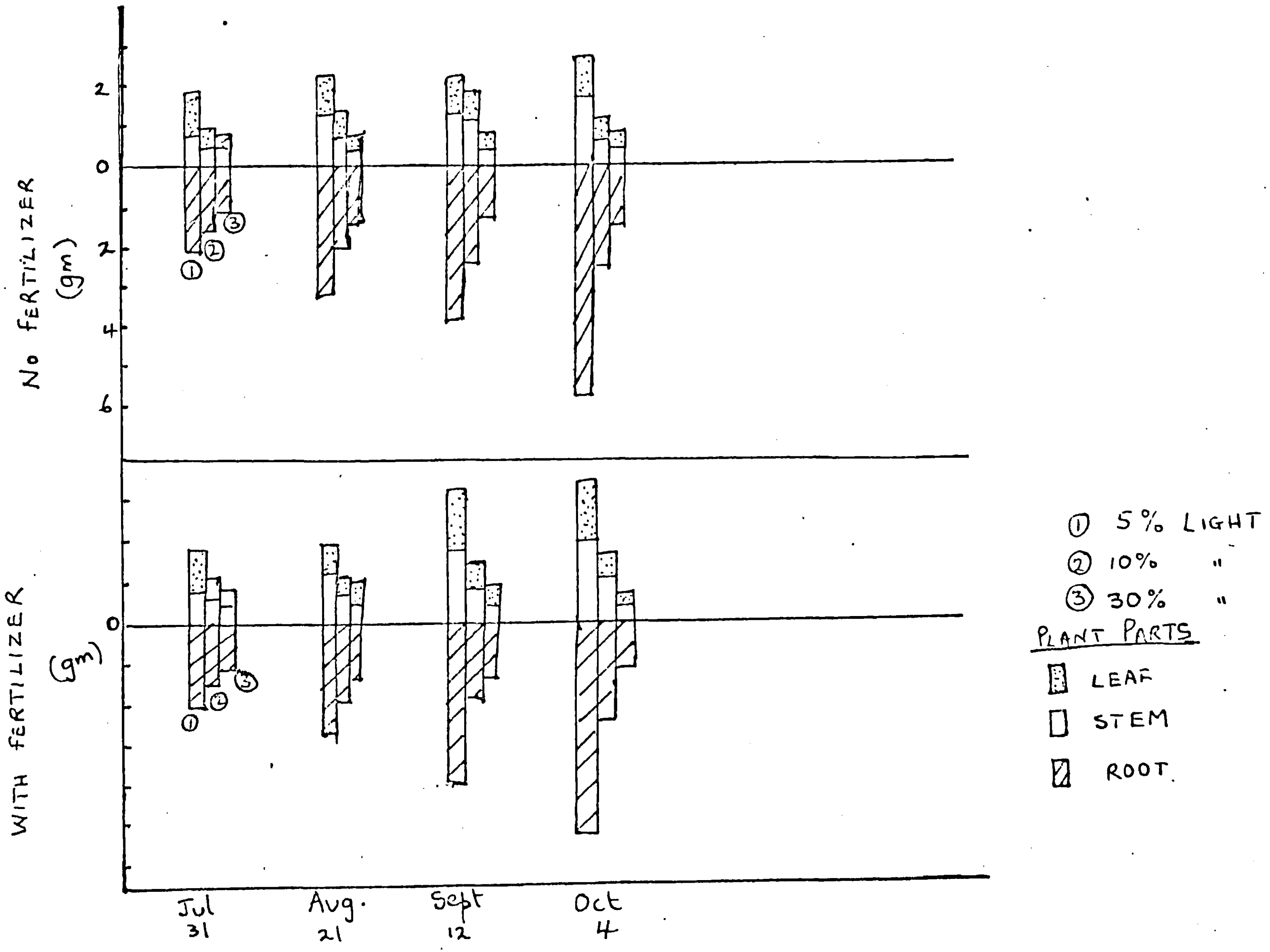
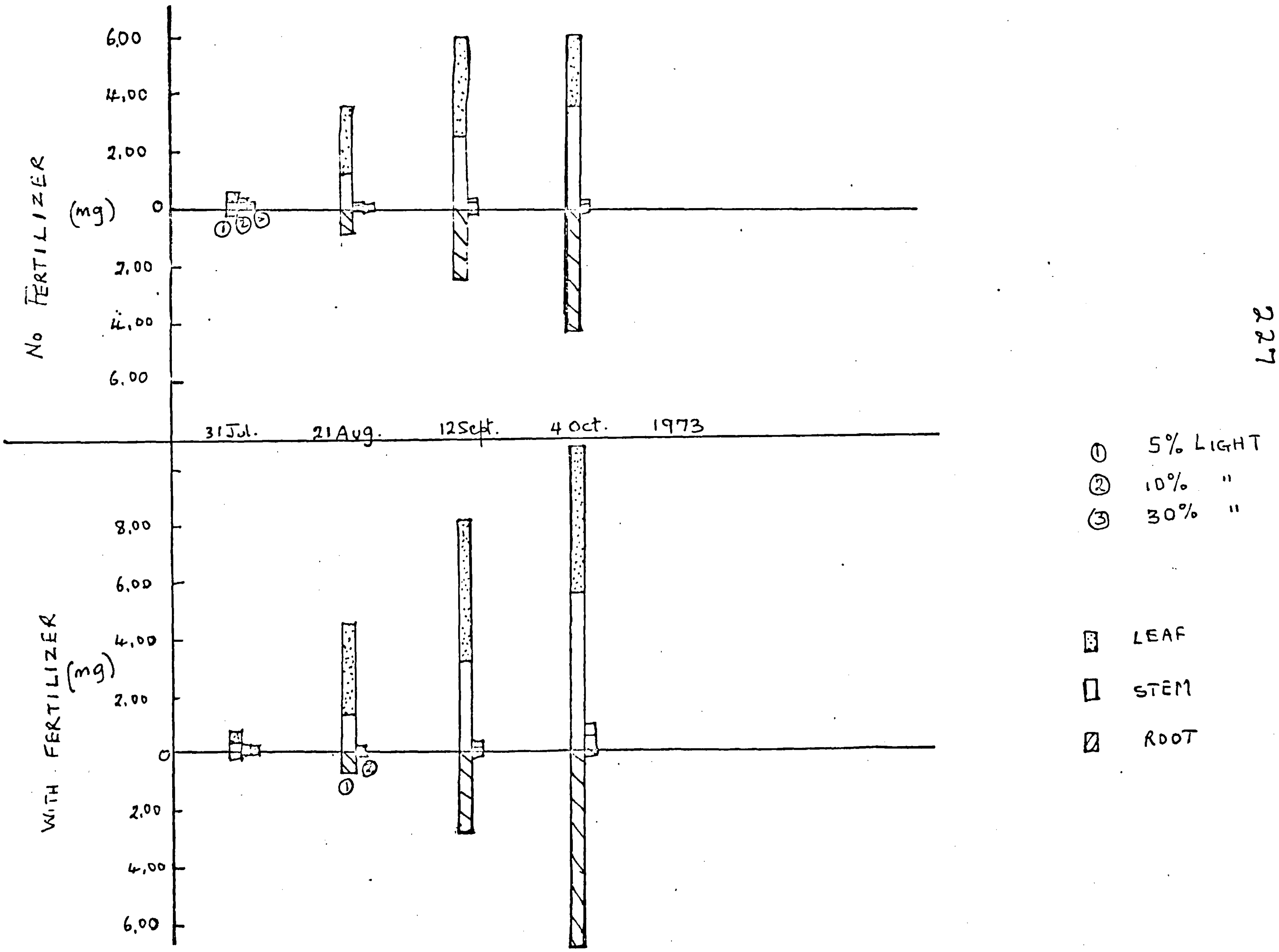


Fig. VI-6 Plant Dry Matter Distribution of B. pendula seedlings grown in 30%, 10% and 5% light with and without fertilizer.



Plant dry matter distribution

Tables VI-7 & 8 give the values and patterns of distribution of plant dry matter within the seedlings of Q. robur and B. pendula during this experiment. The general pattern of greater root production by Q. robur and greater shoot production by B. pendula already observed in the other described experiments, were also observed here. Shade effects obviously prevented either shoot or root growth in the 5% light with or without fertilizer in both species. The death of B. pendula seedlings in this light regime has already been reported.

There was some production of shoot and root dry matter in both species at 10% light. The death of some B. pendula seedlings in this light regime has also been reported.

On the whole it appeared that the fertilizer treatment encouraged no shoot production by Q. robur. Compare values of Q. robur plant part dry matter production on the 12 September and on the 4 October Table VI-7. It was only in the 30% light however that this phenomenon became more apparent. (See Analysis of variance).

The B. pendula seedlings in 30% light grew and developed well, whilst in lower light intensities there was little or no development.

The effect of fertilizer seemed more apparent in B. pendula at 30% light starting from the third harvest on September 12. (Table VI-7 & Fig. VI-4). The highest values of leaf, stem and root dry matter were in the last harvest of the fertilized B. pendula samples at 30% light.

Table VI -13.

Observations on Q. robur seedlings grown in two soil types No F (No fertilizer) (F with fertilizer) and in three light regimes (approx.) 30%, 10% and 5% of total day light. There were four harvests I, II, III, IV on 31 July, 21 August, 12 September and 4 October respectively 1973

Each estimate is the mean of four replicates

SOIL	LIGHT REGIME	LEAF AREA (dm^2)				SPECIFIC LEAF AREA (dm^2/g^{-1}) dry weight			
		I	II	III	IV	I	II	III	IV
NO FERTILIZER	30%	2.45	2.79	1.96	3.06	2.04	2.16	1.96	2.20
	10%	1.18	1.59	2.05	1.36	2.45	2.23	2.38	2.56
	5%	1.47	1.64	1.39	1.23	2.72	3.21	2.81	2.85
	30%	2.84	2.23	3.38	3.75	2.10	2.10	1.75	1.99
	10%	1.50	1.15	1.79	1.89	2.67	2.39	2.41	2.58
	5%	1.36	1.69	1.26	0.91	2.47	2.95	2.60	2.45

Table VI-14.

