PHYSIOLOGICAL STUDIES OF SPROUTING OF TEAK (*Tectona grandis* Linn. f.) PLANTING STUMPS

by

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ORIGINALITY OF THESIS

Except where specific acknowledgement is given, this thesis describes the author's own work.

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ABSTRACT

Stump planting is the commonly practised method in teak plantation establishment. In this method the teak seedling is raised for up to 2 years in a nursery to produce a straight and unbranched tap-root. At planting time, the seedling is lifted and the planting stump prepared by cutting off the shoot and lateral roots, leaving only the main tap-root attached to 3- to 5-cm of the lower stem. The early productivity of teak plantations is, therefore, dependent largely on the potential of the stump to sprout and to regenerate new lateral roots. In this study an investigation has been made of the way environmental and physiological factors influence the sprouting potential of the teak stump. A better understanding of the sprouting phenomenon, and of factors influencing the sprouting potential could be useful in modifying techniques for teak stump planting and increasing the early productivity of plantations.

The thesis is in three main parts, a general background to teak and theories dealing with the sprouting mechanism of plants, field studies of stump planting, and controlled environment studies to help interpret the field observations.

In the first part all available information is summarised dealing with the natural occurrence and phenological development of teak and its artificial regeneration by stump planting. Physiological mechanisms controlling stump sprouting are reviewed.

In a series of field studies carried out in Thailand the effects of the following factors on the survival of the teak stump and the growth rate of stump sprouts are examined : the time of lifting and stumping (or the stage of phenological development at time of lifting), the planting site condition and site and tending treatments, storage of stumps, and time of planting. It is shown that stumps lifted between mid-January and mid-April (the period when the seedlings are at full dormancy or the early bud-break stage) have a relatively higher sprouting potential than those lifted earlier or later than this optimum lifting time. Furthermore, it is shown that the optimum time for planting teak follows the end of the hot-dry season (late April) and the end of May. Since the optimum time for lifting and stumping teak does not coincide with the optimum time for planting, storage of stumps with high sprouting potential is neccessary. Studies on stump storage show that teak stump can be kept safely for as long as 9 months in a dry underground store. The most appropriate storage medium and method of storage of the teak stumps are examined.

Based on the field results, a series of controlled environment studies was carried out to determine the physiological basis for the success of early lifting and stump storage. The effects of temperature and soil moisture regime on the growth and development of the teak seedling, and physiological processes contributing to enhanced sprouting potential are examined. These include photosynthesis, respiration, translocation of photosynthates and the accumulation of photosynthates in the tap-root of the seedling. The teak seedling is very sensitive to the cool temperature and soil moisture stress. Growth of the seedling is markedly restricted where the growing temperature is reduced from warm (30/25° C day/night temperature) to a relatively cool (18/13° C) temperature. Likewise, growth is markedly reduced where the supply of soil water is maintained at or below 40 percent of the difference between the field capacity and the wilting point of the soil. However, neither cool temperature nor severe soil moisture stress reduced the sprouting potential of the teak seedling following stump-replanting. Studies on physiological processes in the teak seedling suggest that cool temperature and possibly drought stress promote the sprouting potential primarily through enhanced translocation of photosynthates and mobilization of the stored starch to labile sugars in the tap-root of the seedling prior to stumping. Plant growth subsances have also been found to play a significant role in controlling the sprouting of teak planting stumps.

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CHAPTER 1

INTRODUCTION

1.1 NATURAL OCCURRENCE AND GROWTH HABITAT OF TEAK (*Tectona grandis* L.)

Teak is one of the most important timber tree species of the tropics. The species occurs naturally only in the Indian Peninsula, Burma, Northern Thailand and Northwestern Laos; and has a distribution from the longitudes of 73°E to 104°30'E (Troup, 1921; Mahaphol, 1954). The northern boundary limit of teak is about 25°30'N lat., that is some distance outside the tropics; while its southern boundary limit lies from 9°N lat. in India through 15–16°N lat. in Burma to 16°30'N lat. in Northeastern Thailand (Figure 1.1) (Troup, 1921; Mahaphol, 1954; Kermode, 1957). There is some doubt whether teak in Java and in the small islands of the Indonesian Archipelago, such as Moena and Boetueng, is an indigenous or introduced species. According to Altona (1922a, 1922b), the species in these areas was introduced from India by the Hindus sometime from the 14th to 16th century.

1.1.1 Climatic Requirements

Teak can grow over a wide range of climatic conditions, from dry localities with annual rainfalls lower than 760 mm (e.g. in some parts of Madras and Bombay in India) to very moist localities with annual rainfalls higher than 3,800 mm (e.g. on the west coast of India where the annual rainfall is 5,080 mm)

(Troup, 1921; Haig, Hubermann and Aung Din, 1958). This species also occurs under a wide range of temperatures, for example, an extreme low temperature of 1.7°C (during the cold season) and an extreme high temperature of 47.8°C (during the hot season) (Anon., 1958; Haig et al, 1958). Actually, teak grows best and reaches its largest dimensions in a warm-moist tropical climate with rainfall ranging from 1,270 to 3,800 mm per annum, absolute minimum and maximum temperatures of 13° and 40°C respectively and a marked dry season of 3-5 months (Troup, 1921; Kermode, 1957; Haig et al, 1958; Champion and Seth, 1968). The climatic conditions in the natural range of teak are mainly influenced by the two local winds: the southwest monsoon and the northeast monsoon (Sternstein, 1962; Kermode, 1964; Champion and Seth, 1968). In Thailand, for example, the climatic classification is based on reversal of the monsoon winds into four seasons as follows:

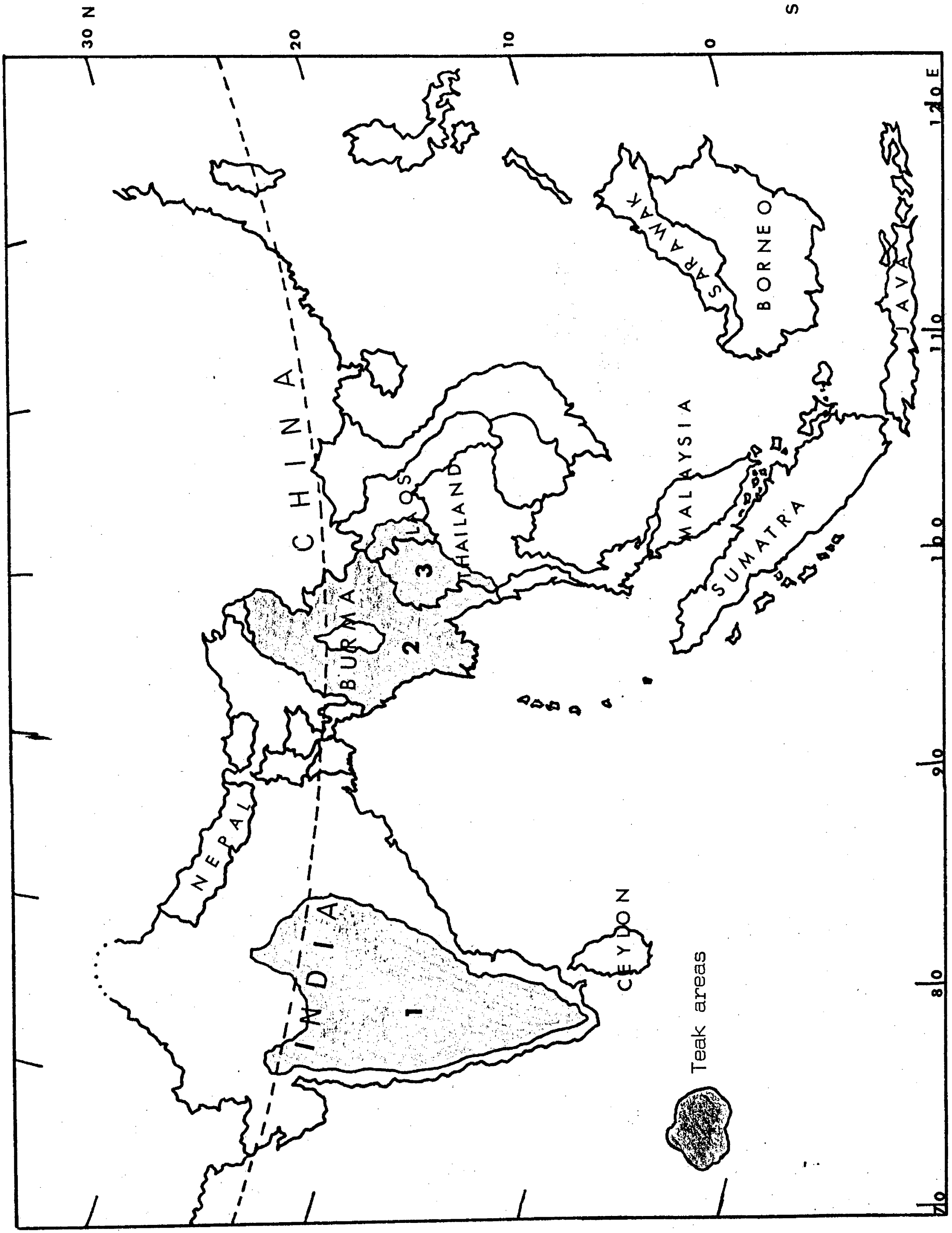
1. the pre-monsoon season (the hot season), from March to April;
2. the southwest monsoon season (the rainy season), from mid-May to mid-September;
3. the post monsoon season (characterized by changeable weather), during October; and
4. the northeast monsoon season (the cold season) from November to February (Sternstein, 1962).

The climatic conditions of the teak zone in Thailand are summarized on the basis of mean monthly maximum and minimum temperatures in Figure 1.2, monthly rainfall in Figure 1.3, isohyets and absolute maximum and minimum temperatures in Figure 1.4, and the range of climatic conditions throughout the teak zone in Table 1.1.

TABLE 1.1 The range of climatic conditions in the teak zone in Thailand. (Data represents the average of records from 1951 to 1970).

Climatic conditions	Locality	
	Min.	Max.
Annual rainfall (cm)	100.0	178.0
Mean temperature (°C)	25.0	28.0
Annual potential evaporation (cm)	143.0	215.0
Moisture index (P/T ratio)	36.0 (dry)	72.0 (wet)
Extreme max. temp. (°C)	41.0	44.0
Extreme min. temp. (°C)	2.0	7.0
Mean temp. during the wet period (May - Oct.) (°C)	27.0	29.0
Mean temp. during the dry period (°C) (Nov. - April or cold - hot seasons)	23.0	27.0

Source: Chunkao *et al* (1972): Meteological and Hydrological Summary of the 16 Northern Provinces of Thailand.



<u>FIGURE 1.1</u> Natural distribution of teak (<u>Tectona grandis</u> L.)

Source: 1. After Puri (1960)
2. After KoKo Gyi (1972)
3. After Mahaphol (1958)

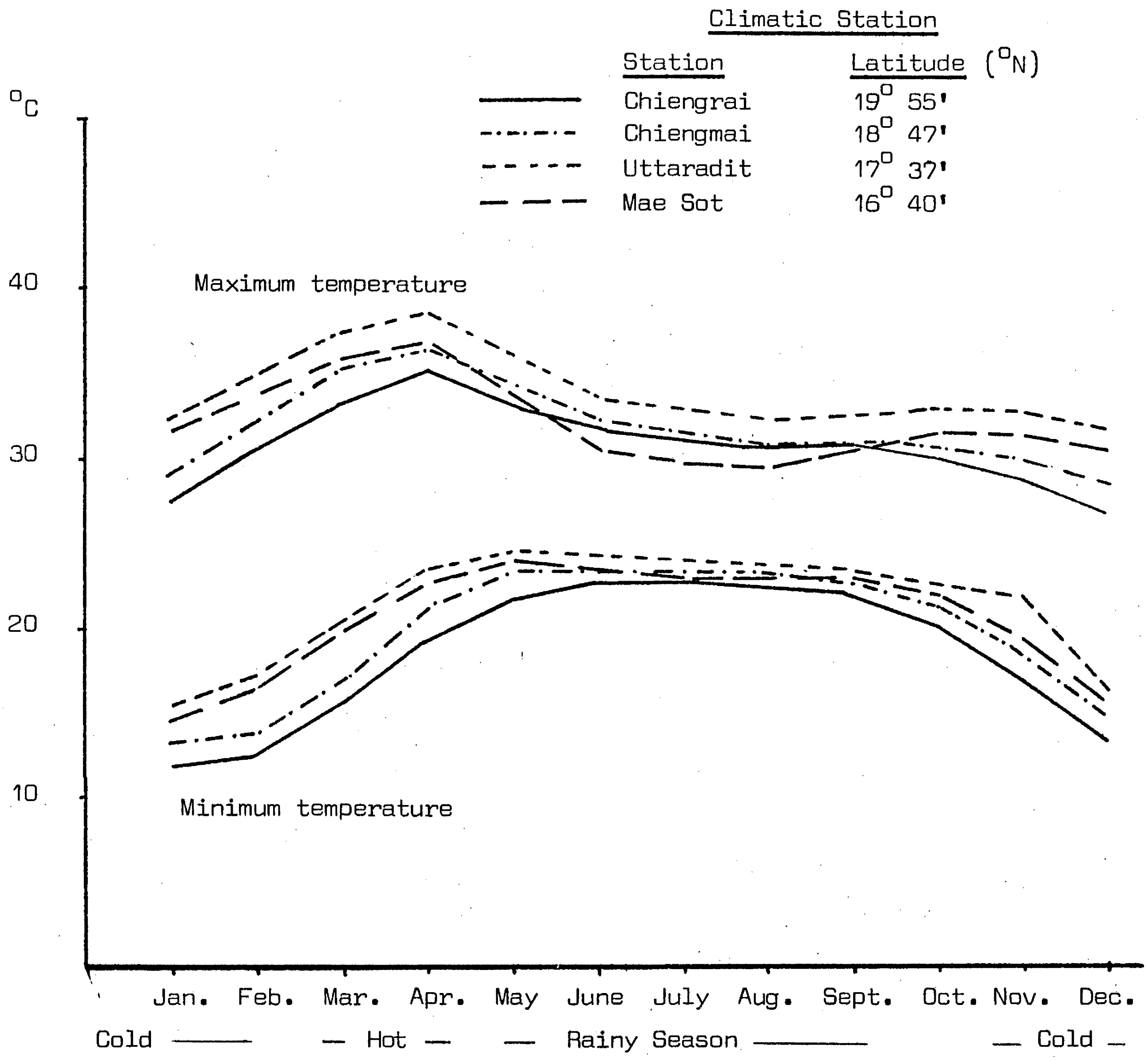


FIGURE 1.2 Mean monthly maximum and minimum temperatures in teak areas in Thailand (1951 - 1970)

Source: Chunkao et al, (1972)

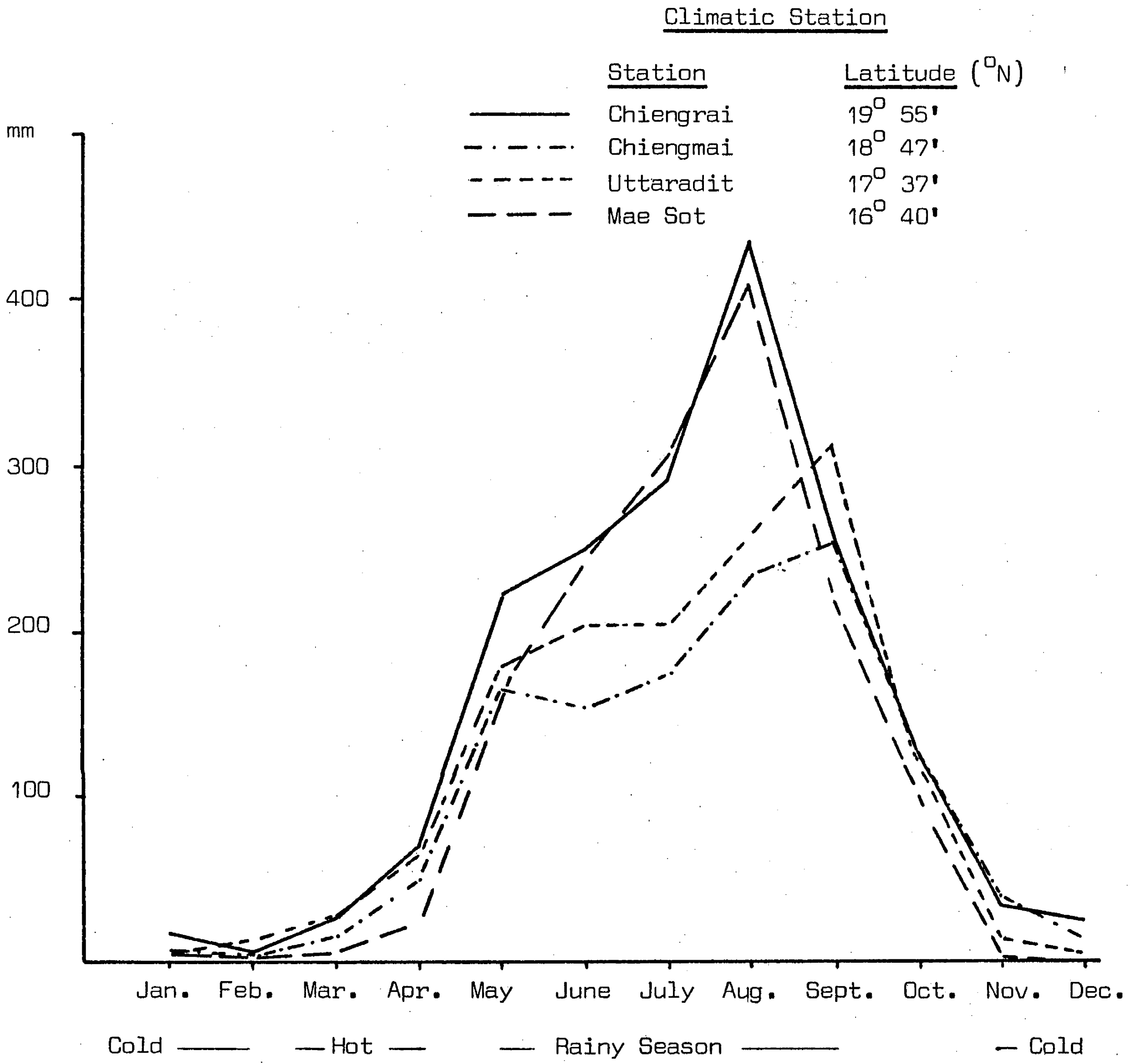
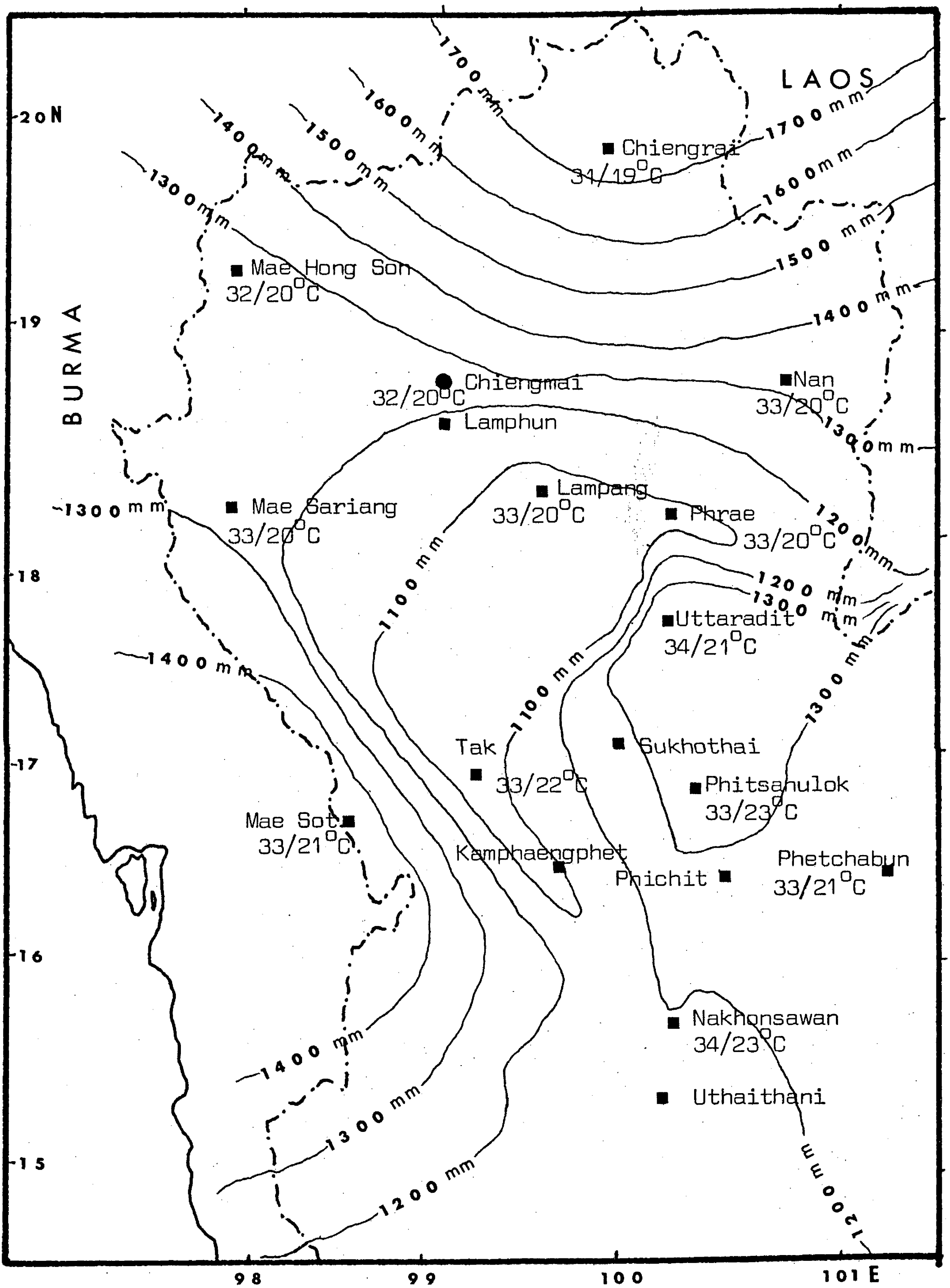


FIGURE 1.3 Mean monthly rainfall in teak areas in Thailand (1951 - 1970)

Source: Chunkao *et al*, (1972)

FIGURE 1.4 Mean annual rainfall (as shown by isohyetal map), mean maximum and mean minimum temperatures (max/min) in the north of Thailand (1951 - 1970)



Source: Chunkao et al, (1972)

1.1.2 Geology and Soil Requirements

Teak occurs on a variety of geological formations such as igneous rock, limestone, granite, gneiss, schist, calcareous crystalline rocks, some sandstones, conglomerate, shale . But it occurs predominantly on the soils derived from trap and river alluvia formed from this rock, even where the overlying soil is shallow and poor (Kulkarni, 1951; Puri, 1951 1960; Bhatia, 1954; Seth and Yadav, 1959). In areas where conglomerate or sandstone underlies the soil, this species may be absent, or appears to be stunted in growth and poor in quality (Heweston, 1951; Kulkarni, 1951; Puri, 1951; Bhatia, 1954; Seth and Yadav, 1959). Kulkarni (1951) studied the relationship between geological formations and natural distribution of teak in India and found that geology plays the most important part in the distribution of teak. The percent stocking of teak and other tree species in relation to geological formation in this study is shown in the following table:

TABLE 1.2 Relationship between geological formation and distribution of teak

Geological formation	Composition of forest Teak %	 Non-Teak %
Deccan Trap (Igneous rock)	80	20
Granitic gneisses	75	25
Calcareous crystalline rock	60	40
Phyllites and schists	50	50
Bagra conglomerate	45	55
Jabalpur conglomerate and haematite	15	85
Pachmarhi sandstone	0	100
Denwa sandstone	0	100
Jabalpur sandstone	0	100

Source: Kulkarni (1951)

Since teak had been known to grow best on soils derived from igneous rocks such as trap, several attempts have been made at a systematic study of soils and geological formations in relation to teak distribution. Kulkarni (1951), for example, found relationships between geological formation, pH value of soil, and the stocking of teak in natural teak forests. He reported that trap and alluvial soils, to which the best teak stands in the region are confined, are either nearly neutral or slightly alkaline. He also found that teak occurs predominantly on soils with pH values ranging from 6.5 to 7.5. The species is totally absent from natural forests where soils are more acidic than 6.0 pH. On the other hand, on alkaline soils with pH values ranging from 7.5 to 8.5, teak deteriorates in quality, and above a pH of 8.5 the presence of excess alkalies in soils seems to be definitely toxic towards teak growth. This has been supported by the work of Puri (1951, 1960), Bhatia (1954), Seth and Yadav (1959). The relationships between geological formation, soil pH, and the stocking of teak in natural forests is shown in the following table:

TABLE 1.3 Relationships between geological formation, pH value of soil, and the percentage of teak in the natural forests.

Name of the parent rock formation	Average pH value of the resultant soils	Percentage of teak in the forest
Deccan trap (Igneous rock)	7.0	80
Alluvium	7.0	80
Granitic gneisses	7.5	75
Phyllites and schists	7.2	50
Calcareous crystalline	7.7	40
Bagra conglomerate	6.8	45
Jabalpur conglomerate	6.5	15
Bijori sandstone	6.0	0
Pachmarhi sandstone	5.6	0
Denwa sandstone	5.5	0

Apart from soil pH, a number of minerals in soil such as calcium and phosphorus have been found to play an important role in controlling the distribution and growth of teak. Several studies suggest that teak requires a large amount of calcium and phosphorus for its growth. For example, Puri and Gupta (1950) analyzed the mineral content of teak and sal (Shorea robusta) leaves collected from the same soil type. They reported that the amount of calcium in leaves of teak is nearly double that of sal, i.e. 2.91% (teak leaves) and 1.46% (sal leaves). Similarly, Puri (1960) analysed the ash of teak wood and reported that the amounts of calcium and phosphorus in teak wood ash are higher than those of any other mineral contained in the same wood ash, i.e. 31.35% (CaO) and 29.69% (P_2O_5). Bhatia (1954) studied the role of geology and soils in relation to the distribution and growth of teak and reported that teak grows best on the igneous rocks which contain higher amounts of exchangeable calcium and phosphorus. Relationships between geological formations, soil pH, and the amounts of exchangeable calcium and phosphorus in soils are shown by Bhatia (1954) in Table 1.4. From this summary it can be seen that teak is a "calciolous" plant which normally grows on soils containing high levels of exchangeable calcium, and on soils which are alkaline, neutral or of relatively low acidity.

TABLE 1.4 The average pH values and the amounts of exchangeable calcium and phosphorus in the soils derived from different geological formations of Madhya Pradesh.

Geological formation	pH	CaO	$Mg_2P_2O_7$
*Granites and gneisses	6.2	0.41	0.28
Vindhyan sandstones, shales and conglomerates	6.0	0.37	0.25
Quarzites	6.0	0.26	0.25
Gondwana sandstones			
Talchirs, Moturs and Barakars	5.8	0.24	0.14
Bagra conglomerates	6.6	0.37	0.33
Jabalpur sandstone	6.0	0.23	0.20
Pachmarhi sandstone	5.6	0.24	0.13
*Igneous rocks			
Deccan trap	7.1	0.73	0.32
Dykes and sills	6.3	0.50	0.38
Calcareous crystalline	7.6	0.76	0.54
*Alluvial soils			
Calcareous	8.3	2.38	0.33
Non-calcareous	8.3	0.56	0.46

After Bhatia (1954) * High stocking of teak

1.1.3 Growth Habits

Teak is a deciduous tree species. It generally starts shedding its foliage about the end of the cold season (mid-January) and is completely defoliated by the middle of the hot season (March - April). New leaves start sprouting within a few weeks after leaf fall is completed. The time of leaf fall and leaf renewal of teak are variable depending on locality and the climate of the particular year. In a long dry season year the species may remain leafless longer than usual, while in a moist locality it may remain in leaf until March or even later. For example, teak cultivated in the wetter area of eastern Java behaves like an evergreen species, but in the periodically dry region of western Java this species loses its leaves during the dry season (Walter, 1962 cited by Alvim, 1964). In a study of seasonal production of litter in teak plantations in Thailand, Arksornkoae et al, (1972) reported that leaf fall of teak occurred from January to September, with a maximum in April (the hottest month) and a minimum in September (the mid of rainy season). This summary suggests that soil moisture and atmospheric humidity play an important role in controlling leaf fall and leaf production of this species.

Teak flowers seasonally, and its flowering usually starts within a few weeks after its leaves are full grown. In Thailand, teak starts flowering in mid-July and continues throughout the rainy season until November (Bryndum and Hedegart, 1969). Teak in plantations normally commences flowering 5 - 7 years from planting; however, in some places or some provenances it may flower as early as 2 years of age (Mahaphol, 1954; Boonkird, 1966). In general, the large white inflorescences are terminal on the main stem as well as on branches of the tree. An inflorescence of teak contains approximately 3,000 (1,200 - 3,700) individual flowers, and the flowering period for individual inflorescences lasts from 2 to 5 weeks (Bryndum and Hedegart, 1969; Hedegart, 1975). The teak flower (6-8 mm in diameter) is perfect and it has an ovary with 4 ovules and a style with a forked stigma (Bryndum and Hedegart, 1969). The individual flower opens for one day only and if in that day pollination does not occur the flower is shed either that evening or the following morning (Bryndum and Hedegart, 1969). Teak is mainly a cross-pollinating species and insects are the main agents of natural pollination (Bryndum and Hedegart, 1969; Hedegart, 1973, 1976). Fruit set after self pollination may still occur but germination of seeds obtained from this fruit is usually very poor compared with that obtained from cross pollination (Bryndum and Hedegart, 1969).

Soon after a flower has been successfully pollinated the ovary develops rapidly into a fruit. Teak fruits usually ripen within 120 and 200 days after pollination and fall gradually throughout the hot season (March - May) (Hedegart, 1973). The fruit of teak is a hard, irregularly globose nut (1.0 - 1.5 cm in diameter), and contains 4 seed chambers. In general, germination of teak seeds (the term "teak seed" means teak fruit) is poor (about 35%) and sporadic (Bryndum, 1966; Boonkird, 1975). In teak nursery practice, seed pre-treatments, such as alternate soaking and drying or removal of the exocarp of the fruit, are normally required to improve the percentage and the rate of germination, in order to obtain uniform seedlings.

After seed germination, the seedling of teak usually develops a large and strong carrot-like tap-root with few, poorly developed laterals (Plate 1.1). The establishment of a strong tap-root during the seedling stage is an important adaptive trait which enables the seedling of this species to withstand the influences of periodic damage to its shoot. In the study of the natural regeneration of teak in Thailand, Kittinanda (1963) found that teak seedlings less than 1.5 metres in height are usually burnt back by running fire during the hot season (March - April), but the underground parts of some of these burnt seedlings still survive and will produce the new shoots by the beginning of the next rainy season. He also reported that with such periodic damage, it will take about 8 to 20 years from the time of germination for teak to develop its root system (mainly the tap-root) which is capable of establishing the vigorous and fire resistant shoot(s) within one growing season. Similar findings have been reported by Sono (1964), who reported that it takes about 7 to 29 years from germination for teak to develop a tap-root which enables it to produce within the one growing season the fire resistant shoot(s). Sono also noted that the minimum size of seedling tap-root which enables it to produce the fire resistant shoot is about 2.5 cm in diameter at the collar level.

1.2 TEAK PLANTATION ESTABLISHMENT

Teak is one of the high commercial value timber tree species. For this reason the species has been introduced to several countries in the tropical and sub-tropical regions.

The plantations of teak can be established either by the direct dibbling of seed or by the stump-planting method. The first method is rarely practised because the price of teak seed is high and the germination of teak seed is usually poor and sporadic, resulting in unreliable establishment of the plants. The latter method is therefore more widely practised in teak plantation establishment.

Teak stump planting was first successfully tried in Burma in 1920 (Anon., 1921), and this method has been adopted as a standard practice since 1932 (Champion and Pant, 1932). The term "stump" in this planting method refers to a "root-shoot cutting" of the seedling. As noted earlier, teak seedlings usually develop a large and strong carrot-like tap-root with a high sprouting potential. The tap-root of the seedling constitutes the major part of the planting stump. To prepare the stump for planting, the seedling is first raised in the nursery for about 1 - 2 years to produce the straight and unbranched tap-root; it is then lifted for stumping one or two days before out-planting. After lifting from the nursery, the stem of the seedling is cut at about 3 - 5 cm above the root collar level, leaving one or two pairs of buds in the stem part for developing into sprouts or new shoots; the lateral roots are entirely trimmed off close to the tap-root. If necessary the

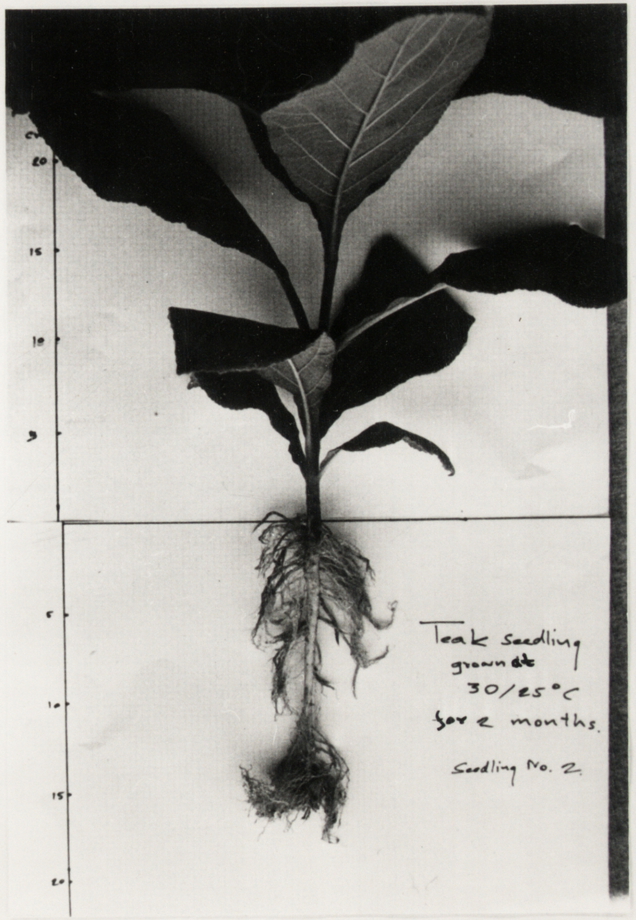


Plate 1.1 Teak Seedling

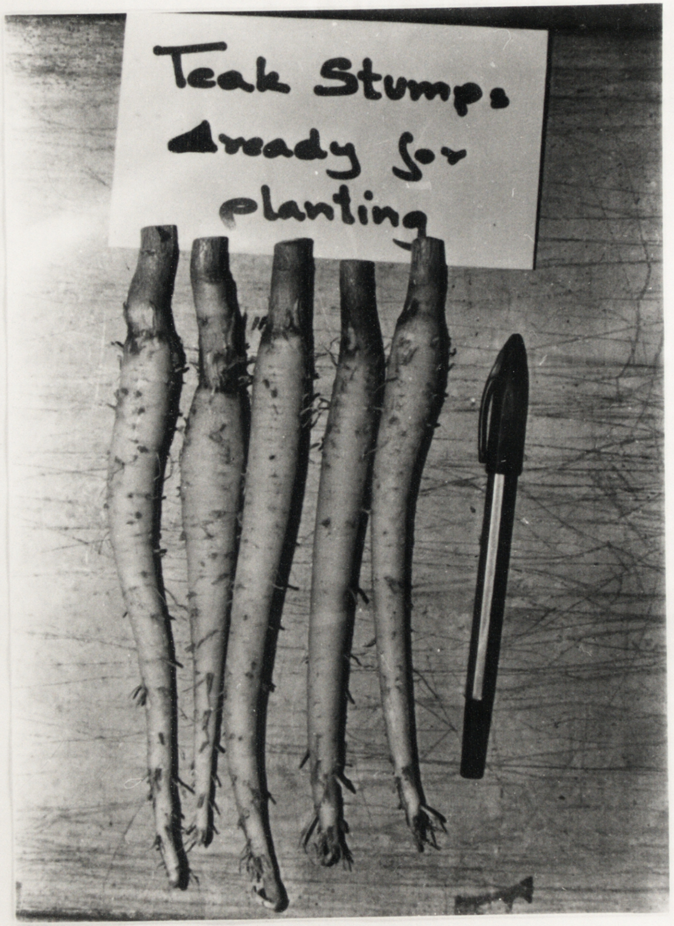
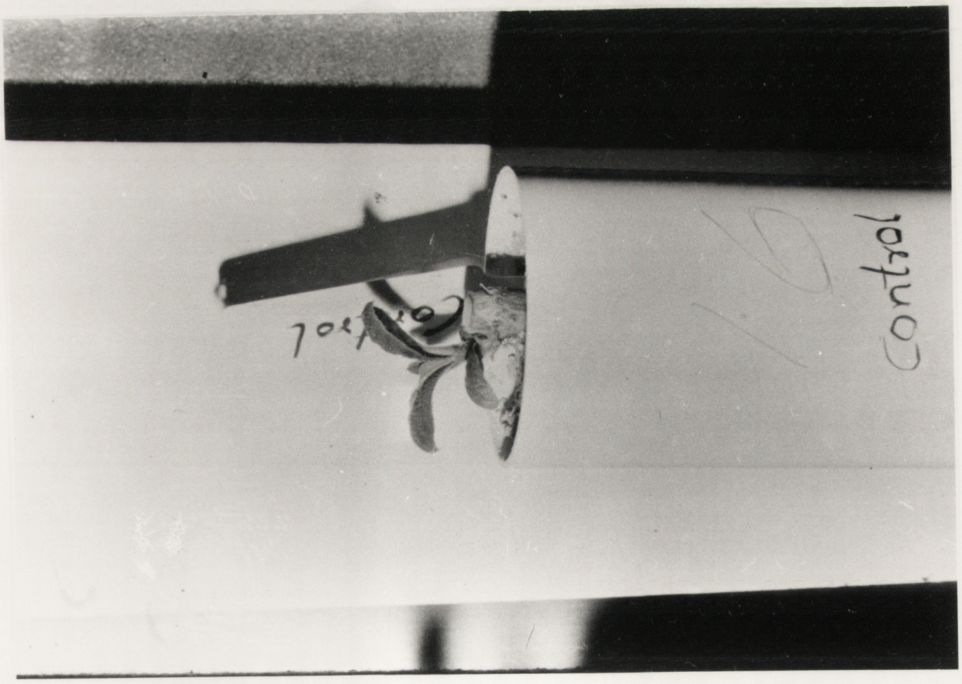
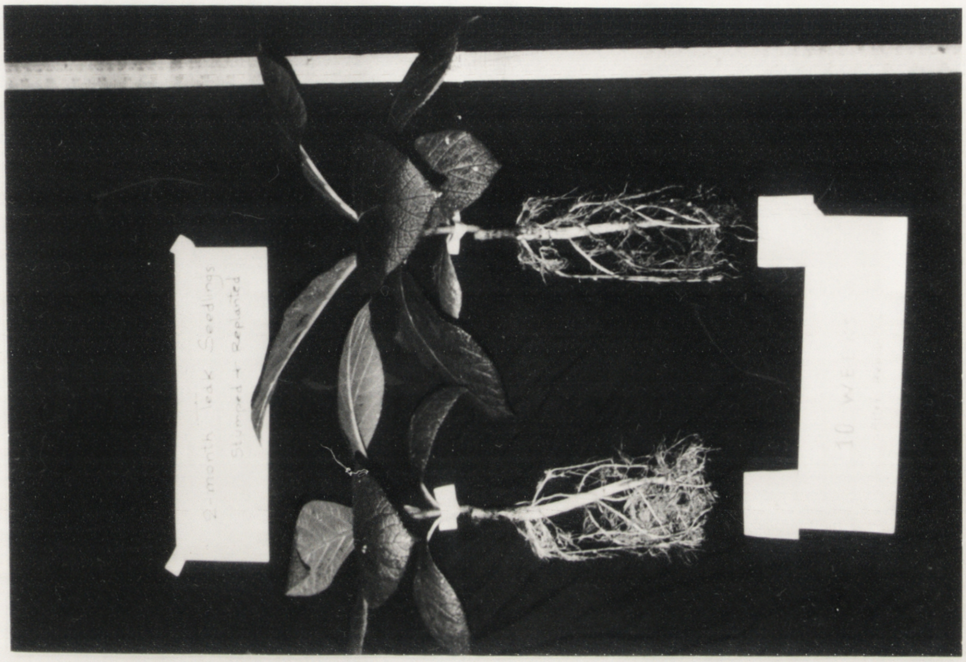


Plate 1.2 Charateristics of Teak Seedling Stump

PLATE 1.3 STUMP SPROUTING



One week after stump-replanting



Ten weeks after stump-replanting

(Showing shoot and lateral root regeneration) tap-root may be cut, the optimum length of stump being between 15 - 20 cm. Characteristics of teak stumps ready for out-planting are shown in Plate 1.2.