Observations on B. pendula seedlings grown in two soil types (No F. without fertilizer, F with fertilizer) and in three light regimes (approx.) 30%, 10% and 5% of total day light. There were four harvests, I, II, III and IV, 31 July, 21 August 12 September 4 October respectively, 1973

(Mean values of 4 replicates)

SOIL TYPES	LIGHT REGIME	LEAF AREA (dm^2)				SPECIFIC LEAF AREA (dm^2/g^{-1})			
		I	II	III	IV	I	II	III	IV
NO FERTILIZER	30%	0.13	1.06	0.97	1.01	4.33	4.41	2.62	3.60
	10%	0.02	0.04**	0.06	0.09	6.66	10.00**	6.00	5.62
	5%	0.003	-	-	-	5.00	-	-	-
FERTILIZER	30%	0.20	1.20	1.83	1.75	4.00	5.00	3.38	3.38
	10%	0.014	0.03	0.08*	0.29*	4.66	7.50	5.35*	7.63*
	5%	0.004	-	-	-	5.71	-	-	-

* ONLY ONE PLANT

** 3 PLANTS ONLY

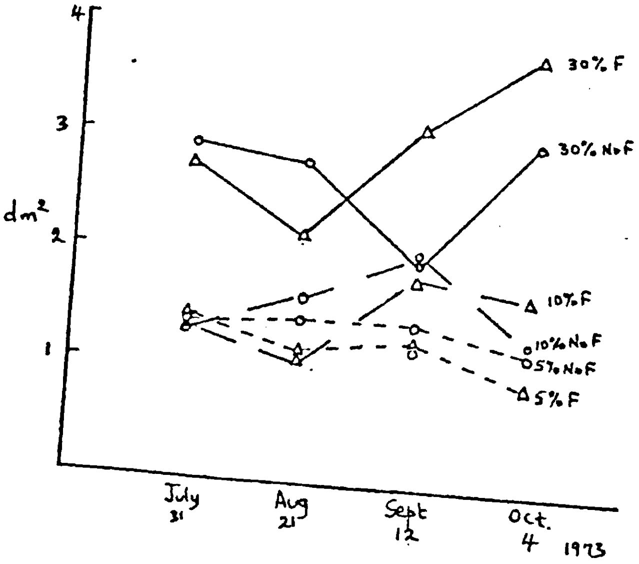
TABLE VI-15

Variance ratio values in the analysis of variance of Q. robur leaf area values of seedlings grown in (T) 30%, 10%, 5% light with F or without (No F) fertilizer

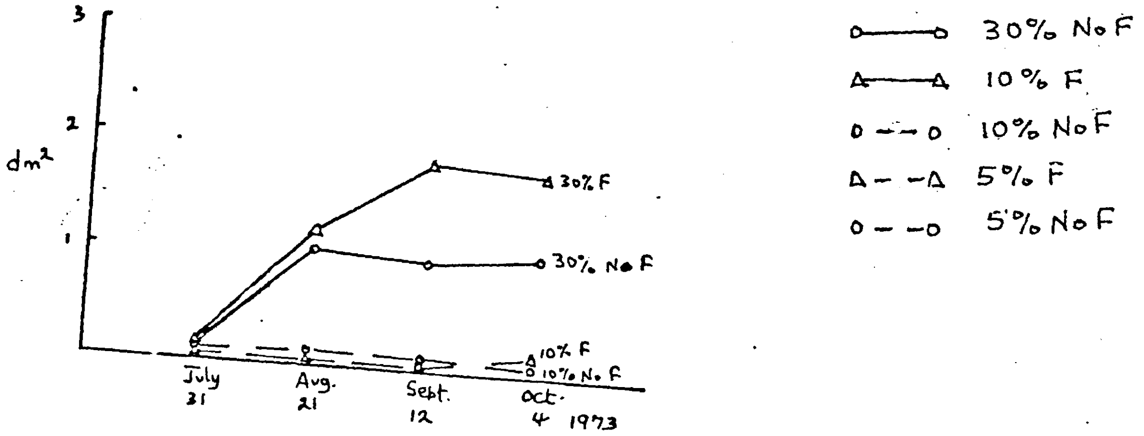
	HARVESTS			
Variables	I	III	III	IV
Fertilizer (F) effect	0.16 NS	1.10 NS	0.38 NS	0.20 NS
Treatment (T_1) (No F & F)	2.55 NS	5.97^{*}	2.00 NS	4.76^{*}
Treatment (T_2) (No F)	2.37 NS	9.83	1.15 NS	3.15 NS
Treatment (T_3) (F)	5.00 NS	6.38^{*}	5.26^{*}	6.46^{*}
F X T_1 (Fertilizer x Shading)	0.11 NS	0.37 NS	0.94 NS	0.24 NS
Replicate (R_1) (NoF&F)	0.22 NS	0.82 NS	0.72 NS	0.48 NS
Replicate (R_2) (No F)	0.15 NS	2.27 NS	1.35 NS	0.84 NS
Replicate (R_3) (F)	1.60 NS	0.44 NS	1.27 NS	0.75 NS

Fig. VI-7 Leaf area values of *Q. robur*, and *B. pendula* seedlings grown in 30%, 10% and 5% light, with (F) and without (No F) fertilizer. (Mean values of four replicates)

a. *Q. robur*



b. *B. pendula*



Plant dry matter production and distribution thus seemed continuous throughout the period of this experiment in *B. pendula* grown in 30% light.

Thus the interaction of light (30%) and fertilizer treatment was more effective on the *B. pendula* seedlings than the *Q. robur*, as far as plant dry matter production was concerned. On the other hand, light alone seemed more important to *Q. robur* for dry matter production than a combination of light and fertilizer at least under the conditions of this experiment.

Leaf Area

The effects of shade and fertilizer on *Q. robur* and *B. pendula* seedling leaf areas can be seen in Tables VI-13 & 14 and Fig. VI-7. These results show that both species especially *B. pendula* were affected greatly in their leaf areas by shade, the effect of the fertilizer treatment was not quite apparent, i.e. shade had a greater influence than nutrients on leaf area extension within the period of the experiment.

The results of *Q. robur* Table VI-13 & Fig. VI-7a show that at 30% light leaf area values were generally higher than those of plants grown in either 10% or 50% light, whether the soil was fertilized or not. Similary *Q. robur* seedlings had higher leaf areas values at 10% light than at 5%. This trend was equally true for *B. pendula* even to a greater extent.

The range of leaf area values of *Q. robur* was 1.96 - 3.06dm^2 in 30% light in a soil without fertilizer, the results from four harvests at 3 week intervals in summer of 1973.

The range for Q. robur at the same light regime, but with fertilizer added to the soil was 2.23 - 3.75dm^2, slightly higher than those from the unfertilized soil in the same light regime.

The leaf area values (range) for Q. robur in 10% was 1.18-2.05dm^2 (without fertilizer), and 1.15-1.89dm^2 (with fertilizer). Both these values are quite comparable, showing the non-significant effect of fertilizer on leaf area extension at the 10% light. These values are however lower than those obtained for Q. robur at 30% light even in a soil without fertilizer. At 5% light, the lowest values for leaf area for Q. robur were obtained 1.23 ti 1.64dm^2 (without fertilizer) and 0.91-1.69dm^2 (with fertilizer). The effects of harvesting (or aging) were not quite as apparent on the rate of leaf area extension than the effects of shade (or light).

In September (the last harvest) Q. robur at 5% light had the lowest leaf area values, leaf necrosis had started in both seedlings with fertilizer or without fertilizer in the 5% light.

The leaf area values at 30% light without fertilizer for B. pendula ranged from 0.13 to 1.06dm^2 in the unfertilized soil and 0.20 to 1.75dm^2 in the fertilized soil. This showed that the values of leaf areas from fertilized samples were generally higher than those from the unfertilized samples at all harvests.

When compared with values at 10% light, B. pendula seedlings had low values whether the soil was fertilized or not. (0.20 - 6.09dm^2) unfertilized; 0.014 - 0.29dm^2 fertilized. At 5% light, the values were even lower 0.001 - 0.005dm^2 unfertilized; 0.004 - 0.007 fertilized. The effects of fertilizer were not important in either the 10% light or 5% light.

The last two figures for *B. pendula* with fertilizer at 10% light were those of one single surviving seedling only and this should be considered with caution (See percentage survival).

The effect of time on rate of leaf area extension was only important in the 30% light for *B. pendula* and was more important in the fertilized samples, where there was a steady increase in leaf area values for three consecutive harvests i.e. up to 12 September when the effects of winter had set in. On the other hand, at 30% light, *B. pendula* seedlings did not appear to be extending their leaf areas in the unfertilized samples right from the second harvest; the leaf area values were more or less constant till the end of the experiment. 0.97 -1.01dm^2 (TableVI-13).

Relative Growth Rate

Tables VI-16 + 17 indicate the relative growth rates (proportional rates of increase in dry weight) obtained for Q. robur and B. pendula seedlings during the experiment. B. pendula had higher values than Q. robur. In both species the highest values were in the 30% light and the lowest in the 5% light; the deaths in B. pendula seedlings had already been reported.

It is clear from the tables that Q. robur with negative growth rates in the 5% light with or without fertilizer were not performing well. The relative growth rates in both species were not constant, rather they fluctuated differently with time. The relative growth rates of Q. robur in 30% light (with fertilizer) were 0.09 - 0.13gwk^{-1} were slightly higher than those in the same light regime without fertilizer. (0.02 - 0.12gwk^{-1}). Q. robur in 10% light, without fertilizer had values which decreased with time to a value of 0.05gwk^{-1} at the last harvest. The relative growth rates in the 5% light of Q. robur with or without fertilizers were generally low. The only positive values were during the first harvest, after that the values were negative in both species, the lower values were in the unfertilized samples, with rates as low as -0.09gwk^{-1}.

The B. pendula seedlings in the unfertilized soil at 30% light, first had very high growth rates 0.77gwk^{-1}, which decreased tremendously to 0.05gwk^{-1} by October, the last harvest (Table VI-17).

Table VI - 16

Observations on Q.robur seedlings grown in two oil types (No.F. without fertilizer and F with fertilizer)and in three light regimes (approx.) 30%, 10%, and 5% of total day light harvested four times I, II, III, IV, 31 July, 21 August, 12 September, 4 October, 1973, respectively

SOIL TYPE	LIGHT REGIME	UNIT LEAF RATE $gdm^{-2}wk^{-1}$			RELATIVE GROWTH RATE $gg^{-1}wk^{-1}$		
		I	II	III	I	II	III
NO FERTILIZER	30%	0.29	0.18	0.42	0.10	0.02	0.12
	10%	0.27	0.16	0.13	0.10	0.07	-0.05
	5%	0.03	-0.05	-0.07	0.02	-0.01	-0.09
FERTILIZER	30%	0.16	0.34	0.24	0.08	0.13	0.09
	10%	0.08	0.09	0.18	0.04	0.05	0.07
	5%	0.09	-0.05	-0.05	0.05	-0.03	-0.05

Table VI-17

Observations on B.pendula seedlings grown in two soil types (no F without fertilizer, F with fertilizer) and in three light regimes (approx.) 30%, 10% and 5% of total day light. There were four harvests I, II, & IV 31 July, 21 August, 12 September, 4 October, 1973 respectively.

SOIL TYPE	LIGHT REGIME	UNIT LEAF RATE $gdm^{-2}wk^{-1}$			RELATIVE GROWTH RATE $g\ g^{-1}wk^{-1}$		
		I	II	III	I	II	III
NO	30%	0.22	0.14	0.05	0.77	0.22	0.05
FERTI-	10%	0.01	0.10	0.11	0.05	0.39	0.24
LIZER	5%	-	-	-	-	-	-
	30%	0.17	0.14	0.33	0.59	0.31	0.23
FERTI-LIZER	10%	0.10	0.03*	0.17*	0.15	0.36*	0.46*
	5%	-	-	-	-	-	-

* ONE PLANT ONLY

The fertilized samples in 30% light did have rates as high as those in in the unfertilized soil during the first harvest, yet the fertilized values did not decrease as low as those of unfertilized samples. B. pendula in unfertilized soil at 10% light had a maximum rate in the middle of the experiment, whereas the fertilized samples in the same light regime had growth rates which increased with time. Again it must be noted that here it was only one plant surviving and any inference on it must be viewed with caution. Similarly there were seedling deaths in 10% light, see Table VI-3. In 5% light, the death of the samples made only one harvest possible.

Unit Leaf Rate

The unit leaf rates (the rate of dry matter increase per unit leaf area) of the Q. robur and B. pendula seedlings are presented in Tables VI-16&17. Generally Q. robur values were higher than those of B. pendula seedlings, and in B. pendula species the effects of the fertilizer seemed to have produced higher unit leaf rates in the fertilized than in the unfertilized samples especially in the 30% light. In almost all the treatments the unit leaf rates were not constant values between harvest, rather the values fluctuated somehow irregularly. In Q. robur, for instance, the range of unit leaf rates in the unfertilized samples were 0.18 – 0.42gdm^{-2}wk^{-1} in the 30% light, the lowest value was 0.18gdm^{-2}wk^{-1} obtained between August and September. The fertilized samples however had values ranging from 0.16–0.34gdm^{-2}wk^{-1} with a peak in the middle of the experiment, whereas in the unfertilized samples, the highest rates were those in the last harvest.

In 10% light *Q. robur* had unit leaf rates decreasing with every harvest and during the period September - October the values were negative $-0.13\mathrm{gdm}^{-2}\mathrm{wk}^{-1}$ (TableVI-16). On the contrary the fertilized samples in this 10% light had unit leaf rates rising with the number of harvests, to a maximum of $0.18\mathrm{gdm}^{-2}\mathrm{wk}^{-1}$ in the September - October period when the unfertilized *Q. robur* seedlings were having negative values.

In the 5% light, *Q. robur* had the lowest unit leaf rates. In the unfertilized samples, the values were rather irregular in pattern, with positive and negative values. The fertilized samples in this 5% light had rates consistently decreasing with time,

In *B. pendula* the 30% light seedlings had the highest unit leaf rates compared with seedlings in the other light treatments. The *B. pendula* samples without fertilizer in 30% light had unit leaf rates progressively decreasing from $0.22-0.05\mathrm{gdm}^{-2}\mathrm{wk}^{-1}$. The fertilized samples however had the unit leaf rates about doubling at the last harvest, when compared with the values at the beginning.

In the 10% light, the unit leaf rates of the *B. pendula* seedlings were quite comparable in the fertilized and unfertilized and unfertilized samples (TableVI-17) In the 5% light, *B. pendula*'s unit leaf rates could not be measured due to the high mortality rate.

TABLE VI-18

Observations on Q. robur seedlings grown in two soil types (No F without fertilizer and F with fertilizer) and in three light regimes (approx.) 30%, 10%, and 5% of total day light harvested four times, I, II, III, IV, 31 July, 21 August, 12 September, 4 October, 1973 respectively

SOIL TYPE	LIGHT REGIME	LEAF WEIGHT RATIO			
		I	II	III	IV
NO FERTILIZER	30%	0.25	0.17	0.13	0.12
	10%	0.23	0.17	0.16	0.12
	5%	0.20	0.18	0.18	0.15
FERTILIZER	30%	0.26	0.17	0.21	0.17
	10%	0.18	0.13	0.18	0.14
	5%	0.21	0.19	0.18	0.16

Table VI-19

Observations on B. pendula seedlings grown in two soil types (No F without fertilizer, F with fertilizer) and in three light regimes (approx.) 30%, 10% and 5% of total day light. There were four harvests I, II, III, and IV 31 July, 21 August, 12 September, 4 October, 1973 respectively

SOIL TYPE	LIGHT REGIME	LEAF WEIGHT RATIO			
		I	II	III	IV
NO FERTILIZER	30%	0.53	0.53	0.41	0.27
	10%	0.50	0.58*	0.52	0.35
	5%	0.33	-	-	-
FERTILIZER	30%	0.61	0.53	0.45	0.29
	10%	0.49	0.48	0.60	0.41
	5%	0.39	-	-	-

* Three plants only.

Specific Leaf Area

The values for the area of leaf per unit of leaf dry weight i.e. specific leaf area are shown in Tables VI-13+14. These results show that the lower the light intensity the higher the specific leaf area values, this trend was more strongly indicated in *B. pendula* than in *Q. robur* seedlings i.e. *B. pendula* specific leaf area values were generally higher than those of *Q. robur* as a result of the treatments. *Q. robur* values in 30% light without fertilizer ranged from 1.96-2.20dm^2/g^{-1}. For *B. pendula* in the same light intensity the values were 2.62-4.41dm^2 without fertilizer and 3.38-5.00dm^2/g-1 with fertilizer. The effect of the fertilizer treatment was not considered serious in either species, whatever the treatment.

In August i.e. at the second harvest *B. pendula* had the highest specific leaf area values in the experiment, these values decreased with time in all treatments with the exception of *B. pendula* seedlings in 10% light, with fertilizer. Here the values tended to rise again after a fall in September at the third harvest. This exception should however be viewed with caution as there was only one plant out of four surviving.

Leaf Weight Ratio

The leaf weight ratio values are presented in Tables . The *B. pendula* values were generally about twice as high as those of *Q. robur* seedlings in all treatments. The *B. pendula* values ranging from 0.27 to 0.61 while the *Q. robur* values were from 0.12 to 0.26 when all the treatments were compared together.

In the *Q. robur* samples, the highest leaf weight ratio values were in the 30% light with those of the fertilized samples slightly higher than the unfertilized, and these were obtained only during the first harvest 31 July TableVII8. Later the leaf weight ratio values in the other treatments were fairly comparable.

In the 30% light, *Q. robur* seedlings without fertilizer had leaf weight ratio values progressively decreasing to about half the original value at the last harvest i.e. 0.25-0.12. This patternof leaf weight distribution was not observed in *Q. robur* in the same light regime, with fertilizer. In the latter, the values kept fluctuating throughout the season, the highest values were those obtained at the early part of the experiment.

Q. robur seedlings in 10% light followed in unfertilized and fertilized soils had a patternof leaf weight ratio values similar to those in the 30% light, *Q. robur* seedlings without fertilizer had values decreasing progressively to about half the original values, but with fertilizer the values were fluctuating like those in the 30% light.

In the 5% light, (fertilized and unfertilized) the leaf weight ratio values of *Q. robur* seedlings were fairly similar. Compare these ranges 0.15 - 0.20 in unfertilized and 0.16 to 0.21 in fertilized soils.

B. pendula seedlings in 30% light had leaf weight ratios which decreased steadily to about half the original values, although the values of the fertilized seedlings were slightly higher than those without fertilizer on the same light regime.

In 10% light, *B. pendula* seedlings had leaf weight ratios fairly high (three harvests) falling slightly only at the last harvest in October.

B. pendula seedlings in 5% light, were only obtained for one harvest as death had set in on the seedlings. The values at this time were lower than those obtained from other treatments during the same period.

The effects of shade and fertilizer on Betula pendula seedlings previously grown in 100% light

Introduction and Methods

The great response of B. pendula seedlings to shading in the last experiment, easpecially the high mortality rate in 5% light showed clearly the non-tolerance of deep shading by these seedlings. The seedlings used in the previous experiment were put into the shading cubes directly after germination, thus it was not possible to determine their response had they been previously grown in 100% day light.

Consequently another experiment was planned to investigate the growth responses of B. pendula seedlings which had been growing in 100% light partly in the greenhouse and partly outdoor and then put into cubes providing 25%, 12.5%, and 2.5% total day light respectively. A batch of seedlings were left in the 100% light and harvested at the same time with other seedlings in the cubes.

The effect of fertilizer on B. pendula seedlings in the last experiment was not conclusive, partly because of the early age at which the seedlings were put into the cubes and partly because it was not possible to continue the investigation for a much longer time. Thus the seedlings were grown in two soil types one with a level of John Innes fertilizer mixed with it and the other without. Germination of the seedlings started in the greenhouse from the 8 April 1974 and were allowed to continue growing till the 23 May for about 6 weeks.

The greenhouse was made of plain glass and the actual percentage of light reaching the floor was approximately 85% of total day light; it was therefore not possible practically to provide 100% light. There was no artificial heating of the greenhouse.

The first assessment of growth was made on the 23 May at the same time of putting some seedlings into the various cubes, see table VI-20. There was a plant per pot and there were four replicates per treatment in a randomized design. There were other two harvests at two weeks interval after the shading commenced.

RESULTS

The heights and plant dry matter production values at the time of shading and two weeks of shading of B. pendula seedlings are given in Table VI-20.

The results of Table VI-20, (before shading) indicate the uniformity in the sizes of seedlings selected in this experiment. The total plant dry weight was 0.1g the leaf contributing about 60% of this, while the stem and root were of the same weights. There was no effect of fertilizer at all at this stage of the seedling growths. The height was about 5cm for most seedlings.

Growth after two weeks of shading

The effect of shading was becoming apparent after two weeks as the results in Table VI-20 indicate at 2.5% light there was no growth at all, whether in fertilized or unfertilized soils 0.9g, this harvest compared with 1.0g. before shading, this slight difference was considered to be due to sampling and not a result of treatment.