Stumps can be more readily planted than whole seedlings. In general, the stump is planted in a hole made by a crowbar slightly bigger in size than the biggest stump (about 2.5 cm in diameter). The method of planting is as follows: The bar is inserted into the ground at an angle, and pushed forward to the upright position. The stump is inserted into the hole, leaving its stem part above ground. The bar is then inserted into the ground at an angle about 5 - 10 cm from the stump, and pushed forward to the stump to firm the soil around the base and the top of the stump. The soil around the stump is then pressed by the planter using his feet.

Under favourable conditions for growth, the stump usually produces sprouts within a few weeks after planting. The biggest sprout on the stump will dominate the smaller sprouts and subsequently it develops into a plant (see Plate 1.3). The ability of stumps to produce sprouts and the mechanism of stump sprouting will be discussed in more detail in Chapter 2.

1.3 PURPOSE AND SCOPE OF STUDY

While stump planting is a standard method used for teak plantation establishment, information on the physiology of the sprouting of teak planting stumps is very limited. In the present study, a series of experiments dealing with some of the factors influencing the sprouting of teak planting stumps are described. The first two studies made under field conditions were designed to examine:

a. whether teak planting stumps could be kept for a long period in an underground (uncooled) storage unit;

b. effects of lifting date and/or the phenological development of the parent seedlings at lifting on the production of stump sprouts after out-planting;

c. effects of planting date and weeding treatment on the production of stump sprouts.

Subsequent studies made under controlled environmental conditions were designed to examine:

a. effects of temperature and soil moisture regimes on growth and development of teak seedlings, and the subsequent production of sprouts of teak planting stumps after planting under the same conditions;

b. effects of temperature and soil moisture regimes on the activity of some of the physiological processes in teak seedlings, including photosynthesis and respiration, translocation and redistribution of photosynthates, carbohydrate levels in seedling organs, and the level of auxin content;

c. the direct effect of carbohydrate reserves and plant growth substances on the production of sprouts of teak planting stumps.

1.4 TERMINOLOGY

Before proceeding further it is necessary to clarify some of the terms which will be used frequently in this study.

Dormant bud: The term dormant or suppressed or inhibited bud is usually used to refer to the undeveloped bud in the axil of the leaf or bud scale on the long shoot of the plant. Normally, this bud is connected to the pith by a bud trace (Kramer and Kozlowski, 1960; Wilson, 1968, 1970; Kozlowski, 1971) and remains inhibited and embedded in the wood or bark of the plant. Although this bud is called dormant, it is still active and grows a little each year to enable the tip or the scale primordia to keep pace with the radially expanding cambium (Kramer and Kozlowski, 1960; Wilson, 1970; Kozlowski, 1971). Dormant buds may develop into a number of dormant shoots under the bark, or may develop into new shoots or branches within a few weeks after leaf fall or after the parent plant has been damaged; but many of them may remain dormant indefinitely or may finally die.

Adventitious bud: The adventitious bud is the bud which originates either from cork cambium, from phloem parenchyma, or from the ray initials of the vascular cambium (Stone and Stone, 1943; Esau, 1960; Kramer and Kozlowski, 1960; Kozlowski, 1971). This bud normally forms on the older portions of the root or stem of the plant, or forms on the callus tissue near or adjacent to a wound. This bud has no connection to the apical meristem.

Stump sprout: Stump sprouts mostly originate and develop from dormant or inhibited buds buried in the bark on the lower part of the stem or on the zone of rapid taper in the roots near the stem

(Kramer and Kozlowski, 1960; Smith, 1962; Wilson, 1968, 1970; Kozlowski, 1971). Working with stump sprouting in red maple, Wilson (1968) showed that there are two types of dormant (inhibited) buds that grow out to form stump sprouts in this species. The most common type is buried in the bark, and the other type is a short-shoot of an external dormant bud which is external to the bark. (This external bud type appears to be very similar to that found on the stem portion of the teak planting stump.) Wilson also reported that both types of buds are inhibited lateral buds that are derived from the original lateral buds on the main axis of the plant.

Stool shoot: A new shoot that differentiates from the callus tissue that develops at the cut surface of the cambial area is called a stool shoot. This shoot is normally short lived because it continues to elongate without bud formation and this new shoot is finally killed by the frost or drought. This type of shoot is not so important in vegetative reproduction of forest tree species.

Epicormic shoot: The term epicormic shoot, epicormic branch, epicormic sprout, or water sprout, normally refers to the shoot or sprout that develops from the dormant bud located on the upper part of the clear bole stem (Kramer and Kozlowski, 1960; Smith, 1962; Kozlowski, 1971). This shoot usually occurs when the tree is artificially pruned or when neighbouring trees are thinned, resulting in sudden and excessive exposure which stimulates development of the dormant bud on the stem.

Root sucker: The term root sucker or root sprout refers to the shoot that develops from the adventitious bud originating on the surface or in the periderm of the root (Kramer and Kozlowski, 1960;

Kozlowski, 1971; Zimmermann et al, 1971). Zimmermann et al, (1971) noted that all buds on the roots are adventitious in origin and they develop exogenously from tissues exterior to the stele. In some cases, these buds may develop endogenously from the pericycle as do lateral roots. In general, these buds become inhibited and exist as dormant buds embedded in the periderm of the roots for several years before being released. Occasionally these buds produce short-shoots underground and leaf primordia annually for several years. Finally they develop into long-shoots above ground (Kormanik and Brown, 1967; Kozlowski, 1971).

Sprouting vigor: This term usually refers to the developmental stage of sprouting which includes the breaking of bud dormancy as well as the subsequent elongation of the sprouts. Normally it is expressed in terms of height and diameter growth and dry weight of the sprouts.

CHAPTER 2

LITERATURE REVIEW

2.1 THE FORMATION OF SPROUTS IN PLANTS

Sprouting is one of the most important types of vegetative propagation for woody plants after cutting, girdling, or fire. This also applies to forest plantation establishment , especially teak, in which seedling stumps (root-shoot cuttings) are commonly used as a method of planting. Sprouting may occur on the roots and on the stems at ground level or within the upper part of the plant stems. Different terms are applied to the sprouts depending on their locations and origins (Section 1.4).

In general, plants produce sprouts when they are seriously damaged, either by physical or biotic agents, due to an upset in the physiological balance within the plants (Kramer and Kozlowski, 1960). Stump sprouting in plantation establishments is similar to that of tree stumps after cutting. Under favourable growth conditions, dormant buds or lateral buds on the planted stumps develop into sprouts and one or two of the biggest sprouts elongate rapidly and become the leading shoots of the new plants. The planted stumps usually sprout within a few weeks of planting, but the capacity of the stumps to produce sprouts with high survival and growth potential would depend on many factors, such as species and season of stump-planting. In a study of the production of stump sprouts after planting of a number of tropical species, Champion and Pant (1932) found that stumps of <u>Terminalia tomentosa</u>, teak, and <u>Gmelina arborea</u>

Note: Owing to the lack of recent publications (1975-76) concerning shoot growth and development and stump sprouting, especially of teak, only a few recent references are cited in the Literature Review and in the General Discussion of the thesis.

seedlings formed sprouts within 2, 10, and 15 days, respectively. They also noted that both the survival and height growth of teak sprouts were much greater than those of the other two species.

2.2 PHYSIOLOGICAL BASES OF PLANT SPROUTING

As stated earlier, sprouting of the plant is a result of the interruption of physiological balance within the plant. Early investigations on the physiology of plant sprouting showed that the formation and growth of sprouts along an elongating stem of the intact plant are strongly inhibited by an actively growing shoot of the plant. If the terminal shoot is removed one or more of the lower lateral buds are released from inhibition and develop into sprouts (Snow, 1925, 1929; Thimann and Skoog, 1933, 1934). This type of correlative inhibition is known as "apical dominance". Phillips (1969, 1975) classified apical dominance as follows:

i. complete or almost complete inhibition of lateral bud growth by the presence of apical buds;

ii. inhibition of the growth of one shoot by the presence of another shoot; and

iii. the influence of the apical part of the shoot on the orientation and development of lateral organs, such as branches, rhizomes stolons.

The capacity of plants to produce sprouts, or in other words, the degree of apical dominance in plants varies considerably with several factors, such as season, species, age, and size of the plant. In studies on seasonal variation in stump sprouting and root suckering of a number of woody plants, it has been shown that the season of cutting and girdling has a marked effect on the formation of stump sprouts and root suckers; more sprouts are formed on stumps or roots of plants cut or girdled during the inactive growth period than on those cut or girdled during the active shoot growth period (Buell, 1940; Stoeckler, 1947; Wenger, 1953; Stoeckler and Macon, 1956; Sterrett et al, 1968; Eliasson, 1971a; Hook and Debell, 1970; Brown, 1971; Cremer, 1973; Schier, 1973). This evidence demonstrates that a high capacity to produce sprouts is associated with the dormant season of the plant. Similarly, the capacity of teak stumps to produce sprouts is high during the inactive growth period (the dry season) and low during the active growth period (the rainy season) (Bose, 1909; Hole, 1910; Troup, 1921). Troup (1921) noted that trees cut during the period of leaf fall and bud break produced more sprouts with better growth than those cut during the period of active shoot growth. Likewise, through their work on the production of epicormic branches in teak plants Briscoe and Nobles (1966) reported that trees pruned during the inactive growth period (February) produced more epicormic branches than those pruned during the active shoot growth period (May – August). In experiments on the use of teak seedling stumps in plantation establishment, a number of workers have shown that teak stumps lifted and planted during the bud break period produce more vigorous plants (sprouts) with a higher survival rate than those lifted and planted during the rapidly growing period of the parent seedling (Champion and Pant, 1932; Griffith, 1938; Anon, 1971; Mathur, 1972).

The physiological mechanism of plant sprouting has been widely studied since 1925 when Snow demonstrated the inhibition of lateral bud growth by the rapidly growing leaves in or near the terminal shoot of Phaseolus vulgaris seedlings. Many theories have been proposed to explain the basic mechanism(s) of this phenomenon. The two main theories involve nutrition and plant growth hormones and are discussed in the following sections.

2.2.1 Nutritional Theory

2.2.1.1 The role of mineral nutrition

Most early investigations, as described in the excellent reviews of "apical dominance" by Phillips (1969, 1975), demonstrated that the inhibition of lateral bud development in the intact plant is due to competition for a limited supply of plant nutrients between the apical and the lateral bud meristems. Upon the removal of the apical meristem, which is assumed to be the greater sink for nutrients, the lateral buds are released from inhibition and develop into shoots or branches. Following the discovery of auxin, like IAA and its inhibitory effect on the development of lateral buds (Thimann and Skoog, 1933, 1934; Skoog and Thimann, 1934), the potential role of plant nutrition was ignored until the work of Gregory and Veale (1957). Gregory and Veale demonstrated that the degree of lateral bud inhibition in flax seedlings (Linum usitatissimum) could be controlled by varying the supply of nitrogen and carbohydrate to the plant. They reported that under nutrient deficiency, growth and development of lateral buds in this plant were entirely inhibited. In support of the work of Gregory and Veale, McIntire (1968) showed that lateral buds in flax seedlings could be released from inhibition by increasing the supply of soil nitrogen. This author also reported that there was an increase in the total nitrogen content in the suppressed buds within 12 hours after the removal of the terminal shoot of the plants. Working with *Agropyron repens* McIntire (1965, 1969, 1971, 1972) concluded that the inhibition of lateral bud development in the rhizome of this species is due primarily to competition for water, nitrogen, and carbohydrate supply between the apical and the lateral buds. In woody plants, several studies have also shown that there is an important effect of some mineral nutrients, particularly nitrogen, on plant sprouting. For example, Stirling (1973) showed that the growth of lateral buds on *Eucalyptus obliqua* and *E. diversicolor* seedling stems could be stimulated by increasing the concentration of nitrogen and phosporus supply. Similarly, the lateral buds in tea seedlings (*Camellia sinensis*) could be released from inhibition by the application of high level of N.P.K. fertilizer (Kulasegaram and Kathiravetpillai, 1972).

There is evidence available which is at variance with the above hypothesis. A number of studies have shown that levels of NPK, amino acid, and carbohydrates in suppressed buds are not lower than those in the rapidly growing buds (cf., Phillips, 1969, 1975). Likewise, direct applications of plant nutrients to suppressed buds have not released them from inhibition (Goodwin and Canfield, 1967; Cutter, 1972a, 1972b). Working with *Eucalyptus obliqua*, Blake (1974) reported that withholding nutrients from the seedlings of this species had no effect in reducing the number of sprouts that developed following decapitation of the seedlings.

From the above evidence it can be seen that a purely nutritional factor cannot be the sole factor governing the production of plant sprouts. Phillips (1975) has stated that plant growth substances and the interaction between them and nutrients might be the most important factors controlling plant sprouting. The role of plant growth substances, particularly auxin, will be discussed in more detail in Section 2.2.2.

2.2.1.2 The role of carbohydrate reserves

As stated by Kramer and Kozlowski (1960), plants use photosynthates in two ways:- (a) in respiration, and (b) in the production of new tissues by assimilation. The surplus products after utilization is then accumulated in vegetative structures (or in fruits and seeds) and subsequently used at a time when it is not supplied directly from photosynthesis. In deciduous plant species a number of studies have shown that the level of carbohydrates, especially in the roots, increases in late summer to a peak in autumn, declines slightly during the winter, and drops rapidly during spring and reaches a minimum in early summer (Jones and Bradlee, 1933; Smyth, 1934; Ishibe, 1935; Wenger, 1953; Wood et al, 1959). This evidence suggests that the early stages of bud opening, leaf expansion, and internode elongation during spring growth of the plant may utilize a large amount of food accumulated during the previous growing season (Wood et al, 1959; Kramer and Kozlowski, 1960; Kozlowski and Keller, 1966; Quinlan, 1969; Kozlowski, 1971a).

The role of carbohydrate reserves in sprouting (which includes stump sprouts and root suckers) in woody plants remains uncertain at present. Several studies have shown that the patterns of seasonal variation in sprouting parallel the levels of plant carbohydrate reserves. This evidence leads to the belief that carbohydrate reserves may play an important role in sprouting; that is, the production of plant sprouts is positively related to the level of carbohydrate reserves (Aldous, 1929; Buell, 1940; Stoeckler, 1947; Kramer and Kozlowski, 1960; Chattaway, 1958; Cremer, 1965; Hook and Debell, 1970). On the other hand, there is evidence that the production of plant sprouts is not primarily dependent on the level of carbohydrate reserves. Wenger (1953), for example, studied the sprouting of sweetgum (Liquidambar styraciflua) in relation to season of cutting and carbohydrate content. This author reported that the stump sprouting in this species varied with the season of cutting but not with the level of carbohydrate content in the stumps. Wenger noted that the carbohydrates in the stumps increased continuously during the accumulation period whereas sprout growth fluctuated during this period. This author suggested that under conditions of non-limiting carbohydrate reserves other factors such as plant hormones may be more important in controlling the stump sprouting in this species. Similar results were obtained in eucalypt stumps (Bachelard and Sands, 1968; Cremer, 1973; Blake, 1974), oak stumps (Vogt and Cox, 1970), eucalypt lignotubers (Blake, 1974), and aspen root cuttings (Tew, 1970; Schier and Zasada, 1973). Kozlowski (1971a) has pointed out that the supply of carbohydrates and other nutrients in plants for shoot growth is often adequate but growth is still inhibited because the utilization of these reserves is controlled by other internal regulatory mechanisms. Similarly, Cremer (1973) concluded that the production of stump sprouts in eucalypt might be controlled by:

i. the existence of buds or the ability of the stumps to form buds;
ii. growth substances which regulate the buds;
iii. reserves which enable buds to start growing into shoots; and
iv. seasonal and other environmental factors which influence shoot growth.

In teak, there is no direct evidence for the effect of carbohydrate reserves on the production of stump sprouts. However, a number of studies on stump size and on split stumps in relation to their subsequent survival and height growth after out-planting could be used to relate the effect of reserves on the planted stump to the capacity of the stump to produce sprouts (Champion and Pant, 1932; Griffith, 1938, 1939, 1942). These authors showed that the optimum diameter of the teak stump for the production of sprouts with high survival and growth potential after planting is between 1.0 and 2.0 cm. Stumps outside this diameter range produce less vigorous sprouts with low survival rate. Likewise, in studies on split stumps Mathur (1972, 1973) reported that there was no difference in the capacity for sprouting (in terms of survival and height growth of stump sprouts) between the half split and the entire stumps. However, when quarter split stumps were planted, sprouts produced were much poorer. From both stump size and split stump studies, it is suggested that under conditions where food reserves are not limiting (as determined by stump size) there is no correlation between the amount of food reserves and the production of stump sprouts.

2.2.2 Hormonal Theory

2.2.2.1 The basic mechanism of plant sprouting in relation to plant growth substances

The role of plant growth substances in the inhibition of plant sprouting has been extensively studied. Early investigations by Snow (1925, 1929) showed that the inhibition of lateral bud development in pea plants (*Phaseolus vulgaris*) was caused by a diffusible substance produced in the apical bud and in the rapidly growing young leaves. When these growing regions were removed the lower lateral buds were released from inhibition. Later, Thimann and Skoog (1933, 1934) and Skoog and Thimann (1934) demonstrated that the applications of auxin like IAA could replace the apical bud in inhibiting the growth of lateral buds in broad bean plants (*Vicia faba*), in that repeated applications of auxin to the cut surface of decapitated plants suppressed lateral bud growth in much the same manner as the apical bud. Furthermore, Thimann and Skoog (1934) found that auxin was synthesized in growing apical buds and in the rapidly growing young leaves, and the amount of auxin decreased markedly with the age of the leaf. These workers suggested that the development of lateral buds in broad bean is inhibited by auxin produced at the apical bud and transported down the stem.

Since this classic work of Thimann and Skoog, there have been many theories proposed, involving many growth substances, in an attempt to explain the basic mechanism of the action of plant hormones, especially auxin, in the inhibition of plant sprouting. The three possible theories based on the fundamental role of auxin propounded at the present time are:

i. the direct theory of auxin inhibition;
ii. the indirect theory of auxin inhibition; and
iii. the blockage of translocation of metabolites.

These three theories will be discussed in more detail in following sections.

2.2.2.1.1 The direct theory of auxin inhibition

This theory proposed by Thimann (1937) assumes that roots, buds, and stems of a plant require auxin for optimal growth at different concentrations in the following order: stems > buds > roots. Growth and development of these organs are inhibited when the auxin concentrations fall beyond the optimal levels required for growth. Thimann (1937) first explained the phenomenon of lateral bud inhibition as follows: auxin produced by the terminal shoot is transported basipetally along the plant stems and enters lateral buds from the stems at concentrations similar to those pertaining in the shoot; this concentration although optimal for stem growth is much too high for bud growth and consequently lateral bud development is inhibited. This assumption is supported by the works of Skoog (1939), Thimann (1952), Kuse (1954) Vardar (1955) and Eliasson (1971a, b). However, evidence contradictory to this hypothesis indicating a more indirect role of auxin in lateral bud inhibition were obtained (Snow, 1937; van Overbeek, 1938; Champagnat, 1955; Jacobs *et al*, 1959). This is discussed in the following Section.

2.2.2.1.2 The indirect theory

The two theories dealing with the indirect effect of plant growth hormones, particularly auxin, on the inhibition of plant sprouting are:

A. the hormone-directed transport of metabolites; and

B. the formation of plant growth inhibitors by auxin stimulation.

A. The hormone-directed transport of metabolites

This theory was first proposed by Went (1936, 1939) as the "nutrient diversion" theory, and subsequently modified to the hormone-directed transport of metabolites theory as described by Phillips (1969, 1975). As discussed in Section 2.2.1.1 the inhibition of lateral bud growth could be due primarily to competition for the limited supply of plant nutrients between the apical and the lateral meristems (Gregory and Veale, 1957; McIntire, 1965, 1969, 1971, 1972). In the hormone-directed theory, it is assumed that metabolites in plants are predominantly moved to the actively growing regions such as the apical bud, the young developing leaves, and the cambium, in response to a stimulus provided by plant growth hormones (mainly auxin) (Phillips, 1969, 1975). Early investigations made by Mitchell and Martin (1937) and Sturt (1938) showed that both nitrogenous compounds and carbohydrates moved to and accumulated at high concentrations in the auxin applied regions of stems in bean. Recent studies using isotope elements such as ^{32}P and ^{14}C have produced evidence supporting this theory. Booth et al, (1962) found that ^{14}C-assimilates accumulated at high concentrations in auxin treated stumps of pea and potato plants within a few hours of auxin application. Similarly, working with poplar plants Davies and Wareing (1965) showed that ^{32}P moved towards and accumulated in the region where auxin was applied exogenously. Apart from auxin, a number of studies have shown that gibberellins and cytokinins also play an important role in stumulating translocation of metabolites to actively growing regions in the plant (Seth and Wareing, 1964, 1967; Davies *et al*, 1966; Wareing and Seth, 1967). These workers also showed that gibberellins or cytokinins alone seemed to have little effect on the accumulation of plant nutrients (^{32}P), but when applied together with auxin the accumulation of nutrients was effectively doubled, compared with that obtained with auxin alone.

B. The formation of plant growth inhibitors by auxin stimulation

In direct contrast to the direct theory of auxin inhibition (Thimann, 1937), Snow (1937) proposed that auxin acts indirectly in inhibiting the development of lateral buds. In his two-shoot pea study, Snow showed that auxin moving down along the stem of the bigger plant stimulates cambial activity and subsequently stimulates (or synthesizes) the production of plant growth inhibitors which can move upwards and inhibit growth and development of the smaller shoot and lateral buds in both shoots. The author assumed that the auxin and the inhibitory substance act antagonistically so that lateral buds are inhibited. Subsequently, Snow (1939) produced evidence to support his previous assumption that the suppressed leafy lateral shoots of *Pisum sativum* contained a growth inhibitory substance whereas the growing shoot did not. Similarly, Hemberg (1949) found that growh inhibitory substances in *Fraxinus pendula* buds decreased markedly as the buds were released from inhibition. In the meantime, the phenolic compounds and the abscisic acid (ABA) were identified as natural plant growth inhibitors, and several workers provided evidence supporting the theory proposed by Snow. (cf, Kozlowski, 1964, 1971;

Phillips, 1969, 1975; Wareing and Phillips, 1970; Steward and Krikorian, 1971). Tucker and Mansfield (1972, 1973) observed that the level of ABA in the suppressed buds of Xanthium strumarium plants, was between 50 and 250 times greater than in any other parts of the plant. These authors also reported that the level of ABA in the inhibited buds of this plant decreased markedly after the removal of the terminal shoot.

2.2.2.1.3 The blockage translocation of metabolites by auxin

This theory assumes that auxin at high concentrations blocks the transport of plant nutrients from the main stem to the inhibited buds in plants. This theory was first proposed by van Overbeek (1938) and subsequently modified by Gregory and Veale (1957). Gregory and Veale studied the differentiation of vascular tissues in relation to the development of lateral buds in flax seedlings. They found that the inhibited buds lacked properly-developed vascular connexions with the vascular strands of the main stem. Further they found that auxin plays a role in preventing the formation of the vascular traces to the auxillary buds in this plant which results in the starvation and inhibition of these buds. Further evidence in support of the above theory comes from Sachs (1968, 1969, 1970) who studied the control of bud growth by the differentiation of vascular tissues in a number of plant species. He concluded that:

a. the formation of direct contacts between new and pre-existing vascular strands can be inhibited if the pre-existing vascular strands are artificially supplied with auxin or if the pre-existing vascular strands are in the procambial stage and lead to the growing leaf primordia;

b. the growth of lateral buds released from inhibition is associated with the formation of new vascular connections; and

c. an actively growing shoot inhibits the formation of contacts between the vascular strands of a new apex and its own vascular system.

Sachs (1970) suggested that the control of vascular tissue is a major mechanism for control of lateral bud growth by the growing shoot.

2.2.2.2 Evidence for the hormonal control of sprouting in woody plants

The previous section (Section 2.2.2.1) has been concerned with the theories of the mechanism of plant sprouting in relation to plant growth hormones. Although most theories proposed are based on studies carried out on herbaceious plants, the basic mechanism of inhibition of plant sprouting would be similar in both herbaceous and woody plants (Phillips, 1969a).

It was noted earlier that trees cut or girdled during the inactive growth period, usually produce a higher number of sprouts and also more vigorous sprouts than those cut or girdled during the active growth period. Wenger (1953) demonstrated that stump sprouting in sweetgum is seasonal but not related to the amount of food reserves in the stump. He suggested that a hormone system related to that controlling apical dominance, is the main factor governing the seasonal trend of stump sprouting in sweetgum. This suggestion was later supported by the work of Eliasson (1969, 1971a, 1971b) and Schier (1973). In studies on the relation of auxin content to the capacity of root suckering in Populus tremula, Eliasson (1969, 1971a, 1971b) found that there was a negative relationship between the amount of auxin content in the root and the capacity of the root to produce sprouts. He concluded that auxin transported from the growing shoot into the root, prevents the formation and development of root suckers. Eliasson (1971a) showed that roots of the intact plant collected in early spring and summer contained greater amounts of auxin than those collected in the autumn. Similarly, Schier (1973) reported that the capacity of root suckering in Populus tremuloides was high when auxin content in roots of the intact plant was low. Reducing the amount of auxin content in roots either by (a) removal of the growing shoot; (b) girdling the stem with an application of triodobenzoic acid (TIBA) to block the basipetal transport of auxin; or by (c) stopping shoot growth by short day treatment, resulted in an increase in, or stimulation of the formation and development of root suckers in aspen plants (Eliasson, 1971b). In studies on the effect of exogenous auxin on stump sprouting and root suckering, a number of workers have shown that an application of auxin on the cut surfaces of stumps and root cuttings had a marked effect on the inhibition of stump sprouting and root suckering of many species (Farmer, 1962; Steerett and Chappell, 1967; Bowersox and Ward, 1968; Bachelard, 1969a; Loan, 1969; Vogt and Cox, 1970; Blake, 1974; Smith, 1975). Bachelard (1969a) for example, found that low concentrations of auxin (1 - 10 ppm) markedly inhibited the production of sprouts on stem segments of Eucalyptus polyanthemos and stimulated cambial activity. He suggested there was a competative relationship between cambial activity and the production of sprouts, such that the production of sprouts is inhibited at times when the cambium is active. This assumption was later supported by the work of Smith (1975) who studied the direct effect of plant growth substances on the production of sprouts and cambial activity in the decapitated seedlings of Eucalyptus viminalis and E. regnans. She noted that auxin, gibberellin, and the interaction between them inhibited the production of sprouts and at the same time stimulated the activity of cambium in these decapitated seedlings. She suggested that there was a negative relationship between cambial activity and plant sprouting.

2.3 SUMMARY

Plants usually sprout when they are seriously damaged. Under normal conditions, lateral buds along the stem are usually inhibited from developing into sprouts or shoots by the rapidly growing terminal shoot. Two main theories (namely nutritional theory and hormonal theory) involving plant nutrients and plant hormones have been proposed to explain this inhibition.

According to the nutritional theory, the inhibition of lateral bud development is due primarily to the competition for the limited supply of plant nutrients between the inhibited lateral buds and the rapidly growing terminal buds. Removal of the growing terminal buds (assumed to be a bigger sink for nutrients) would release nutrients for the development of the suppressed buds. However, there are evidence to suggest that this theory could not totally explain the inhibition of lateral bud development. Studies in a number of woody plants suggest that the production of both stump sprouts and root suckers is not totally dependent on the amount of food reserves in the stumps or roots; rather stump sprouting and/or root suckering depends largely on (a) the existence of buds or the ability of stumps or roots to form buds, (b) growth hormones which regulate bud development, (c) food reserves which enable buds to start growing into shoots; and (d) seasonal and other environmental factors influencing shoot growth.

Plant growth hormones, especially auxin, have been found to play an important role in controlling the production of stump sprouts and root suckers. Early investigations showed that auxin produced primarily in the terminal shoot and in the rapidly growing leaves is transported basipetally along the stem and inhibits the development of lateral buds. Removal of the terminal shoot would result in one or more of the lower lateral buds being released from inhibition. Subsequently, there have been a number of theories proposed to explain the role of plant growth hormones in the inhibition of lateral bud development. The three main theories are:

a. direct auxin inhibition;

b. indirect auxin inhibition; and

c. the blockage of translocation of metabolites by auxin.

The direct theory of auxin inhibition assumes that roots, buds, and stems have a different optimum auxin concentration requirements for their development and that growth and development of these three organs are inhibited at non-optimal auxin concentrations. Lateral buds have a smaller auxin concentration optimum than stems and hence concentrations which stimulate stem growth are inhibitory to lateral bud growth. In other words, the observed inhibition of lateral bud development is due to the supra-optimal auxin concentration reaching the lateral buds from the apical meristems.

There are two main assumptions for the indirect theory of auxin inhibition : (a) metabolites predominantly move to the rapidly growing regions in response to stimulus provided by plant hormones, especially auxin, and result in the starvation and inhibition of lateral buds; and (b) auxin moving down along the plant stem stimulates the production of plant growth inhibitors which enter the buds and inhibit development.

The third theory of auxin inhibition proposes that high concentrations of auxin inhibit the formation or differentiation of vascular connections between the vascular strands of the main stem and the vascular supplies of the lateral buds, resulting in the starvation and inhibition of lateral bud development.

CHAPTER 3

FIELD STUDY

EFFECTS OF LIFTING DATE, STORAGE, PLANTING TIME, AND PLANTING SITE CONDITION ON FIELD PERFORMANCE OF TEAK PLANTING STUMPS

3.1 INTRODUCTION

The success of the establishment of forest plantations depends on several factors: (a) the nature and condition of planting stock; (b) the condition of planting site; (c) the time or season of planting; and (d) cultural practices maintained during the growth of the plant. During the past two decades the effects of lifting date, storage, and planting time or planting season on the establishment and survival of forest tree seedlings after out-planting to the field have been intensively investigated. The lifting date or the stage of phenological development at time of lifting from nursery beds of seedlings has been found to influence their field performance. Seedlings lifted during the inactive growth (dormant) period often perform better, in terms of subsequent survival and growth after out-planting than those lifted during the period of active shoot growth (Stone and Schubert, 1959; Stone et al, 1962; Winjum, 1963; Lavender, 1964; Hermann, 1967; Hermann and Lavender, 1967; Lavender and Hermann, 1970, 1976; Hocking and Nyland, 1971; Hermann et al, 1972). These differences are due largely to the physiological dormancy or physiological potential in establishment and survival at the time of lifting of the seedling. Seedlings lifted during the inactive growth period or at the time just before the bud break dormancy usually have a relatively higher physiological potential than those lifted during the period of active shoot growth (Stone and Schubert, 1959; Stone et al, 1962; Winjum, 1963; Lavender, 1964; Hermann, 1964, 1967; Krueger and Trappe, 1967; Zaerr, 1967; Hermann and Lavender, 1967; Hocking and Nyland, 1971; Lavender and Hermann, 1976). Several studies have demonstrated that planting stocks lifted or prepared during the inactive growth period often have a relatively higher root regeneration potential (Stone and Schubert, 1959; Stone et al, 1962, 1963; Winjum, 1963; Lavender, 1964; Lavender and Hermann, 1970; Stone and Jenkinson, 1970, 1971); higher ability to withstand exposure of the root system (Jobling, 1960; Hermann, 1962, 1964, 1967); higher carbohydrate and other nutrient reserves (Winjum, 1963; Kruger, 1967; Krueger and Trappe, 1967); and lower auxin content (Zaerr, 1967; Eliasson, 1971a; Schier, 1973) than those lifted or prepared during the active shoot growth period. Lavender and Hermann (1976) have investigated the role of seedling physiology in the production of forest planting stocks and plantation establishments. These authors concluded that the ability of conifer seedlings to survive and establish after lifting, storing, and subsequently out-planting increases through the autumn to a maximum in the period December until the buds begin to enlarge in the following spring, and then declines thereafter.

In practice, the time when nursery seedlings have reached a peak in physiological potential for establishment and growth may not coincide with the most favourable time for field planting. To maintain this physiological quality, the seedlings may be lifted from nursery beds and stored under suitable conditions and then subsequently out-planted when site conditions are favourable for plant growth. Studies have shown that the physiological quality of planting stock can be maintained longer by storage of nursery seedlings than by retention of the seedlings in nursery beds (Stone and Schubert, 1959; Aldous and Atterson, 1963; Brown, 1971; Hocking and Nyland, 1971; Stone and Jenkinson, 1971).

Storage of planting stock can be done by several methods: cold storage (Aldous, 1964, 1972; Mullin, 1966; Brown, 1971; Hocking and Nyland, 1971; Hocking, 1971); underground or pit storage (Ursic, 1960; Dierauf and Marler, 1972); and storage in moisture proof materials at normal room temperature or under shade (Pamay, 1966; Aldous, 1972). Apart from maintaining the physiological quality of the planting stock, additional benefits of plant storage include:

a. efficiency in lifting, preparing, packing and shipping of planting stock;

b. possibility of holding over the surplus stock after out-planting;

c. the provision of an area in the nursery for early operations; and

d. improved planning for the distribution of planting stock because the amount of available planting stock can be determined accurately.

The establishment of teak plantation by stump planting method has been practised since 1920 (Champion and Pant, 1932), but the role of seedling physiology or the role of lifting date, storage, and planting time in the establishment and survival of the planting stumps after out-planting to the field has not yet been recognized. Several studies have shown that teak planting stumps could not be stored or kept longer than two weeks after lifting from nursery beds (Champion and Pant, 1932; Venkateramany, 1956; Maung Gale and Soe Tint, 1969; Anon, 1970; Mathur, 1972). But these investigations were carried out with unprotected routine stumps. In contrast, more critical studies have indicated that teak planting stumps may be early lifted and stored safely for a period of nine weeks either in sealed plastic bags or in sawdust boxes kept in a room at 22-32°C (Louridsen, 1973). This author also reported that stumps lifted and stored during the bud break period performed better in both survival and growth than those lifted and stored when they had already sprouted. Louridsen suggested that the lifting date or the stage of phenological development of seedlings at the time of lifting and storing might have an important influence on the field performance of teak planting stumps. In this chapter, the effects of lifting date, planting time, and planting site condition on subsequent survival and growth of teak planting stumps after out-planting, and the method of storage of teak planting stumps will be discussed.