RESULTS

Table VI-20

B. pendula. seedlings grown in various light regimes, with or without fertilizer

Soil Type	Light %	Height (cm)	Total Plant Dry Weight	Leaf	Stem	Root
(a) Before shading				Mean of 4 replicantes		
				(g)		
No Fertilizer	85	5.55	0.10	0.06	0.02	0.02
Fertilizer	85	5.00	0.10	0.06	0.02	0.02
(b) 2 weeks of shading						
No Fertilizer	85	8.50	0.29	0.18	0.06	0.05
	25	10.10	0.28	0.17	0.06	0.05
	12.5	12.20	0.20	0.11	0.06	0.03
	2.5	8.50	0.09	0.05	0.02	0.02
Fertilizer	85	11.50	0.35	0.22	0.08	0.05
	25	10.50	0.31	0.19	0.07	0.05
	12.5	10.60	0.18	0.10	0.05	0.03
	2.5	8.10	0.09	0.06	0.02	0.01

For analysis of variance see Table VI - 22

The effects of shade and fertilizer on B. pendula seedlings previously grown in 100% light. Mean of four replicates

Table VI-21

4 weeks of shading

Soil Type	Light %	Leaf Area (dm^2)	Height (cm)	Total Plant Dry Weight	Leaf	Stem	Root
No Fertilizer	85	0.77	13.50	0.57	0.29	0.13	0.15
	25	0.81	15.75	0.53	0.29	0.14	0.10
	12.5	0.85	18.00	0.35	0.19	0.10	0.06
	2.5	0.34	9.87	0.10	0.06	0.03	0.01
Fertilizer	85	1.27	18.25	0.88	0.49	0.22	0.17
	25	1.35	21.87	0.77	0.43	0.21	0.13
	12.5	1.06	20.37	0.45	0.24	0.14	0.07
	2.5	0.37	9.87	0.11	0.07	0.03	0.01

For analysis of variance see Table VI - 23

TABLE VI - 22

Variance ratio values from the Analysis of Variance of B. pendula dry weights of seedlings grown in (T) 85%, 25%, 12.5% and 2.5% light with (F) or without (No F) fertilizer (2 weeks after shading)

Variables	Plant Parts			
	Total Plant	Leaf	Stem	Root
Fertilizer (F) effect	2.66 NS	5.17*	0.83 NS	0.03 NS
Treatment (T_1) (No F & F)	17.83***	11.86**	6.50**	9.66***
Treatment (T_2) (No F)	2.05 NS	21.5***	7.0**	16.49***
Treatment (T_3) (F)	26.33***	27.87***	14.50***	22.57***
(F X T_1)	1.20 NS	0.27 NS	0.66 NS	0.03 NS
Replicate (R_1) (No F & F)	0.13 NS	0.24 NS	0.50 NS	0.40 NS
Replicate (R_2) (No F)	1.33 NS	1.66 NS	1.50 NS	2.12 NS
Replicate (R_3) (F)	0.09 NS	1.49 NS	1.50 NS	1.14 NS

NS Not Significant

* Significant at 5% probability level

** Significant at 1% probability level

*** Significant at 0.1% probability level.

TABBLE VI-23

Variance Ratio values from the Analysis of Variance of <u>B. pendula</u> seedling dry weights grown in (T) 85%, 25%, 12.5% and 2.5% light with (F) or without (No F) fertilizer (4 weeks after shading)

Variables	Plant Parts				
	Total Plant	Leaf	Stem	Root	Leaf Area
Fertilizer Effect (F)	20.09^{***}	14.16^{**}	5.53^{*}	0.80 NS	10.04^{**}
Treatment (T_1) (No F & F)	57.18^{***}	30.00^{***}	11.56^{**}	21.86^{***}	10.25^{***}
Treatment (T_2) (No F)	31.66^{***}	30.00^{***}	17.50^{***}	28.8^{***}	13.50^{**}
Treatment (T_3) (F)	42.72^{***}	36.25^{***}	28.8^{***}	31.0^{***}	39.0^{***}
F X T_1	3.00 NS	2.33 NS	0.72 NS	0.13 NS	1.12 NS
Replicate (R_1) (No F & F)	0.53 NS	1.0 NS	0.59 NS	0.13 NS	0.70 NS
Replicate (R_2) (No F)	1.16 NS	1.26 NS	0.83 NS	1.0 NS	0.81 NS
Replicate (R_3)	1.25 NS	1.50 NS	3.10 NS	0.33 NS	5.5 NS

NS	Not Significant
*	Significant at 5% probability Level
**	Significant at 1% probability level
***	Significant at 0.1% probability level.

Table VI-24 The specific leaf area and Leaf Weight Ratio Values of *B. pendula* seedlings grown in various light conditions with and without fertilizer (4 weeks after shading)

Soil Type	Light %	Specific Leaf Area dm^2/g	Leaf Weight Ratio
No Fertilizer	85	2.65	0.50
	25	2.79	0.54
	12.5	4.47	0.55
	2.5	5.66	0.60
With Fertilizer	85	2.58	0.55
	25	3.13	0.55
	12.5	4.41	0.53
	2.5	5.28	0.63

The seedlings in both 85% and 25% light had fairly comparable values (0.28–0.29g without fertilizer) and 0.35–0.31g with fertilizer in total plant dry weights in 85% and 25% total light respectively. These values were about three times higher that those of two weeks earlier (TableVI-20b), and were also higher than those of seedlings grown in 12.5% light with or without fertilizer.

The values of plant dry weight for the fertilized samples in both 85% and 25% light were generally higher than those of unfertilized samples in the same light conditions. Thus at this stage, the fertilizer effect was beginning to show only in the higher light intensities of 85% and 25%. The leaf, stem and root weights followed the same pattern described for samples harvested before shading, i.e. the leaf contribution more than dry weights for these B. pendula seedlings.

All the seedlings increased in height, while those in 85% and 25% light might be considered as normal growths, those in the 12.5% and 2.5% light were abnormally tall and thin.

Growth after 4 weeks of shading

At this stage, the leaves of B. pendula seedlings in unfertilized samples in both 85% and 25% light were getting yellowish, and a few leaves had necrotic edges. This phenomenon was however not observed in the unfertilized samples growing in 12.5 and 2.5% light. The leaves of all the fertilized seedlings irrespective of light treatment remained green.

A few older leaves in the 2.5% light became necrotic but there were no deaths. It appeared the B. pendula seedlings in 12.5% light were expanding their leaves as a result of the shading; the leaf petioles were long, the leaf area values were measured to record the changes now apparent in the leaves. B. pendula seedlings in 12.5% -85% (with or without fertilizer) had greater leaf area values than those in 2.5% light and the seedlings in 12.5%-85% light with fertilizer had higher leaf area values than those in the same light regimes but without fertilizer.

The height measurements indicate a similar patternto that just described for leaf area values. The fertilized samples in 12.5%-85% light about doubled their heights in two weeks.

The results of the specific leaf area and leaf weight ratios (TableVI-24) indicate that the specific leaf area values changed due to shading, while the latter remained fairly constant irrespective of treatment. The effect of fertilizer was not apparent on the specific leaf area values.

Plant Dry Weights

The total plant dry weights (TableVI-21) indicate the overall responses of the B. pendula seedlings to shading and fertilizer conditions after 4 weeks. The results show that there was apparently no growth at all by seedlings in 2.5% light, yet there was no decrease in dry matter production either i.e. the rate of photosynthesis balanced out the rate of respiration in this low light regime.

The dry weight values for unfertilized samples in 85% and 25% light were quite comparable 0.57g and 0.53g total dry weights respectively, these values were higher than those in the other light regimes amongst unfertilized samples.

The dry weight values tended to increase with increase in percentage light available. The dry weight values for the unfertilized samples were generally lower than those of the fertilized samples with the exception of those in 2.5% light. The same patter of responses just described was also observed amongst the fertilized samples.

The total dry weights for fertilized samples in 85% light was 0.88g and for 25% light 0.77g, higher than those in the same corresponding light regimes without fertilizer. The 12.5% fertilized samples with a total dry weight of 0.45g was also higher than the value for the unfertilized samples 0.35g. Thus at this last harvest, the plant dry weights of the unfertilized seedlings in 12.5%–85% light were almost double the values two weeks earlier, while the fertilized samples in the same light more than doubled their values two weeks earlier. This phenomenon was also observed in the various plant parts as Table VI-21 indicates, the leaves again being the most responsive plant parts in this experiment, and the roots the least.

DISCUSSION

Seedling mortality and survival at 5% light

The results of this experiment confirm the views of many workers that Q. robur resists shading while B. pendula is intolerant of shade. See Salisbury (1916; Watt, 1919 Tansley, 1919; Jones, 1959 and Grime, 1966).

The results indicate that Q. robur with large fruit reserve was only able to keep on surviving at 5% light, and the suggestion is that the compensation point was about 5%. This is possible because the results show no indication of continued growth after germination by Q. robur seedlings in 5% light, on the other hand there were no mortalities during the period of this experiment. It was also likely the plant might remain alive for much longer at this 5% light intensity.

For B. pendula, it is clear that the seedlings (freshly germinated) could not survive in this 5% light condition for up to a month (see Table VI-3). B. pendula seedlings with little fruit reserves in 5% light became elongated, and collapsed suddenly in a few days.

Watt, (1919) had observed that Deschampsia flexuosa and Pteridium spp. are the agents of light reduction in an oak-birch heath vegetation. Salisbury (1916) obtained 41-49% light in the light phase, and 0.16-1.0% of total illumination in the shade phase of an Oak - Hornbeam woodland. The complete disappearance of germinated seedlings of Quercus spp. within a few years from British oakwoods has been associated with mildew attack Watt (1919).

The above observations in relation to the present investigations show that Q. robur could survive mildew attack within the period of this experiment,but might not do so if the experiments continued over a number of years. That fungi action was on in the 5% light was indicated by the high mortality rate of the B. pendula seedlings in the 5% light conditions in which Q. robur seedlings were were also growing. For B. pendula, poor growth generally was a precussor to fungal attack, in the 5% light. Fungal growth was observed on the dead seedlings. Other workers who have observed seedling mortality being associated with shade and fungal attack include Grime (1966), Hutchinson (1967) and Vaartaja (1952).

It is remarkable that the effect of fertilizer increased mortality rate among B. pendula seedlings. The fertilizer in the 5% light probably increased fungal activity and thus caused deaths of seedlings at 5% light and also had some effects on mortality at 10% light. This explains why B. pendula had a higher mortality amongst fertilized samples than in unfertilized samples. Fertilizer application requires the right balancing of the light situation. This phenomenon has also been observed by Shaw (personal communication) in relation to Q. petraea.

The survival and establishment of seedlings in a natural wood-land are different but related disciplines. For instance B. pendula could not survive at 5% light, thus there would be no chance of the seedlings being established in the course of time. Q. robur was able to survive at 5% light (at least for a growing season), but in order to establish itself on any site there must be further growth.

There was no such evidence of renewed growth by Q. robur throughout this experiment whether fertilized or not. Species able to grow at such low light intensities stand better chances of establishing themselves, rather than these two species, other conditions being equal in natural sites.

Consequently, this experiment indicates that both species would require higher light intensities than 5% for seedling establishment. Performances of both species in higher light intensities are now considered.

Seedling performances at higher light intensities

There is evidence that both Q. robur and B. pendula put on some growth at 10% light. The height and dry weight results Tables and Fig. confirm this statement. Q. robur seedlings remained dormant in 5% light, but in 10% light the buds in many seedlings were opened and growth resulted. Q. robur normally produces one or two "flushes" in a particular growing season, the 10% light was therefore favourable enough for such growth.

All plant parts of Q. robur seedlings showed growth responses in 10% light. The non-significant effect of fertilizer treatment on the Q. robur seedling groth shows that growth was still dependent on fruit reserve or the slow rate of growth at this light intensity did not cause an efficient utilization of the extra mineral resources in the soils fertilized. With B. pendula the situation was fairly similar; plant dry matter increase with time shows the seedlings were growing in this light intensity.