3.2 PURPOSES OF STUDY

Very little information is available on teak planting stumps dealing with the effects of lifting date, storage method, and storage period on the field performance of the stumps after out-planting. This study has been carried out to examine:

1. the effects of early lifting time and long storage period on the field performance of teak stumps;
2. the effects of the lifting time or the stage of phenological development of teak seedlings at the time of lifting on the field performance of the planting stumps; and
3. the most favourable time for planting of teak stumps.

3.3 STUDY 1 : EFFECTS OF LIFTING DATE, STORAGE, STORAGE MEDIUM AND PLANTING SITE

3.3.1 Materials and Methods

3.3.1.1 Materials

A. Plant Material: Teak seeds collected from Mae Sai Kam natural forest, Lampang, were sown in the Northern Teak Nursery Center (N.T.N.C.) in Ngao, Lampang on May 27-28, 1970. The experiment was started in January 18, 1971 when the first seedlings were lifted from nursery beds. Climatic conditions at the N.T.N.C. during the experiment are given in Appendix 2.

B. Underground Store and Storage Medium: An underground (uncooled) store was constructed at the Teak Improvement Center (T.I.C.) about 2 km from the N.T.N.C., by excavating a 1.0 x 3.0 x 1.5 m (width x length x depth) trench. A cross section of the store is illustrated in Appendix 3.

Three different materials were used as a storage medium : dry sawdust, dry rice husk and the clear plastic wraps.

3.3.1.2 Experimental Treatments and Procedures

A. Lifting: Seedlings of about 1.5 cm diameter at the root collar level were lifted, stumped and immediately placed in the store at 15-day intervals from January 18 to May 3, 1971 giving a total of 8 lifting/storing dates. At each lifting date, about 350 seedlings were lifted from nursery beds at random throughout the 50 x 50 m nursery plot. Of these 240 uniform seedlings with unbranched tap-roots were selected for the experiment.

B. Storage and Storage Medium: At each lifting date, 240 seedlings were divided into 30 groups of 8 seedlings. The seedling groups were assigned at random according to the out-planting experimental design (Appendix 4) to 30 treatment combinations (3 x 2 x 5); i.e. 3 storage media, 2 field trials, and 5 blocks. The seedlings from all groups were then stumped and arranged in the store following the storing design given in Appendix 3.

C. Storage Period: Stored stumps were out-planted at the same time as the routine (control) stumps which were lifted one day before out-planting. Both stored and routine stumps were out-planted on June 16, 1971; the longest period of storage was about 5 months and the shortest was 45 days.

D. Planting Site and Planting: The effects of lifting date and storage on subsequent survival and growth of teak planting stumps were examined on two different sites : one wet and one dry. The "wet" site was located approximately 50 km north of the T.I.C., and the "dry" site was located approximately 250 km south of the T.I.C. (Appendix 1). The average annual rainfall and the mean temperature at the "wet" site were 1,715 mm and 25°C respectively; and those at the "dry" site were 1,048 mm and 27°C. The climatic conditions in both sites during the experiment are given in Appendix 2.

A split-plot design with 2 factors (storage medium and lifting date) and 5 blocks was applied to each planting site. Within each block, three main plots were allocated for three storage media and each main plot was divided into 9 sub-plot for 9 lifting dates (8 for stored stumps and 1 for the routine stumps). There were 27 (3 x 9) treatment combinations in each block, and each of these treatments contained 8 stumps. The total number of stumps planted at each site was 1,080. The experimental layout after randomization at each site is shown in Appendix 4.

The planting espacement used in this experiment was 1 x 1 m. Both planting sites were kept continuously free of weeds throughout the first growing season.

3.3.1.3 Measurements

A. Phenological Development Stage of Seedlings at the Time of Lifting: The stages of phenological development of the seedlings at the time of lifting were recorded in terms of bud dormancy and leaf development. The following information were recorded at each lifting date:

1. the number of mature leaves (pair) : full size leaves with firm, upper surfaces glossy;

2. the number of dormant buds (pair);
3. the number of leaves (pair) in the following categories:
   a. less than 5 cm in length,
   b. between 5 and 10 cm in length, and
   c. greater than 10 cm in length.

The degree of seedling dormancy or seedling sprouting was determined as a percentage of the total number of leaf and bud pairs in each seedling, as given in Appendix 7.

B. Survival and Height Growth: The number of live or sprouting stumps and height growth of stump sprouts were tallied and measured at the end of the first growing season - January 25, 1972 for the "wet" site and February 26, 1972 for the "dry" site.

C. Statistical Analyses: The methods of Cochran and Cox (1957) and Snedecor and Cochran (1971) were used. The analysis of variance for stump survival was calculated using the ArcSin$\sqrt{\%}$ transformed values, while for sprout height the analysis was based on height in centimetres. Least significant difference values (L.S.D.) were calculated for individual factors and interactions when variance ratios suggested that significant differences existed between means at the 5% level.

Note: The test of homogeneity of variances of data is shown in Appendix 11.

3.3.2 Results

Experimental results of the relative survival (%) and the height growth (cm) of sprouts produced by stumps which were lifted at different times, stored in different storage media, and out-planted at different sites ("wet" and "dry" sites) are presented in Appendix 8 and illustrated graphically in Figures 3.1 – 3.2. The analyses of variance for relative survival and height growth are presented in Tables 3.1 and 3.2, respectively.

3.3.2.1 Statistical Analyses

A. The analysis of variance for plant survival (Table 3.1) shows that:–

a. there was no significant difference between storage media at either planting site;

b. there were highly significant differences between lifting dates at both planting sites; and

c. there was no significant interaction between lifting date and storage medium at the "dry" site, but there was a highly significant interaction at the "wet" site.

B. For height growth, the analysis of variance (Table 3.2) shows that:

a. there was no significant difference between storage media at either planting site;

b. there were highly significant differences between lifting dates at both planting sites; and

c. there was no significant interaction between lifting date and storage medium at either planting site.

FIGURE 3.1a

"Wet" Site

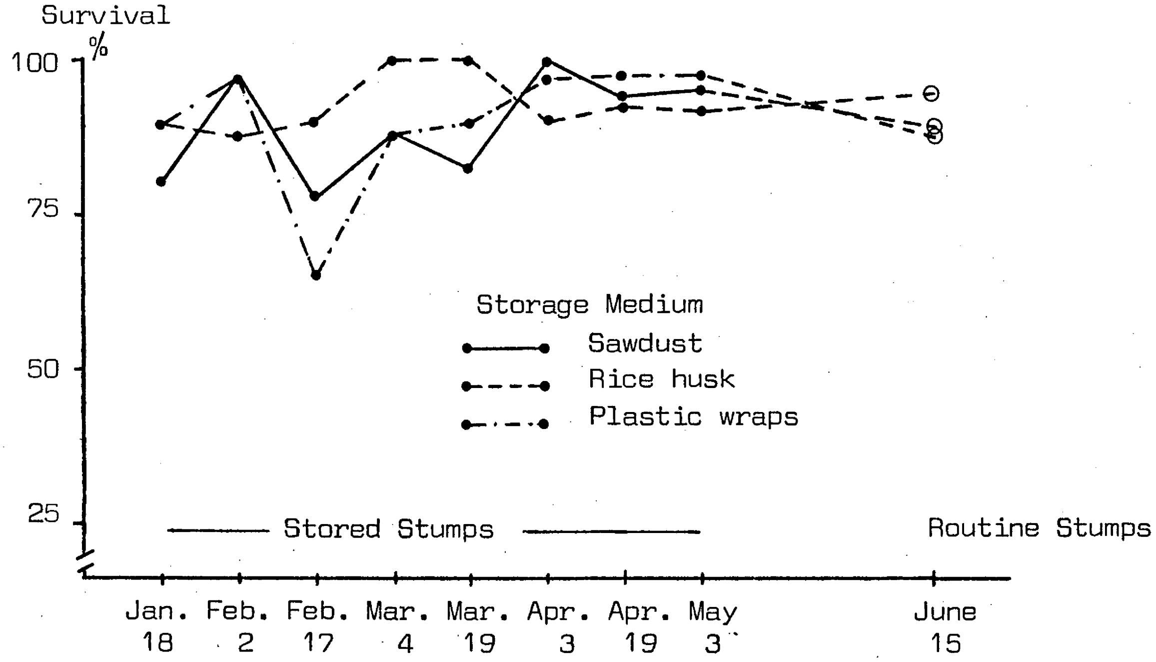


FIGURE 3.1b

"Dry" Site

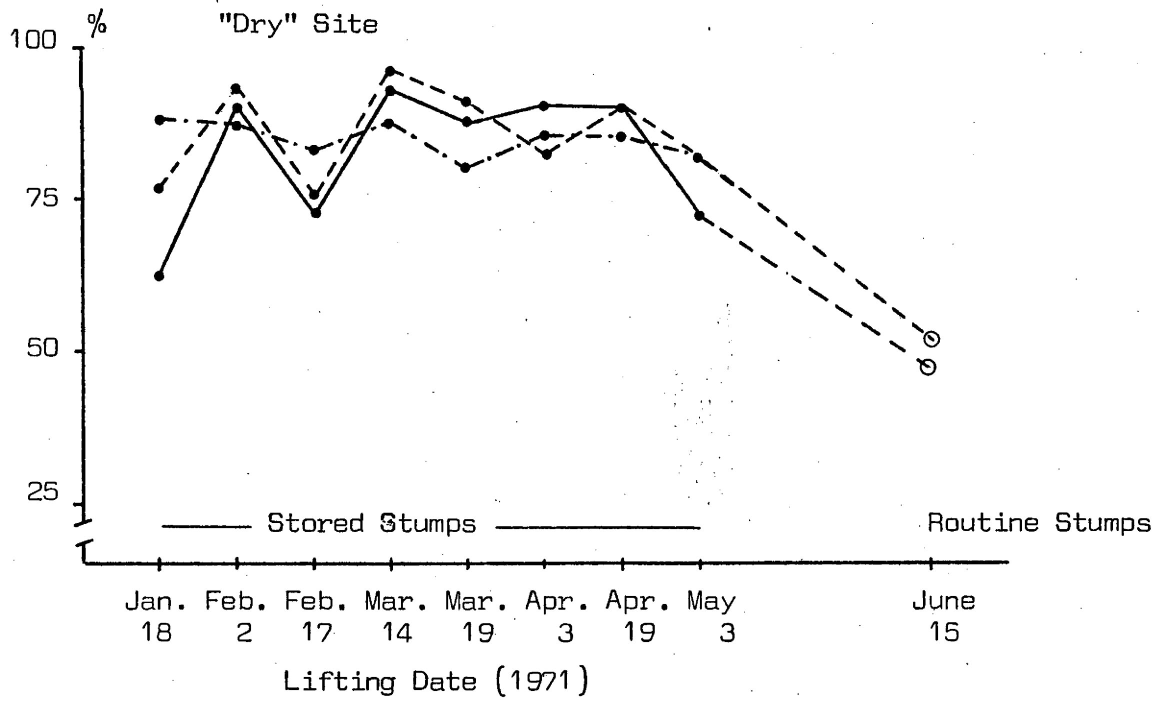


FIGURE 3.1 Effects of lifting date and storage medium on subsequent survival of teak planting stumps after out-planting to "wet" and "dry" planting sites.
(All stumps were out-planted on June 16, 1971)

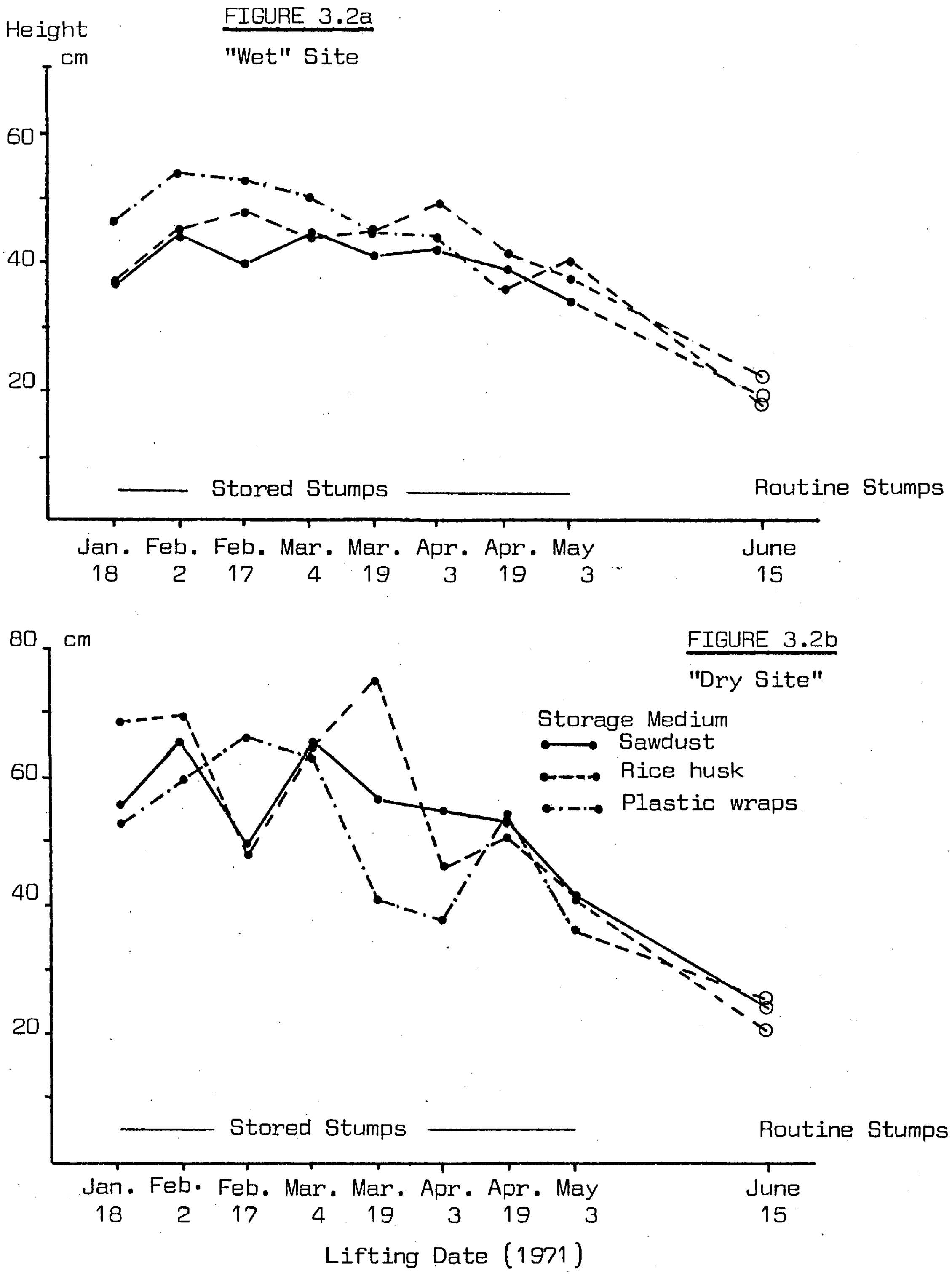


FIGURE 3.2 Effects of lifting date and storage medium on subsequent height growth of teak planting stumps after out-planting to "wet" and "dry" planting site
(All stumps were out-planted in June 16, 1971; height growth at the "wet" site was measured on Jan.25, 1972, at the "dry" site was measured on Feb.25, 1972).

TABLE 3.1 Analyses of variance for survival of stumps after out-planting for one growing season at "wet" and "dry" planting sites. (Data represent the ArcSin$\sqrt{\%}$ transformation values).

Source of Variation	df	s.s	m.s	F	
	"Wet Site"				
Blocks	4	516.4	129.1	1.1	ns
Storage medium	2	201.0	100.5	0.8	ns
Error (a)	8	969.1	121.1		
Lifting dates	(8)	(2231.9)	(279.0)	4.8	**
Stored vs Routine	1	2.7	2.7	0.1	ns
Among stored stumps	(7)	(2229.2)	(318.4)	5.4	**
Linear	1	709.9	709.9	12.1	**
Quadratic	1	25.5	25.5	0.4	ns
Cubic	1	217.1	217.1	3.7	ns
Deviations	4	1276.6	319.2	5.4	*
Lifting x Medium	(16)	(2080.9)	(130.0)	2.2	*
Stored vs Routine	2	49.4	24.7	0.4	ns
Among stored stumps	(14)	(2031.5)	(145.1)	2.5	**
Sawdust vs Rice husk	7	437.3	62.5	1.1	ns
Sawdust + Rice husk vs plastic	7	1594.1	227.7	3.9	**
Error (b)	96	5635.5	58.7		
Total	134	11634.6			
Among stored stumps + Int.	(21)	(4260.6)	(202.9)	3.5	**
Among plastic stored	7	487.9	69.7	1.2	ns
Sawdust vs Rice husk int.	7	437.3	62.5	1.1	ns
Sawdust + Rice husk	(7)	(3335.3)	(476.5)	8.1	**
Linear	1	803.2		13.7	**
Quadratic	1	204.1		3.5	ns
Cubic	1	193.8		3.3	ns
Deviations	4	2134.2	533.6	9.1	**

(Cont'd)

TABLE 3.1 (Cont'd)

Source of variation	df	s.s	ms	F	
	"Dry Site"				
Blocks	4	443.3	110.8	1.4	ns
Storage medium	2	90.3	45.2	0.6	ns
Error (a)	8	617.2	77.1		
Lifting date	(8)	(8779.6)	(1097.4)	8.1	**
Stored vs Routine	1	6541.6	6541.6	48.0	**
Among stored stumps	(7)	(2238.0)	(319.7)	2.4	*
Linear	1	68.2		0.5	ns
Quadratic	1	682.0		5.0	*
Cubic	1	3.0		0.02	ns
Deviations	4	1484.8	371.2	2.7	ns
Lifting x Medium	16	1351.1	84.4	0.6	ns
Error	96	13076.9	136.2		
Total	134	24358.4			

* significant difference at the 5% level
** significant difference at the 1% level
ns no significant difference at the 5% level

TABLE 3.2 Analysis of variance for height growth (cm) for plants on "wet" and "dry" sites

Source of Variation	d.f	Sum square	mean square	F	
"Wet Site"					
Blocks	4	5,345.4	1,336.4	8.5	**
Storage medium	2	588.3	294.2	1.9	ns
Error (a)	8	1,263.4	157.9		
Lifting date	(8)	(9,124.2)	(1,140.5)	14.7	**
Stored vs Routine	1	7,368.6	7,368.6	95.2	**
Among stored	(7)	(1,755.6)	(250.8)	3.2	**
Linear	1	525.5	525.5	6.8	*
Quadratic	1	850.5	850.5	11.0	**
Cubic	1	125.2	125.2	1.6	ns
Deviations	4	254.4	254.4	0.8	ns
Lifting x Medium	16	977.4	63.6	0.8	ns
Error (b)	96	7,433.5	77.4		
Total	134	24,732.3			
"Dry Site"					
Blocks	4	3,879.1	969.8	2.7	ns
Storage medium	2	664.4	332.2	0.9	ns
Error (a)	8	2,890.0	361.2		
Lifting date	(8)	(20,941.0)	(2,617.6)	9.9	**
Stored vs Routine	1	12,826.4	12,826.4	48.6	**
Among stored	(7)	(8,114.6)	(1,159.2)	4.2	**
Linear (-)	1	4,410.1	4,410.1	16.7	**
Quadratic	1	908.0	908.0	3.4	ns
Cubic	1	0.5	0.5		ns
Deviations	4	2,795.9	699.0	2.6	*
Lifting x Medium	16	5,029.7	314.4	1.2	ns
Error (b)	96	25,363.3	264.2		
Total	134	58,767.6			

3.3.2.2 Effects of Storage Medium

There were no overall significant differences in both survival and height growth of stump sprouts between the three storage media - sawdust, rice husk, and plastic wraps (Table 3.3). This suggests that there was no difference in the qualities of maintaining the survival and growth potential of teak planting stumps during storage in the underground store between these three different types of materials. However, the analysis of variance for stump survival at the "wet" site shows that there was significant interaction between storage medium and lifting date (Table 3.1). It indicates that the effect of storage medium on stump survival varied significantly with lifting date and planting site. Alternatively, the effect of lifting date on stump survival varied with storage medium and planting site. These findings will be presented in detail in the next section.

TABLE 3.3 Effects of storage medium on survival and height growth of teak planting stumps
(Data represents the mean of 8 lifting/storing dates and 5 blocks)

Storage Medium	"Wet" Site			"Dry" Site		
	Survival		Height	Survival		Height
	ArcSin $\sqrt{\%}$	%	cm	ArcSin $\sqrt{\%}$	%	cm
Sawdust	71.4	89.4	39.8	66.7	82.5	55.3
Rice husk	72.4	90.3	43.0	68.0	84.7	57.8
Plastic wrap	74.1	92.8	45.6	68.5	85.6	51.1
	ns		ns	ns		ns
S.E. (8df)	± 2.3		± 2.7	± 1.9		± 4.0
L.S.D.05	5.3		6.1	4.3		9.2

ns = no significant difference at the 5% level
% = the observed mean values

3.3.2.3 Effects of Lifting Date and Storage Period

A. The Difference Between Stored and Routine Stumps

There is clear evidence that stored stumps performed as well as or better than, routine stumps in terms of survival after out-planting to the field at the same time. Stored stumps were also superior to routine stumps in terms of the height growth of sprouts produced (Table 3.4). On the "wet" site there was no difference in survival between stored and routine stumps (90.8% for stored stumps and 90.7% for routine stumps); whereas on the "dry" site the survival of the stored stumps (84.2%) was much greater than that of the routine stumps (50.7%). The overall height growth of sprouts produced by the stored stumps was about twice as great as that of sprouts produced by the routine stumps for both "wet" and "dry" planting sites.

TABLE 3.4 Average survival and height growth of sprouts produced by stored and routine stumps after out-planting at the same time
(Data represent the mean of 8 lifting dates, 3 storage media, and 5 blocks for stored stumps; and represent the mean of 120 plants for routine stumps)

	"Wet" Site			"Dry Site"		
	Survival		Height	Survival		Height
	%	ArcSin $\sqrt{\%}$	cm	%	ArcSin $\sqrt{\%}$	cm
Stored Stumps	90.8	72.6	42.8	84.2	67.8	54.8
		ns	**		**	**
Routine Stumps	90.7	72.2	19.3	50.7	45.6	23.7

ns = no significant difference at the 5% level.
** = significant difference at the 1% level.
% = observed mean
ArcSin $\sqrt{\%}$ = ArcSin transformed mean

B. The Differences Among Stored Stumps

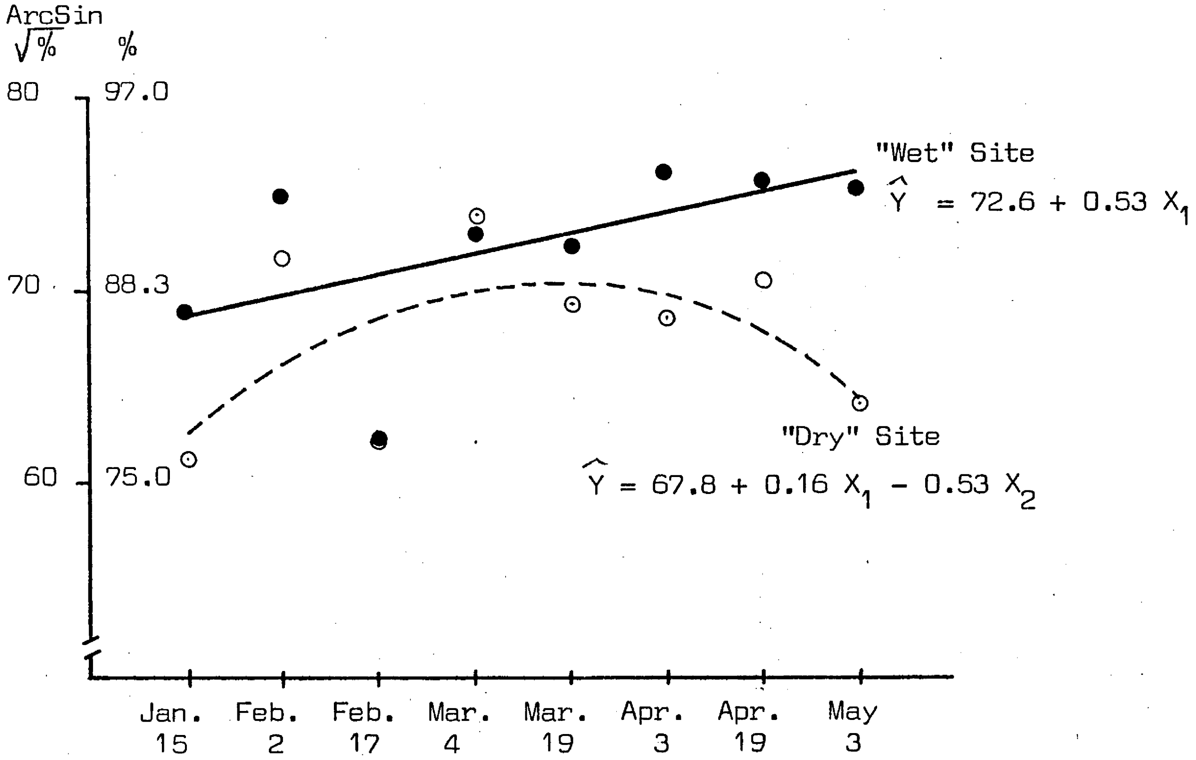
While stored stumps performed better than routine stumps, especially in terms of sprout height, the lifting date (and hence the storage period) was found to have some influences on the performance of stored stumps. The analyses of variance show that there were highly significant differences in both survival and height growth of stump sprouts between lifting dates of the stored stumps (Tables 3.1 and 3.2).

The survival of stored stumps after out-planting at the same time varied with lifting date from 77.5% (mid-February lifting) to 95.8% (early April lifting) at the "wet" site, and from 70.0% (mid-January lifting) to 92.5% (early March lifting) at the "dry" site (Table 3.5). The trend analyses showed significant linear and quadratic effects of lifting date on stump survival at the "wet" and "dry" sites respectively (Table 3.1). This suggests that the effects of lifting/storing date on stump survival were variable and would depend on site conditions. The fitted curves (Figure 3.3a) showed that the survival of stored stumps at the "wet" site increased progressively with the date of lifting and storing. In other words, the survival of stored stumps increased progressively with the decrease in the storage period. The effects of lifting date on the survival of stored stumps were more variable at the "dry" site (Figure 3.3a). This increased progressively with lifting date from mid-January, reached a maximum at mid-March lifting, and then declined markedly to early May lifting.

While the above results demonstrate the effects of lifting date on stump survival, there was significant interaction between lifting date and storage medium on stump survival at the "wet"

FIGURE 3.3a

Survival



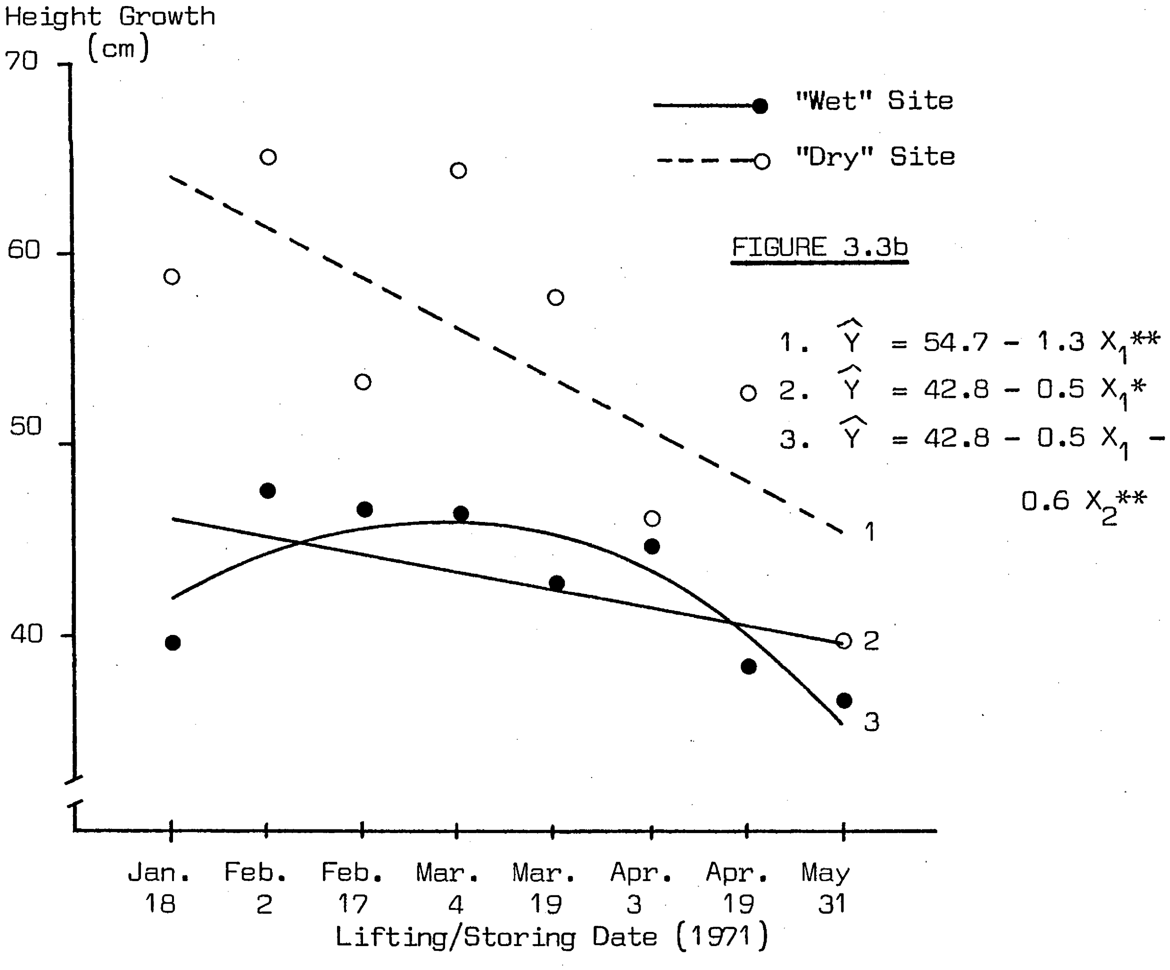


FIGURE 3.3 Effects of lifting/storing date on subsequent survival and height growth of teak planting stumps after out-planting to "wet" and "dry" planting sites

planting site (Table 3.1). This suggests that the differences in stump survival between lifting dates, at least in the "wet" site, varied significantly with the storage medium. Alternatively, the difference in stump survival between the three storage media varied with lifting date and planting site. The results summarized in Table 3.6 show that there was no significant difference in survival between the 8 lifting dates when the stumps were stored in plastic wraps, but there were highly significant differences between lifting dates when the stumps were stored either in sawdust or in rice husks. At the "dry" site, on the other hand there was no significant interaction between lifting date and storage medium. This clearly suggests that the differences in stump survival between lifting dates at this planting site were not influenced by the storage medium. These findings suggest that the influence of lifting date on stump survival could be ignored only when the stumps were kept in plastic wraps in the underground store and subsequently out-planted to the "wet" site.

The above evidence suggests that the overall survival of stored stumps would depend on the influence of both the lifting date and the interaction between the lifting date and the storage medium in the "wet" site. However, the relative influence of these factors and the interaction between them on stump survival is not determined. In contrast, the survival of the stored stumps in the "dry" site was influenced only by the lifting date.

In terms of height growth, there were highly significant differences in sprout height between lifting dates at both planting sites (Tables 3.1 and 3.2). At the "wet" site, the height of stump sprouts varied from 36.6 cm (early May lifting) to 47.6 cm (early February lifting), with an overall average of 42.8 cm. At the "dry" site, it varied from 39.8 cm (early May lifting) to 65.1 cm (early February lifting), with an overall average of 54.7 cm. There was no significant interaction between lifting date and storage medium at both the "wet" and "dry" sites (Table 3.2). This suggests that the differences in the height growth of sprouts produced were due primarily to the influence of the lifting date rather than to the influence of the storage medium. The trend analyses showed that there was a highly significant quadratic effect of lifting date on sprout height at the "wet" site, but a highly significant negative linear effect at the "dry" site (Table 3.2). Again, this would suggest an interaction effect between the lifting date and planting site condition on the subsequent growth of stump sprouts. The fitted curves (Figure 3.3b) showed the relationship between the sprout height and lifting date of stumps after out-planting at the same time. There was clear evidence that the height growth of stump sprouts decreased progressively from 63.8 cm (mid-January lifting) to 45.6 cm (early May lifting) with the lifting date at the "dry" site. At the "wet" site, the height growth of stump sprouts also tended to decrease with progressive lifting date, but the rate of decrease, however, was not constant. Based on the quadratic effect of lifting date, the height growth of sprouts at the "wet" site increased progressively from mid-January lifting (42.1 cm), reached a maximum at early March lifting (46.3 cm) and then declined markedly to early May lifting (35.1 cm).

These results suggest that there was a negative relationship between the lifting date and the height growth of sprouts after out-planting to the field at the same time. That is, the height growth of stump sprouts tended to decrease progressively with the date of lifting.

3.3.2.4 Summary of the Results

The results of the present study can be summarized as follows:-

1. Teak planting stumps can be lifted early from nursery beds and kept in the underground (uncooled) store for a period of 5 months (i.e. from mid-January to mid-June) without deterioration until the time of planting.

2. The field performance (in term of survival) of the stored stumps was equal to or better than that of the routine stumps; height growth of sprouts produced by the stored stumps was much greater than that of sprouts produced by the routine stumps after out-planting at the same time under the same planting condition.

3. There were no significant differences between the three storage media - sawdust, rice husk, and plastic wraps - in their abilities to maintain the survival and growth potential of the stored stumps; on the "wet" planting site the evidence suggest that the survival of stumps kept in the plastic wraps did not vary significantly with the date of lifting/storing whereas the survival of stumps kept in both sawdust and rice husk varied significantly with the date of lifting/storing of the stumps.

4. The survival of stumps after out-planting tended to increase progressively with lifting/storing date while sprout height, in contrast, tended to decrease progressively with the date of lifting/storing.

These findings will be discussed in further detail in Section 3.5.

TABLE 3.5 Effects of lifting date and storage period on survival of teak planting stumps after out-planting at the same time. (Data represent the mean of 3 storage media and 5 blocks)

Lifting Date (1971)	Storage Period (Month)	Observed Mean ($\bar{Y}$)				Adjusted Mean ($\hat{Y}$)	
		"Wet" Site		"Dry" Site		"Wet"	"Dry"
		%	ArcSin √%	%	ArcSin √%	ArcSin √%	
Stored stumps:							
Jan. 18	5.0	86.7	69.1	75.8	61.5	68.9	63.0
Feb. 2	4.5	94.2	75.2	90.0	71.8	70.0	66.5
Feb. 17	4.0	77.5	62.9	76.7	62.2	71.0	68.9
Mar. 4	3.5	91.7	73.3	92.5	73.9	72.1	70.3
Mar. 19	3.0	90.8	72.6	85.8	69.3	73.1	70.6
Apr. 3	2.5	95.8	76.4	85.8	68.8	74.2	69.9
Apr. 19	2.0	95.0	75.9	88.3	70.5	75.3	68.1
May 3	1.5	95.0	75.7	79.2	64.1	76.3	65.0
Routine stumps:							
June 15	0	90.8	72.2 **	50.8	45.6 **		
Standard error (96 df)			± 2.8		± 4.3		
LSD .05			5.6		8.4		
.01			7.4		11.2		

** significant difference at the 1% level.

Adjusted mean ($\hat{Y}$) :

"wet" site : $\hat{Y} = 72.6 + 0.53\, X_1$

"dry" site : $\hat{Y} = 67.8 + 0.16\, X_1 + 0.53\, X_2$

where X_1 and X_2 for $n = 8$ read from Table A 17 in Snedecor and Chochran (1971).

TABLE 3.6 Effects of lifting date and storage medium on the percentage of stump sprouting on the wet planting site (Data represent the mean of 5 blocks)

Lifting Date (1971)		Storage Medium				
		Saw-dust	Rice husk	Plas-tic		Mean Sawdust + Rice husk
		Survival (ArcSin$\sqrt{\%}$)				
Stored stumps:						
Jan. 18	ns	64.0	71.6	71.6	ns	67.8
Feb. 2	ns	77.7	77.7	70.3	ns	77.7
Feb. 17	**	62.7	54.3	71.6	**	58.5
Mar. 4	*	70.1	70.1	79.8	*	70.1
Mar. 19	*	65.8	72.2	79.8	*	69.0
Apr. 3	ns	79.8	77.7	71.6	ns	78.7
Apr. 19	ns	75.6	77.7	74.3	ns	76.6
May 3	ns	75.6	77.7	73.7	ns	76.6
		**	**	ns		**
S.E. (96 df)		± 4.8	± 4.8	± 4.8		± 3.4
L.S.D. .05		9.6	9.6	9.6		6.8
.01		12.7	12.7			9.0

Difference between two mean of storage media:

S.E. = ±5.1, L.S.D. .05 = 10.4

.01 = 14.0

*	significant difference at the 5% level
**	significant difference at the 1% level
ns	no significant difference at the 5% level

TABLE 3.7 Effects of lifting date or storage period on height growth (cm) of teak stump sprouts after out-planting at the same time. (Data represent the mean of 3 storage media and 5 blocks)

Lifting Date (1971)	Storage Period (month)	Observed mean ($\check{Y}$) "Wet" Site	Observed mean ($\check{Y}$) "Dry" Site	Adjusted mean ($\hat{Y}$) "Wet" Site Linear	Adjusted mean ($\hat{Y}$) "Wet" Site Quad.	Adjusted mean ($\hat{Y}$) "Dry" Site Linear
		(cm)	(cm)	(cm)	(cm)	(cm)
Stored stumps:						
Jan. 18	5.0	39.8	58.8	46.3	42.1	63.8
Feb. 2	4.5	47.6	65.1	45.3	44.7	61.2
Feb. 17	4.0	46.4	53.1	44.3	46.1	58.6
Mar. 4	3.5	46.3	64.6	43.3	46.3	56.0
Mar. 19	3.0	42.8	57.9	42.3	45.3	53.4
Apr. 3	2.5	44.6	45.9	41.3	43.1	50.8
Apr. 19	2.0	38.5	52.9	40.3	39.7	48.2
May 3	1.5	36.6	39.8	39.3	35.1	45.6
Routine stumps:						
June 15	0	19.3 **	23.7 **	*	**	**
Standard error		± 3.2	± 5.9			
L.S.D. .05		6.4	11.8			
.01		8.4	15.6			

* significant difference at the 1% level
** significant difference at the 5% level

Adjusted mean ($\hat{Y}$) :

"wet" site : linear function $\hat{Y} = 42.8 - 0.5\,X_1$

quadratic function $\hat{Y} = 42.8 - 0.5\,X_1 - 0.6\,X_2$

"dry" site : linear function $\hat{Y} = 54.7 - 1.3\,X_1$

where X_1 and X_2 for $n = 8$ read from Table A 17 in Snedecor and Cochran (1971).

3.4 STUDY 2 : EFFECTS OF LIFTING DATE, STORAGE, PLANTING TIME AND WEEDING TREATMENT

The previous study (Study 1) on the effects of lifting date and storage on subsequent survival and height growth of teak planting stumps after out-planting to the field indicated:

1. that teak stumps can be lifted early and kept safely in the underground (uncooled) store;
2. that the survival and height growth of the stored stumps were generally greater than that of the routine stumps after out-planting at the same time.

This second study further investigates and re-examines the effects of lifting date, long term storage, planting time, and weeding treatment on the field performance of teak planting stumps. In this study, teak stumps were lifted from nursery beds and kept in the underground store at one month intervals from mid-October (the end of the rainy season) to mid-March (the beginning of the following rainy season). These stored stumps were out-planted together with the routine or the freshly prepared stumps at four different times, starting from the end of April to mid-July at approximately one month intervals, and under two different weeding treatments (slashing and scraping). The longest period of the storage of teak planting stumps in this study was about 9 months, that is, the stumps were lifted and stored in mid-October and out-planted in mid-July.

The main purposes of this study are:-

(a) to re-examine the effectiveness of the underground (uncooled) store which provided satisfactory results in maintaining the survival and growth potential of teak planting stumps in Study 1;

(b) to examine the effects of long term storage, the effects of lifting date on the field performance of teak planting stumps;

(c) to determine the optimum time for planting of teak stumps; and

(d) to examine the effects of weeding methods on both survival and height growth of teak stumps.

The experimental detail and the experimental results obtained in this study are described in the following sections.

3.4.1 Materials and Methods

This study was conducted in Thailand in 1971-1973.

3.4.1.1 Materials

A. Plant Materials: Teak seeds collected from natural forests in Lampang were sown in the N.T.N.C. on April 10-13, 1971. The first seedlings were lifted for the experiment on October 15, 1971. The climatic conditions at the N.T.N.C. while this study was conducted are given in Appendix 2.

B. Underground Store and Storage Medium: The underground store was the same as that used for Study 1 (Section 3.3.1.1 - B). The results in Study 1 showed that there was no significant difference in the ability to maintain the survival and growth potential of the stored stumps between storage media (i.e. sawdust, rice husk, and plastic wrap). Consequently sawdust (the cheapest storage material) was used as the storage medium.

C. Site for Field Trial: The trial was established at about 48 km north of the T.I.C. Climatic conditions of this site during the experiment are given in Appendix 2.

3.4.1.2 Experimental Treatments

A. Lifting Date: Seedlings of about 1.5 cm diameter at the root collar level were lifted, stumped, and immediately stored at one month intervals from October 15, 1971 to March 15, 1972, giving a total of 6 lifting and storing dates. The stored stumps were out-planted with the routine stumps (the control) which were lifted and prepared one day before out-planting.

B. Planting Date: The stored stumps were out-planted together with the routine stumps (the control) at four different times ranging from the end of the hot season to the middle of the rainy season i.e. April 27, May 22, June 15, and July 11, 1972.

C. Weeding Treatment: Two weeding methods - slashing and scraping or hoeing - were applied to the trial. Slashing is the most common method used in teak plantation establishment in Thailand. The weeds were slashed at approximately 5 - 15 cm above ground. In the scraping plots, the weeds were scraped out and the ground was kept free of weeds throughout the duration of the experiment.

3.4.1.3 Experiment Designs and Procedures

This experiment used a completely randomized design for lifting the seedlings from nursery beds and a split-split plot design with 3 factors and 4 blocks for field trial.

A. Lifting: The nursery beds were divided into 125 plots of size 1 x 25 m. Five plots were selected at random for lifting the seedlings at each lifting date and 120 seedlings were lifted at random from each plot - a total of 600 seedlings were lifted at each lifting date. Only 512 uniform seedlings with good form and unbranched tap-roots were selected for the experiment.

The routine stumps (the control) were lifted at each planting time. A total number of 128 routine stumps were used at each planting time.

B. Storage: At each lifting date, the 512 seedlings were divided at random into 4 groups - one for each of the four planting dates - of 128 seedlings each. The seedlings were stumped and placed in the underground store as illustrated in Appendix 5.

C. Planting: A 4-block split-split plot design for 3 factors (i.e. weeding, planting, and lifting) was used in the field trial (Appendix 6). Each block was divided into 2 main plots for 2 weeding methods; each main plot was divided into 4 sub-plots for 4 planting times; each sub-plot was divided into 9 sub-sub-plots for 7 lifting dates (6 for stored stumps and 1 for the routine stumps or the control) plus 2 blanks. All main plots, sub-plots, and sub-sub-plots were allocated at random and the experimental layout after randomization is illustrated in Appendix 6.

There were 16 stumps being planted in each sub-sub-plot and the total number of stumps used in this experiment was 3,584. The planting espacement was 1 x 1 m.

3.4.1.4 Measurement

A. Phenological Development Stages of Seedlings at Lifting: The stages of phenological development of the seedlings at each lifting date were recorded in terms of size, colour, and the maturity of seedling leaves. The number of seedlings at each lifting date, were recorded in the following classifications:

1. seedlings with fully matured leaves;
2. seedlings with old or brown or yellowish leaves;
3. leafless seedlings;
4. sprouting seedlings.

The data on the phenological development of seedlings are given in Appendix 7.

B. Survival and Height Growth: The number of live or sprouting stumps and height growth of stump sprouts were tallied and measured at the end of the first growing season, i.e. January 22-23, 1973.

C. Statistical Analyses: The analysis of variance of the split-split plot design for both survival and height growth were calculated as in Study 1 (Section 3.3) on the ArcSin$\sqrt{\%}$ and the logarithmic transformation values, respectively.

One lifting date (November 15, 1971) has been deleted from the analysis of stump survival. During packing of the stored stumps for out-planting it was observed that a number of stumps lifted and stored in mid-November were dry and had decayed during storage. This was probably due to some error in storing technique. The survival of these stumps was extremely low in comparison with that of stumps lifted and stored at any other date (Appendix 9). The results for

November lifting were considered to be biased and were not included in the analysis of variance for plant survival.

Note: The test of homogeneity of variances of data is shown in Appendix 11.

3.4.2 Results

All experimental data are summarized in Appendix 9 and illustrated in Figures 3.4 and 3.5. This shows the mean values for survival (%) and height growth (cm) of sprouts produced by stumps which were lifted and stored at different dates and planted at different times in plots where different weeding methods were used.

3.4.2.1 Statistical Analyses: The analysis of variance for survival (ArcSin $\sqrt{\%}$) and height growth (log cm) are presented in Tables 3.8 and 3.9 respectively.

A. The analysis of variance for plant survival (Table 3.8) shows that:-

(a) there was no significant difference between the two weeding methods;

(b) there were highly significant differences between planting times and between lifting dates;

(c) there were no significant interactions between planting time and weeding method, and among lifting date, weeding method and planting times; and

(d) there were significant interactions between lifting date and weeding method, and between lifting date and planting time.

B. The analysis of Variance for Height Growth (Table 3.9) shows that:-

(a) there were significant differences between the two weeding methods, between planting time, and between lifting dates;

TABLE 3.8 Analysis of variance for survival (ArcSin $\sqrt{\%}$) of teak planting stumps. (Excluded November lifting)

Source of variation	df	SS	MS	F	
Blocks	3	2,046.4	682.1	1.5	ns
Weeding method	1	1,989.8	1,989.8	4.4	ns
Error (a)	3	1,353.1	451.0		
Planting date	(3)	(2,543.7)	(847.9)	6.4	**
Linear	1	1,186.6		9.0	**
Quadratic	1	1,150.0		8.8	**
Cubic	1	207.1		1.6	ns
Planting X Weeding	3	326.0	108.6	0.8	ns
Error (b)	18	2,365.0	131.4		
Lifting date	(5)	(1,668.5)	(333.7)	3.5	**
Stored vs Routine	1	1,144.7	1,144.7	6.8	*
Among stored stumps	4	523.8	130.9	1.7	ns
Lifting x Weeding	(5)	(1,084.4)	(216.9)	2.3	ns
Stored vs Routine	1	875.4	875.4	5.2	*
Among stored stumps	4	209.0	52.3	0.7	ns
Lifting x Planting	(15)	(2,706.1)	(180.4)	1.9	*
Stored vs Routine	3	978.8	326.3	1.9	ns
Among stored stumps	12	1,727.3	143.9	1.9	ns
Error (c)	(120)	(11,353.0)	(94.6)		
Stored vs Routine	24	4,052.6	168.9	2.2	**
Among stored stumps	96	7,300.4	76.0		

ns no significant difference at the 5% level

* significant difference at the 5% level

** significant difference at the 1% level

TABLE 3.9 Analysis of variance for height growth (log cm) of stump sprouts. (Included November lifting)

Source of variation	df	SS	MS	F	
Blocks	3	0.6486	0.2162	1.0	ns
Weeding method	1	6.3416	6.3416	30.4	*
Error (a)	3	0.6248	0.2083		
Planting date	(3)	(2.8550)	(0.9517)	10.0	**
Linear	1	2.2099		2.3	ns
Quadratic	1	0.5198		5.5	*
Cubic	1	0.1253		1.3	ns
Planting x Weeding	3	0.2570	0.2244	2.4	ns
Error (b)	18	1.7084	0.0949		
Lifting date	(6)	(2.1430)	(0.3572)	22.9	**
Stored vs Routine	1	1.0818	1.0818	69.3	**
Among stored stumps	(5)	(1.0612)	(0.2133)	13.7	**
Linear	1	0.4756		30.9	**
Quadratic	1	0.0238		1.5	ns
Cubic	1	0.2690		17.5	**
Deviation	2	0.2928	0.1464	9.5	**
Lifting x Weeding	(6)	(0.2570)	(0.0428)	2.7	*
Stored vs Routine	1	0.0612	0.0612	3.9	ns
Among stored stumps	5	0.1958	0.0392	2.5	**
Lifting x Planting	(18)	(0.6508)	(0.0362)	2.3	**
Stored vs Routine	(3)	(0.2164)	(0.0721)	4.6	*
Linear	1	0.1525		9.8	**
Quadratic	1	0.0005		0.03	ns
Cubic	1	0.0633		4.1	ns
Among stored stumps	(15)	(0.4344)	(0.0290)	1.9	*
Linear	5	0.1349	0.0270	1.7	ns
Quadratic	5	0.1602	0.0320	2.0	ns
Cubic	5	0.1393	0.0279	1.8	ns
Error (c)	(144)	(2.2432)	(0.0156)		
Stored vs Routine	24	0.3983	0.0166		
Among stored stumps	120	1.8449	0.0154		

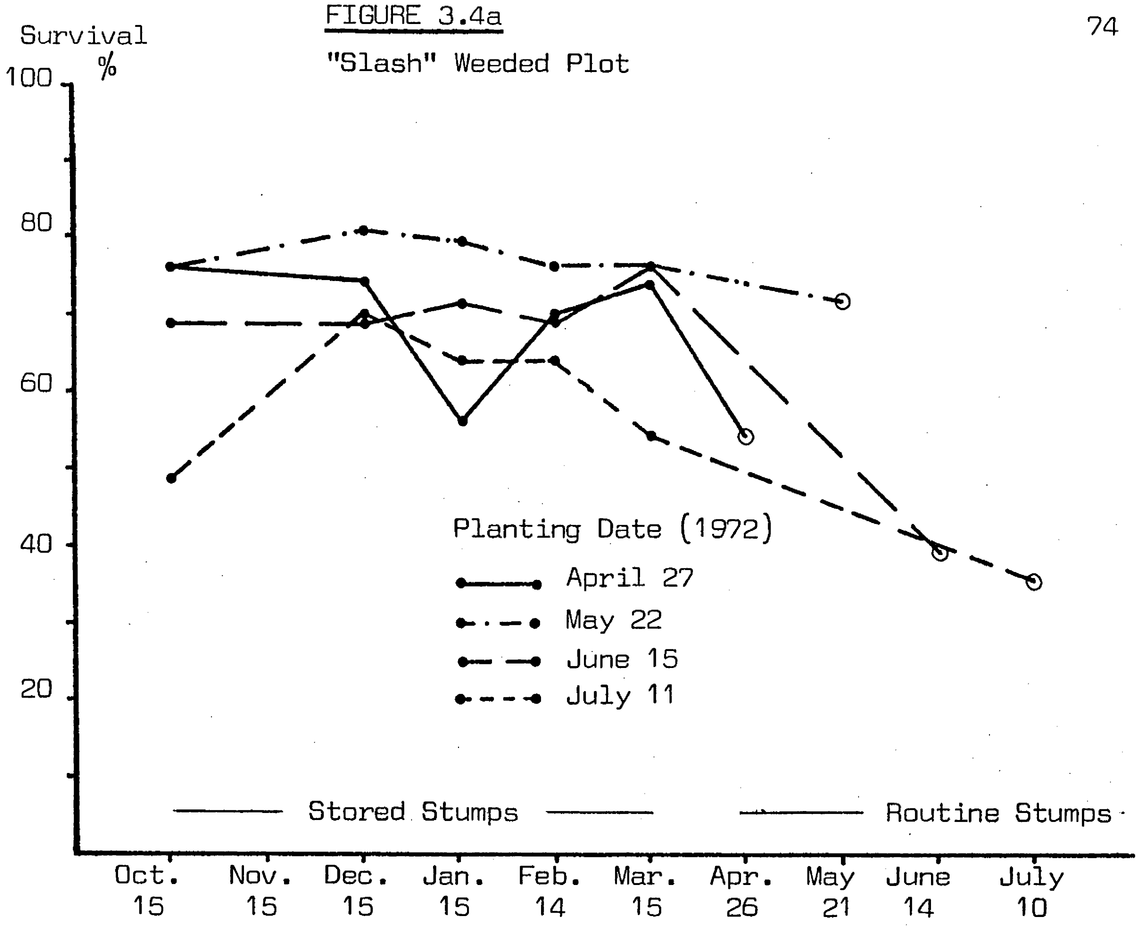


FIGURE 3.4a

"Slash" Weeded Plot

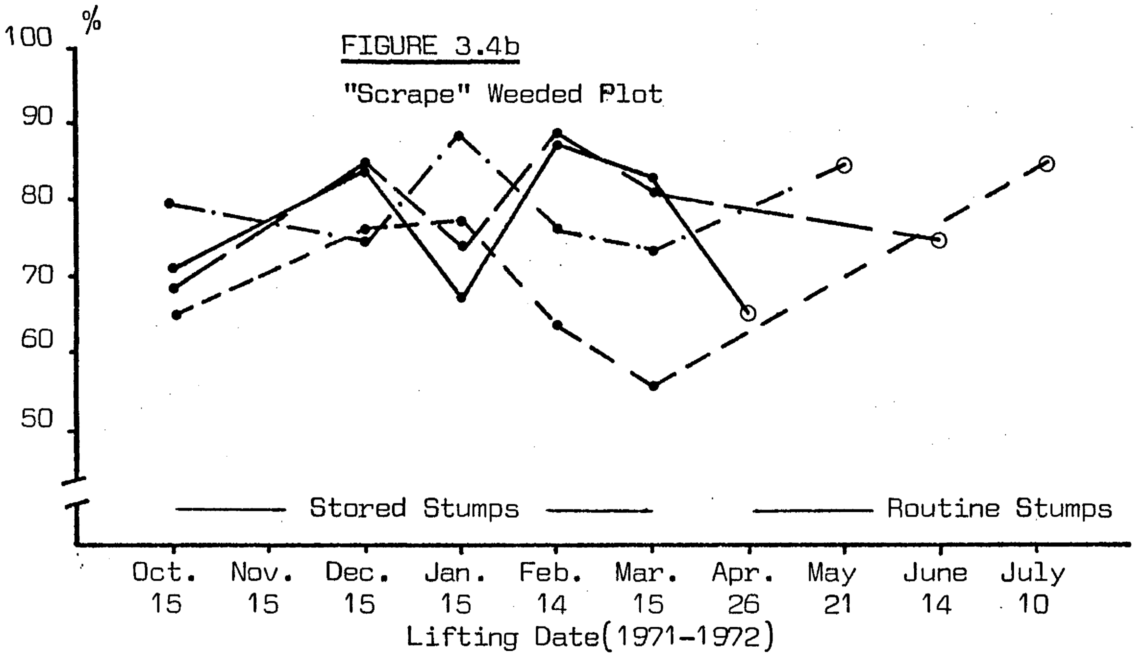


FIGURE 3.4b

"Scrape" Weeded Plot

FIGURE 3.4 Effects of lifting date and planting time on subsequent survival of teak planting stumps after out-planting under the two weeding treatments

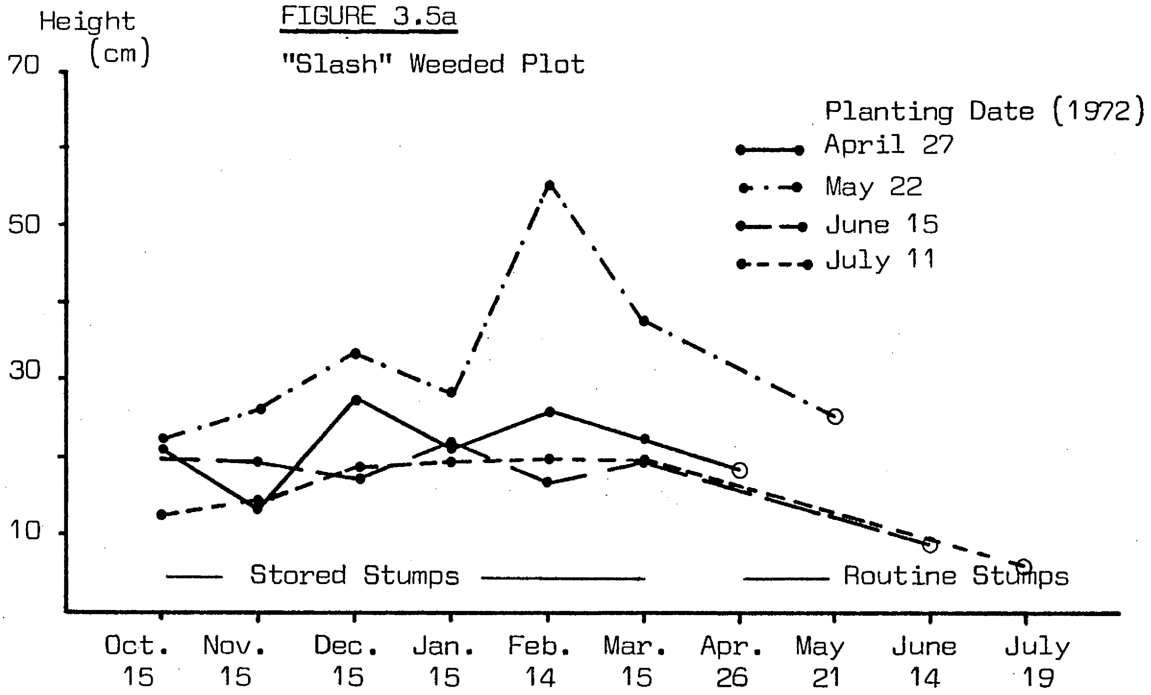


FIGURE 3.5a

"Slash" Weeded Plot

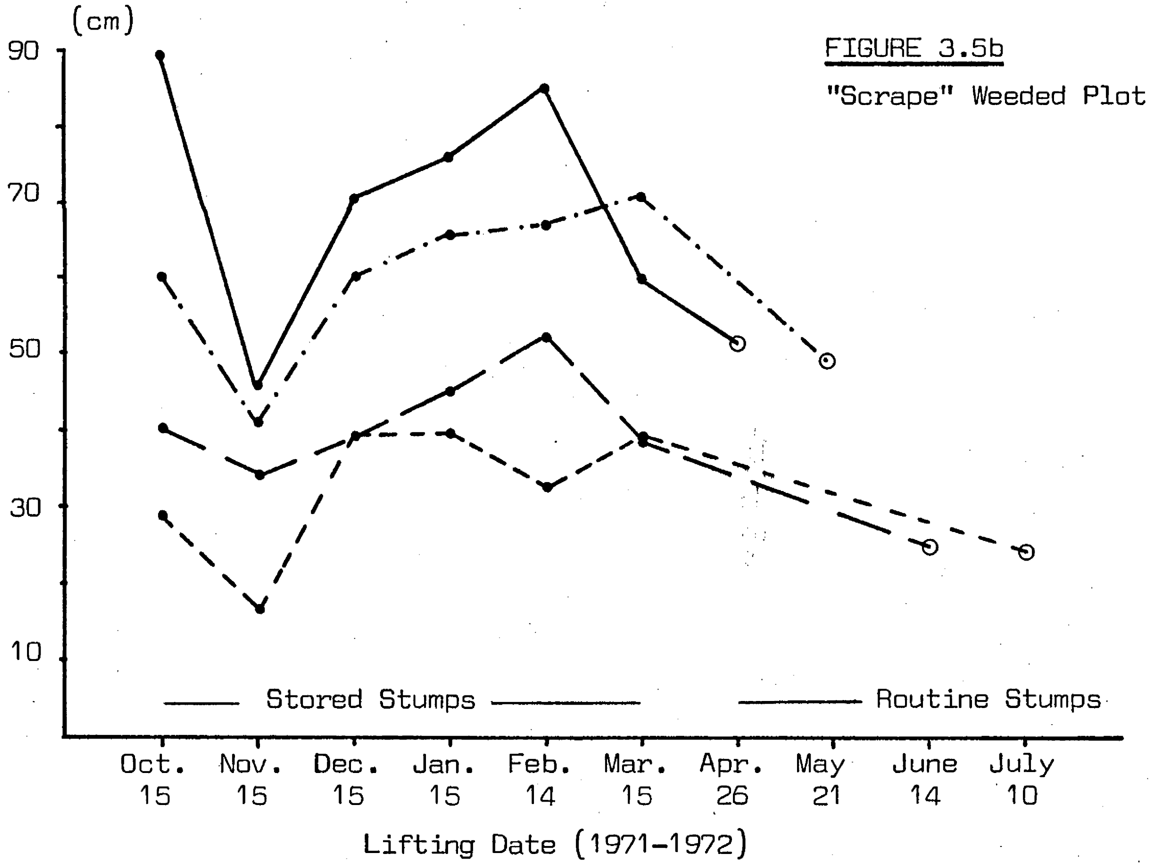


FIGURE 3.5b

"Scrape" Weeded Plot

FIGURE 3.5 Effects of lifting date and planting time on subsequent height growth of teak planting stumps after out-planting under the two weeding treatments

(b) there were no significant interactions between planting date and weeding method, or among lifting date, weeding method, and planting time; and

(c) there were significant interactions between lifting date and weeding method, and between lifting date and planting date.

3.4.2.2 Effects of Weeding Treatment

A. Survival: The results summarized in Table 3.10 show that there was no significant effect of weeding treatment on stump survival: the survival of teak stumps grown in the "slash" weeded plot was 66.6% and those grown in the "scrape" weeded plot was 75.9%. Moreover, the analysis of variance for plant survival shows that there were no significant interactions between weeding treatment and planting time, between weeding treatment and lifting date, and among weeding treatment planting time and lifting date. These results clearly indicate that at any planting time or lifting date there was no difference in stump survival between the two weeding treatments (Tables 3.11 and 3.12). In other words, the survival of teak stumps during the first year after out-planting to the field was not dependent on the method of weeding practice.

TABLE 3.10 Effects of weeding treatment on survival and growth of teak planting stumps
(Data represent the mean of planting times, lifting dates, and 4 blocks)

Weeding Method	Survival		Height Growth	
	ArcSin $\sqrt{\%}$	%	log cm	cm
Slashing	55.5	66.6	1.32	22.1
Scraping	62.0	75.9	1.65	49.9
	ns		*	
S.E. (3 df)	± 3.1		±0.06	
L.S.D. .05	9.8		0.19	
.01	–		0.36	

(%) and (cm) : the observed value means

TABLE 3.11 Effects of planting time and weeding method on subsequent survival and height growth of teak planting stumps
(Data represent the mean of 7 lifting dates and 4 blocks)

Planting Time (1972)	Weeding Method					
	Slashing		Scraping	Slashing		Scraping
	ArcSin$\sqrt{\%}$			log cm		
April 27	56.2	ns	62.1	1.30	**	1.82
May 22	62.4	ns	64.9	1.46	*	1.76
June 15	54.8	ns	62.6	1.34	*	1.57
July 11	48.6	ns	58.2	1.17	*	1.46
	**		ns	**		**
L.S.D. .05	7.0		7.0	0.17		0.17
.01	9.5		9.5	0.24		0.24
S.E. (18 df)		± 3.3			± 0.08	

Comparisons between two means of weeding method for the same planting time:

Survival : S.E. = ± 4.2, L.S.D. .05 = 11.2
Height = S.E. = ± 0.09, L.S.D. .05 = 0.23
.01 = 0.39

TABLE 3.12 Effects of lifting date and weeding method on the production of sprouts of stored stumps
(Data represent the mean of 4 planting dates and 4 blocks)

Lifting Date (1971-72)	Survival			Height Growth		
	Slashing		Scraping	Slashing		Scraping
	ArcSin $\sqrt{\%}$			log cm		
Stored stumps:						
October 15	55.8	ns	58.2	1.26	**	1.70
November 15	-		-	1.26	*	1.48
December 15	60.1	ns	64.9	1.40	*	1.70
January 15	56.5	ns	62.8	1.38	**	1.73
February 14	57.0	ns	64.6	1.44	*	1.75
March 15	58.5	ns	60.0	1.39	*	1.70
Routine stumps:	45.3	*	61.3	1.11	**	1.52
	*		ns	**		**
L.S.D. .05	6.8		6.8	0.09		0.09
.01				0.11		0.11
S.E.		± 3.4 (120 df)			± 0.04 (144 df)	

Comparisons between two means of weeding methods for the same lifting date:

Survival : S.E. = ± 4.4, L.S.D. .05 = 11.3
.01 = 18.4

Height : S.E. = ± 0.07, L.S.D. .05 = 0.21
.01 = 0.35

B. Height Growth: The results obtained in this study show that the weeding treatment had a marked influence on height growth of stumps sprouts. On the average, height growth of sprouts grown in the "scrape" weeded plot (49.9 cm) was about twice as great as that of sprouts grown in the "slash" weeded plot (22.1 cm) (Table 3.10). The analysis of variance for these results show that there was significant interaction between weeding treatment and lifting date, and there were no significant interactions between weeding treatment and planting time and among weeding treatment, planting time, and lifting date. The significant interaction between weeding treatment and lifting date implies that the difference in sprout height between the two weeding treatments varied significantly with the date of lifting stumps, or alternatively the difference in sprout height between the seven lifting dates varied significantly with weeding treatment. The results summarized in Tables 3.11 and 3.12 show the differences in sprout height between the two weeding treatments at each planting time and each lifting date. There is clear evidence that, at any planting time (Table 3.11) and any lifting date (Table 3.12) the height growth of stump sprouts grown in the "scrape" weeded plot was significantly greater than that of sprouts grown in the "slash" weeded plot.

3.4.2.3 Effects of Planting Time

The analyses of variance for both survival and height growth show significant effects of planting time on the field performance of teak planting stumps. Within the four planting times, the overall survival and height growth of stump sprouts were both maximal at the May planting (78.3% for survival and 46.3 cm for height), and minimal at the July planting (63.3% for survival and 29.9 cm for height) (Table 3.13). The trend analyses (Tables 3.8 and 3.9) indicate highly significant linear and quadratic effect of planting time on stump survival, and a significant quadratic effect of planting time on sprout height. The fitted parabolic curves for both survival and height growth of stump sprouts in relation to planting time are shown in Table 3.13 and Figure 3.6. The survival of stumps increased markedly from the April planting to a maximum at the May planting, and then declined progressively with the time of planting to the July planting (Figure 3.6a). Similarly, height growth of stump sprouts was maximal when planting was done between the end of April and the end of May, and it declined progressively with the time of planting from the end of May to mid-July. The differences in both survival and height growth of stump sprouts obtained in this study may be due either to the conditions of climate at the time of planting or to the length of the growing period, i.e. from the time of planting to the end of the experiment. However, these factors affecting the performance of the teak stumps after out-planting would not be determined.

The analyses of variance show that there were significant interactions between planting time and lifting date for both survival and height growth of stump sprouts, and there were no significant interactions between planting time and weeding treatment, and among planting time lifting date and weeding treatment for both survival and height growth. The significant planting time and lifting date interactions suggests that the differences in both survival and height of stump sprouts between the four planting times varied with the date of lifting stumps. Alternatively, the differences in both survival and

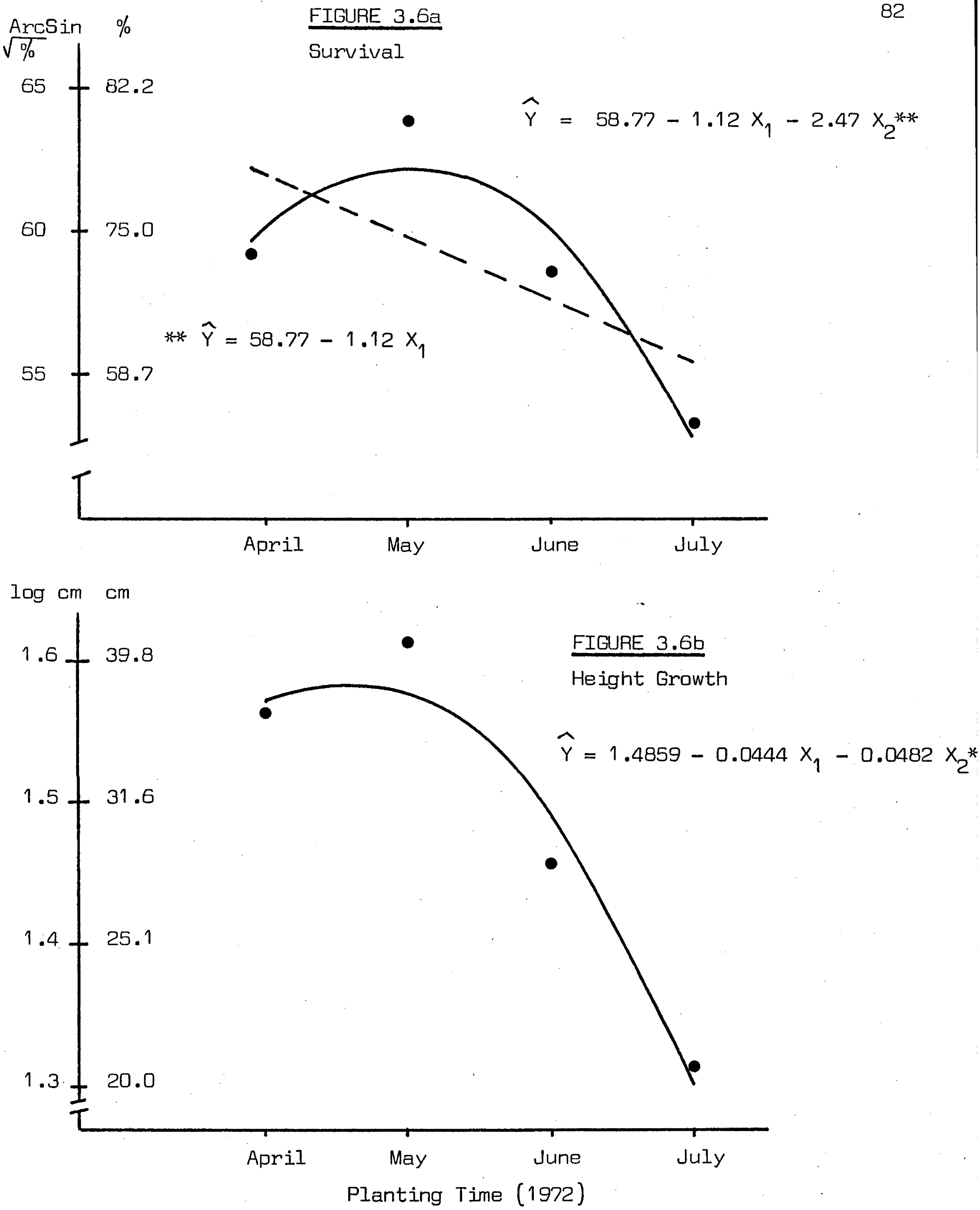


FIGURE 3.6 Effects of planting time on survival and height growth of teak planting stumps

TABLE 3.13 Effects of planting time on survival and height growth of teak planting stumps
(Data represent the mean of lifting dates, weeding methods and 4 blocks)

Planting Time (1972)	Survival		Height Growth		Parabolic adjusted mean values		
					Survival	Height	
	ArcSin$\sqrt{\%}$	%	log cm	cm	ArcSin $\sqrt{\%}$	log cm	(cm)
April 27	59.2	72.2	1.56	45.3	49.7	1.57	(37.2)
May 22	63.8	78.3	1.61	46.3	62.4	1.58	(38.0)
June 15	58.7	71.3	1.46	28.7	60.1	1.49	(30.9)
July 11	53.4	63.3	1.32	23.9	52.9	1.30	(19.9)
	**		**				
S.E. (18 df)	± 2.3		± 0.06				
L.S.D. .05	4.9		0.12				
.01	6.7		0.18				

** significant difference at the 1% level,

ArcSin $\sqrt{\%}$ and log cm : the means of the transformed values

% and cm : the means of the observed values,

Parabolic adjusted mean values:

Survival : $\hat{Y} = 58.8 - 1.12\,X_1 - 2.47\,X_2$

Height : $\hat{Y} = 1.49 - 0.04\,X_1 - 0.05\,X_2$

where X_1 and X_2 are from the orthogonal set of multipliers at 4 n (From Table A17, Snedecor and Cochran, 1971)

TABLE 3.14 Effects of planting time and lifting date on survival and height growth of teak planting stumps (Data represent the mean of 2 weeding treatments and 4 blocks)

Lifting Date (1971-1972)	Planting Date (1972)					
	April 27	May 22	June 15	July 11		
	Survival (ArcSin√ %)					
Stored stumps:						
October 15	59.6	63.6	56.3	49.1	**	
November 15	-	-	-	-		S.E. ±5.0
December 15	63.6	63.3	62.9	60.1	ns	L.S.D.
January 15	52.5	68.3	59.7	58.1	**	.05 = 10.3
February 14	63.7	62.1	64.1	53.4	*	.01 = 13.4
March 15	64.2	61.5	63.1	48.3	**	
Routine stumps:	51.5	64.0	46.1	51.6	**	
	**	ns	**	**		

S.E. = ± 4.9 (120 df)

L.S.D. (.05) = 9.6, L.S.D. (.01) = 10.5

	Height Growth (log cm)					
Stored stumps:						
October 15	1.63	1.55	1.45	1.27	**	
November 15	1.38	1.49	1.45	1.15	**	S.E. = ±0.08
December 15	1.63	1.64	1.50	1.43	*	L.S.D.
January 15	1.60	1.62	1.58	1.43	*	(.05) = 0.17
February 14	1.66	1.77	1.55	1.39	**	(.01) = 0.22
March 15	1.56	1.69	1.48	1.45	**	
Routine stumps:	1.46	1.52	1.20	1.08	*	
	**	**	**	**		

S.E. = ± 0.06 (144 df)

L.S.D. (.05) = 0.12, L.S.D. (.01) = 0.16

height of stump sprouts between the lifting dates varied with the time of planting. The results given in Table 3.14 show the differences in both survival and height growth of stump sprouts between the four planting times at each lifting date. It appears that there was no significant effect of planting time on stump survival at the mid-December lifting, whereas the survival of stumps which were lifted at the remaining dates differed significantly between planting times. At any lifting date, there was a significant difference in sprout height between planting times.