The fact that fertilizer effect was also non-significant at this 10% light level indicates a sub-optimum nutrient uptake condition because *B. pendula* normally has very small fruits.

It is reasonable to suggest that *Q. robur* and *B. pendula* have chances of establishing themselves in wood conditions where the light was as low as 10% of full illumination.

Q. robur seedlings in 30% light did not show any significant effect of fertilizer even in the last harvest. The soil type (Chapter V)experiment showed that *Q. robur's* dependency on acorn nutrient supply could be terminated within a growing season under green-house conditions. The soil type experiment was performed in the glass house which had an additional heating facility and higher light intensities.

In view of this, *Q. robur* probably did not respond to fertilizer treatment at 30% light, because other factors in the environment (e.g. temperature) were not quite optimum, though there is enough reason to suggest that 30% light was fair enough for this tree. Secondly this shading experiment was started later in the season, and thus had few hot days than the soil type experiment.

B. pendula seedlings performed similarly to *Q. robur* in this 30% light, except that *B. pendula* showed a significant fertilizer effect at the last harvest Table VI-5 and Fig. VI-4. Binns (1966) working on tree seedling fertilizer requirements asked for factors that could be limiting apart from soil and nutrients. This experiment suggests that an adequate light condition is a pre-requisite to an efficient fertilizer utilization especially in *B. pendula*.

Secondly, natural regeneration of *Q. robur* and *B. pendula* seedlings is also possible in shade conditions of 10% and 30%, but not likely in 5% light by either species.

The factors of seed reserves, seedling establishment and mortality, nutrient or fertilizer requirement and dormancy are among other factors relevant to the whole life cycle of a plant in a shade environment (Watt, 1919 and Grime, 1966).

The analysis of vegetative growth in response to shading is a fairly new technique for studying plant behaviour in such conditions over a growing season Coombe (1966). The growth behaviour of *Q. robur* and *B. pendula* seedlings over part of a growing season is hereby discussed.

Plant Growth Analysis

The following are summaries of the general trends expressed by the various components of relative growth rate analysed for *Q. robur* and *B. pendula* grown under various shading regimes.

Q. robur has higher leaf area values than *B. pendula* generally, yet *B. pendula* had higher values of leaf weight ratio, specific leaf area and leaf area ratio, irrespective of treatment. These differences originate from the varying natures of both species; for instance *Q. robur* produces large leaves from germination while *B. pendula* normally starts life with small leaves. Secondly, at least at this early seedling stage, *Q. robur* produces less shoot than root and *B. pendula* more shoot than root (Tables VI-7&8). Various factors are used to distinguish between "sun plants and shade" plants.

Coombe (1966) stated that shade plants are associated with high specific leaf area values and sun plants with low values. Increase in leaf area ratio (of which specific leaf area is a component) is also described as a characteristic of plants of a shady habitats Blackman and Wilson (1951 a & b). *Q. robur* seedlings in the present experiment had slightly higher specific leaf area and leaf area ratio values in plants growing in the lower light regimes. This phenomenon is even more clearly shown in the *B. pendula* seedlings, (the dead seedlings did not becloud the overall trends. (Tables VI-13,14).This is rather strange as *Q. robur* is generally thought to be more shade tolerant and *B. pendula* more light loving. Or could this be some attempt by *B. pendula* seedlings to adapt themselves to the poor light conditions? Further work (to be discussed later) was done to investigate this point. Jarvis (1964) also found the specific leaf area values of *Q. petreae* increased by shading, the leaf area ratio values were equally affected.

The unit leaf rates and relative growth rate values of *Q. robur* seedlings in the higher light regimes (with or without fertilizer) were higher than those in the lower light conditions. While the negative values in the 5% light indicate some critical situation for survival (approaching compensation point) the rising values with higher light intensities also indicate the requirements by the seedlings for normal growth. Thus marked differences between growth values in low and high intensities indicate the point that photosynthetic efficiency of the *Q. robur* seedlings could be impaired by poor light conditions. The response of relative growth rate to shading closely parallels that of the unit leaf rate for *Q. robur* as Jarvis also found for *Q. petraea*.

With *B. pendula* seedlings there was no such parallel relationship between unit leaf rate and relative growth rate as a result of shading. The unit leaf rate values in 30% light were higher than those in 10% light, (5% light seedlings were dead within a month). The fall in growth rate (at high light intensities) with increasing size of seedling was also observed in the soil type experiment (soil type IV Chapter V). This limitation of studies of seedling plants in explaining overall growth cycles has been pointed out by Hughes (1966). This is an ontogenetic drift which must be accounted for when assessment of the relative importance of different factors on the overall performance of an individual plant is being considered.

The fertilizer application was of relatively little importance to the various components of relative growth rates of the *Q. robur* seedlings. The *B. pendula* seedlings were slightly affected by the fertilizer treatments. Perhaps the most marked effects were on the unit leaf rates and relative growth rates (Tables VI-16&17). The different sizes of the fruits of the *Q.robur* and *B. pendula* seedlings had varied influences on the responses to fertilizer. The *Q. robur* acorn buffered the seedlings from immediate influence of fertilizer, especially in the sub-optimum light conditions available. The *B. pendula* seedlings were more easily influenced. The influence of fertilizer on *B. pendula* seedlings was investigated further, by using more mature seedlings.

Changing light climate and mineral uptake by *B. pendula* seedlings

The light climate in deciduous woodlands has two main phases - light (autumn to spring) and shade phase (mid-May to Autumn). Salisbury (1916)&Tansley (1919).

Salisbury stated that it is the light phase that is really critical for seedling establishment in British woodlands. Thus the previous growth of the B. pendula seedlings in 100% light before shading them is analogous to giving the seedlings two light phases. The results of this experiment indicate that if B. pendula seedlings were able to germinate and grow for a couple of days before the canopy closes in summer, they might survive the shading effect due to the reserve material accumulated within the light period.

That is, the death of the B. pendula seedlings in 5% light within a month, could have been prevented if the seedlings had been exposed to an initial period of sunlight. The situation whereby the seedlings in 2.5% light remained fairly constant in dry weight through this experiment indicates that the rate of respiration was about equal the rate of photosynthesis. Thus 2.5% light appears near the compensation point for B. pendula seedlings. Secondly the seedlings had sufficient reserve to overcome collapse due to fungal attack in the 2.5% light. However it was not thought likely that the seedlings could survive for long if kept much longer in the 2.5% light. Although the seedlings performed better with increasing light intensity, the differnce between the 25% and 85% values was not significant. Thus at 25% light B. pendula seedlings were fairly efficient in light utilization.

It is however remarkable that *B. pendula* seedlings growing in 25% light with fertilizer had better performances not only than seedlings in 25% light without fertilizer, but also those in 85% light without fertilizer. This interaction between light and fertilizer has also been recognised in cocoa *Theobroma cacao* by Murray and Nichols (1966). The theory that the light regime for optimum yield is a function of nutrition has been advanced. This supports the view of Hewitt (1966) that forest trees could respond to nutrient requirements as much as other crop species do. Secondly it also illustrates the fact that fertilizer application to forest tree seedlings needs to be balanced with an optimum light regime to preverent seedling mortality in very dark shades and to optimize nutrient uptake and thus plant growth.

It is fair to say that *Q. robur* is shade tolerant due mainly to the fruit reserve, while *B. pendula* could tolerate shade if it had the chance of previous growth in sufficient light.

CHAPTER VII

GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

The experimental results presented here indicate that at least in the early stages of seedling development, Q. robur is relatively nutrient-sufficient (Experiment I on nutrient deficiency). Q. robur would probably thrive better on phosphorus-deficient rather than nitrogen-deficient soil. Newnham and Carlisle (1969) have observed that sites in Lancashire deficient in phosphorus have been supporting oakwoods for a long time, but it must be remembered that in many situations plants occur in 'suboptimal' environmental conditions. It is also possible that soil phosphorus deficiency at present may have been caused by removal of soil phosphate into the tissues of the oak trees.

The deficiency experiment using artificial growing medium must be interpreted with caution, as the mycorrhizal roots which are generally common in natural conditions did not appear to develop in this experiment. Consequently, the behaviour of B. pendula and Q. robur seedlings in these nutrient-deficient solutions should be confirmed using either field conditions or using natural soils in the greenhouse for a better control of variables. However, the deficiency experiments indicate that due to its small sized fruits, B. pendula may fail to establish on very poor soils, especially where availability of phosphorus is very low.

Plants in nature are normally under stress from their neighbours. This stress derives from the forced sharing of the environmental resources and the resultant modification of individual physiology Harper (1967).

An attempt to study an aspect of this phenomenon was made by growing the Q. robur and B. pendula seedlings in pots of varying volumes. While this method does not estimate "population stress," it assumes that a certain minimum amount of soil volume must be available in any plant population for a normal growth of the individual to occur. The pot-size experiment results suggest that Q. robur seedlings withstand soil volume restriction more than B. pendula seedlings. The Q. robur results confirm the observations of Jones (1959) of Q. robur trees performing better in dense planting than in an open one. Secondly, there is a basis for close spacing of Q. robur trees in a plantation. In view of the sensitivity of B. pendula to restricted soil volume, dense seedling populations would not be expected to favour good tree development. This experiment also illustrates that for B. pendula seedlings, even though the soil may be good in terms of nutrient availability, over-population of seedlings might prevent efficient root system development. The small seedlings of the small pots (B.pendula) are analogous to small, thin plants often observed in a dense population of plants. This casts some doubt on the usual assumption that unbranched habit in crowded conditions is a mutual shading effect. A frequently occurring vegetational succession in Britain is a heath - birch - oak situation (Salisbury 1916 and Tansley 1919). This situation is however reversible according to the pressures acting on the ecosystem.

The behaviour of the Q. robur and B. pendula seedlings in different types of soil indicate that both species could do fairly well on various sites if other conditions were qual. These conditions include light (to be discussed later) and other aspects of the environment, not easily definable.

This experiment has been useful in identifying physiological plant responses to varied soil conditions. Iversen (1964) stated that "retrogressive succession takes place when the yearly disintegration of the plant debris no longer keeps pace with the fresh supply from the living plants, and, consequently a layer of mor (raw humus) is accumulated on top of the mineral soil." This is very common in many pine forest soils, which have to be cleared before fresh planting could take place. Rapid decomposition and nutrient release from humus may be the major cause of best growth of Q. robur, B. pendula and T. ivorensis on soil type IV Thus all the seedlings in this soil type had very high relative growth rates to start with, which declined with time. This was expected as the plants were grown in a pot with a limited supply of soil. The relatively poorer growth of the seedlings in soil types II & III indicates the more mature nature of these soils with very little litter, a mineral kind of soil. The higher relative growth rate values of the B. pendula seedlings in these soil types 2 & 3 gives an indication that other factors being normal, they have better chances of survival than the other two species. This is interesting for two reasons (i) the B. pendula fruits were the smallest to start with, yet the seedlings seem to be performing better relatively, on these poor sites; (ii) the soils were generally poor in major nutrients including nitrogen, phosphorus and potassium. Here the mycorrhizal relationship might have assisted, or some other factors not yet investigated. The death of a number of T. ivorensis seedlings on the calcareous soil was not surprising as the trees have not been observed on calcareous soils before. The poor growth of Q. robur on this calcareous soil however contradicts the observations of Jones (1959). Newnham and Carlisle (1969) found satisfactory growth of Q. robur and Q. petraea on soils over carboniferous limestone in Lancashire, but these soils may not have been calcareous in the upper layers.