3.4.2.4 Effects of Lifting Date

Although the analyses of variance show highly significant differences between lifting dates, the effects of lifting date on the field performance of teak planting stumps may be oversimplified because there are many factors such as planting time, weeding method and stump storage involved in these differences. Therefore, comparisons of stored and routine stumps, and of lifting date among the stored stumps in both survival and height growth are described separately in an attempt to explain the effect of lifting date on the performance of teak stumps after out-planting.

A. The Differences Between Stored and Routine Stumps: The overall field performance (in terms of survival and height growth) of the stored stumps was significantly better than that of the routine stumps. The average survival and height growth of the stored stumps were 73.0% and 37.7 cm, respectively; whereas those of the routine stumps were 62.5% and 25.8 cm (Table 3.15). For these comparisons, the analyses of variance show a significant interaction between lifting date and weeding treatment for stump survival and show a significant interaction between lifting date and planting time for height growth. These imply that the difference in survival between the stored and routine stumps varied significantly with the method of weeding practice, and the difference in sprout height between the stored and routine stumps varied with the time of planting. Alternatively, the difference in survival between weeding treatments varied with stored and routine stumps, and the difference in sprout height between the time of planting varied with stored and routine stumps.

From comparisons of stored and routine stumps at each weeding treatment (Table 3.15), there was no significant difference in survival between the stored and routine stumps in the "scrape" weeded plot (76.1% for stored stumps and 74.8% for routine stumps), whereas in the "slash" weeded plot the difference between these two types of stumps was significant (69.9% for stored stumps and 50.3% for routine stumps). In terms of height growth, the performance of the stored stumps was much better than that of the routine stumps under both weeding treatments.

From comparisons of stored and routine stumps at each planting time (Table 3.16), there were no significant differences in survival between the stored and routine stumps which were out-planted at the same time in April, May and July respectively. Stumps planted in June provided the one exception to this pattern, that is, the survival of stored stumps was significantly greater than that of the routine stumps. Since there was no significant interaction between lifting date and planting time in the comparison of stored and routine stumps (Table 3.8), the difference in survival between the stored and the

TABLE 3.15 Effects of weeding treatment on survival and height growth of stored and routine stumps

Weeding Method	Survival					Height Growth				
	Stored Stumps			Routine Stumps		Stored Stumps			Routine Stumps	
	(%)	ArcSin $\sqrt{\%}$			(%)	(cm)	log cm			(cm)
Scraping	(76.1)	62.1	ns	63.3	(74.8)	(52.2)	1.68	**	1.52	(36.6)
Slashing	(69.9)	57.6	*	45.3	(50.3)	(23.3)	1.35	**	1.11	(15.0)
Average	73.0	59.8	*	53.3	62.5	37.7	1.51	**	1.32	25.8

Difference between stored and routine stumps for the same weeding method:

Survival : - SE = ± 4.6 (24 df) Height growth:- SE = ± 0.05 (24 df)

L.S.D. .05 = 9.5 L.S.D. .01 = 0.13
.01 = 12.8

TABLE 3.16 Effects of planting date on survival and height growth of stored and routine stumps

Planting Date	Survival			Height Growth		
	Stored		Routine	Stored		Routine
	ArcSin$\sqrt{\%}$			log cm		
April 27	60.7	ns	51.5	1.58	ns	1.46
May 22	63.7	ns	63.9	1.63	ns	1.52
June 15	61.2	*	46.1	1.50	**	1.20
July 11	53.8	ns	51.6	1.35	**	1.08

Difference between stored and routine stumps for the same planting date:-

Survival:- SE = ± 6.5 (24 df) Height growth:- SE = ± 0.06 (24 df)

L.S.D. .05 = 13.4 L.S.D. .05 = 0.13
.01 = 18.2 .01 = 0.18

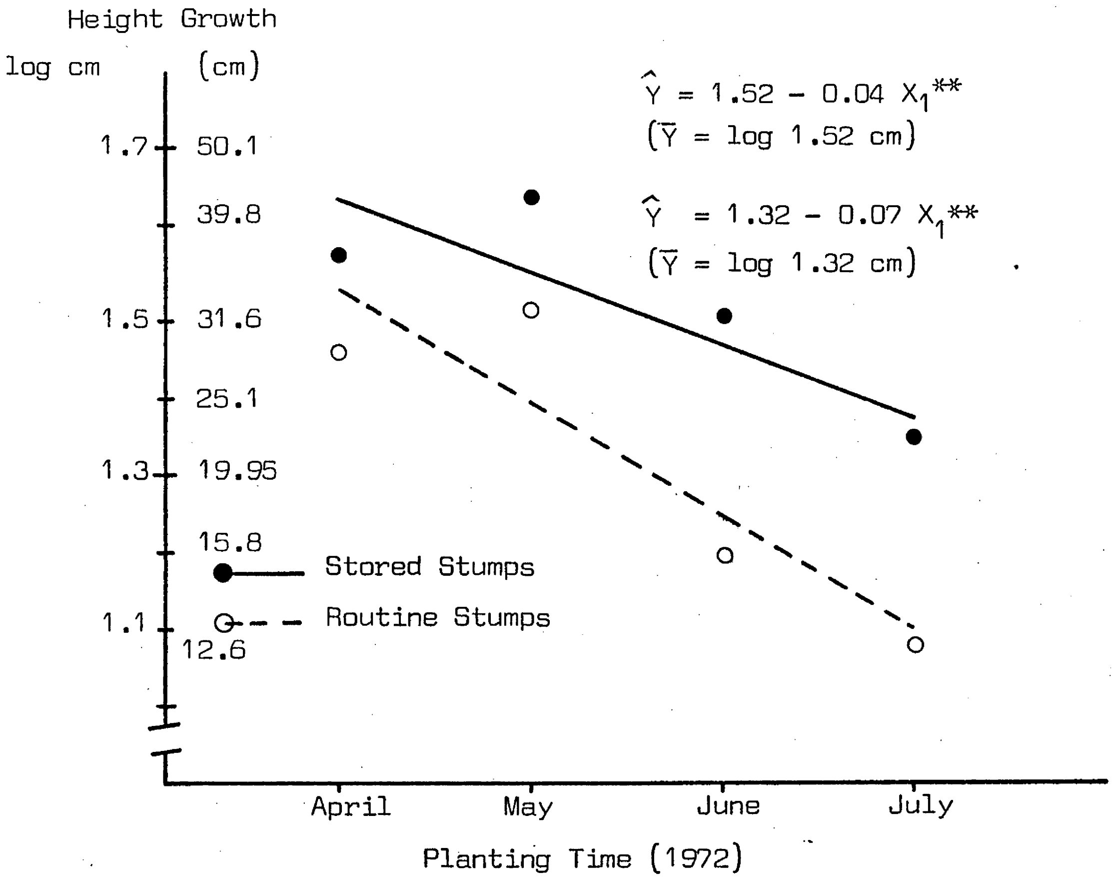


FIGURE 3.7 Effects of stump storage and planting time on subsequent sprout height

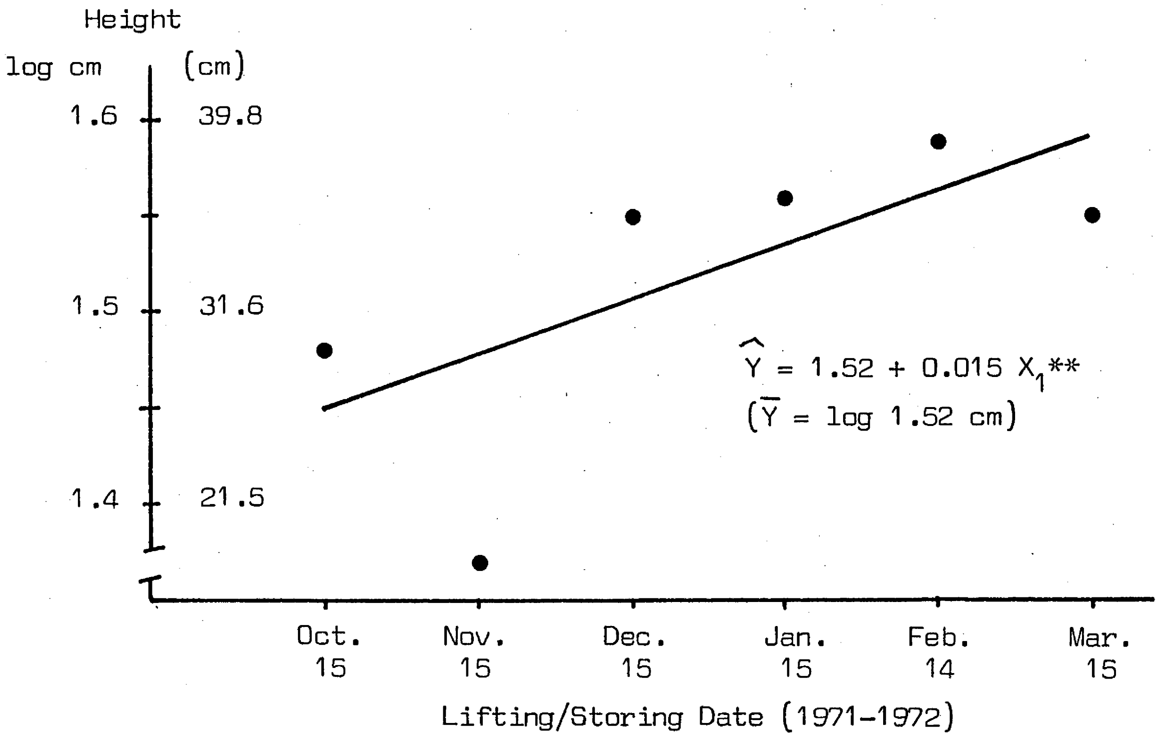


FIGURE 3.8 Effect of lifting date on subsequent height growth of teak stored stumps

routine stumps at the June planting can be ignored. In terms of height growth, the results summarized in Table 3.16 show that there were no significant differences between the stored and routine stumps at the April and May plantings. However, the difference in sprout height was highly significant at the latter planting times : the June and July plantings. A trend analysis (Table 3.9) shows highly significant linear effect of planting time on height growth of sprouts produced by the stored and the routine stumps, that is, height growth of sprouts produced by both types of stumps decreased progressively with the time of planting (Figure 3.7). However, the rate of decrease in sprout height with progressive planting time of the routine stumps was considerably greater than that of the stored stumps (Figure 3.7), that is, the difference in sprout height between the stored and the routine stumps increased progressively with the time of planting. The later the planting was done the greater the relative advantage for the stored stumps.

B. The Differences Among Stored Stumps: While stored stumps clearly performed better than routine stumps, especially in terms of height growth, it is important to determine the effects of early lifting and storage on the performance of teak stumps after out-planting to the field.

The analysis of variance for plant survival shows that there was no significant difference between lifting dates of stored stumps, and there were no significant interactions between lifting date and weeding treatment and between lifting date and planting time (Table 3.8). These findings clearly suggest that at any weeding treatment and any planting time there was no significant differences in survival between stumps lifted and stored during the period of mid-October to mid-March.

In other words, there was no significant effect of lifting/storing date (and hence storage period) on the survival of teak planting stumps, and this applies particularly when the stumps were lifted and kept in the underground store between mid-October and mid-March and subsequently out-planted between the end of April and mid-July. The results presented in Table 3.17 show the survival of the stored stumps at each lifting/storing date.

In terms of height growth, the analysis of variance shows that there was highly significant difference in sprout height between the lifting/storing dates. However, the results given in Table 3.17 show that there were no significant differences in sprout height between stumps lifted and stored during the period mid-December to mid-March, and these stumps lifted and stored during this period grew much better than those lifted and stored in the period mid-October – mid-November. Although the results given in Table 3.17 do not show the significant difference in sprout height between stumps lifted and stored between mid-December and mid-March, the trend analysis shows that there was a highly significant linear relationship between sprout height and the time of lifting/storing of the stumps (Table 3.9), that is, height growth of the sprouts tended to increase progressively with the time of lifting from mid-October to mid-March (Figure 3.8). The results presented in Table 3.17 show the adjusted value of the sprout height at each lifting date. Since the analysis of variance shows significant interactions between lifting date and weeding treatment and between lifting date and planting time for the stored stumps, it suggests that the differences in sprout height between lifting dates varied significantly with the method of

TABLE 3.17 Effects of lifting date on survival and height growth of teak planting stumps after out-planting at the same time. (Data represent the mean of 4 planting times, 2 weeding treatments, and 4 blocks)

Lifting/Storing Date (1971–1972)	Survival		Height Growth		
			Observed $\bar{Y}$	Mean	Adjusted mean $\hat{Y}$
	ArcSin $\sqrt{\%}$	%	log cm	cm	log cm
<u>Stored stumps</u>:					
October 15	57.0	69.2	1.48	37.3	1.45
November 15	–	–	1.37	26.6	1.48
December 15	62.4	77.0	1.55	38.7	1.50
January 15	59.6	72.4	1.56	40.1	1.53
February 14	60.8	74.5	ns 1.59	44.9	1.56
March 15	59.2	72.0	1.55	38.8	1.59
	ns		**		
S.E. (96 df)	± 2.2		±0.03 (120 df)		
L.S.D. .05			0.06		
.01			0.08		

Adjusted mean ($\hat{Y}$) for height growth:

$$\hat{Y} = 1.52 + 0.0146\, X_1$$

where X_1 for n = 6 reads from Table 17 A Snedecor and Cochran (1971).

weeding practice and with the time of planting. Alternatively, the differences in sprout height between weeding treatments or between planting times varied significantly with lifting date of the stumps (Table 3.12 and 3.14).

3.4.2.5 Summary of the Results

The results obtained in the present study can be summarized as follows:-

1. Weeding treatment had no effect on the survival of teak planting stumps during the first year after out-planting. Height growth of the stump sprouts, on the other hand, was markedly influenced by the weeding treatment, that is, sprouts of teak stumps planted in the "scrape" weeded plot were much greater than those of stumps planted in the "slash" weeded plot.

2. Planting time had marked effects on the field survival and height growth of teak stumps. There were parabolic relationships between the time of planting and both stump survival and height growth. Both survival and height growth increased markedly from the April planting to the May planting, and then declined progressively from the May planting to the July planting. However, there is evidence to suggest that the differences in both survival and height growth between the four planting times were partly influenced by the date of lifting/storing of the stumps.

3. In term of field survival, stored stumps generally performed as well as or better than the routine or the fresh-dug stumps. Height growth of sprouts produced by the stored stumps was much greater than that of routine stumps. There is evidence to suggest that the

differences in sprout height between the stored and routine stumps varied markedly with the time of planting. There was no significant difference in sprout height between the two types of stumps when planting was done in the period April-May, but this difference was highly significant when planting was done in the period June-July.

4. There was no significant effect of the date of lifting/storing on the survival of the stored stumps after out-planting at the same time but height growth of sprouts varied significantly with lifting/storing date. Furthermore there was a linear relationship between sprout height and the date of lifting/storing of the stumps. Height growth of the sprouts increased progressively with lifting date from the mid-October lifting to the mid-March lifting. However, the difference in sprout height between stumps lifted and stored in the period of mid-January and mid-March was not significant.

The effects of lifting date and storage on the field performance in terms of both survival and height growth of teak planting stumps will be discussed in further details in the following section.

3.5 DISCUSSION

3.5.1 Possibility of Storage of Teak Planting Stumps

It has been shown that teak planting stumps could be stored in dry sawdust in the underground (uncooled) store without any deterioration for as long as 5 to 9 months. Evidence has been provided that under any planting condition the field survival and height growth of the stored stumps were at least as well as or greater than those of the routine stumps after out-planting at the same time. These findings suggest that the stored stumps are generally superior to the routine stumps in both survival and height growth potential.

TABLE 3.18 The differences between stored and routine stumps in field performance after out-planting at the same time

Experimental Condition	Survival (%)			Height Growth (cm)		
	Stored		Routine	Stored		Routine
STUDY 1:						
"Wet" Site	90.8	ns	90.8	42.8	***	19.3
"Dry" Site	84.3	***	50.8	54.8	***	23.7
STUDY 2:						
Overall	73.3	*	62.6	37.7	***	25.8
Weeding Treatment:						
Slashing	69.9	*	50.4	23.3	**	15.0
Scraping	76.1	ns	75.0	52.2	**	36.6
Planting Time:						
April 27	76.4	ns	60.1	47.1	ns	34.6
May 22	78.3	ns	78.0	47.7	ns	37.4
June 15	75.2	*	52.0	30.9	**	15.9
July 11	64.5	ns	60.1	25.3	**	15.3

STUDY 1: Stored stumps were lifted between 18 January and 3 May, 1971.
Routine stumps were lifted in 15 June 1971.

STUDY 2: Stored stumps were lifted between 15 October 1971 and 15 March 1972.
Routine stumps were lifted between 27 April and 11 July, 19 72.

ns = no significant difference at the 5% level
* = significant difference at the 5% level
** = significant difference at the 1% level
*** = significant difference at the 0.5% level

Among the stored stumps, the results obtained in the Study 1 have indicated that the type of the storage medium did not affect the field survival and growth potential of the stumps. The success of storage of teak stumps in this study is therefore believed to be due largely to the 2 factors:

(1) The influence of the underground store in reducing temperature fluctuation during storage.

(2) The influence of storage medium in preventing stump desiccation.

These findings are consistent with the results obtained in the work of Louridsen (1973) who found that teak stumps could be stored safely either in sawdust or in plastic bags in a room at 22 - 32°C for a period of nine weeks. This author also reported that under similar conditions, the stumps kept "open" or without any special protection even for 3 weeks could not survive when out-planted to the field. In the same study, the overall fresh weight of the "open" stumps and stumps kept in sawdust and plastic bags at the end of the storage period were reduced by about 53% (44-59%), about 42% (18-55%), and about 6% (2-12%), respectively. Louridsen has suggested that the extremely high mortality of stumps kept "open" would be due primarily to the desiccation of the stumps during storage; and teak planting stumps should not be kept without any special protection even for 3 weeks at normal room temperature or under shade. Unfortunately, the experiments reported in this study did not determine the desiccation of the stumps after storage and the store temperature. However, the stored stumps used in this study were likely to suffer less desiccation than those reported by Louridsen, because the stumps kept in this type of store were more protected or isolated than those kept in the ordinary room.

3.5.2 Effects of Lifting Date

A. The Differences Between Stored and Routine Stumps: The results summarized in **Table 3.18** show the differences between stored and routine stumps in field performance after out-planting at the same time in both Study 1 and Study 2. It has been clearly shown that under any planting condition, e.g. site and weather conditions, the survival of the stored stumps was at least as great as, but mostly greater than that of the routine stumps. Height growth of stump sprouts, on the other hand, was much greater for the stored stumps than for the routine stumps after out-planting at the same time in the same site. This suggests that these stored stumps had a relatively higher physiological potential in field survival and growth than the freshly dug or the routine stumps. It is not known whether this difference was due to the influence of the date of lifting or to the influence of storage or to both of these factors. However, in the following section the effects of lifting date on field performance of the stored stumps will be discussed in detail.

B. The Differences Among the Stored Stumps: In term of stump survival, it has been shown in the Study 1 that there were differences between stumps lifted and stored at different dates (between mid-January and early May) at both "wet" and "dry" planting sites. In contrast, in the Study 2 the differences in survival between stumps which were lifted and stored during the period mid-October - mid-March were not significant. There was evidence suggesting that the significant differences in stump survival between lifting/storing dates exhibited in the Study 1 were not due mainly to the influence of lifting date, but these differences also varied significantly with storage medium and planting site. For example, the field survival of stumps, which were stored in plastic wraps and subsequently out-planted to the "wet" planting site, did not differ signficantly between lifting dates. The above evidence has suggested that the effects of lifting/storing date on the field survival of teak planting stumps could be ignored when these stumps were kept under suitable storage conditions and subsequently out-planted to the relatively wet planting site.

Studies on the effects of lifting and storing of seedlings of a number of coniferous species including Douglas-fir, Norway spruce, Sitka sprouce, ponderosa pine, red pine, Scoth pine and others, similarly, emphasise the flexibility in the lifting time of nursery seedlings where the seedlings are kept in cold storage and subsequently out-planted when environmental conditions are favourable (Walters and Soos, 1961; Winjum, 1963, Aldhous, 1964; Lavender, 1964; Novotny, 1966; Bunting, 1970; Nyland, 1970; Hocking and Nyland, 1971). Winjum (1963), for example, lifted Douglas-fir seedlings from nursery beds at 4 week intervals from October to May and held them for 4 weeks at 2°C before out-planting. This author reported that there were no differences in field survival between seedlings lifted and stored during the period October-April. Similarly, Lavender (1964) showed that lifting date had little effect on the field survival of Douglas-fir seedlings when these seedlings were lifted and stored between mid-November and early March; however, the survival of seedlings lifted in September, October and April was considerably lower than those lifted in the remaining months. This author has suggested that the relatively lower survival of seedlings lifted prior to December, or after buds start to enlarge in the spring (April) is due to the disruption of the seedling physiology, and seedlings lifted from December until buds begin to enlarge the following spring are more resistant to adverse environment .

In terms of height growth, it has been clearly shown in both studies that the time of lifting/storing teak planting stumps had an important effect on their field performance after out-planting at the same time. Height growth of stumps sprouts differed significantly between lifting times. The results presented in the following figure (Figure 3.9) show the general patterns of the growth response of teak planting stumps in the field to the time of their lifting/storing in the nursery in both studies at the same planting site (i.e. the "wet" site). Within the limit of lifting times in both studies, the optimum time for teak stump lifting was betwen mid-January (the first lifting date) and mid-April for Study 1 and between mid-January and mid-March (the final lifting date) for Study 2 (Figure 3.9). In Study 2, the decrease in sprout height would be expected when the stumps were continuously lifted and stored further from mid-March because there was evidence showing that the routine stumps which were lifted in the period April – July produced much smaller sprouts than the stored stumps (Figure 3.9).

The above evidence has suggested that there was a marked response in height growth of stump sprouts to the time of lifting/storing of teak planting stumps. Height growth of stump sprouts increased progressively in stumps lifted from mid-October, reached a peak in mid-February to mid-March, and then declined progressively in stumps lifted after mid-March. However, the optimum time for teak stump lifting and storing was in the period mid-January and mid-April. In terms of the relationship between height growth of stump sprouts and the stage of phenological development of the seedlings at the time of lifting and

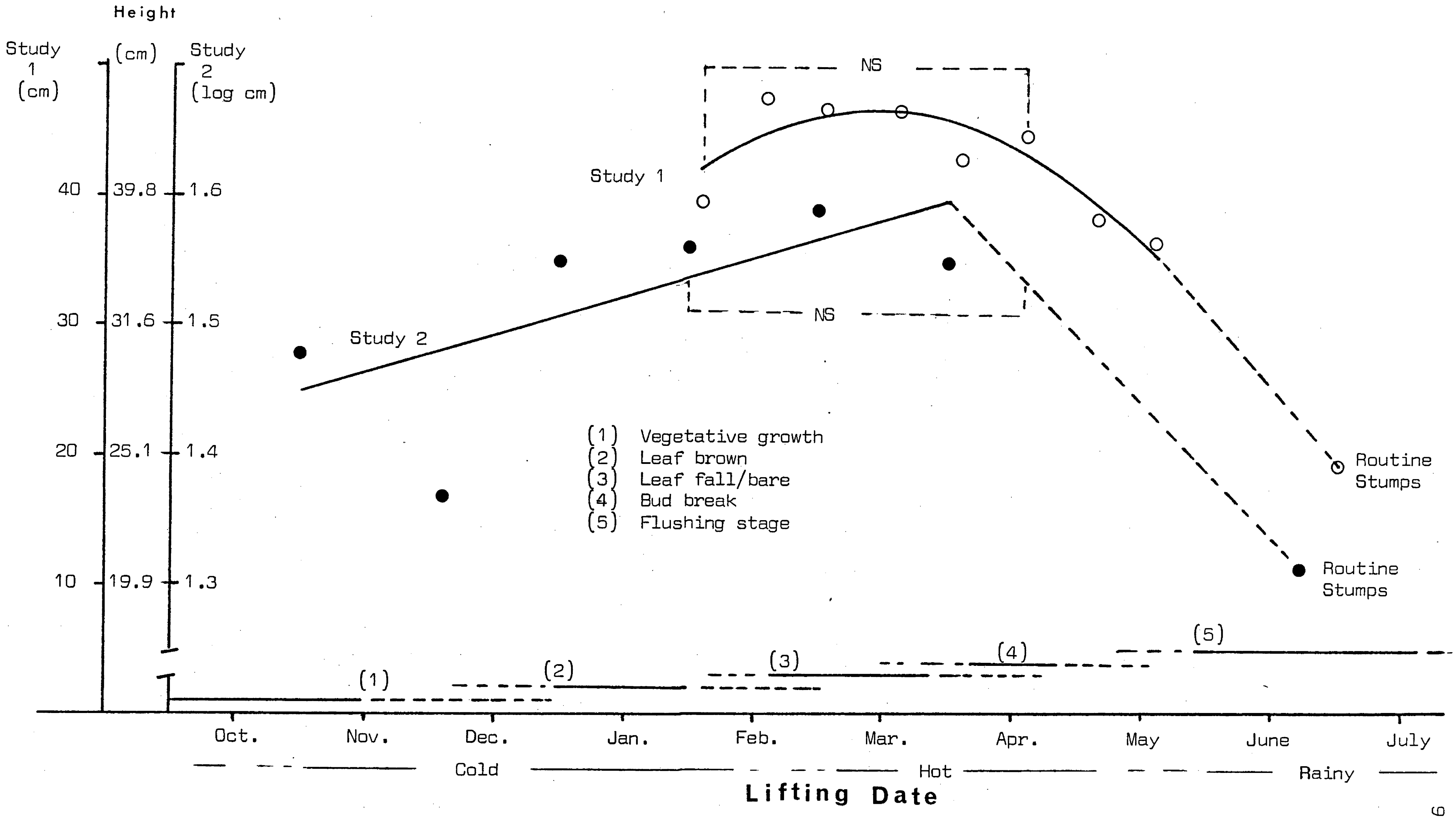


FIGURE 3.9 Effects of vegetative phenological stages on sprouting potential of teak planting stumps

storing, the results summarized in Figure 3.9 show that stumps lifted during the dormant or inactive growth period (i.e. between the period of leaf fall and bud break) in the dry season months were superior to those lifted prior to the leaf fall period, or after the buds had sprouted in the beginning of the rainy season months.

The findings of these present studies are consistent with those of Louridsen (1973) who worked with the same species. Louridsen (1973) reported that teak planting stumps lifted and stored during the bud break period (March) produced more vigorous sprouts than those lifted after the leaf flushing period in May after out-planting at the same time, Several other studies on season of cutting in relation to the ability of the cut stumps to produce sprouts have shown that there is a close relationship between the time of cutting and the vigor of stump sprouts. Stumps cut during the inactive growth (dormant) period often produced more vigorous sprouts than those cut during the period of active growth (Aldous, 1929; Stoeckler, 1947; Clark and Liming, 1953; Wenger, 1958; Wilson, 1968). Stoeckler (1947), for example, related the ability of a stump to produce sprouts following cutting to the stage of phenological development in aspen and cherry plants and found that both aspen and cherry stumps cut when their leaves were nearly full size in late spring produced less vigorous sprouts than those cut earlier. Working with red maple (*Acer rubrum*), Wilson (1968) found that the rate of leaf expansion and leaf production, internode elongation, and the final size of leaves and internodes were all greater in sprouts produced by the winter-cut stumps than in sprouts produced by the spring-cut stumps.

The differences in height growth of teak planting stumps caused by the influence of the time of lifting/storing obtained in these two studies may be explained in two ways. Firstly, stumps lifted during the inactive growth or dormant period (i.e. between mid-January and mid-April) may contain relatively higher carbohydrate and other food reserves than those lifted after the leaf flushing period (i.e. after mid-April), resulting in the production of more vigorous sprouts after out-planting. This assumption could be supported by the results obtained in the work of Aldous (1929), Buell (1940), Stoeckler (1947), Chattaway (1958), Cremer (1965) and Hook and Debell (1970). Secondly, stumps lifted during the dormant period may have a relatively weaker degree of the apical dominance (bud inhibition) than those lifted during the period of active shoot growth, so that the lateral buds on the stumps are readily released from inhibition after out-planting under favourable conditions for shoot growth. Consequently, the sprouts take advantage of the most favourable climatic conditions for rapid expansion of the leaves and elongation of the new shoots. It has been shown in Study 2 that the most favourable time for rapid growth and development of the teak planting stumps appear to be only during the beginning of the rainy season (May). This second assumption has been supported by the work of Wenger (1958), Eliassion (1971a), and Schier (1973). The respective role of food reserves and plant growth substances in the production of stump sprouts have already been discussed in detail in Section 2.2 in Chapter 2.

In the case of teak, there is clearly a need for more research into the effects of environmental and internal factors during seedling development on the subsequent production of stump sprouts after out-planting. This research is developed in the following Chapters in this thesis.

CHAPTER 4

INTRODUCTION TO CONTROLLED ENVIRONMENT STUDIES

4.1 INTRODUCTION

The general background of teak in terms of its natural distribution, growth habit, artificial regeneration by stump planting, and the basic mechanism of stump sprouting have been described in Chapter 1 and Chapter 2. In Chapter 3, the field studies have demonstrated the techniques of lifting and storage of teak planting stumps. They also illustrated the importance of the time of lifting/storing of teak stumps on the field performance after out-planting under different planting conditions and at different planting times. Stumps lifted and stored during the dormant or the inactive shoot growth period (i.e. between mid-January and mid-April) were, generally, superior in terms of both the field survival and growth potential to those lifted before or after this optimum period. But very little is known about factors or mechanisms contributing to these observations. Therefore, it is very appropriate to examine the physiological basis of sprouting phenomena in a more controlled environment.

The studies reported in the following chapters (Chapter 5 - Chapter 8) were designed to examine the effects of temperature and soil moisture on the following :

1. growth and development of teak seedlings;
2. the subsequent sprouting of teak stumps after replanting;
3. photosynthesis and respiration, translocation of photosynthates and the accumulation of carbohydrates in seedling stumps; and

4. the amount of plant growth substances and their influences on sprouting ability of teak stumps.

4.2 GENERAL MATERIALS AND METHODS

The following sections outline the general methodology and controlled environment facilities.

4.2.1 Controlled Environmental Conditions

Most of the experiments reported in Chapter 5 to Chapter 8 were carried out in the Canberra Phytotron, a unit of the C.S.I.R.O. Division of Plant Industry. Inside the phytotron, the fifteen naturally lit glasshouses were operated at 15° – 36°C temperature in the day (9 hours) and 10° – 31°C temperature in the night (15 hours). The mean temperature throughout the area in each glasshouse was within 1.5°C of the controlled temperature. The relative humidity was kept above 40%, ranging between 50 and 85%. L.B.H. growth chambers (lit by fluorescent and incandescent lights) were also used for photosynthesis and translocation of photosynthates studies. Temperature in these growth chambers were ranged from 4 to 45°C. Light sources were provided by V.H.O. (140 watt) fluorescent tubes supplemented by incandescent bulbs. The total radiation was 4,000 f.c. at the bottom and 5,000 f.c. at mid height.

4.2.2 Growing Materials

A. Pots: Cylindrical pots were used in most studies in this part. The pots were made from 9 and 11 cm diameters P.V.C. Tubing. The length of the smaller tube was 22 cm, and that for the bigger tubes was 25 cm. The smaller tubes were closed one end with cloth shade screens, while the bigger tubes were closed with a cap. Drainage holes were made in the bigger tubes.

B. Growth Media: The growth media used in most experiments, except the moisture experiments, was a mixture of an equal part of vermiculite and perlite.

C. Water and Nutrient Solution Supply: The seedlings were water twice daily: once in the morning with a modified "Hoagland's" nutrient solution, and once in the afternoon with ordinary tap water. The composition of the modified "Hoagland's" nutrient solution is given in Appendix 10.

4.2.3 Preparing of Seedlings for the Experiment

Teak seeds were obtained from the C.S.I.R.O. Division of Forest Research, Canberra. The seeds were pretreated before sowing by alternately soaking and drying. The seeds were soaked in the running tap water at room temperature for 24 hours and dried in the 36/31°C day/night temperature glasshouse for 48 hours. This process was repeated five times before the seeds were sown.

The seeds were sown in the germination trays containing equal parts of vermiculite and perlite in the 30/25°C glasshouse. After germination, when the radicle emerged from the seed coat, they were transplanted singly in the pots containing a standard growth mixture. All seedlings were grown at day/night temperature of 30/25°C for approximately 8 weeks, in most cases, before they were used for the experiments.

4.2.4 Measurements and Harvesting

Height growth of the seedling was measured from the cotyledon to the apex of the stem. Stem diameter was measured at the point just below the lowest node.

When harvesting was commenced, all leaves of the seedling were removed first by cutting at the top of the petioles. Sprouting leaves with brown colour at the apex and leaf petioles were included as part of the stem (Evans, 1972). Leaf fresh weight and leaf area of each seedling were determined immediately after harvesting. Leaf area was measured by an automatic area meter. After measuring the area, the leaves were placed in paper bags for drying. The rest of the seedling was removed from the pot and the stem was separated from the root system at the root collar level. The stem fresh weight was determined and subsequently cut into small pieces and placed in paper bags for drying. The root system was carefully washed free of growth media (vermiculite and perlite or soil) and the lateral roots were then separated from the main tap-root. Leaves, stem, lateral roots and tap-roots of the harvested seedling were oven dried at 85°C for 3 days, then weighed.

4.2.5 Analyses of Growth and Structural Parameters

Where comparisons were required of growth and structure of seedlings, at different stages and different treatments under the study, analyses of growth parameters (RGR and NAR) and structural parameters (LAR, LWR, SLA, and root/shoot) were calculated using the formula given by Ledig (1974) as follows:

$$\mathrm{RGR} = (\underline{\ln} W_2 - \underline{\ln} W_1) / (t_2 - t_1)$$

$$\mathrm{NAR} = (W_2 - W_1)(\underline{\ln}\, LA_2 - \underline{\ln}\, LA_1) / (LA_2 - LA_1)(t_1 - t_1)$$

$$\mathrm{LAR} = LA/W$$

$$\mathrm{LWR} = LW/W$$

$$\mathrm{SLA} = LA/LW$$

where RGR is the relative growth rate, which is the index of productivity of an overall growth;

NAR is the net assimilation rate, which is an index of physiological activity or the photosynthetic efficiency;

LAR is the leaf area ratio, which is an index of leafiness expressing the proportion of assimilatory surface to respiratory mass;

LWR is the leaf weight ratio, which is an indication of the productive investment in photosynthetic tissues;

SLA is the specific leaf area, which is an index of leaf structure;

W_1 and W_2 are the total plant dry weights at times t_1 and t_2 respectively;

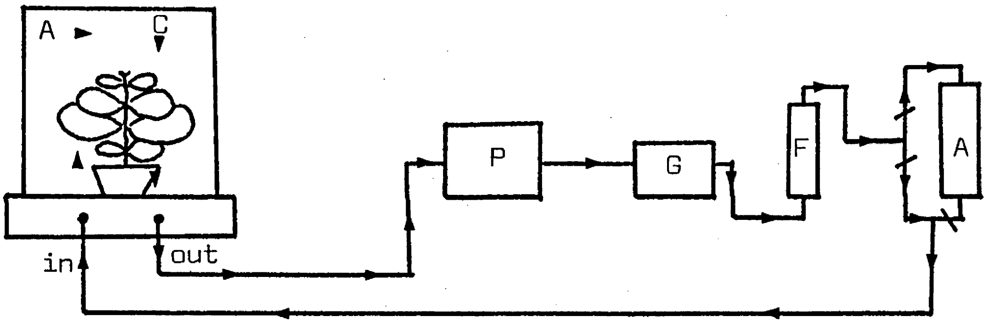
LA_1 and LA_2 are the total leaf areas of plants at times t_1 and t_2 respectively;

LW is the total leaf dry weight, and $\underline{\ln}$ is natural logarithm.

4.2.6 Translocation of ^{14}C-Photosynthates in Teak Seedlings

Two studies (described in Chapter 7) dealing with the effects of temperature and soil moisture regimes on the translocation of photosynthates in teak seedlings were made. The methods used in those studies are described as follows:

FIGURE 4.1 Schematic representation of the gas circuit used for $^{14}CO_2$ assimilation



Legend

A.C = Assimilation Chamber
P = Pump
G = Generator
F = Flow Meter
A = Column Absorber (soda lime)

A. $^{14}CO_2$ Assimilation: The seedling to be exposed to $^{14}CO_2$ was placed in a 30 (wide) x 61 (long) x 40 (tall) cm assimilation chamber. The chamber was placed in the LBH growth chamber in which the light was supplied by 28 x 140 W VHO daylight influorescent tubes, supplied by 4 x 1,000 W incandescent bulbs. The assimilation chamber was connected to a closed circuit apparatus as shown in Figure 4.1. $^{14}CO_2$ was generated from 10 mg $Ba^{14}CO_3$ (Sp.Act. 1.06 mCi/mM) or from 0.05 ml $Na^{14}CO_3$ (Sp.Act. 1.0 mCi/mM) by 50% (v/v) lactic acid. The seedling was exposed to $^{14}CO_2$ for 10 minutes and then transferred to the naturally lit glasshouse for the experiment.