Q.robur or Q. petraea were not found growing at all on soil type I where the soil was obtained. Beech was the dominant plant, with a few planted conifers. It is therefore probable that there are other factors associated with calcium abundance which allows presence or absence of Q. robur seedlings in such sites. This needs further investigations as well.

The B. pendula seedlings seemed to have overcome the calcium carbonate "shock" easily in the experiment and again it had the highest relative growth rate values when compared with other species. All the species showed leaf chlorosis. Beech trees in soil type I were observed in summer to have developed chlorosis in the upper leaves. This beech chlorosis did not appear to have had any appreciable adverse effect on the growth of the trees. Thus the B. pendula seedlings appeared to be adapting to the calcareous condition. Perhaps light is the over-riding environmental factor affecting plant distribution, especially in forest situations. (Salisbury 1930; Grime, 1965; Hughes; 1966 and Hutchinson, 1967.) High rates of seedling mortality due to shading have been observed. The shading experiment has been able to point out in relationship to Q. robur and B. pendula three aspects of the light environment (i) fate of fruits and seedlings in shade most of the time (ii) the effect of shading on seedlings which had made appreciable previous growth in full day light (iii) the interaction of light (or shade) as it affects nutrient uptake.

While no experiment was performed to determine the effect of shade on germination of these tree seedlings, the results of this experiment show clearly that B. pendula would not be able to establish itself in light about 5% of total day light. Q. robur did not grow at all in this 5% light.

Here, the fruit reserves came into play again and while Q. robur seedlings were able to survive a growing season in this shade, B. pendula without a reserve of material died within days.

The ecological importance of this is the fact that Q. robur with its fairly shade tolerant attitude might be able to persist in the forst for years until a break in the canopy or some thinning programme creates the necessary light condition for a further growth. Thus as far as shade is concerned B. pendula seemed inadequately made up to compete with other plants. It is not surprising therefore that B. pendula seedlings are usually found in freshly cleared sites or in open canopy types of woodland.

The ability of B. pendula seedlings previously grown in 100% light to withstand shading at least for a while suggests that B. pendula seedlings might take the advantage of early spring open canopy of the forest to accumulate dry matter, which sustains it during the summer months of closed canopy. It would be interesting to study the behaviour of these seedlings during the light/shade phases of the natural forest.

Finally the relationship between light and nutrient uptake has been long observed in forest conditions Wilde (1946). It seems from this work that Q. robur is not affected by this light-nutrient effect as much as B. pendula is. The non-response of Q. robur to fertilizer treatment even at 30% light is a clear example. Perhaps this might have been important if the experiment was performed for a couple of years. However the fact remains that at least in the first year of growth and in light conditions 30% or below Q. robur did not respond to fertilizer treatment.

There was very little response (in terms of better performance) by *B. pendula* seedlings grown directly in the shades. The only effect was the adverse one of the fertilizer encouraging seedling mortality through fungal attack. The *Q. robur* seedlings were able to overcome this probably as a result of the fruit reserve.

Grime (1966) described five types of habitats in temperate regions on the basis of the intensity of illumination near the ground surface, with variations within the main groups in terms of spectral quality of light experienced:- (i) Discontinuous turf on dry unproductive sites (ii) Recently cleared, moist, productive sites (iii) Closed grassland (iv) Open woodland and scrub and (v) Dense woodland and forest.

Betula spp. were observed regenerating in the recently cleared moist productive sites. Apparently the first habitat, was too dry and poor nutritionally to support birch regeneration, while (from the results of this work) the abscence of *Betula* spp. in the closed grassland was due to the dense shade present in these sites. There is need to establish the optimum range of light requirement for these species. Ovington and Macrae (1960) have observed in the field that in dense woodland, the *Quercus* spp. seedlings might persist for several years but with declining vigour. They observed that cover (shade) proved to be more effective than soil type in controlling seedling growth. This view is also supported by the results of this work.

Ovington and Macrae suggested that careful manipulation of the tree canopy would be of primary importance in promoting regeneration. While this work has shown that at about 5% light *Quercus* spp. could not grow, it is desirable to know the optimum range of light requirement of *Quercus* spp. and *Betula* spp. before this "careful manipulation" could be attempted.

There is an overwhelming evidence that tree seedlings require specific environmental conditions for their regeneration. Further study is required to clarify the light-nutrient requirements of these seedlings.

BIBLIOGRAPHY

Aldrich, D.G. and Buchanan, J.R. (1954). Phosphorus content of soils and their parent rocks in Southern California. Soil Sci. 77 : 369-376.

Allen, S.E., Grimshaw, H.M. and Holdgate, M.W. (1967). Factors affecting the availability of plant nutrients on an Antarctic Island. J. Ecol. 55 : 381-396.

Anderson, M.C. (1964a). Studies of the woodland light climate. I The photographic computation of light conditions. J. Ecol. 52 : 27-41.

Anderson, M.C., (1964b) Light relations of terrestrial plant communities and their measurement. Biol. Rev. 39 : 425-486.

Anderson, M.C., (1964c). Studies of the woodland light climate II Seasonal variation in the light climate. J. Ecol. 52 : 643-663.

Anderson, M.C., (1966). Some problems of simple characterization of the light climate in plant communities. In "Light as an ecological factor." ed. R. Bainbridge, G.C. Evans and O. Rackham pp. 77-90. Blackwell, Oxford.

Arnold, P.W., (1969). Cation equilibria and competition between ions. In "Ecological aspects of the mineral nutrition of plants" ed. I.H. Rorison pp. 115-125. Blackwell, Oxford.

Bamgbala, E.O. and A.B. Oguntala (1973). Merchantable yields and stand projection in Akure natural high forest reserve, Western Nigeria. Paper delivered at the Nigerian Forestry Conference, Zaria, 1971.

Barber, D.A. (1969). The influence of the microflora on the accumulation of ions by plants. In "Ecological aspects of the mineral nutrition of plants"ed. I.H. Rorison pp. 191-200.
Blackwell, Oxford.

Barva, D.N. (1969). Light as a factor in metabolism of the tea plant. In "Physiology of tree crops."ed. L.C. Luckwill and C.V. Cutting. pp. 307-322.
Academic Press, London.

Binns, W.O. (1966). Current fertilizer research in the (British) Forestry Commission. In "Physiology in Forestry". Forestry (Suppl.) pp. 60-69.

Blackman, G.E. and Rutter, A.J. (1947). Physiological and ecological studies in the analysis of plant environment. II The interaction between light intensity and mineral nutrient supply in the growth and development of the _Scilla_ _non-scripta_ .
Ann. Bot, N.S. _11_ : 125-158

Blackman, G.E. and Wilson, G.L. (1951b). Physiological and ecological studies in the analysis of plant environment VII. An analysis of the different effects of light intensity on the net assimilation rate, leaf area ratio and relative growth rate of different species.
Ann. Bot. N.S. _15_ : 373-408.

Blackman, G.E. and Black, J.N. (1959). Physiological and ecological studies in the analyses of plant environment XII. The role of the light factor in limiting growth. Ann. Bot. N.S. 23 : 131-145.

Bocock, K.L. and Gilbert, O.J.W. (1957). The disapperance of leaf litter under different woodland conditions. Plant and Soil 9 (2) : 179-185.

Bould, C. (1969). The nutrition of fruit trees. In "Physiology of tree crops." ed. L.C. Luckwill and C.V. Cutting. pp. 223-234. Academic Press, London.

Bouma, D. and Dowling, E.J. (1962). The physiological assessment of the nutrient status of plants. I Preliminary experiments with phosphorus. Aust. J. Agric. Res. 13 : 791-800.

Bradshaw, A.D. (1969). An ecologist's viewpoint. In "Ecological aspects of the mineral nutrition of plants." ed. I.H. Rorison. pp. 415-427. Blackwell, Oxford.

British Forestry Commission, (1972). Research Report H.M.S.O., London.

Broeshart, H., Ferwerda and Kovachick W.G., (1957). Mineral deficiency symptoms of the oil palms. Plant and Soil VIII : 289-300.

Brown, A.H.F., Carlisle, A., and White, E.J. (1966). Some aspects of the nutrition of Scots pine on peat. In "Physiology in Forestry." Forestry (Suppl.) pp. 78-87.

Brown, I. C. (1943). A rapid method of determining exchangeable hydrogen and total exchangeable bases of soils.
Soil Sci. 56 : 353-357.

Bunt, A,C. and Kulwiec, Z.J., (1970). The effect of container porosity on root environment and plant growth. I Temperature.
Plant and Soil 32 : 65-80.

Burnett, J. H., (ed.) (1964). "The vegetation of Scotland".
Oliver and Boyd, Edinburgh.

Büsgen, M., Münch, E., and Thomson, T. (1929). "The structure and life of forest trees."
Chapman and Hall, London.

Carlisle, A., Brown, A.H.F., and White, E.J., (1967). The nutrient content of the tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland.
J. Ecol. 55 : 615-627.

Chapman, S.B., (1967). Nutrient budgets for a dry heath ecosystem in the south of England.
J. Ecol. 55 : 677-689.

Clapham, A.R., Tutin, T.G., and Warburg, E.F. (1962). Flora of the British Isles.
University Press, Cambridge.

Clapham, A.R. (1968). 'Introduction'. In "Ecological aspects of the mineral notrition of plants"ed. I.H. Rorison.
pp. XV - XXl.
Blackwell, Oxford.

Clarkson, D. T. (1969). Metabolic aspects of aluminium toxicity and some possible mechanisms for resistance. In "Ecological aspects of the mineral nutrition of plant" ed. I. H. Rorison pp. 381-397. Blackwell, Oxford.

Clymo, R. S. (1962). An experimental approach to part of the calcicole problem. J. Ecol. 50 : 707-731

Cochran, W. G. and Cox, G. M. (1957). "Experimental Designs". 2nd (Ed) New York.

Conway, E. J., (1947). Microdiffusion analysis and volumetric error 2nd (Ed.) Crosby Lockwood, London.

Coombe, D. E. (1960). An analysis of plant growth of *Trema guineesis* J. Ecol. 48 : 219-231

Coombe, D. E., and Hadfield W. (1962). An analysis of the growth of *Musanga cecropoides*. J. Ecol. 50 : 221-234.

Coombe, D. E., (1966). The seasonal light climate and plant growth in a Cambridgeshire wood. In "Light as an ecological factor" ed. R. Bainbridge, G.C. Evans and O. Rackam. Blackwell, Oxford.

Cousens, J. E. (1972). Notes on the status of sessile and pedunculate oaks in Scotland and their identification. Scot. For. 16 (3): 170-177.

Cox. D. R., (1958). Planning of experiments.
Chapman and Hall, London.

Cunningham, R. K., Smith, R. W., and Hurd, R. G. (1961). A cocoa shade and manurial experiment at the West African Cocoa Research Institute, Ghana.
J. Hort. Sci. 36 : 116-125.

Dijkshoorn, W. (1969). The relation of growth to the chief ionic constituents of the plant. In "Ecological aspects of the mineral nutrition of plants." ed. I. H. Rorison.
pp. 201-213.
Blackwell, Oxford.

Dimbleby, G. W. (1952). The root sap of birch on a podzol.
Plant and Soil 4 : 141-153.

Dimbleby, G. W. (1952). Soil regeneration on the North East Yorkshire moors.
J. Ecol. 40 : 331-341.

Dimbleby, G. W. (1953). Natural regeneration of pine and birch on the heather moors of North East Yorkshire.
Forestry 24 (1) : 41-53.

Eavis, B. W., (1972). Soil physical conditions affecting seedling root growth. I Mechanical impedance, aeration and moisture availability as influenced by bulk density and moisture levels in a sand loam soil.
Plant and Soil 36 : 613-622.

Eldin, H.L., (1963). A modern "Sylva" or A discourse of forest trees 4. oak.
Quart. J. For. 57 (1): 20-28

Evans, G.C., (1939). Ecological studies on the Rain Forest of Southern Nigeria. II. The atmospheric environmental conditions.
J. Ecol. 27 : 436-482.

Evans, G.C. (1956). An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks.
J. Ecol. 44 : 391-428.

Evans, G.C. (1966). Model and measurement in the study of woodland light climates. In "Light as an ecological factor" ed. R. Bainbridge, G.C. Evans and O. Rackam.
pp. 53-76
Blackwell, Oxford.

Evans, G.C. (1972). The quantitative analysis of plant growth Vol.1.
Blackwell, Oxford.

Evans, L.T. (1963). Extrapolation from controlled environments to the field. In "Environmental control of plant growth" ed. L.T. Evans. pp. 421-435.
Canberra.

Fairbairn, W.A. (1954). Preliminary light-intensity study under sessile and pedunculate oak.
Forestry 27 (1) : 1-6.

Ferry, B.W. (1973). Personal communication.

Fields, M., King, P.S.T., Richardson, J. P., and Swindale, L.D. (1951). Estimation of exchangeable cations in soils with the Beckman flame spectrophotometer.
Soil Sci. 72 : 219-232.

Fisher, R. A. and Yates, F. (1963). Statistical tables for biological, agricultural and medical research.
Oliver and Boyd, London.

Ferwerda, J. D. (1961). Growth, production and leaf composition of the African oil palm as affected by nutritional deficiencies. In "plant analysis and fertilizer problems." ed. W. Reuther. pp. 148-158.
Washington, D. C.

Fisher, R. A. (1920). Some remarks on the methods formulated in a recent article on the quantitative analysis of plant growth.
Ann. appl. Biol. 7 : 367-372.

Fowells, H. A. and Krauss, R. W. (1959). The inorganic nutrition of loblolly pine and Virginia pine with special reference to nitrogen and phosphorus.
Forest Sci. 5 : 95-112.

Fraser, A. I. (1966). Current (British) Forestry Commission root investigations. In "Physiology in Forestry".
Forestry (Suppl.) pp. 88-97.

Gardiner, A. S. (1968). The reputation of birch for soil improvement: a literature review. (British) Forestry Commission Research and Development Paper No. 67.

Goodall, D. W., and Gregory, F. G. (1947). Chemical composition of plants as an index of their nutritional status. Tech. Comm. Imp. Bur. Hort. Plantn.Crops No.17.

Goodman, P. J. (1969). Intra-specific variation in mineral nutrition of plants from different habitats. In "Ecological aspects of the mineral nutrition of plants." ed. I. H. Rorison. pp. 237-253. Blackwell, Oxford.

Grime, J. P. (1966). Shade avoidance and shade tolerance in flowering plants. In "Light as an ecological factor" ed. R. Bainbridge, G.C. Evans, and O. Rackam. pp. 187-207. Blackwell, Oxford.

Grime, J. P. and Hudgson, J.G. (1969). An investigation of the ecological significance of lime chlorosis by means of large-scale comparative experiments. In "Ecological aspects of the mineral nutrition of plants" ed. I.H. Rorison. pp. 67-69. Blackwell, Oxford.

Grime, J. P. and Hutchinson, T. C. (1967). The incidence of lime-chlorosis in the natural vegetation of England. J. Ecol. 55 : 557-566.

Grime, J. P. and Jeffrey, D. W. (1965). Seedling establishment in vertical gradients of sunlight. J. Ecol. 53 : 621-642.

Grunes, D. L., Haas, H. J., Shih, S. H.(1955). Effect of oflong term dry land cropping on available phosphorus of cheyene fin saudy loam.
Soil Sci. **30** : 127-138,

Hackett, C. (1964). Ecological aspects of the nutrition of *Deschampsia flexuosa* (L.) Trin. II. The effects of Al, Ca, Fe, K, Mn, N, P and pH on the growth of seedlings and established plants.
J. Ecol. **53** : 159-167.

Hackett, C. (1967). Ecological aspects of the nutrition of *Deschampsia flexuosa* (L.) Trin. III.
Investigation of phosphorus requirements and response to aluminium in water culture, and a study of growth in soil.
J. Ecol. **55** : 831-840.

Harris, G.P. (1971). The ecology of corticholous lichens. I The zonation of oak and birch in South Devon. II. The relationship between physiology and the environment.
J. Ecol. **59** (2) : 431-452.

Harley, J. L. (1969). 'A physiologist's viewpoint'. In "Ecological aspects of the mineral nutrition of plants." ed. I.H. Rorison.
pp. 437-447.
Blackwell, Oxford.

Harper, J. L. (1967). A Darwinian approach to plant ecology.
J. Ecol. **55** : 247-271.

Harper, J.L., Williams, J.T. and Sagar, G.R. (1965). The behaviour of seeds in the soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed.
J. Ecol. 53 : 273-286.

Heald, W.R. (1965). 'Calcium and magnesium'. In "Methods of Soil Analysis" ed. C.A. Black, D.D. Evans, White, J.L., Ensminger, L.E. and Clark, F.E. pp. 999-1058.
Amer. Soc, Agron. Inc. Publi., Wisconsin.

Hesse, P.R. (1971). A text-book of soil chemical analysis.
John Murray, London.

Hewitt, E.J. (1952). Sand and water culture methods used in the study of plant nutrition.
Tech. Commun. Commonw. Bur. Hort.
Plantn Crops. No 22.

Hewitt, E.J. (1966). The use of sand and culture methods in the study of plant nutrition 2nd Edn.
Tech. Commun. Common. Bur. Hort.
Plantn. Crops. No. 22.

Hewitt, E.J. (1966). A physiological approach to the study of forest nutrition. In "Physiology in forestry."
Forestry (suppl.) pp. 49-59.

Hoyle, M.C. (1971). Effects of the chemical environment on yellow-birch root development and top growth.
Plant and Soil 35 : 623-633.

Hughes, A.P. (1966). The importance of light compared with other factors affecting plant growth. In "Light as an ecological factor". ed. R. Bainbridge, G.C. Evans and O. Rackam. pp. 121-146.
Blackwell, Oxford.

Hutchinson, T.C. (1967). Comparative studies of the ability of species to withstand prolonged periods of darkness.
J. Ecol. 55 : 291-299.

Ingestad, T. (1957). Studies on the nutrition of forest tree seedlings. I Mineral nutrition of birch.
Physiologia Pl. 10 : 418-439.

Ingestad, T. (1959). Studies on the nutrition of forest tree seedlings. II Mineral nutrition of spruce.
Physiologia PL. 12 : 568-593.

Ingestad, T. (1960). Studies on the nutrition of forest tree seedlings. III. Mineral nutrition of pine.
Physiologia PL. 13 : 513-533.

Iversen, J. (1964). Retrogressive vegetational succession in the post-glacial.
J. Ecol. 52 (Suppl.) : 59-70.

Jackson, M.L. (1958). Soil Chemical Analysis
Constable, London.

Jarvis, P.G. (1963). The effects of acorn size and provenance on the growth of seedlings of sessile oak.
Quart. Journal of For. 57 : 11-28.

Jarvis, P.G. (1964). The adaptability to light intensity of seedlings of Quercus petraea (Matt.) Liebl.
J. Ecol. 52 : 545-571.

Jarvis, G.D. and Jarvis, M.S. (1964). Growth rates of woody plants.
Physiol. Plant. 17 : 654-666.

Jefferies, R.L., Laycock, P., Stewart, G.R. and Sims, A.P. (1969). The properties of mechanisms involved in the uptake and utilization of calcium and potassium by plants in relation to an understanding of plant distribution. In "Ecological aspects of the mineral nutrition of plants." ed. I.H. Rorison.
Blackwell, Oxford.

Jefferies, R.L. and Willis, A.J. (1964). Studies on the calcicole-calcifuge habit. I. Methods of analysis of soil and plant tissues and some results of investigations on four species.
J. Ecol. 52 : 121-138.

Jenny, H., Gessel, S.P. and Bingham, F. T. (1949). Comparative study of decomposition rates of organic matter in temperate and tropical regions.
Soil Sci. 68 : 419-432.

Jones, E.W. (1959). Biological flora of the British Isles. Quercus L.
J. Ecol. 47 : 169-222.

Jones, J. P. (1929). Deficiency of magnesium, the cause of chlorosis in corn.
J. Agric. Res. 39 : 873-892.

Kinnaird, J. W. (1970). Birch regeneration in relation to site characteristics.
Nature Conservancy Research in Scotland Report for 1968-70.

Kinnaird, J.W. (1974). Effect of site conditions on the regeneration of birch *Betula pendula* Roth. and *B. pubescens* Erh..
J. Ecol. 62 : 467-472.

Kinnaird, J. W. and Kemp, E. (1970). Effect of shade on the growth of birch.
Nature Conservancy Research in Scotland Report for 1968-70.

Kramer, P.J. and Kozlowski, T.T. (1960). Physiology of trees.
McGraw - Hill, New York.

Lamb, A.F.A. and Ntima, O.O. (1971). Fast growing timber species of the lowland tropics. *Terminalia ivorensis*.
Commonwealth Forestry Institute, Oxford.

Larsen, S. and Sutton, C.D. (1963). The influence of soil volume on the absorption of soil phosphorus by plants and on determination of labile phosphorus.
Plant and Soil *18* : 77-84.

Leyton, L. (1957). The relationship between the growth and mineral composition of the foliage of Japanese larch. II Evidence from manurial trials.
Plant and Soil *9* : 31-48.