B. Determination of ^{14}C-activity: At the end of the experiment, the seedlings were harvested and leaves, stems, tap-roots, and lateral roots were oven-dried separately. The dried materials were weighed and subsequently ground separately in a Wiley mill. A 30 mg powder sample was taken from each seedling component, placed in a 1 cm diameter planchet, and counted for the radioactivity on a Tracerlab-Omni/Guard Scaler Model SC 520 M, using the method modified by O'Brien and Wardlaw (1961). The results were expressed in terms of relative specific activity (cpm/mg) and percentage distribution (Wardlaw, 1965).

4.2.7 Determination of Carbohydrate Reserves

Two studies dealing with effects of temperature and soil moisture regimes on carbohydrate levels in teak seedlings were presented in Chapters 5 and 6. In those studies, the amount of carbohydrates, as described in terms of soluble sugars and starch, were determined using the anthrone colour reaction method as modified by Fasternack and Danbery (1968) and Blake (1974). The procedures of extraction are as follows:

A. Preparation of Plant Material for Extraction: Teak seedlings were harvested and oven-dried at 70°C for 1 day as an initial drying and then the temperature was increased to 105°C and the specimens dried for 2 days at this temperature. After drying the specimens were weighed, and then ground to pass a 150 mesh sieve in a micro-Wiley mill, and held in a desicator until extraction.

B. Extraction of Water Soluble Sugars: Two independent extractions were carried out on 0.2 gm each of the ground tissues. The sample was transferred to a 100 ml volumetric flask and 50 ml of distilled water was added. The sample was frozen in a deep freeze (at -25°C) for 18 hours. The purpose was to achieve bursting of cell walls and more efficient subsequent extraction. After thawing, the flasks were sealed with rubber caps dipped into toluene to prevent fungal contamination and extracted for 1½ days in a water bath at 30°C, with occasional shaking. The contents were filtered, the residues dried, and stored for starch extraction. The filtrates were deproteinized using the method of Somogyi (1945)modified by Blake (1974) as follows: to 10 ml of the filtrate was added 1 ml of zinc sulphate and 0.3 N barium hydroxide was added to neutralize the excess zinc sulphate. The precipitate was filtered and the clear filtrate was deionized using the method of Lewis and Harley (1965), modified by Blake (1974), by shaking with a small quantity of a mixture of Amberlite IRA-120 and Amberlite IR-45(OH) ion exchange resins. The concentration of sugars content in the filtrate was determined using the procedure given in Section 4.2.7D.

C. Extraction of Starch: The method adopted was that of enzyme hydrolysis of starch in the left-over residue from Section 4.7.2 B and extraction with warm water. The method, as described by Pasternack and Danbery (1968) and Blake (1974) is as follows:

A sample of 0.1 gm of the oven-dried residue was transferred to a 100 ml volumetric flask containing 50 ml of distilled water, 1 ml of acetate buffer pH 5.3 added then boiled for 3 minutes. The acetate buffer pH 5.3 was prepared from a mixture of 18 ml of 0.2 N acetic acid and 82 ml of 0.2 M sodium acetate. After cooling, 1 ml of 5% diastase was added to hydrolize the starch and the flask was placed in a hot water bath of 50°C for 3 hours. The flask was cooled, the content was filtered and the filtrate was made up to 500 ml with distilled water. The determination of starch content in the filtrate was given in the following Section.

D. Determination of glucose Equivalent: A reagent was prepared from 0.2 gm of pure anthrone in 100 ml of sulphuric acid at the concentration of 5 : 2 (v/v of conc. acid/water). The reagent was prepared 30 - 40 minutes in advance and used within 12 hours.

1 ml of the filtrate from the sugar or starch extraction (Sections 4.2.7B and 4.2.7C was pipetted into a test tube containing 5 ml of the anthrone reagent standing in an ice bath. At the same time, 1 ml of distilled water and 1 ml each of standard glucose solutions of known concentrations were pipetted into test tubes containing the anthrone reagent. Test tubes were loosely stoppered, the solutions were mixed by shaking, and placed into boiling water for 13.7 minutes to allow full colour development (Yemm and Willis, 1954) and then immediately cooled in icy cold water for 5 minutes.

The optical density of the solution was read at 630 millimicrons (Yemm and Willis, 1954) with a spectrophotometer.

Equivalent glucose content of the filtrate was determined from a reference curve prepared by using the optical densities of a range of glucose solution of known concentrations.

In the case of starch determinations, to calculate the amount of starch from the reference curve of glucose the optical density reading of the unknown sample was multiplied by 0.9 to account for the hydrolysis as reported by Somogyi (1945) and Pasternack and Danbery (1968).

The level of sugars and starch content in the dried tissue was calculated as follows:

$$\text{Sugar content (\% o.d.w.)} = \frac{\text{mg glucose equivalent} \times (50 \text{ X } Y) \times 10^2}{10^3 \times 0.2}$$

$$\text{Starch content (\% o.d.w)} = \frac{\text{mg glucose equivalent} \times 500 \times 10^2}{10^3 \times 0.1}$$

where Y is the amount of zinc sulphate and barium hydroxide (ml.).

CHAPTER 5

THE PHYSIOLOGICAL RESPONSE OF TEAK SEEDLINGS TO TEMPERATURE

5.1 INTRODUCTION

It has long been accepted that growth and development of plants is dependent on a temperature regime suitable for metabolic activity in plants. According to Kramer and Kozlowski (1960), temperature plays an important role in controlling plant growth and development by altering rates of and relations among several physiological processes including at least photosynthesis, respiration, cell division and elongation, and absorption of water and minerals. Every plant has temperature limits (upper and lower) for growth and development; and the optimum range of temperature for maximum growth varies markedly from species to species and even among populations and individuals of a single species.

Teak is one of the most valuable timber tree species of the tropics but surprisingly little is known about the effect of temperature on its growth and development. As noted earlier, the species occurs naturally over a wide range of climatic conditions, varying from one locality where the maximum temperature may be as high as 48°C for the hottest month to a locality where the minimum temperature may be as low as 2°C for the coldest month. It appears to grow best in the localities with the mean monthly maximum temperature of about 40°C and mean monthly minimum temperature of about 13°C. A study on growth and development of teak seedlings under controlled temperatures made by KoKoGyi (1972) showed that there was a marked trend for all growth parameters measured to increase with an increase in day/night temperature regimes from 15/10^{o} to 27/22^{o}C; and that teak seedlings grew best under day/night temperature ranging from 27/22^{o} to 36/31^{o}C. KoKoGyi has suggested that the critical maximum and minimum day/night temperatures for growth and development of teak seedlings are about 36/31^{o}C and 21/16^{o}C, respectively; above or below these temperature limits growth of the seedling ceases. This suggestion was later supported by the work of Kanchanaburangura (1976). Night temperature has been found to play an important role in influencing growth and dry matter production of teak seedlings (KoKoGyi, 1972; Kanchanaburangura, 1976). KoKoGyi (1972), for example, reported that under the favourable day temperature of 30^{o}, 33^{o} and 36^{o}C, growth and dry matter production was better at the high night temperature of 31^{o}C than at the low night temperature of 22^{o}C. Similarly, Kanchanaburangura showed that under the favourable day temperature of 30^{o}C growth and dry matter production of teak seedlings increased markedly with an increase in night temperature from 19^{o} to 26^{o}C. Furthermore, when grown under the day/night temperatures of 30/13^{o}, 33/25^{o} and 36/19^{o}C seedlings growth was best at 33/25^{o}C and poorest at 30/13^{o}C. Kanchanaburangura has suggested that the optimum night temperature for teak seedling growth would be between 25^{o} and 28^{o}C.

The effect of growing temperature on the production of sprouts of teak planting stumps is still unknown at the present time. It was noted in field studies presented in Chapter 3 that teak stumps lifted and stored during the cold season (January - February) performed better in terms of sprouting vigour than stumps lifted during the rainy season after out-planting at the same time. Similar behaviour has been found with several other woody species. Working with *Eucalyptus polyanthemos*, Bachelard (1969a) reported that there is a marked seasonal variation in the production of sprouts of stem segments under controlled conditions; the production of sprouts was greatest on stem segments collected in winter and least on stem segments collected in summer. Similarly, Blake (1974), who worked with *Eucalyptus obliqua*, showed that there is a seasonal variation in the sprouting of decapitated eucalypt lignotubers, with a maximum in winter and minimum in late spring and summer. In a further study, Blake provided evidence that the production of sprouts in eucalypt seedlings could be stimulated by cold night pretreatment, and the degree of day/night temperature variation might be important in the seasonal variation of sprout production in eucalypt seedlings. According to Bachelard (1969a) the winter-increase in sprouting of eucalypt stem segments appears to be associated with a time when cambial activity of the parent tree is expected to be minimum. In a further study, Bachelard found that applications of sucrose, water alone, and a variety of plant growth promoting substances, all inhibited the sprouting of stem segments; and the sprouting of stem segments was negatively related to the cambial activity in stem segments. From these results Bachelard has interpreted there is a competative relationship between the production of sprouts and cambial activity in eucalypt stems; that is, the formation of sprouts is favoured at times when the cambium is dormant. He has suggested that the supply of any factor which stimulates cambial activity could inhibit the production of plant sprouts. This suggestion was later supported by the work of Smith (1975) who studied the sprouting of decapitated *Eucalyptus viminalis* seedlings in relation to the activity of cambium after the supply of a variety of plant hormones.

From evidence provided above, it has been suggested that there are relationships between environmental factors, cambial activity, and the production of sprouts in plants; such that the restriction of cambial growth by any factor such as low temperatures might stimulate the production of sprouts under the favourable conditions for plant growth. If this hypothesis is accepted it might be applied to the sprouting of teak planting stumps.

In the present Chapter, the effects of fluctuating temperatures on growth and development of teak seedlings and on subsequent sprout production of stumps have been examined. The upper temperature regime used was 30/25^{0}C which is close to the average mean temperature during the active growth period of teak in its natural range; the lowest temperature was 18/13^{0}C which is close to the average mean temperature during the cold season or the inactive growth period of teak.

5.2 STUDY 1: EFFECTS OF TEMPERATURE ON SEEDLING GROWTH AND DEVELOPMENT AND SUBSEQUENT STUMP SPROUTING IN TEAK

5.2.1 Materials and Methods

Teak seeds from trees introduced to Melville Island, Australia were used for the experiments. The seeds were pretreated and sown (see Section 4.2.3), and the seedlings were grown singly in 9 cm diameter cylindrical pots containing a mixture of equal parts of perlite and vermiculite. All seedlings were well supplied with water and nutrient solution and grown in the 30/25^{0}C day/night temperature glasshouse until the experimental treatments were applied.

5.2.1.1 EXPERIMENT 1:

Eight weeks after germination, 60 uniform seedlings were selected for the experiment. The seedlings were divided into 3 groups each of 18 seedlings. The remaining 6 seedlings were harvested immediately. The seedling groups were allocated at random to one of the following temperature treatments:

A. Control: Seedlings were grown continuously under a day/night temperature of 30/25°C throughout the duration of experiment.

B. Gradual Change in Temperature: The temperature was lowered gradually from 30/25° to 18/13°C (3°C per week) during the 9th to the 12th week, and subsequently returned gradually from 18/13° to 30/25°C (3°C per week) during the 13th to the 16th week.

C. Abrupt Change in Temperature: The temperature was lowered abruptly from 30/25° to 18/13°C at the end of the 8th week, and subsequently returned abruptly from 18/13° to 30/25°C at the end of the 12th week.

Measurement and Harvesting: Height and diameter growth of seedlings were assessed at one week intervals from seedling germination to the final harvest 16 weeks after germination.

Seedlings were harvested at 4 week intervals from germination to 16 weeks after germination. Six seedlings were taken from each treatment at each harvest. The procedures have already been given in Section 4.2.4.

Analysis of Plant Growth and Statistical Analysis: Mean relative growth rates (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) were calculated using formulae given in Section 4.2.5. Comparisons of the treatment means for all plant growth parameters were based on analysis of variance. Where the variance ratios indicated significant differences between treatment means at the 5% level, L.S.D. values were calculated.

5.2.1.2 EXPERIMENT 2:

On the basis of the results of the Experiment 1 all temperature treatments were repeated in this experiment. Eight weeks after germination, 112 uniform seedlings were selected for the experiment. Ninety six of these seedlings were divided into 3 groups each of 32 seedlings. The remaining 16 seedlings were stumped (S_1) and immediately replanted singly in the same pots containing a mixture of equal parts of vermiculite and perlite in the 30/25°C day/night temperature glasshouse. The groups were allocated at random to treatments A, B, and C as shown in Table 5.1.

As shown in Table 5.1, 16 uniform seedlings from each treatment were selected for stump-replanting at 12 weeks (S_2) and 16 weeks (S_3) respectively. The selected seedlings were harvested, stumped, and immediately replanted singly in the same pots containing a mixture of equal parts of vermiculite and perlite in the 30/25°C day/night temperature glasshouse. The procedures used for preparing teak stumps for planting was described in Section 1.2. Replanted stumps were allowed to develop sprouts for 10 weeks at 30/25°C, and they were well supplied with water and nutrient solution.

Parameters Measured: Ten weeks after stump-replanting sprouts were harvested. The following measurements were made on sprouts; height and diameter growth, leaf area, leaf, stem, and total shoot of sprouts dry weights.

TABLE 5.1 Experimental Treatment

End of week from germination	Temperature Treatment			Operation	
	A	B	C	Expt. 1	Expt. 2
4	30/25^0	30/25^0	30/25^0	Harvest* (H_1)	
8	"	"	"	Harvest (H_2)	Stumping** (S_1)
9	"	27/22^0	18/13^0		
10	"	24/19^0	"		
11	"	21/16^0	"		
12	"	18/13^0	"	Harvest (H_3)	Stumping (S_2)
13	"	21/16^0	30/25^0		
14	"	24/19^0	"		
15	"	27/22^0	"		
16	"	30/25^0	"	Harvest (H_4)	Stumping (S_3)

* Harvest for growth analyses (H_1, H_2, H_3 and H_4)

** Stumps were immediately replanted and allowed to develop sprouts under the day/night temperature of 30/25^0 for 10 weeks.

S_1 = 8-week-old stump

S_2 = 12-week-old stump

S_3 = 16-week-old stump

5.2.2 Results

5.2.2.1 EXPERIMENT 1

5.2.2.1.1 Seedling Growth:

The response of teak seedlings to fluctuating temperatures in terms of height and diameter growth and leaf area production are presented in Table 5.2.

A. Height Growth: The height of seedlings grown under the constant warm condition (Treatment A) was much greater than that for seedlings grown under the fluctuating temperature treatments (Treatments B and C). The results show quite clearly that the teak seedling is very sensitive to cool conditions (Figure 5.1). As the temperature was lowered either gradually or abruptly from $30/25^{\circ}$ to $18/13^{\circ}$C height growth of the seedlings declined markedly. Four weeks later the height of seedlings in treatments B and C were 23.7± 0.7 and 19.9± 0.8 cm, respectively, while the height of seedlings in treatment A was 36.3± 1.5 cm.

Height growth of seedlings increased markedly when the temperature was raised from $18/13^{\circ}$ to $30/25^{\circ}$C; particularly when the temperature approached $30/25^{\circ}$C. At final harvest mean height of seedlings was 27.0± 0.9 cm for treatment B, 29.0± 1.0 cm for treatment C and 41.5 cm ± 1.9 for treatment A.

B. Diameter Growth: The diameter response was similar to that of height growth. The diameter of seedlings grown under treatment A was significantly greater than that of seedlings grown under both B and C treatments (Table 5.2).

C. Leaf Area Production: The treatments had a marked effect on leaf area production (Table 5.2). The total leaf area of seedlings

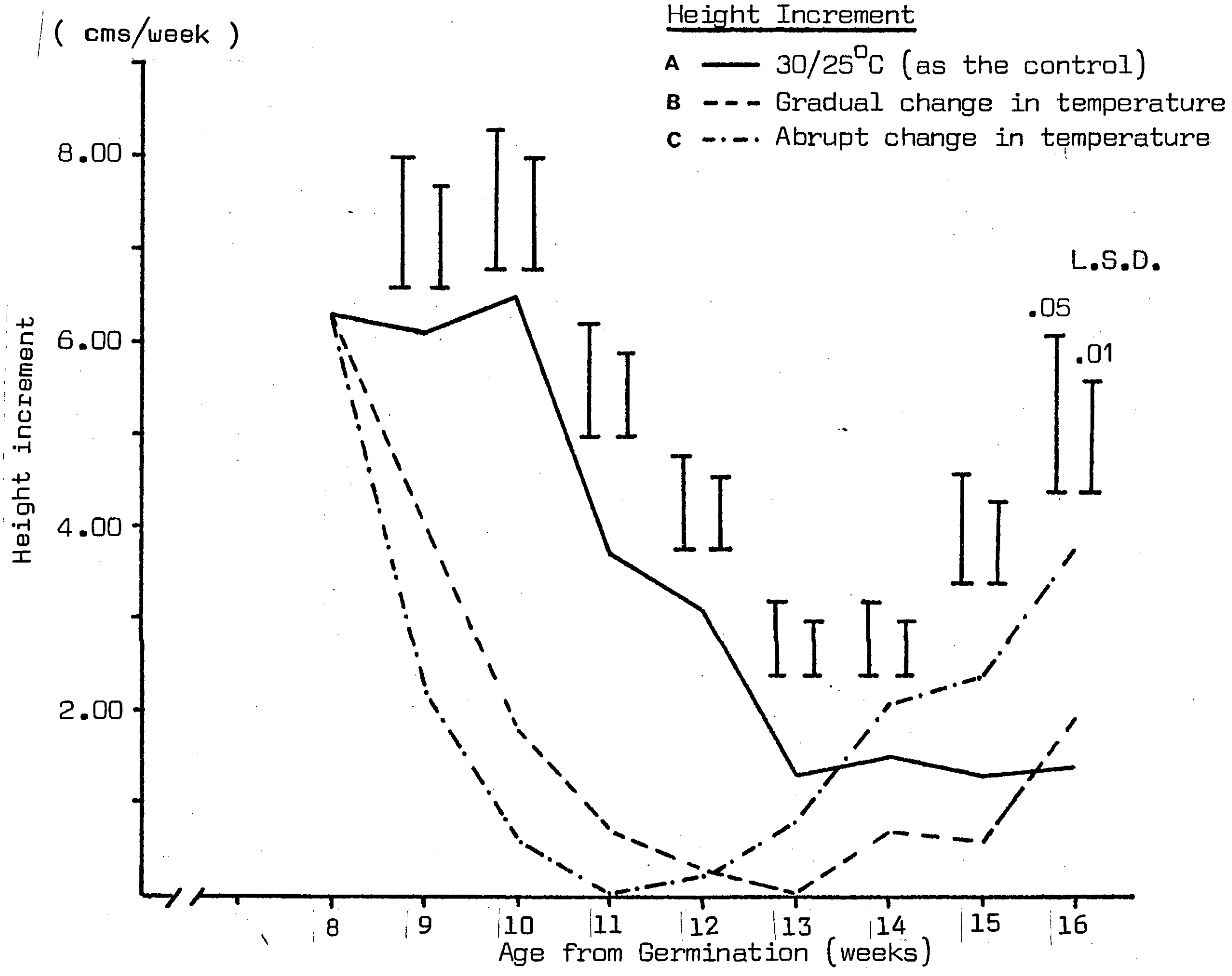


FIGURE 5.1 Effect of temperature on height growth response of teak seedlings

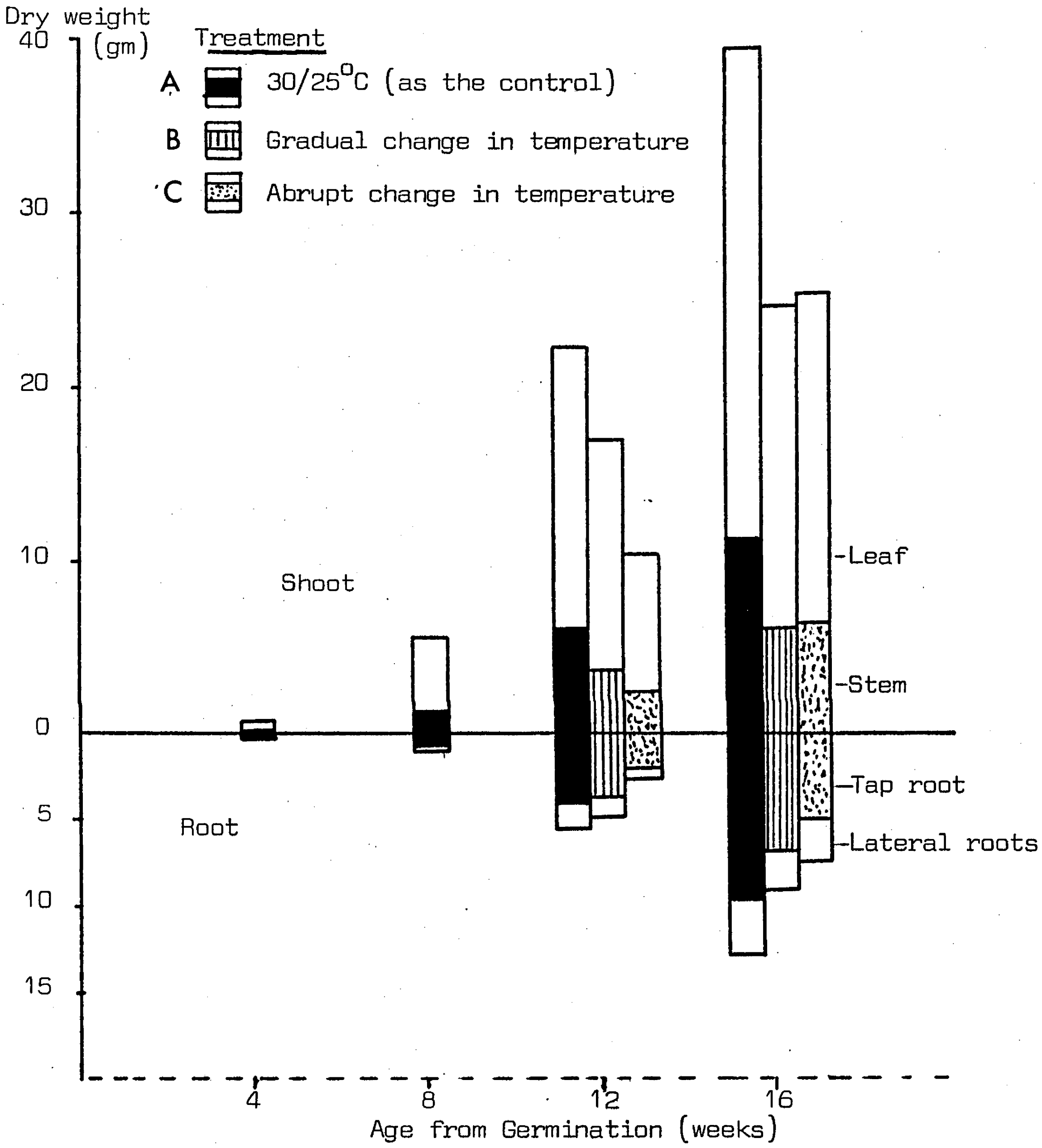


FIGURE 5.2 Effects of temperature on dry matter production of teak seedlings

grown under treatment A was much greater than that of the seedlings grown under treatments B and C. Seedlings in treatment B produced more leaf area than seedlings in treatment C during the temperature reduction phase but returning to 30/25°C, the difference between these two treatments in total leaf area was not significant. In fact, the abrupt change in temperature from 18/13° to 30/25°C produced a marked stimulus in leaf area production (Table 5.2).

From observation, under the cool day/night temperature of 18/13°C all leaves of the seedlings became yellowish indicating incipient senescence. The leaves appeared to be thicker than those of seedlings grown at 30/25°C, and this was confirmed by the SLA values given in Section 5.3.1.3. When the temperature was raised abruptly to 30/25°C, seedling shoots flushed rapidly, and new leaves expanded rapidly. The old leaves did not recover and some of them fell at this stage.

5.2.2.1.2 Dry Matter Production

For all plant components, dry matter production of seedlings grown under treatment A was considerably greater than that of seedlings grown under treatments B and C (Table 5.3 and Figure 5.2). When the temperature was lowered progressively from 30/25° to 18/13°C dry matter production decreased, but at 12 weeks (H_3), total dry matter production did not differ from seedlings grown at 30/25°C. When the temperature was changed abruptly from 30/25° to 18/13°C, dry matter was markedly reduced (at the 1% level of significance). However, at the end of week 16 of the experiment there was little difference between the two fluctuating temperature treatments (Table 5.3) and both were significantly less than for treatment A.

The dry matter production patterns for the individual plant components are generally similar to total dry weight production. For all components, recovery after a period of 4 weeks at 18/13°C was rapid with the exception of tap-root production.

5.2.2.1.3 Growth Parameter

A. RGR: Under treatment A the RGR of seedlings decreased as is usual with age from germination (Table 5.4). This applied to the total dry weight and the weight of each of the plant components. RGR decreased significantly with the reduction in temperature from 30/25° to 18/13°C, and this decrease was greater where the temperature was changed abruptly.

As the temperature was raised from 18/13° to 30/25°C, there was a marked difference between treatments in RGR. In treatment C, there was an increase in RGR but for both treatments A and B, RGR continued to decline. The increase in RGR under treatment C reflected the rapid growth recovery of plants in the 12-16 week period noted earlier.

B. NAR: NAR patterns were similar to those for RGR (Table 5.4). The NAR of seedlings grown under treatment A decreased with seedling age through the greater part of the experiment. The NAR of seedlings grown under treatment B also decreased significantly through the experiment. Under treatment C there was a particularly marked decline in NAR following reduction in temperature from 30/25° to 18/13°C, but this was followed by a marked increase in NAR when temperature was abruptly raised again to 30/25°C.

TABLE 5.2 Effects of fluctuating temperature on growth and development of teak seedlings
(Data represent the mean of 6 seedlings)

Age from Germination (week)		Day/Night Temperature Treatment			L.S.D.	
		A	B (mean ± s.e)	C	.05	.01
Height growth (cm):						
H_1	4	7.1 ± 0.4				
H_2	8	16.8 ± 0.5				
H_3	12	36.3 ± 1.5	23.7 ± 0.9	19.9 ± 0.8	3.1	4.2
H_4	16	41.5 ± 1.9	27.0 ± 0.9	29.0 ± 1.0	3.9	5.2
Diameter growth (mm):						
H_1	4	5.0 ± 0.0				
H_2	8	6.8 ± 0.2				
H_3	12	11.2 ± 0.2	9.8 ± 0.2	8.4 ± 0.3	0.6	0.9
H_4	16	15.4 ± 0.3	14.4 ± 0.6	13.4 ± 0.3	1.2	1.6
Leaf area production (dm^2):						
H_1	4	2.0 ± 0.1				
H_2	8	11.9 ± 1.3				
H_3	12	32.2 ± 3.4	23.5 ± 2.4	14.5 ± 1.3	7.6	10.5
H_4	16	49.8 ± 2.5	31.2 ± 3.4	34.4 ± 1.5	7.8	10.8
Leaf area increment (dm^2):						
4 - 8		9.9 ± 1.2				
8 - 12		20.3 ± 2.3	11.6 ± 1.1	2.6 ± 0.5		
12 - 16		17.6 ± 1.5	7.7 ± 1.3	19.9 ± 0.6		

TABLE 5.3 Effect of fluctuating temperature on dry matter production of teak seedlings
(Data represent the mean of 6 seedlings)

Age from Germination		Day/Night Temperature Treatment			L.S.D.	
		A	B (mean ± s.e.)	C	.05	.01
Leaf dry weight (gm):						
H_1	4	0.7 ± 0.1				
H_2	8	4.5 ± 0.7				
H_3	12	16.2 ± 2.0	13.3 ± 1.6	8.0 ± 0.7	4.6	6.4
H_4	16	28.3 ± 1.0	18.7 ± 2.4	19.1 ± 0.6	4.5	6.3
Stem dry weight (gm):						
H_1	4	0.1 ± 0.0				
H_2	8	1.2 ± 0.2				
H_3	12	6.1 ± 0.8	3.8 ± 0.5	2.4 ± 0.3	1.7	2.3
H_4	16	11.2 ± 0.3	6.1 ± 0.9	6.2 ± 0.3	1.7	2.3
Tap-root (stump) dry weight (gm):						
H_1	4	0.04 ± 0.01				
H_2	8	0.7 ± 0.2				
H_3	12	4.0 ± 0.6	3.6 ± 0.3	2.0 ± 0.3	1.2	1.7
H_4	16	9.6 ± 0.6	6.9 ± 1.0	5.0 ± 0.5	2.3	3.2
Lateral roots dry weight (gm):						
H_1	4	0.01 ± 0.01				
H_2	8	0.32 ± 0.09				
H_3	12	1.7 ± 0.2	1.1 ± 0.2	0.55 ± 0.07	0.5	0.7
H_4	16	3.3 ± 0.1	2.2 ± 0.2	2.3 ± 0.2	0.6	0.8

TABLE 5.3 (Cont'd)

Age for Germination (week)		Day/Night Temperature Treatment			L.S.D.	
		A	B (mean ± s.e.)	C	.05	.01
Total shoot dry weight (gm):						
H_1	4	0.78 ± 0.07				
H_2	8	5.7 ± 0.9				
H_3	12	22.3 ± 2.7	17.0 ± 2.2	10.4 ± 0.9	6.3	8.7
H_4	16	39.5 ± 1.0	24.8 ± 3.1	25.2 ± 0.8	5.9	8.2
Total roots dry weight (gm):						
H_1	4	0.14 ± 0.01				
H_2	8	1.06 ± 0.32				
H_3	12	5.7 ± 0.7	5.0 ± 0.5	2.5 ± 0.3	1.6	2.2
H_4	16	12.9 ± 0.7	9.1 ± 1.2	7.4 ± 0.6	2.6	3.6
Total plant dry weight (gm):						
H_1	4	0.94 ± 0.07				
H_2	8	6.8 ± 1.2				
H_3	12	28.0 ± 3.4	21.8 ± 2.5	12.9 ± 1.2	7.6	10.6
H_4	18	52.5 ± 1.5	33.9 ± 4.2	32.7 ± 0.9	7.8	10.9

TABLE 5.4 Effects of fluctuating temperature on growth parameters of teak seedlings

(Data represent the mean of 6 seedlings)

Age from Germination (week)	Day/Night Temperature Treatment			L.S.D.	
	A	B	C	.05	.01
Leaf relative growth rate (LRGR) (cm^2/cm^2/week):					
4 - 8	0.45 ± 0.01				
8 - 12	0.25 ± 0.01	0.17 ± 0.01	0.05 ± 0.01	0.03	0.04
12 - 16	0.11 ± 0.01	0.07 ± 0.01	0.22 ± 0.01	0.04	0.05
Shoot relative growth rate (SRGR) (mg/mg/week):					
4 - 8	0.49 ± 0.01				
8 - 12	0.35 ± 0.01	0.28 ± 0.01	0.16 ± 0.02	0.04	0.06
12 - 16	0.15 ± 0.02	0.09 ± 0.01	0.23 ± 0.01	0.05	0.07
Root relative growth rate (RRGR) (mg/mg/week):					
4 - 8	0.47 ± 0.04				
8 - 12	0.45 ± 0.03	0.42 ± 0.04	0.25 ± 0.03	0.11	0.15
12 - 16	0.21 ± 0.02	0.15 ± 0.02	0.27 ± 0.01	0.06	0.08
Relative growth rate (RGR) (mg/mg/week):					
4 - 8	0.48 ± 0.02				
8 - 12	0.36 ± 0.02	0.30 ± 0.02	0.17 ± 0.02	0.05	0.07
12 - 16	0.17 ± 0.02	0.11 ± 0.01	0.24 ± 0.02	0.05	0.07
Net assimilation rate (NAR) (mg/cm^2/week):					
4 - 8	2.56 ± 0.26				
8 - 12	2.59 ± 0.06	2.23 ± 0.09	1.21 ± 0.11	0.27	0.37
12 - 16	1.61 ± 0.25	1.09 ± 0.11	2.21 ± 0.19	0.57	0.79
Leaf area ratio (LAR) (cm^2/gm):					
H_1 4	201.4 ± 1.6				
H_2 8	186.0 ± 13.4				
H_3 12	116.4 ± 3.6	108.4 ± 1.7	113.0 ± 4.3	ns	
H_4 16	94.9 ± 4.1	92.8 ± 2.3	105.0 ± 3.2	9.9	-
Leaf weight ratio (LWR):					
H_1 4	1.72 ± 0.16				
H_2 8	1.08 ± 0.14				
H_3 12	0.58 ± 0.01	0.61 ± 0.01	0.62 ± 0.02	ns	
H_4 16	0.54 ± 0.01	0.55 ± 0.00	0.58 ± 0.01	0.03	0.04
Specific leaf area (SLA) (cm^2/gm):					
H_1 4	291.9 ± 6.0				
H_2 8	277.6 ± 18.5				
H_3 12	201.5 ± 5.5	179.4 ± 5.1	182.3 ± 2.4	13.7	19.0
H_4 16	175.6 ± 6.2	168.2 ± 3.4	179.9 ± 4.6	ns	

C. LAR, LWR, and SLA: Under treatment A the LAR, LWR and SLA of the seedlings decreased with age. When compared with treatment A, either the B or the C treatment did not have a pronounced effect on the LAR, LWR and SLA of the seedlings in this study.

5.2.2.2 EXPERIMENT 2:

5.2.2.2.1 Growth of Seedlings Before Stumping

The growth of teak seedlings under the three temperature treatments was similar to that obtained in Experiment 1 (Table 5.5). Seedlings grown under the constant warm condition (treatment A) performed better in all growth parameters than seedlings grown under the fluctuating temperature treatments B and C. In treatment B only the stump size at S_2 did not differ significantly from those of seedlings from treatment A. In treatment C the seedlings at S_2 were markedly affected in all growth parameters. They were significantly smaller than seedlings from treatments A and B. At final harvest (S_3), the seedlings grown under treatments B and C did not differ significantly in any growth parameter. This clearly showed that, under treatment C recovery of the seedlings was rapid in all growth parameters when the temperature was raised from 18/13^o to 30/25^{o}C.

5.2.2.2.2 Stump Sprouting

A. Number of Sprouting Stumps: In treatment A the number of sprouting stumps increased markedly with seedling age. Only 6 out of 16 of the 8-week-old stumps produced sprouts, whereas all stumps in all three treatments produced sprouts when prepared at 12 and 16 weeks after germination (S_2 and S_3). The difference in sprouting capacity between the 8-week and older stumps may have been due to the difference in stump size.

B. Sprouting Vigor: The cool temperature treatments had significant effects on seedling growth as well as on the subsequent production of stump sprouts. The development of sprouts on the S_2 stumps from treatment A for all parameters of sprout performance are recorded in Table 5.6. At this stage, sprouts produced by the S_2 stumps of treatment C were superior to those produced by the stumps of treatment B in leaf area and leaf dry weight and in stem as well as total shoot dry weight, but not in height and diameter or lateral root dry weight. Since the S_2 stumps from treatment C were much smaller than those from treatments A and B, it is clear that the abrupt temperature reduction greatly enhanced the potential of these plants to produce vigorous sprouts when returned to the 30/25°C regime following stumping.

The pattern of sprout response on the S_3 stumps was very much different from that on the S_2 stumps. The sprout performance on stumps from treatment C was significantly reduced for all parameters recorded (Table 5.6). This marked change in response is the reverse of what was found in the previous experiment. This will be discussed later.

Under treatment B, there were significant differences in growth parameters of sprouts between the S_2 and the S_3 stumps (Table 5.6). The height of sprouts on the S_3 stumps was smaller than for the S_2 stumps, but leaf area and both leaf and shoot dry weight increased. Stem dry weight was almost the same, but new root production of the S_3 stumps declined.

Under treatment A, the sprout performance of stumps tended to remain more or less constant with stump age (S_1, S_2 and S_3 stumps). New root production tended to increase with stump age and sprout height to decrease with stump age.

5.2.2.2.3 Root Regeneration

The root regenerating potential of stumps in treatment A was poor at 8 weeks from germination (S_1), but increased markedly with age (Table 5.6). The S_2 stumps of seedlings grown under treatments B and C had a much greater root regeneration capacity than treatment A,similar to the capacity of the stumps for shoot production. There was no difference between treatments B and C in the root regenerating potential of the S_2 stumps. Root regnerating potential of these stumps decreased markedly after the seedlings were returned to the high temperature of 30/25°C, particularly in treatment C.