Loach, K. (1966). Relations between soil nutrients and vegetation in wet-heaths. I Soil nutrient content and moisture conditions.
J. Ecol. 54 : 597-608

Longmans, K.A. (1973). Personal communication.

Lowe, R.G. (1973). Personal communication.

Lowe, R.G. (1973). Plots in managed plantation crops in the high forest zone of Nigeria. Research paper (Forest series) Fed. Dept. of For. Res., Nigeria Bulletin No.17.

Lundegardh, H. (1931). Klima und Boden in ihrer wirkung auf das pflanzenleben. "Environment and Plant Development."
Translated by E. Ashby.
Arnold, London.

Magnitski, K.P. (1961). The diagnosis of mineral nutrition of plants according to chemical composition of leaves.
In "Plant analysis and fertilizer problems." ed. W. Reuther.
pp. 159-179.
Institute of Biological Science
Washington 6. D.C.

Martin, J. P., Harding, R.B. and Murphy, W.S. (1953). Effects of various soil exchangeable cation ratios on growth and chemical composition of citrus plants.
Soil. Sci. 76 : 285-295.

Mattson, S. and Wiklander, L. (1939). The laws of soil colloidal behavious.
Soil Sci. 49 : 109-152.

Meyer, B.S. and Anderson, D.B. (1952).
Plant Physiology (2nd Ed.)
D. Van Nostrand, Toronto.

Milles, J. (1972). Experimental establishment of seedlings on Southern English heath.
J. Ecol. 60 : 225-234.

Milles, J. (1973). Early mortality and survival of self sown seedlings in Glenfeshire. Invernesshire.
J. Ecol. 61 : 399-412

Miller, G.R., Nicholson, I.A. and McCowan, D. (1970). Grazing and the regeneration of shrubs and trees. Nature Conservancy Research in Scotland.
Report for 1968-70.
pp. 33-35.

Murray, D.B. and Nichols, R. (1966). Light, shade and growth in some tropical plants. In "light as an ecological factor." ed. R. Bainbridge, G.C. Evans and O. Rackam.
pp. 249-263.
Blackwell, Oxford.

McVean, D.N. (1964). Woodland and Scrub. In "The vegetation of Scotland". ed. J.H. Burnett.
Oliver and Boyd, Scotland.

McVean, D.N. and Ratcliffe, D.A. (1962). Monographs of the Nature Conservancy No.1.
H.M.S.O., London.

Newnham, R.M. and Carlisle, A. (1969). The nitrogen and phosphorus nutrition of seedlings of Quercus robur L. and Q. petraea (Mattuschka) Liebl.
J. Ecol. 57 : 271-284.

Newbould, P.J. (1967). Methods for estimating the primary production of forests.
Blackwell, Oxford.

Newbould, P.J. (1969). The absorption of nutrients by plants from different zones in the soil. In "Ecological aspects of the mineral nutrition of plants". ed. I.H. Rorison. pp. 177-190.
Blackwell, Oxford.

Njoku, E. (1960). An analysis of plant growth in some West African species. II. The effect of shading.
JL. W. Afr. Sci. Ass. 6 : 1-17.

Oguntala, A.B. (1973). Classification of canopy, stem, crown status and climber infestation in natural forest.
Fed. Dept. of For. Res. Nigeria.
Bulletin No. 14.

Okali, D.U.U. (1971). Rates of dry matter production in some tropical forest tree seedlings.
Ann. Bot. 35 : 87-97.

Okali, D.U.U. (1972). Growth rates of some West African forest-tree seedlings in shade.
Ann. Bot. 36 : 953-959.

Olsen, S.R., Cole, C.V., Watanable, F.S. and Dean, L.A. (1954).
Estimation of available phosphorus in soils by
extraction with sodium bicarbonate.
U.S. Dept. Agr. Circ. 939.

Olsen, S.R., Watanable, F.S. and Cole, C.V. (1960). Soil properties
affecting the solubility of calcium phosphates.
Soil Sci. 90 : 44-50.

Ovington, J.D. and Macrae, (1960). The growth of seedling of
Quercus petraea.
J. Ecol. 48 : 549-555.

Ovington, J.D. and Madgwick, H.A. (1959). The growth and composition of
natural stands of birch. 1.
Dry matter production.
Plant and Soil 10 : 271-283.

Ovington, J.D. and Madgwick, H.A. (1959). The growth and composition
of natural stands of birch. 2.
The uptake of mineral nutrients.
Plant and Soil 10 : 389-400.

Peterken, G.F. and Llyod, P.S. (1967).
Biological flora of the British Isles.
Ilex aquifolium L.
J. Ecol. 55 : 841-858.

Penistan, M. J. (1974). Growing oak. In The British Oak. ed. M.G.
Morris, F.H. Perring.
pp. 98-112.
Classey, Faringdon, Berkshire.

Pigott, C.D. and Taylor, K. (1964). The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. J. Ecol. 50 (Suppl.) : 175-185.

Piper, C.S. (1943). Soil and Plant Analysis. University of Adelaide.

Phares, R.E. (1971). Growth of Red Oak. *Q. rubra* L. seedlings in relation to light and nutrients. Ecology 52 : 669-672.

Reed, J. F. and Cummings, R.W. (1945). Soil reaction - Glass electrode and colorimetric methods for determining pH values of soils. Soil Sci. 59 : 97-104.

Richards, P.W. (1952). The tropical rain forest. Cambridge University Press.

Richards, B.N. (1968). Effect of soil fertility on the distribution of plant communities as shown by pot cultures and field trials. Commonwealth For. Rev. 47 : 200-223.

Robinson, R.L. (1927). Mortality among oak. Quart, J. For. 21 : 25-27.

Rorison, I.H. (1960b). Some experimental aspects of the calcicole-calcifuge problem. II. The effects of mineral nutrition on seedling growth in solution culture. J. Ecol. 48 : 679-688.

Rorison, I.H. (1967). A seedling bioassay on some soils in the Sheffield area.
J. Ecol. 55 : 725-741.

Rorison, I.H. (1968). Ecological inferences from laboratory experiments on mineral nutrition. In "Ecological aspects of the mineral nutrition of plants." ed. I.H. Rorison.
Blackwell, Oxford.

Russel, W. W. (1969). A soil scientists' view point. In "Ecological aspects of the mineral nutrition of plants". ed. I.H. Rorison.
Blackwell, Oxford.

Rutter, A.J. (1957). Studies in the growth of young plants of Pinus sylvestris L. I. The annual cycle of assimilation and growth.
Ann. Bot. 21 : 399-426.

Sagar, G.R. and Harper, J.L. (1961). Controlled interference with natural populations of Plantago lanceolata, P. major and P. media
Weed Research 1 : 163-176.

Salisbury, E.J. (1916). The Oak-Hornbeam woods of Hertifordshire. Parts I & II.
J. Ecol. 4 : 83-117.

Schollenberger, C.J. and Simon, R.H. (1945). Determination of exchangeable capacity and exchangeable bases in soil. - Ammonium acetate method.
Soil. Sci. 59 : 13-24.

Shaw, M.W. (1968). Factors affecting the natural regeneration of sessile oak Quercus petraea in North Wales. I. Preliminary study of acorn production, viability and losses.
J. Ecol. 56 : 565-583.

Shaw, M.W. (1968). Factors affecting the natural regeneration of sessile oak. Q. petraea in North Wales. II. Acorn losses and germination under field conditions.
J. Ecol. 56 : 647-660.

Shaw, M.W. (1974). Personal communication.

Sheik, K.H. (1969). The effects of composition and nutrition on the inter-relations of some wet-heath plants.
J. Ecol. 57 : 87-99.

Spurr, S.H. and Barnes, B.V. (1973). Forest Ecology. (2nd Ed.)
Ronald Press, New York.

Steward, F.C. (ed.) (1963). Plant Physiology Vol. III.
Academic Press, New York.

Steward, F.C. (1965). Plant Physiology Vol. IVA.
Academic Press, New York.

Streeter, D. T. (1974). Ecological aspects of oak woodland conservation. In "The British Oak". ed. M.G. Morris and F.H. Perring. pp. 341-354.
Classey, Faringdon, Berkshire.

Sutcliffe, J. F. (1962). Mineral salts absorption in plants. Pergamon Press, Oxford.

Tansley, A.G. (1939). The British Isles and their vegetation. Cambridge University Press.

Tansley, A.G. (1944). Ecological principles involved in the practice of forestry. J. Ecol. 32 : 83-115.

Tansley, A. G. (1949). The British Isles.and their vegetation Vol. 1 and 2. Cambridge University Press.

Thiman, K. V. (ed.) (1958). The physiology of forest trees. Ronald Press, New York.

Toth, S.J. and Prince, A.L. (1949). Estimation of cation, exchange capacity and exchangeable Ca, K and Na contents of soils by flame photometer techniques. Soil Sci. 67 : 439-445.

U.K. Nature Conservancy (1958). Tree growth, forest productivity and soil type. Rep. Nat. Conservancy, London, 1957/58. pp. 65-67.

Vaartaja, O. (1952). Forest humus quality and light conditions as factors influencing damping-off. Phytopathology 42 : 501-506.

Vaartaja, O. (1962). The relationship of fungi to survival of shaded tree seedlings. Ecology, 43 : 547-549.

Wadsworth, R.M. and Lawton, J.R.S. (1968). The effect of light intensity on the growth of seedlings of some tropical tree species.
JL. W. Afr. Sci. Ass. 13 L 211-214.

Wallace, T. (1943). The diagnosis of mineral deficiencies in plants. A colour atlas and guide.
H.M.S.O., London.

Wareing, P.F. (1966). The physiologist's approach to tree growth. In "Physiology in Forestry."
Forestry (Suppl.). pp. 7-18.

Warnaars, B.C. and Eavis, B.W. (1972). Soil physical conditions affecting seedling root growth. II. Mechanical impedance, aeration and moisture availability as influenced by grain-size distribution and moisture content in silica sands.
Plant and Soil 36 : 623-634.

Watt, A.S. (1919). On the causes of failure of natural regeneration in British Oak-woods.
J. Ecol. 7 : 173-203.

Watt, A.S. (1923). On the ecology of British beechwoods with special reference to their regeneration. Part 1.
The causes of failure of natural regeneration of the beech (Fagus silvatica L)
J. Ecol. 11 : 1-48.

Watt, A.S. and Fraser, G.K. (1933). Tree roots and the field layer. J. Ecol. 21 : 404-414.

Whittaker, R.H., and Woodwell, G.M. (1969). Structure, production and diversity of the oak-pine forest at Brookhaven, New York. J. Ecol. 57 : 155-174.

Wilde, S. A. (1946). Forest soils and forest growth. Chronica Botanica, Waltham, Mass.

Williams, R.F. (1946). The physiology of plant growth with special reference to the concept of net assimilation rate. Ann. Bot. 10 : 41-72.