TABLE 5.5 Growth parameters of teak seedlings at stumping times as affected by temperature regime (Data represent the mean of 16 seedlings)

Stumping Time	Temperature Treatment			L.S.D.	
	A	B	C	.05	.01
Parent stumps (seedlings)					
Height growth (cm):					
S_1	25.8 ± 1.0				
S_2	42.7 ± 1.8	33.6 ± 1.6	28.9 ± 1.1	4.4	5.9
S_3	51.9 ± 1.8	41.6 ± 0.9	43.2 ± 1.9	4.6	6.1
Diameter at collar (mm):					
S_1	8.6 ± 0.3				
S_2	12.5 ± 0.2	11.7 ± 0.2	10.3 ± 0.6	1.2	1.6
S_3	14.7 ± 0.2	13.9 ± 0.2	13.8 ± 0.2	0.5	0.7
Leaf area (dm^2):					
S_1	15.8 ± 1.3				
S_2	34.7 ± 1.5	27.4 ± 1.1	20.9 ± 0.5	3.1	4.2
S_3	47.3 ± 0.6	33.4 ± 1.1	32.9 ± 1.5	3.3	4.4
Leaf dry weight (gm):					
S_1	5.9 ± 0.5				
S_2	17.4 ± 0.7	15.6 ± 0.6	11.5 ± 0.3	1.7	2.3
S_3	29.4 ± 0.4	22.1 ± 0.7	20.4 ± 0.8	2.0	2.7
Stump fresh weight (gm):					
S_1	8.9 ± 0.7				
S_2	22.8 ± 1.7	22.8 ± 1.2	15.3 ± 1.3	4.0	5.4
S_3	33.8 ± 1.8	28.4 ± 1.2	26.3 ± 1.0	3.9	5.2

TABLE 5.6 Effects of temperature regime on the subsequent production of sprouts of teak planting stumps (Data represent the mean of 16 stumps)

Harvest (10 weeks after stump & planting	Temperature Treatment			L.S.D.	
	A	B	C	.05	.01
		Sprouts (10 weeks after planting)			
Height growth (cm):					
H - S_1	8.4 ± 0.7				
H - S_2	6.9 ± 0.7	9.4 ± 1.1	11.9 ± 1.0	2.8	3.7
H - S_3	6.2 ± 0.5	6.9 ± 0.5	4.8 ± 0.3	1.6	2.1
Diameter (mm):					
H - S_1	7.2 ± 0.5				
H - S_2	8.0 ± 0.4	8.9 ± 0.3	9.6 ± 0.2	0.9	1.2
H - S_3	9.1 ± 0.4	9.6 ± 0.3	7.8 ± 0.2	0.9	1.2
Leaf area (dm^2):					
H - S_1	10.6 ± 1.6				
H - S_2	10.4 ± 1.1	14.8 ± 1.4	18.7 ± 0.9	3.3	4.4
H - S_3	11.1 ± 1.7	17.0 ± 1.2	7.0 ± 0.8	3.7	4.9
Leaf dry weight (gm):					
H - S_1	5.8 ± 1.0				
H - S_2	6.0 ± 0.7	8.6 ± 0.8	11.0 ± 0.5	1.9	2.5
H - S_3	6.5 ± 1.0	10.3 ± 0.8	4.4 ± 0.5	2.2	3.0
Stem dry weight (gm):					
H - S_1	0.81 ± 0.16				
H - S_2	0.90 ± 0.14	1.42 ± 0.18	2.00 ± 0.15	0.44	0.59
H - S_3	0.92 ± 0.18	1.40 ± 0.16	0.51 ± 0.07	0.41	0.55
Total shoot dry weight of sprout (gm):					
H - S_1	6.6 ± 1.2				
H - S_2	6.9 ± 0.8	10.0 ± 0.9	13.0 ± 0.6	1.1	1.5
H - S_3	7.5 ± 1.1	11.7 ± 0.9	4.9 ± 0.6	2.6	3.5
New lateral root dry weight (gm):					
H - S_1	1.1 ± 0.2				
H - S_2	1.6 ± 0.2	2.4 ± 1.2	2.6 ± 0.2	0.5	0.8
H - S_3	1.8 ± 0.2	1.9 ± 0.1	1.3 ± 0.2	ns	

5.2.3 Discussion

A. Seedling Growth and Development

The results obtained in this Chapter have clearly shown that teak seedlings require a relatively warm climate (about 30/25°C temperature) for rapid growth and development. This was in agreement with the results obtained in the work of KoKoGyi (1972) and Kanchanaburangura (1976) who studied the effects of day/night temperature regimes on growth and dry matter production of teak seedlings. In the present study, it was shown that where the growing temperature was lowered from 30/25° to 18/13°C, either progressively or abruptly, all growth parameters of the seedlings were reduced. The height growth of seedlings, for example, declined a little where the temperature was reduced from 30/25° to 27/22°C (for 1 week) and declined markedly where the temperature was reduced further to 24/19°C. Seedlings ceased height growth when the temperature approached 18/13°C. The reduction of seedling growth under the cool treatment in this study is consistent with that observed by KoKoGyi (1972) and Kanchanaburangura (1976).

The NAR of seedlings was reduced markedly when the temperature was lowered from 30/25° to 18/13°C, particularly when lowered abruptly. This suggests that the capacity of the seedling leaves to photosynthesize and distribute the photosynthate within the plant was apparently curtailed quite suddenly. This finding has been supported by the work of Kanchanaburangura (1976) who studied the effects of temperature regime on rates of photosynthesis and respiration in teak seedlings. Kanchanaburangura showed that both photosynthetic and respiratory rates of the teak seedlings decreased markedly with a reduction of temperature from 30^{o} to 24^{o}C; and the rate of photosynthesis of seedlings at 30^{o}C was twice that of seedlings at 24^{o}C. Reduction of NAR in plants under low temperatures has been reported by a number of workers. Warren Wilson (1966), for example, found that cold climate reduced both NAR and RGR but increased the leaf carbohydrate content in seven herbaceous plant species. He suggested that low temperatures reduce the NAR through a process that decreases the rate at which photosynthates are utilized in respiration and new growth; this causes photosynthates to accumulate in the leaves to levels at which they depress NAR. This hypothesis was later supported by the work of Neales and Incoll (1968). Thus, the results of this study and those obtained by Kanchanburangura (1976) for teak, where growth and respiratory rate of seedlings decreased markedly with the reduction in growing temperatures, could be explained using the hypothesis proposed by Warren Wilson (1966). However, more studies dealing with the effects of low temperatures on photosynthesis, translocation of photosynthates, and levels of carbohydrate content in teak seedlings are required.

Growth of the seedlings increased again when the temperature was raised from 18/13^{o} to 30/25^{o}C, either progressively or abruptly, but there was a marked difference in the rate of increase between treatments. Growth of seedlings increased rapidly when the temperature was raised abruptly from 18/13^{o} to 30/25^{o}C, but only slowly when the temperature was raised progressively from 18/13^{o} to 30/25^{o}C. Both RGR and NAR of the seedlings in treatment C increased markedly, while that for seedlings in treatment B continued to decline. This suggests that all the physiological processes for growth were stimulated very rapidly and that utilization of photosynthates proceeded almost immediately resulting in rapid growth and increase in dry weight.

From the results of this study, it can be concluded that teak seedlings require a relatively high temperature (about 30/25^{o}C) for rapid growth and development. The seedlings are very susceptible to the cold conditions. Under the cold conditions, all physiological activities in the seedlings are depressed and reduction of growth and dry matter production results. These processes, however, can recover rapidly when the temperature is raised to the warm condition of 30/25^{o}C.

B. Stump Sprouting

The results of this study have shown that temperature has a marked influence not only on growth and development of teak seedlings but also on the capacity of sprouting of teak planting stumps. Evidence has been provided that seedlings maintained at 30/25^{o} continuously do not sprout vigorously after stumping and planting under favourable conditions for growth. By contrast, where the seedling growth was restricted by cool temperature the sprouting capacity of the stumps increased markedly. These results are consistent with those obtained from the field studies (see Chapter 3) where stumps lifted during the cold season, when the seedlings were nearly fully dormant, produced more vigorous sprouts than stumps lifted in late spring or during the rainy season. As noted in Chapter 2, the sprouting of lateral buds in plants is mainly controlled by the hormonal and nutritional status of the plant; increasing auxin levels or lowering photoassimilates in the plant resulting in the inhibition of sprouting

(Phillips, 1969a, 1975). According to Larson (1964) and Brown (1971), there are close relationships between environmental factors, plant growth, and auxin production; any factor that enhances rapid shoot growth and continued leaf production results in high levels of auxin production and increases stem auxin. Conversely, low temperatures, drought, and short photoperiods that adversely affect shoot growth and leaf production lowers the levels of auxin production and subsequently reduces stem auxin. Working with *Eucalyptus obliqua*, Blake (1974) found that a reduction in stem elongation of eucalypt seedlings caused by both too warm and too cold conditions stimulated the formation of epicormic shoots on the seedling stems. Furthermore, he concluded that environmental factors stimulating elongation of the main stem (i.e. light and temperature) reduced the sprouting, while environmental treatments inhibiting height growth of the main stem stimulated bud release. From the results of the present study, it could be interpreted that temperature through its direct effect on net assimilation and shoot growth influences the levels of auxin and/or other plant hormones and subsequently affects the capacity of stump sprouting; such that lowering of the temperature reduces net assimilation, shoot growth, and alters the hormone balance in the stump and subsequently increases the capacity of stump sprouting of teak. Further investigations into the effects of a lowering of temperature on some of physiological processes such as photosynthesis, respiration, translocation of photosynthates, and the hormone balance in teak seedlings are required.

5.3 STUDY 2: EFFECT OF TEMPERATURE AND STORAGE ON CARBOHYDRATE RESERVES AND SUBSEQUENT SPROUTING OF TEAK SEEDLING STUMPS

5.3.1 Purpose of Study

The previous study clearly showed that temperature has a marked effect on the growth and subsequent stump sprouting of teak seedlings. There was clear evidence that growth of teak is strongly inhibited at a low day/night temperature regime (18/13°C). In contrast, the stump sprouting potential increased markedly after seedlings had been transferred from 30/25°C to grow at 18/13°C for 4 weeks prior to stump-replanting.

There are a number of factors which might explain the enhanced potential for stump-sprouting after a period of temperature induced growth inhibition. These have been reviewed in Chapter 2. In this Section, a study is made of the effect of the temperature treatments and stump storage on the reserve carbohydrate content in teak stumps, and the relationship between carbohydrate content in the stump and its capacity for sprouting.

5.3.2 Materials and Methods

A. Plant Materials: Teak seeds from Laos were used for the experiment. The seeds were pretreated and sown (Section 4.2.3), and the seedlings were grown singly in 9 cm diameter cylindrical pots containing a mixture of equal parts of vermiculite and perlite. All seedlings were grown under the day/night temperature of 30/25°C and were well supplied with water and nutrient solution until the experiment treatments commenced.

B. Experimental Treatments: Eight weeks after germination, 104 uniform seedlings were selected for the experiment. This stage will be referred to as "time zero". The experimental treatments and experimental procedures are scheduled in Figure 5.3 and details of the experimental procedures are as follows:

Ninety nine of the selected seedlings were divided into 2 groups. The first group of 47 seedlings was retained at 30/25°C, and the second group of 52 seedlings were transferred abruptly to grow at 18/13°C. The remaining 5 seedlings were harvested and oven-dried for carbohydrate extraction (i.e. at time zero).

Four weeks from time zero, 5 seedlings from each of the two groups were harvested and oven-dried for carbohydrate extraction. The remaining 42 seedlings in the first group (30/25°) were divided into 2 sub-groups, each containing 21 seedlings. The first sub-group continued to grow at 30/25°C, and the second sub-group was stumped (Section 1.2) and stored in a metal box containing dry perlite at room temperature (about 25°C). In the second group (at 18/13°), the remaining 47 seedlings were divided into 3 sub-groups. The first subgroup containing 21 seedlings continued to grow at 18/13°C; the second sub-group containing 21 seedlings was stumped and stored in a box containing dry perlite; and the third sub-group containing 5 seedlings were transferred abruptly back to 30/25°C.

Eight weeks from time zero, 5 seedlings from each intact sub-group and 5 stumps from each storage group were harvested and oven-dried for carbohydrate extraction. The remaining 16 seedlings from each intact sub-group were stumped and replanted together with the remaining 16 stumps from each storage group. Stumps from all treatments were replanted singly in 9 cm diameter pots containing a

Note: The use of dry perlite for storage of teak stumps in this study is to simulate the dry sawdust and/or dry rice husk as used in the field experiment.

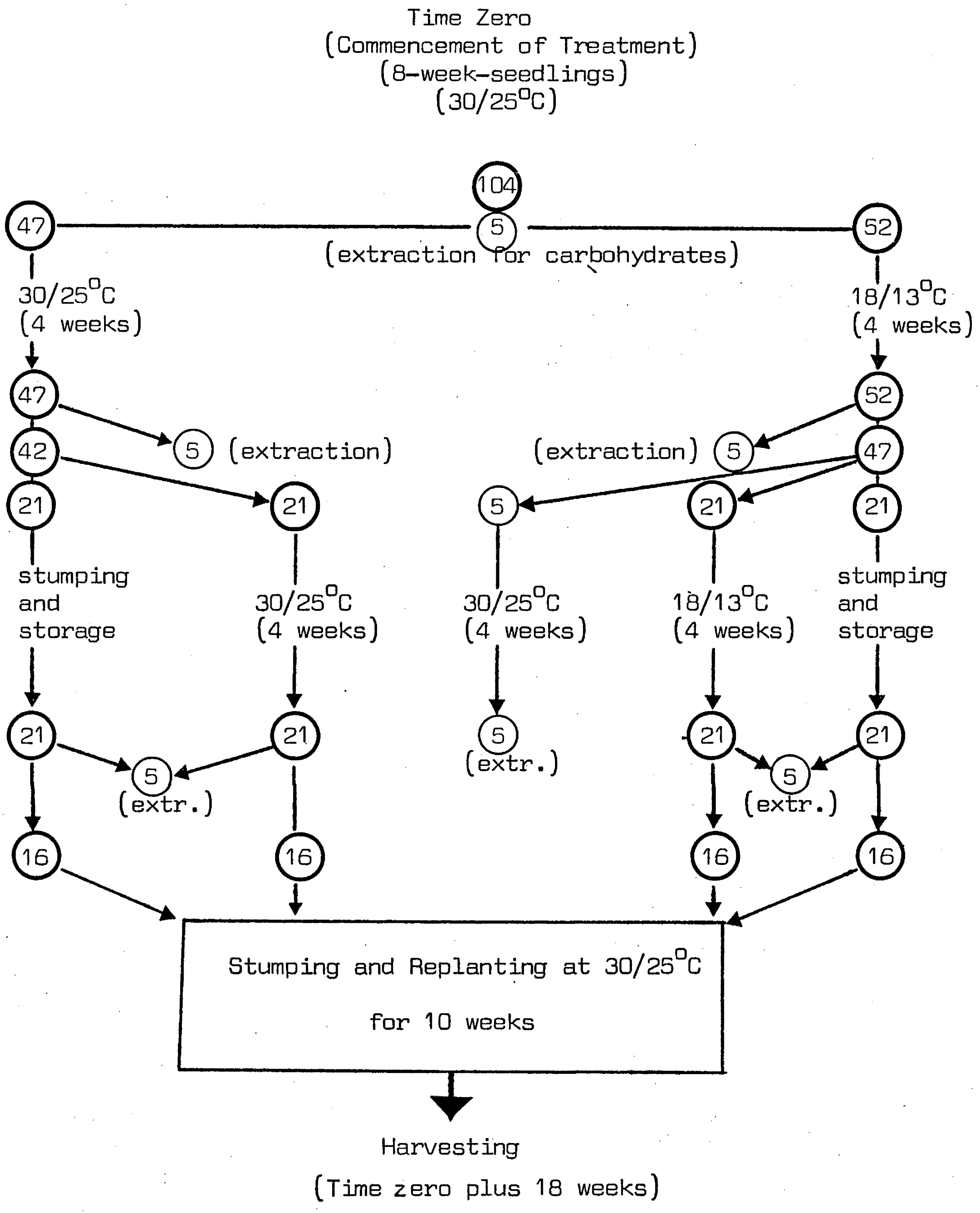


FIGURE 5.3 Experimental Schedule

mixture of vermiculite and perlite, placed in the 30/25°C controlled day/night temperature glasshouse, and supplied with water and nutrient solution.

Ten weeks after stump-replanting (i.e. 18 weeks after time zero) all stump sprouts from each treatment were harvested. Height growth, leaf area, and dry weight of the sprouts were determined.

Determination of Carbohydrates: Water soluble sugar and starch contents in stumps were extracted using the methods described in Section 4.2.7. To prepare the material for extraction, 5 oven-dried stumps from each treatment were ground individually in a Wiley mill to pass a 150 mesh sieve and held in a desiccator. An 0.5 gm sample was taken from each ground stump and these were bulked within a treatment to give a 2.5 gm sample of dry material per treatment. Two 0.2 gm sub-samples were then taken from each bulked sample, and were extracted for water soluble sugars and subsequently extracted for starch.

Statistical Analyses : Four weeks after stump-replanting, stump sprouts were attacked by red spider mites (*Metatetranychus ulmi*) causing a relatively large variance in all growth parameters and treatments at final harvest. In order to minimise the effect of variance due to this factor, the analyses of variance were carried out using a logarithmic transformation of the 5 biggest stump sprouts from each treatment.

5.3.3 Results

5.3.3.1 Carbohydrate Reserves

A. Sugar Reserve: Under constant conditions, the level of stump sugars increased with time from initiation of the experimental treatments (Figure 5.4a). However, the rate or change in stump sugars

FIGURE 5.4a

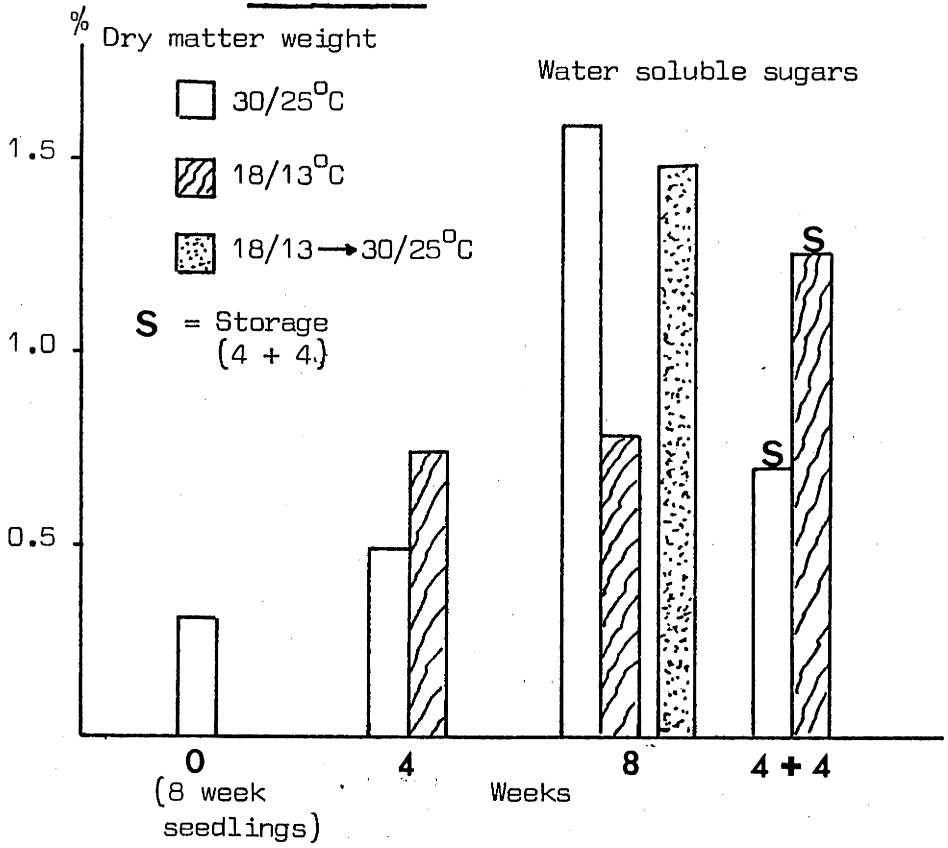


FIGURE 5.4b

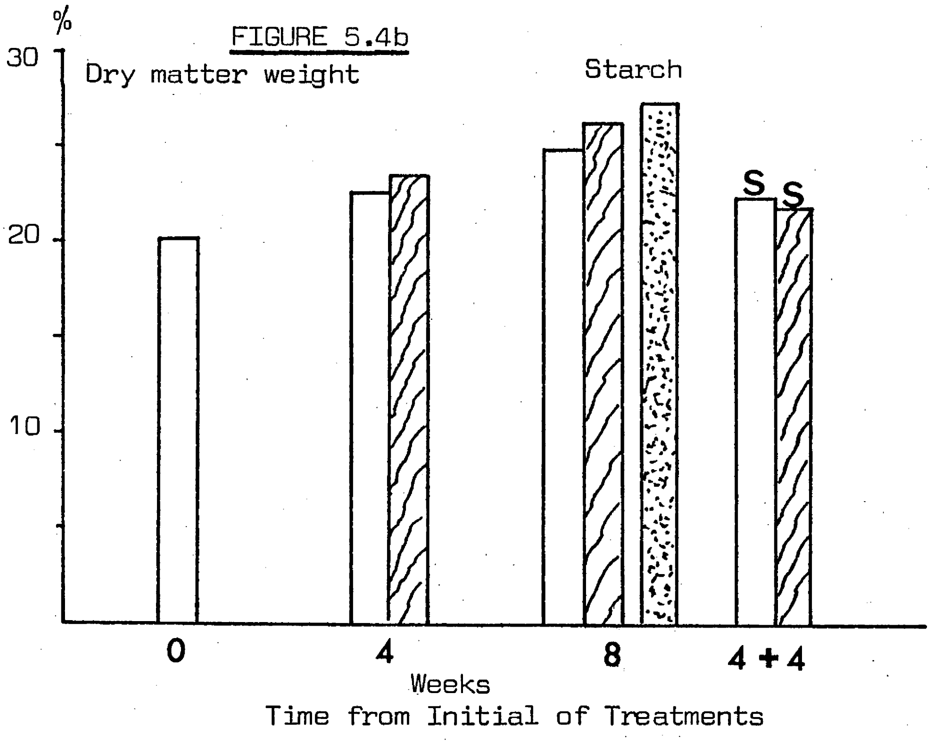


FIGURE 5.4 Effects of temperature and storage on carbohydrate reserves content in teak seedling stumps (see text)

TABLE 5.7 Effects of temperature regime and storage on the level of carbohydrate reserves in teak seedling stumps. (Data represent the mean of 2 x 4 extractions)

Treatments	Sugars	Starch	Total	
	%*	%**	%	gm***
Freshly prepared stumps:	(% of dry matter weight)			
Time zero at 30/25°C (8 weeks old)	0.32 ± 0.00	20.13 ± 0.10	20.4	0.40
4 weeks at 30/25°C	0.49 ± 0.01	22.58 ± 0.12	23.1	0.98
8 weeks at 30/25°C	1.59 ± 0.03	24.90 ± 0.38	26.5	2.66
4 weeks at 18/13°C	0.74 ± 0.01	23.54 ± 0.43	24.3	0.79
8 weeks at 18/13°C	0.78 ± 0.01	26.11 ± 0.16	26.9	1.47
4 weeks at 18/13°C + 4 weeks at 30/25°C	1.48 ± 0.01	27.31 ± 0.39	28.8	1.25
Stored stumps:				
4 weeks at 30/25°C + 4 weeks storage	0.70 ± 0.01	22.23 ± 0.21	22.9	0.97
4 weeks at 18/13°C + 4 weeks storage	1.26 ± 0.02	21.86 ± 0.30	23.1	0.75

$$*\% \text{ sugars} = \frac{\text{mg glucose equivalent} \times \text{dilution factors } (50 \times 1.3) \times 10^2}{10^3 \times 0.2 \text{ (gm dry material)}}$$

$$**\% \text{ starch} = \frac{\text{mg glucose equivalent} \times \text{dilution factors } (5 \times 10^2) \times 10^2}{10^3 \times 0.1 \text{ (mg)}}$$

$$*** \text{ gm} = \frac{\text{stump dry weight} \times \text{carbohydrate content } (\%)}{100}$$

Note:- Standard error of the mean as presented shows reliability of extraction technique rather than that of treatment mean.

at 30/25°C differed markedly with the growth pattern of the seedlings as measured by RGR. At the constant temperature of 30/25°C, the concentrations of stump sugars were 0.32 (time zero), 0.49 (4 weeks from time zero), and 1.59 (8 weeks from time zero) % of dry weight of stump. According to the result of Experiment 1 (Section 5.2), the RGR of seedlings at time zero and 4 weeks from time zero was much greater than that of the seedlings at 8 weeks from time zero. This suggests that at the constant 30/25°C there was a small increase in stump sugars during the rapid continuing growth of the seedlings; but as the relative growth rate of seedlings declined there was a marked increase in stump sugars.

Stumps of seedlings transferred from 30/25°C to grow at 18/13°C for 4 weeks exhibited a marked increase in the sugar concentration (Table 5.7). The concentration of stump sugars in seedlings held at 18/13°C for 4 weeks was 0.74%, whereas that in seedlings maintained at 30/25°C for 4 weeks was 0.49%. However, the level of stump sugars in seedlings held at 18/13°C remained relatively static when the seedlings were maintained at this temperature beyond 4 weeks and at 8 weeks was 0.78%. The increase in stump sugars during the first 4 weeks after reduction of temperature from 30/25° to 18/13°C might be the result of the decreased RGR of the seedlings as reported in Section 5.2, and this will be discussed in Section 5.3.4. Surprisingly, where seedlings held at 18/13°C for 4 weeks were transferred back to 30/25°C for 4 weeks, the stump sugar concentration doubled, to about the same level as in stumps of seedlings grown continuously for 8 weeks at 30/25°C (Table 5.7).

Storage of stumps caused an increase in stump sugars associated with a decrease in stump starch (Table 5.7). The concentrations of sugars in stumps of seedlings held at 30/25° and 18/13°C, respectively, for 4 weeks from time zero prior to stump storage were 0.49 and 0.74%. Four weeks after storage, the concentrations of sugars in these stumps rose to 0.70 and 1.26%, respectively, almost twice the concentration in stumps prior to storage. It will be shown that an increase in stump sugars as a result of storage for 4 weeks was accompanied by a decrease in stump starch; and the amount by which sugars increased was approximately equivalent to that by which the starch decreased. This clearly suggests that storage of stumps may cause hydrolysis of starch to sugars, and this will be discussed in detail in Section 5.3.4.

B. Starch Reserves: Under constant conditions the concentrations of starch in teak stumps also increased progressively after initiation of the treatments (Figure 5.4b). For example, at constant 30/25°C the concentration of starch in stumps increased from 20.1% (time zero) to 22.6 and 24.9% at 4 and 8 weeks respectively from time zero.

Temperature had a marked influence on the level of starch in stumps of teak seedlings. There is evidence that an abrupt reduction of temperature from 30/25° to 18/13°C caused an increase in starch concentration in stumps (Figure 5.4b). Starch concentration at time zero was 20.1%. When transferred to 18/13°C the concentration of starch rose to 23.5 and 26.1% at 4 and 8 weeks, respectively. The concentration of starch in stumps of seedlings grown continuously at 30/25°C rose to 22.6 and 24.9% at 4 and 8 weeks respectively.

Interestingly, where seedlings held at 18/13°C for 4 weeks were transferred back to 30/25°C for 4 weeks, the concentration of stump starch increased substantially from 23.5 to 27.3% that is very similar to the starch content of seedlings kept for the whole 8 week period at 18/13°C.

Storage of stumps obtained from seedlings which had been grown at 30/25°C for 4 weeks had no effect on, or caused a slight decrease in stump starch concentration. However, storage resulted in a decrease in the stump starch of seedlings which had been held for 4 weeks at 18/13°C (Table 5.7). The starch concentrations in stumps of the "30/25°" and "18/13°"C seedlings prior to storage were 22.6 and 23.5%, respectively. After 4 weeks of stump storage, the concentrations of starch were 22.2 and 21.9%, respectively. As suggested above, the decrease in starch as a result of storage might be the result of the hydrolysis of starch to sugars as there was an approximately equivalent increase in sugars. This will be discussed in detail in Section 5.3.4.

5.3.3.2 Stump Sprouting

A. Effect of Temperature: Temperature had an important influence on the subsequent sprouting of teak seedling stumps. Conditioning of seedlings by cool temperature (18/13°C) prior to either stump storage or stump replanting caused an increase in the sprouting ability of seedling stumps (Table 5.8). For example, in comparing the sprouting ability of the two sets of stored stumps, it is clear that stumps of seedlings which had been held at 18/13°C for 4 weeks performed much better than sprouts produced by stumps of

TABLE 5.8 Effects of temperature and storage on stump sprouting in an experiment to monitor carbohydrate content (Data represent the mean of 5 stump sprouts, 10 weeks after stump-replanting)

	30/25°C Stumps		18/13°C Stumps		L.S.D.	
	Stored (4 + 4 weeks)	Fresh-prepared (8 weeks) (see text)	Stored (4 + 4 weeks)	Fresh prepared (8 weeks)	.05	.01
Sprouting stumps (% of 16 stumps)	36	100	100	100		
Height (cm)	*0.50 ± 0.04 ** (3.16)	0.59 ± 0.03 (3.89)	0.86 ± 0.02 (7.24)	0.78 ± 0.05 (6.03)	0.11	0.15
Diameter (mm)	0.72 ± 0.02 (5.25)	0.81 ± 0.01 (6.46)	0.88 ± 0.02 (7.59)	0.86 ± 0.02 (7.24)	0.05	0.07
Leaf area (cm^2)	2.17 ± 0.23 (147.9)	2.54 ± 0.06 (346.7)	3.06 ± 0.06 (1148.1)	2.87 ± 0.10 (741.3)	0.39	0.54
<u>Dry matter production (log mg, and gm)</u>:						
Leaf	2.79 ± 0.25 (0.62)	3.27 ± 0.06 (1.86)	3.76 ± 0.05 (5.75)	3.50 ± 0.09 (3.16)	0.41	0.57
Stem	1.93 ± 0.17 (0.085)	2.38 ± 0.08 (0.24)	2.85 ± 0.07 (0.71)	2.61 ± 0.11 (0.41)	0.34	0.48
Total	2.85 ± 0.24 (0.71)	3.33 ± 0.05 (2.14)	3.81 ± 0.05 (6.46)	3.56 ± 0.09 (3.63)	0.40	0.55
New Roots	2.32 ± 0.18 (0.21)	3.07 ± 0.04 (1.17)	2.76 ± 0.33 (0.56)	2.68 ± 0.07 (0.48)	0.30	0.42

* log x

** (anti log x)

seedlings which had been held for 4 weeks at 30/25°C. This applies both to survival and growth of sprouts. In respect to the fresh or unstored stumps, sprout production by stumps of seedlings which had been held for 8 weeks at 18/13°C was as great in leaf area and total dry matter production, and significantly greater in height and diameter growth than sprout production by stumps of seedlings which had been held for 8 weeks at 30/25°C. In the previous study (Section 5.2), there was a similar effect of low temperature on sprouting ability of teak seedlings stumps. That is, stumps of seedlings which had been held at 18/13°C for 4 weeks produced more vigorous sprouts than stumps of seedlings which had been held at 30/25° for 4 weeks. The findings of the present study are therefore consistent with previous results.

B. Effect of Stump Size: Stump size had no effect on the sprouting potential of the stump. For example, the estimated dry weight of stumps of seedlings which had been held for 8 weeks at 30/25°C was about twice that of stumps of seedlings which had been held for 8 weeks at 18/13°C, and about three times that of stored stumps of seedlings which had been held for 4 weeks at 18/13°C. The estimated dry weights of these three sets of stumps were 9.9, 5.5 and 2.6 gm, respectively. Despite this range in stump size, sprout production of the "30/25°C" stumps was either similar to, or smaller than that of the "18/13°C" stumps depending on the growth parameter (Table 5.8).

C. Effect of Stump Storage: Storage of stumps prior to replanting had a marked effect on stump sprouting. In fact the effect of storage and temperature interactions seems to be greater than that of temperature alone. The greatest sprout production was associated with stumps of seedlings which had been held for 4 weeks at 18/13°C prior to 4 weeks storage. Both survival and subsequent growth of sprouts produced by these stumps were much greater than those of sprouts produced by stumps of seedlings which had been held for 4 weeks at 30/25°C prior to storage (Table 5.8). For example, only 36% of the stored "30/25°C" stumps produced sprouts after replanting, whereas all of the stored "18/13°C" stumps produced sprouts. The average total dry weight of sprouts produced by the stored "30/25°C" stumps was only 0.71 gm and that of sprouts produced by the stored "18/13°C" stumps was 6.47 gm.

Sprout production of stored stumps of seedlings which had been held at 18/13°C for 4 weeks prior to 4 weeks storage was also much greater, in all growth parameters, than that of stumps of seedlings which had been held for 8 weeks at 30/25°C. Within the low temperature regime, sprout production of stored stumps (i.e. 4 weeks at 18/13°C plus 4 weeks storage) did not differ significantly from that of stumps of seedlings held continuously at 18/13°C (i.e. 8 weeks at 18/13°C). On the other hand, for seedlings grown only at 30/25°C, stump storage for 4 weeks had a depressive effect on the subsequent sprouting vigor.

D. Effect of Carbohydrate Reserves: There is no apparent relationship between the carbohydrate reserve in the stump and the vigor of stump sprouting. The results in Figure 5.5 show that the

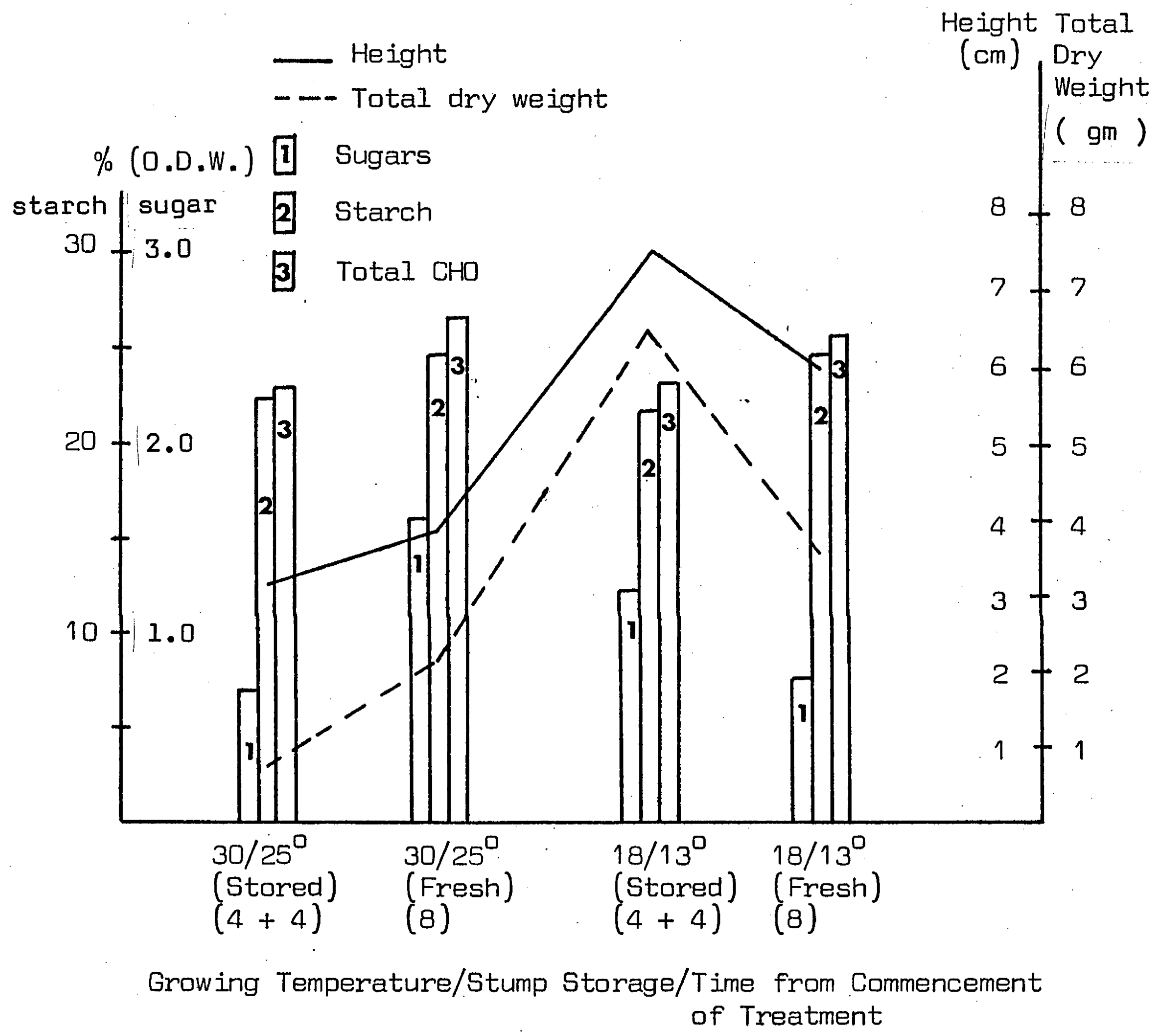


FIGURE 5.5 Relationship between stored carbohydrates in teak planting stumps and the vigour of sprouting

general pattern of growth and dry matter production of stump sprouts did not reflect the level of carbohydrate in the planted stumps, including sugars, starch, and total extractable carbohydrates. For example, stumps of seedlings held for 8 weeks at 30/25°C contained more sugars and starch than stumps of seedlings held at 18/13°C for 4 weeks plus 4 weeks storage, yet sprout production of the latter stumps was about three times greater, in dry weight, than that of the former stumps. The average total dry weight of sprouts produced by stumps of the "30/25°C" seedlings was 2.15 gm, whereas that of sprouts produced by stored stumps of the "18/13°C" seedlings was 6.46 gm. This suggests at least that while the reserve carbohydrate content in the planted stumps may play some role in stump sprout vigor, it is not the only factor affecting the sprouting potential of teak planting stumps. This will be discussed in more detail in the next section.

5.3.4 Discussion

A. Carbohydrate Reserves

Starch is the principal form of carbohydrate accumulated in teak seedling stumps, comprising about 20 - 30% of dry weight. Sugars, on the other hand, are present in the stumps of the teak seedlings at relatively small concentrations, i.e. less than 2% of dry weight. Since the starch concentration in the teak stump is relatively high, large fluctuations are, therefore, not to be expected, compared with possible fluctuations in sugar concentrations.

The starch content of the stump increases with time at both temperature regimes, that is 30/25° and 18/13°C. However, there is evidence that the increase in starch concentration is slightly greater at 18/13° than at 30/25°C. For sugars, the largest increase in concentration occurred at the constant 30/25°C regime between 4 and 8 weeks from initiation of the treatment; at 8 weeks this concentration was double that of seedlings maintained at a constant 18/13°C. This might result from changes in growth patterns reflected by the changes in RGR and NAR. At the constant 30/25°C, RGR declined during the 4 to 8 week period (Table 5.4, Section 5.2), accompanied by a build-up of sugars in the stump. At the constant 18/13°, sugars might have been expected to remain static between the 4 and 8 week period when growth was more or less static. However, stump sugars did increase during the first 4 weeks at 18/13°C. Apparently there was translocation of a considerable proportion of the products of declining photosynthesis to the root system. An increase in sugars in various plant organs caused by low temperatures has been observed by several workers (for example, Parker, 1963; Levitt, 1972p. 138-150). In his study of cold tolerance in relation to some physiological activities in plants, Levitt (1972) concluded that cold tolerance is normally accompanied by an accumulation of one or more substances including sugars, amino acids, proteins, nucleic acids, lipids, and perhaps several other substances synthesized by the plant, and that this is at least partly due to a cessation of or a decrease in the breakdown reactions of the metabolism that supports the growth and development of the plant. He further suggested that at low temperatures photosynthesis continues in excess of respiration, slow growth rate fails to use up the excess products of photosynthesis, and therefore accumulation of these excess products occurs. The increase in plant sugars under low temperatures may also be the result of an increase in the activity of hydrolytic enzymes or a conversion of starch to sugars (Parker, 1963; Marvin et al, 1971; Levitt, 1972). A number of studies cited by these workers have shown that there is an inverse relationship between temperature and enzyme activity; that is, low temperatures lead to increased enzyme activity, particularly the activity of peroxidase. However, this increase is not associated with the cold tolerance of the plant (Levitt, 1972).

In the present study, the most marked treatment response was that associated with 4 weeks at 18/13°C followed by 4 weeks at 30/25°C. The transference of seedlings back to the warmer temperature caused a substantial increase in stump starch (i.e. from 23.5 to 27.3%) and a doubling of stump sugars (i.e. from 0.74 to 1.48%). This is more difficult to interpret. One possible explanation is that an abrupt increase in temperature caused a marked increase in the relative growth rate of the root system (as reported in the previous study, Section 5.2), resulting in an increased demand for photosynthates to support the increased root activity. Consequently, a larger proportion of the photosynthetic products were translocated to the root system.
In studies on seasonal variations in carbohydrate content of roots, many workers have reported that the concentration of carbohydrate reserves of the roots usually reaches a maximum in the spring and summer (Hepting, 1945; Satoo and Takegosi, 1952; Shiroya et al, 1966). Shiroya and co-workers (1966), for example, showed that there are two active periods of translocation of the products of photosynthesis to the roots of young Pinus strobus, one in the spring and a second in the autumn, coinciding with increased root respiration. These co-workers have suggested that the increased activity of the roots acts to pull the products of photosynthesis from the shoot to the root system.

With stump storage, starch either remained constant or declined slightly, but there was a substantial rise in the concentration of sugars in the stored stumps and this rise was most marked for stumps of seedlings which had been held for 4 weeks at 18/13^{o}C. For seedlings which had been held for 4 weeks at 30/25^{o}C, the rise in stump sugars was from 0.49 to 0.70% after 4 weeks storage, and for seedlings which had been held for 4 weeks at 18/13^{o}C a substantial rise in stump sugars occurred during storage from 0.74 to 1.26%. It seems that metabolic activity in the stump continues to result in a conversion of starch to sugars during storage, especially in stumps of seedlings which had been maintained for a period under cool condition (18/13^{o}C) prior to stumping and storage. This conversion of the stored starch into sugars in stored stumps might be associated with the desiccation observed in the stumps. In this study, storage of teak planting stumps for 4 weeks appeared to cause a marked reduction in their fresh weight, especially in stumps of the cool treated seedlings. A reduction in the stump fresh weight of about 14 and 20% were observed in stumps of the "30/25^{o}C" and the "18/13^{o}C" seedlings, respectively. A number of observations have provided evidence that plants when subjected to soil water stress often convert the stored starch into sugars, that is, they exhibit a marked increase in sugars and an approximately equivalent decrease in the stored starch (Eaton and Ergle, 1948; Iljin, 1957; Maraville and Paulsen, 1970; Stewart, 1971). This conversion has been suggested to be due to an increase in activity of some hydrolytic enzymes during the water stress. The effect of soil water stress on the carbohydrate metabolism in teak seedlings will be examined further in the next chapters.

B. Stump Sprouting: The results obtained in this study have clearly shown the importance of the growing condition (temperature) prior to stumping of teak seedlings on both the success of storage of teak stumps and the growth potential of sprout produced after stump-replanting under favourable conditions. Stumps of the cool treated or the restricted growth seedlings (i.e. the "18/13°C" seedlings) appeared to be superior to those of the warm grown or the active growth seedlings (i.e. the "30/25°C" seedlings). This applies to both the success of storage and growth potential after replanting of the stumps. These findings are consistent with the results obtained both from the field studies (Chapter 3), where storage of stumps lifted during the cool or the inactive growth period did not reduce the field survival and growth potential of the stumps, and from the controlled environment studies (Chapter 5, Section 5.2), where stumps of the cool treated seedlings produced more vigorous sprouts than stumps of the active growth seedlings.

Other factors may be involved in the sprouting ability of teak planting stumps. But the findings obtained in this study have suggested that the growth potential of sprout produced was not primarily dependent upon the amount of stored carbohydrates in the planting stumps. As illustrated in Figure 5.5, there was no positive correlation between the amount (or the concentration) of stored carbohydrates in teak planting stumps and the growth potential of the sprout produced. For example, while the maximum growth of stump sprouts was associated with the stored "18/13°C" seedling-stumps, the maximum stored sugars appeared to be associated with the freshly prepared "30/25°C" seedling-stumps. Moreover, stumps of seedlings which had been maintained at 18/13°C for 4 weeks and then transferred back to $30/25^{\circ}C$ for another 4 weeks were found to contain a relatively higher level of stored carbohydrates (Table 5.7), but the growth potential of sprouts produced by these stumps as reported in Section 5.2 was considerably very poor. The above evidence suggests that the amount of stored carbohydrates in teak planting stumps is not likely to be the principal factor governing the growth and development of the sprout produced. This finding agrees with a number of other observations on woody plants (see for example in Section 2.2.1.2 in Chapter 2). Wenger (1953), for example, showed that the ability of sprouting of sweetgum stumps following cutting did not depend primarily on the amount of stored reserves, especially the stored carbohydrates, in stumps of the cut trees. A similar study was reported by Cremer (1973) on the ability to recover from cutting and severe defoliation of the young trees of many moist forest species including *Eucalyptus regnans*, *E. obliqua*, and *E. delegatensis* in relation to the amount of stored reserves in the remaining parts of the treated plants. He suggested that there was no positive correlation between the ability to recover of the plants (in terms of survival and growth of sprout produced) and the amount of stored reserves including sugars, starch, hemicelluloses, fats, and proteins, in the remaining parts of the treated plants. However, both authors suggested that the hormonal factor might play an important role in controlling the ability of stump sprouting of the species observed in their studies. With respect to teak stump sprouting, the effects of plant growth hormones on the ability to produce sprouts of teak planting stumps will be examined further in Chapter 8.

The amount of stored carbohydrates in teak planting stumps was found to be of lesser importance in governing the ability of stump sprouting in this species. But there is evidence to suggest that the capability for mobilization of the stored starch into labile sugars of the stumps might play a significant role in influencing both the success of storage and growth potential of teak planting stumps in this study. It was demonstrated earlier that a reduction of growing temperature from 30/25° to 18/13°C for about 4 weeks caused a marked increase in stored carbohydrates, especially in the form of sugars, in the stumps. In addition, dry storage of stumps of these cool treated seedlings for about 4 weeks caused a substantial increase in sugars and a corresponding decrease in the stored starch in these stored stumps. The increase in sugars in teak stumps caused by the influences of these two treatments (i.e. cool temperature and cool temperature plus dry storage treatments) was suggested to be the result of a stimulated mobilization process, in which the stored starch is converted into labile sugars. Since the ability of sprouting of stumps from these two treatments were considerably high, it is suggested that the ability of stumps to sprout and the success of storage of teak stumps might be influenced more by the capability for mobilization of the stored reserves in the stumps. Stump with a relatively greater capability for mobilization of stored reserves generally have a greater sprouting potential and could be stored safely for a longer period than those with a lower capability for mobilization of their stored reserves. Further studies on the effects of environmental factors on the mobilization of stored reserves and the ability of sprouting in teak stumps are required to help in understanding of the sprouting phenomenon.

CHAPTER 6

EFFECTS OF SOIL MOISTURE AVAILABILITY ON GROWTH AND DEVELOPMENT, CARBOHYDRATE RESERVES AND SUBSEQUENT STUMP SPROUTING OF TEAK SEEDLINGS

6.1 INTRODUCTION

The availability of soil moisture is one of the most important environmental factors influencing growth and distribution of plants. Kramer (1969) has pointed out the importance of water to plants as follows:-

(a) water is an important constituent of protoplasm or physiologically active tissue;

(b) water is an essential reagent in many important physiological processes including photosynthesis and hydrolytic processes such as the hydrolysis of starch to sugars;

(c) water is the solvent in which gases, minerals, and other solutes enter plants and move from tissue to tissue or organ to organ; and

(d) water is essential to maintain sufficient turgidity for growth and cell enlargement; cell turgidity also is important in the maintenance of the form of leaves and other slightly lignified structures, in stomatal opening, and other structures whose position is governed by the turgidity of cells.

The effect of the availability of water on plant growth, therefore, appears to be both direct, through its effect on cell enlargement by the maintenance of the turgidity, and indirect, through its effects on physiological processes such as food and growth hormone synthesis and the transport of these products to other plant organs.

The effects of soil moisture availability on growth and development of forest tree seedlings have been widely investigated (see for instance references cited by Kramer and Kozlowski, 1960; Kozlowski, 1964, 1971a; Zahner, 1968; Kramer, 1969). It has been consistently shown that there is a close relationship between the availability of soil moisture and growth of the seedlings. Seedlings subjected to soil moisture stress have often exhibited a marked reduction in all growth parameters measured. Water stress has also been found to affect many plant processes including water and mineral absorption and transport, transpiration, photosynthesis, respiration and translocation of assimilates (Kozlowski, 1964; Crafts, 1968; Kramer, 1969; Rook, 1973). An accelerated conversion of starch to sugars during water stress has been observed by several workers (Eaton and Ergle, 1948; Hodges and Lorio, 1969; Parker, 1970; Maranville and Paulsen, 1970; Stewart, 1971; Parker and Patton, 1975). Stimulated amylase activity in plants subject to water stress is believed to be involved in a decrease in starch content and an associated increase in sugars (Spoehr and Malner, 1939; Maranville and Paulsen, 1970; Stewart, 1971). However, a number of workers have suggested that the reduction of starch in dry plants is due to inhibited photosynthesis and continuing growth of the plants (Woodhams and Kozlowski, 1954; Eaton and Ergle, 1948; Hodges and Lorio, 1969; Levitt, 1972).

In respect to teak, there has been little study of the effects of soil moisture availability on physiological activity and growth of seedlings. It has been noted earlier that teak occurs naturally over a wide geographic range, from very dry to very moist regions with an average annual rainfall ranging from 760 to 5,080 mm. However, the species appears to avoid both very dry and very moist regions. On dry sites where severe drought stress occurs in the hot season, teak is found to be stunted and shrubby probably due to reduced growth and early loss of apical control. On very moist sites, on the other hand, the tree is usually large and fluted and tends to be replaced by a variety of evergreen forest species. Within its natural range, where the climate is markedly seasonal with distinct dry and rainy seasons, teak loses its foliage during the dry season and produces new leaves shortly after the onset of rains. Alvim (1964) has suggested that the periodicity of leaf fall in this species might be influenced by soil moisture and atmospheric humidity. Walter (1962) cited by Alvim (1964) showed that in the periodically dry region of western Java teak loses its leaves during the dry season, but when grown in the wetter area of eastern Java this species behaves like an evergreen.

In the present study, three experiments were carried out to examine -

(i) the effect of soil moisture supply on growth and development of the teak seedling;

(ii) carbohydrate reserves in the various organs of the plant, and

(iii) the subsequent sprouting of the teak stump.

Seedlings used in these experiments were from the same source and grown under controlled conditions, so that variations in genetical and environmental factors other than soil moisture were eliminated. The experimental details are described in the following sections.

6.2 MATERIALS AND METHODS

Two studies were carried out in the 30/25°C controlled day/night temperature glasshouse in the C.S.I.R.O. Phytotron.

Teak seeds from Laos were used in both studies. The seeds were pretreated and sown (Section 4.2.3). The seedlings were grown singly in 11 cm diameter cylindrical pots containing, 2,300 gm of oven dry soil. The soil used was a mixture of soil : river sand : peat, in the proportion of 3 : 1 : 1 by volume; its moisture characteristics, as measured by pressure membrane and pressure plate apparatus, are given in Table 6.1. All seedlings were well supplied with water and nutrient solution until the experimental treatments were applied.

TABLE 6.1 Moisture characteristics of the soil used in Experiments 1 and 2 (Data represent the mean of 6 samples)

	Percentage * soil moisture	Equivalent ** water content in each pot (gm)
Soil water content at:		
a. near saturation (Treatment A)****	18.9 ± 0.5	435.4
b. field capacity (-0.3 bar)	13.8 ± 0.1	317.4
c. 40% of "available water"***	9.3	213.4
d. wilting point (-15 bars)	6.2 ± 0.2	143.9

* Gravimetric moisture content $= \frac{\text{grams water content}}{\text{grams oven dry soil}} \times 100$

** Amount of soil in each pot : 2,300 gm (oven dried at 105°C)

***40% of water held by a soil between "field capacity" (-0.3 bar) and the wilting point (-15 bars)

**** Pots stood in 7 cm water : soil in the top (0 - 18 cm) section would have been maintained near field capacity of capillary action; that between 18 - 25 cm section would have been saturated.

Eight weeks after germination, 30 uniform seedlings were selected for the experiment. The seedlings were divided into 3 groups each of 10 seedlings. The groups were allocated at random to one of the following soil moisture treatments:-

A. "Constant High Soil Moisture": Seedlings were grown in near saturated soil throughout the duration of the experiment (water table maintained 18 cm below soil surface).

B. "Moderate Moisture Stress": Seedlings were subjected to a fluctuating soil moisture content in which the soil moisture was replenished to field capacity when 60% of the difference in moisture content between 'field capacity' (-0.3 bar) and 'wilting point' (-15 bar) had been used.

C. "Severe Moisture Stress": Seedlings were subjected to a fluctuating soil moisture content in which the soil moisture was replenished to field capacity when wilting point had been reached.

In treatment A the pots were free draining, but were placed singly on 4 cm deep saucers kept full of water throughout the experiment. The mean soil moisture content in this treatment was thus maintained at about 19% (Table 6.1). In treatments B and C, the drainage holes of the pots were sealed with wax paper tape. The soil surface in each pot was covered with 100 gm of polythene beads and sealed with a layer of aluminium foil (Plate 6.1) to prevent water loss by evaporation. The soil moisture content was monitored by daily weighing and where appropriate enough water was added to bring the soil moisture back to field capacity. Estimation of soil moisture content in the undrained pot containing a seedling was based on the following formula:

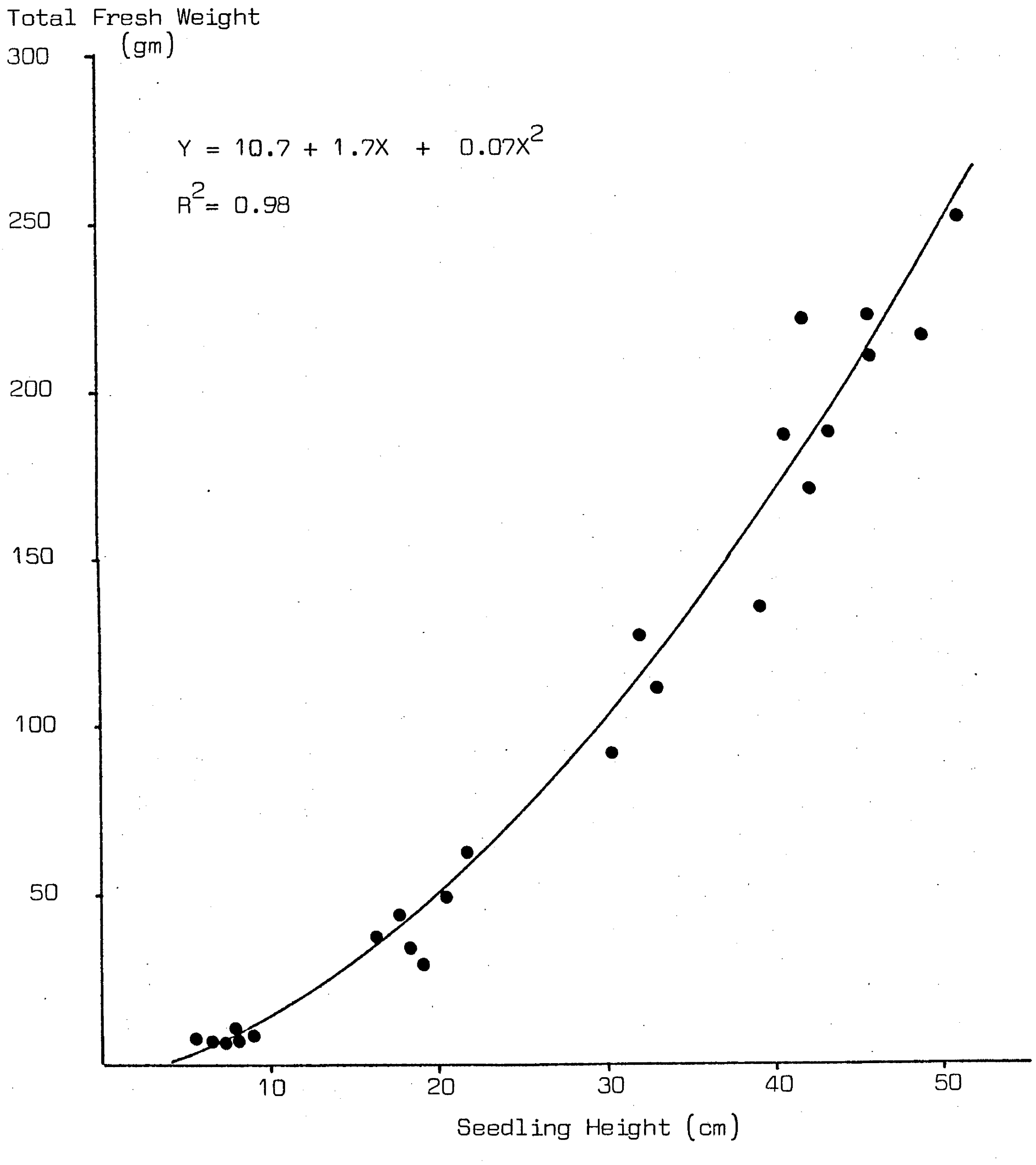


FIGURE 6.1 Relationship between height growth and plant fresh weight of teak seedlings at 30/25°C (day/night temperature)

$$M.C = T - K - P$$

where M.C is the soil moisture content (gm), T is total pot weight (gm), K is a constant value for each pot (pot wt. + oven dry soil + polythene beads, or pot wt. + 2,400 gm), and P is total plant fresh weight (gm). The total plant fresh weight (P) was estimated from data described in Chapter 5, where total plant fresh weight was plotted against height growth for individual seedlings grown at 30/25°C day/night temperature. The relationship between these two parameters for teak seedlings is shown in Figure 6.1.

Measurements and Plant Harvesting in Experiment 1

(a) Plant Water Deficit: Water deficit in seedlings as affected by soil moisture stress was determined once at the end of the experiment using **Stoker's** technique modified by Weatherley (1951). Four seedlings from each treatment were selected at the end of the drying cycle, and three 1 cm discs were punched from a single leaf on each seedling. The fresh weight of the discs was determined immediately, and they were then floated on distilled water in the dark for 4 hours. After floating, the saturated weight of the discs was determined. Subsequently the discs were oven dried for 24 hours and their dry weights obtained. Leaf water deficit in seedlings was calculated using the following formulae:-

$$\text{Relative turgidity} = \frac{(\text{fresh wet. - dry wt.})}{(\text{saturated wt. - dry wt.})} \times 100\%$$

$$\text{Water deficit} = 100 - \text{relative turgidity}\ \%$$

$$\text{Water content} = \frac{(\text{fresh wt. - dry wt.})}{\text{dry wt.}} \times 100\%$$

(b) Growth and Dry Matter Production: The height of seedlings was measured at weekly intervals throughout the experiment. Eight weeks after the soil moisture treatments were initiated seedlings from all treatments were harvested (Section 4.2.4). Leaf area, shoot dry weight and root dry weight were determined.

Experiment 2

A second experiment was carried out to determine the effects of soil water deficits on (a) the level of carbohydrate reserves in various organs of teak seedlings and (b) the sprouting of teak planting stumps.

The three soil moisture treatments: A, B and C, described in Experiment 1 were reapplied in this study. Eight weeks after seed germination, 30 uniform seedlings were allocated at random to one of the three treatments, i.e. there were 10 seedlings per treatment. The procedures used in controlling soil water in the undrained pots are as described for Experiment 1.

Eight weeks after the seedlings had been subjected to their respective treatments, 7 seedlings from each treatment were stumped (Section 1.2) and immediately replanted singly in the same pots containing a mixture of equal parts of vermiculite and perlite. The remaining 3 seedlings from each treatment were harvested (Section 4.2.4), oven-dried, and ground in a Wiley mill to pass a 1 mm mesh sieve for the extraction and determination of carbohydrate levels in leaves, stems, tap-roots, and lateral roots. The replanted stumps were all placed in the 30/25°C controlled day/night temperature glasshouse and were well supplied with water and nutrient solution. They were allowed to form new shoots under these conditions for 10 weeks before they were finally harvested.

Measurements and Plant Harvesting: Stem height and diameter, leaf, area, leaf dry weight, stem dry weight, and stump fresh weight of the treated seedlings were recorded at stumping time.

Ten weeks after stump-replanting, stem height and diameter, leaf area and leaf and stem dry weights of the sprouts were determined.

Determination of Carbohydrate Reserves: Soluble sugar and starch contents were extracted from leaves, stems, tap-roots, and lateral roots of seedlings grown under the three soil moisture regimes following the method described in Section 4.2.7. The preparation of material for extraction was as follows: for each treatment and each seedling organ, one gram samples from each of the three seedlings were mixed to give 3 gram samples of leaf, stem, tap-root, and lateral roots, respectively. Two sub-samples each of 0.2 gm were taken from each of the 3 gm samples, transferred to 100 ml flasks, and extracted for the soluble sugars and starch contents.

6.3 RESULTS

6.3.1 Experiment 1

6.3.1.1 Plant Water Deficit

The results presented in Table 6.2 show the effects of the three soil moisture regimes on the water balance in seedlings. The water deficit of seedlings grown under severe moisture stress (C) was much higher than that of seedlings grown under moderate moisture stress (B) or under constant high soil moisture (A).

TABLE 6.2 Effects of soil moisture regime on water balance in teak seedlings

Soil Moisture Treatment	Leaf Water Status		
	Water Content	Relative Turgidity	Water Deficit
	(% o.d.w.)	(%)	(%)
A. Constant high soil moisture	177.0 ± 8.1	90.7 ± 0.5	9.3 ± 0.5
B. Moderate moisture stress	156.2 ± 2.6	71.0 ± 1.0	21.0 ± 1.0
C. Severe moisture stress	131.8 ± 3.3	61.8 ± 1.9	38.2 ± 1.9

6.3.1.2 Seedling Growth

A. Height Growth: The height increment and height growth of seedlings grown under the three soil moisture regimes are presented in Tables 6.3 and 6.4, respectively.

Under Treatment A seedling height growth was much greater than that under Treatments B and C. Mean seedling height was 20.78 ± 1.30 cm in Treatment A when the experiment was terminated, while that of seedlings grown under Treatments B and C was 9.77 ± 0.71, and 9.35 ± 0.75 cm, respectively. There was no significant difference in height between seedlings grown under Treatments B and C.

B. Diameter Growth: As for height growth, the diameter of seedlings grown under Treatment A was significantly greater, at the 1% level, than that of seedlings grown under Treatments B and C (Table 6.4). However, there was a significant difference, at the 1% level, between seedlings grown under Treatments B and C. At the termination of the study, the mean diameters of seedlings were 1.56 ± 0.03, 1.09 ± 0.06, and 0.81 ± 0.04 cm, respectively, for Treatments A, B and C.

C. Leaf Area Production: Teak seedlings grown under the constant high soil moisture produced more than 4 times the leaf area of seedlings grown under the two soil moisture stress regimes (Table 6.4). There was no difference in leaf area production between seedlings grown under the two moisture stress regimes. The total leaf area of seedlings grown under Treatment A was 46.45 ± 2.09 dm^2, and under Treatments B and C were 10.72 ± 0.74 and 8.71 ± 1.14 dm^2 respectively.

6.3.1.3 Dry Matter Production

The effects of soil moisture supply on the dry matter production of teak seedlings are presented in Table 6.4. Total dry matter production, and dry matter production for each component separately (leaf, stem, tap-root, lateral roots, total shoot, and total root) decreased sharply with decreased soil moisture supply. The total plant dry weight of seedlings grown under Treatment A was 55.09 ± 2.05 gm, that of seedlings grown under Treatments B and C was 18.50 ± 1.62 and 11.82 ± 1.33 gm, respectively. Differences between Treatments B and C were highly significant (i.e. at the 1% level) for the tap-root, lateral roots, total roots, and total plant dry weight. However, differences in leaf, stem, and total shoot dry weight between seedlings grown under Treatments B and C were not significant.

6.3.1.4 Structural Parameters

A. Number of Leaf and Bud Pairs: There was no significant difference between treatments in the number of pairs of dormant buds (Table 6.4). Seddlings grown under constant high soil moisture produced more pairs of leaves than seedlings grown under the two moisture stress treatments, but there was no significant difference between the two stress treatments.

B. Root/Shoot Ratio: The analysis of root/shoot ratio clearly shows that teak seedlings grown under the constant high soil moisture regime channelled a much higher proportion of available photosynthates into shoot growth than into root growth (Table 6.4). The root/shoot ratios of teak seedlings grown under different soil moisture conditions were significantly different at the 1% level. The greatest root/shoot ratio value was for seedlings grown under Treatment B (0.93 ± 0.07), and lowest for seedlings grown under Treatment A (0.36 ± 0.20). The root/shoot ratio value for seedlings grown under Treatment C was 0.65 ± 0.05.

C. Leaf Area Ratio (LAR), Leaf Weight Ratio (LWR), and Specific Leaf Area (SLA); The analyses of variance for LAR, LWR and SLA of teak seedlings grown under different soil moisture regimes show significant difference at the 1% level in the LAR and LWR but no significant difference in SLA. Both the LAR and LWR of seedlings grown under constant high soil moisture were greater than for seedlings grown under the two soil moisture stress regimes (Table 6.4). However, the LAR and LWR of seedlings grown under the moderate moisture stress treatment were significantly lower, at the 1% level, than those of seedlings grown under the severe moisture stress treatment.

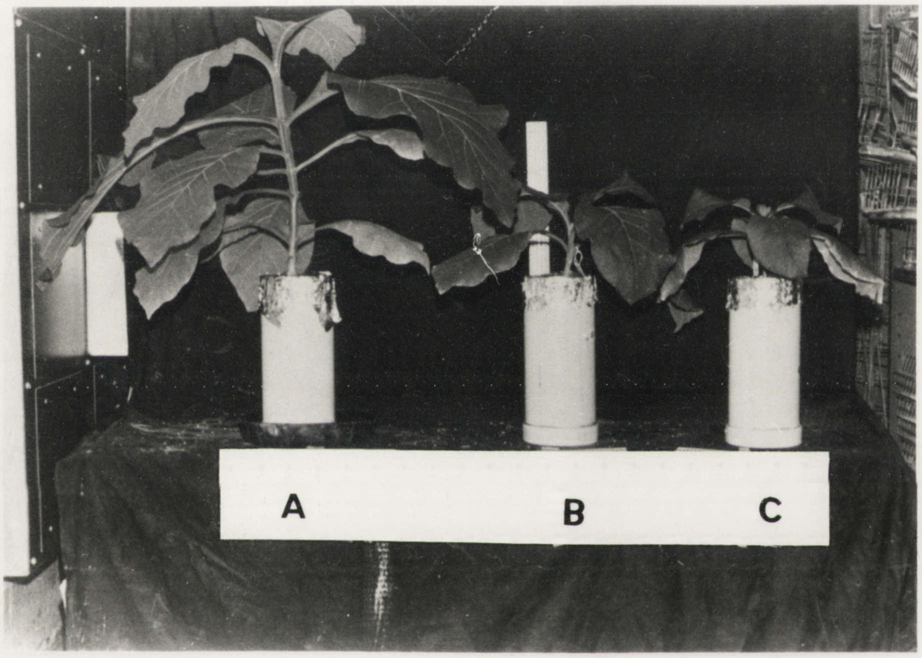


Plate 6.1 Effects of soil moisture availability on growth and development of teak seedlings (8 weeks after treatment)

Treatment A : Constant high soil moisture
B : Moderate soil moisture stress
C : Severe soil moisture stress

TABLE 6.3 Effect of soil moisture regime on height growth increment of teak seedlings
(Data represent the mean of 10 seedlings)

Week After Treatment	Soil Moisture Regime (see text)		
	A	B	C
	Height Increment (cm)		
1st	0.82 ± 0.22	0.42 ± 0.14	0.45 ± 0.13
2nd	2.34 ± 0.34	0.88 ± 0.15	0.68 ± 0.11
3rd	3.10 ± 0.35	0.56 ± 0.12	0.33 ± 0.08
4th	2.50 ± 0.48	0.15 ± 0.03	0.12 ± 0.04
5th	1.91 ± 0.43	-	-
6th	0.98 ± 0.22	-	-
7th	0.73 ± 0.28	-	-
8th	0.67 ± 0.16	-	-

TABLE 6.4 Effects of soil moisture regime on growth and dry matter production of teak seedlings (Data represent the mean of 10 seedlings)

	Soil Moisture Regime (see text)			L.S.D.	
	A	B	C	.05	.01
Seedling growth:					
Height (cm)	20.8 ± 1.3	9.8 ± 0.7	9.4 ± 0.8	2.8	3.7
Diameter (cm)	1.6 ± 0.0	1.1 ± 0.1	0.8 ± 0.0		0.2
Leaf area (dm^2)	46.4 ± 2.1	10.7 ± 0.7	8.7 ± 1.1	4.2	5.6
Dry matter weight (gm):					
Leaf	32.8 ± 1.2	7.9 ± 0.8	6.0 ± 0.8	2.7	3.7
Stem	7.6 ± 0.4	1.7 ± 0.2	1.4 ± 0.2	0.7	1.0
Tap-root	8.6 ± 0.4	5.0 ± 0.5	2.8 ± 0.3		1.6
Lateral roots	6.1 ± 0.5	3.8 ± 0.5	1.6 ± 0.2		1.8
Total shoot	40.4 ± 1.4	9.6 ± 0.9	7.4 ± 0.9	3.1	4.2
Total roots	14.7 ± 0.9	8.9 ± 0.9	4.5 ± 0.4		3.0
Total plant	55.1 ± 2.0	18.5 ± 1.6	11.8 ± 1.3		6.6
Structural Parameters:					
No. bud (pair)	5.3 ± 0.7	5.3 ± 0.5	5.7 ± 0.6	ns	
No. leaf (pair)	5.0 ± 0.3	3.3 ± 0.3	3.2 ± 0.2	0.8	1.1
Root/shoot	0.36 ± 0.20	0.93 ± 0.07	0.65 ± 0.05		0.2
LAR (cm^2/gm)	84.5 ± 2.8	60.4 ± 1.7	72.5 ± 2.3		9.2
LWR	0.6 ± 0.0	0.4 ± 0.0	0.5 ± 0.0		0.05
SLA (cm^2/gm)	141.8 ± 4.2	143.3 ± 3.2	145.4 ± 3.9	ns	

6.3.2 Experiment 2

It has been shown that the availability of soil water has a marked effect on growth and development of teak seedlings; that is teak seedlings are strongly inhibited by even moderate soil moisture deficits. In the second experiment an examination was made of the effects of the same soil moisture regimes on carbohydrate reserves within teak seedling organs, and their subsequent effects on the sprouting of the seedling stumps after replanting.

6.3.2.1 Growth Characteristics of Seedlings Before Stump-Replanting

There were significant differences in growth and dry matter production between seedlings grown under the three soil moisture regimes, with a maximum for the "A" treatment seedlings and a minimum for the "C" treatment seedlings (Table 6.5). Thus the general pattern of seedling response to soil moisture stress was consistent with that shown in Experiment 1. The size of stumps, as expressed in terms of diameter at collar and stump fresh weight, declined markedly with a reduction of soil water supply. The fresh weight of the "A" stumps (30.3 gm) was about 2 and 4 times greater than that of the "B" (14.4 gm) and "C" (8.1 gm) stumps, respectively.

One of the notable features of this experiment was that seedlings from Treatment B exhibited a relatively larger distribution of their total dry weight to the root system, as compared with seedlings from Treatments A and C. The results presented in Table 6.5 show that the total dry weights of the root system of the "A", "B" and "C" seedlings were 28.4, 44.5 and 35.2% of total plant dry weight, respectively. Similar results were obtained in Experiment 1, where the proportion of total dry weight in the root system of the "A", "B" and "C" seedlings were 26.7, 48.1 and 38.1%, respectively. Within the root system, there is evidence to suggest that seedlings from Treatment B tended to produce relatively more lateral roots, as compared with seedlings from Treatments A and C. The weight of lateral roots of the "B" seedlings was about 54% of the total root system, whereas the weights of lateral roots of the "A" and "C" seedlings were about 38 and 39% of their total root system, respectively. These findings suggest that the capability for accumulation of assimilates in the tap-roots of the "A" and "C" seedlings was considerably greater than that of the "B" seedlings.

6.3.2.2 Carbohydrate Reserves

The amounts of carbohydrate reserves in leaves, stems, tap-roots, and lateral roots of teak seedlings as influenced by the availability of soil moisture are presented in terms of water soluble sugars and the starch in Table 6.6. The results clearly show that the great part of the extractable carbohydrate in all parts of the teak seedling is in the form of starch, and a much smaller part is in the form of water soluble sugars. This is consistent with previous results (Section 5.3). The effects of soil moisture availability on the levels of sugars and starch in various organs of teak seedlings are described in detail as follows:-

A. Sugar Reserves: On the basis of averaging the concentration of sugars in leaves, stem, tap-root, and lateral roots and expressing this as a percentage of tissue dry weight, the concentration of sugars in the whole plant increased markedly with reduction of soil water supply (Table 6.6-A). The concentrations of sugars in the "A", "B" and "C" treatment seedlings were 0.23, 0.36 and 0.40% respectively.

TABLE 6.5 Growth and dry matter production of teak seedlings as influenced by soil moisture regime

	Soil Moisture Regime			L.S.D.	
	A	B	C	0.5	0.1
A. Growth of stump-replanted seedlings: (average from 7 seedlings)					
Height (cm)	23.4 ± 1.4	11.3 ± 1.0	11.5 ± 1.2		5.0
Diameter (mm)	15.8 ± 0.3	10.4 ± 0.5	8.6 ± 0.5		0.2
Leaf area (dm^2)	48.2 ± 2.7	9.9 ± 0.9	8.8 ± 1.6	6.4	8.8
Shoot dry weight (gm)	41.4 ± 1.5	9.4 ± 1.2	7.6 ± 1.3	4.2	5.7
Stump fresh weight	30.3 ± 1.5	14.4 ± 1.7	8.1 ± 1.0		5.6

B. Dry matter production and distribution of dry weight in teak seedlings: (average from 3 seedlings and for carbohydrate extraction)

	gm	%*	gm	%	gm	%
Leaf	30.8	57.9	8.9	44.5	6.1	52.6
Stem	7.3	13.7	2.2	11.0	1.4	12.1
Tap-root	9.4	17.7	4.1	20.5	2.5	21.5
Lateral roots	5.7	10.7	4.8	24.0	1.6	13.8
Total	53.2	100	20.0	100	11.6	100
R : S	0.4		0.8		0.6	

* % of total dry weight

Within the seedling, the concentration of sugars in the shoot parts was much higher than that in the root systems. This applies to seedlings from all treatments. Under the constant high soil moisture (treatment A) the sugar concentration in the seedling shoot (0.28%) was almost three times greater than that in the root systems (ca. 0.10%). Under dry conditions (treatments B and C) the sugar concentration in shoot parts (0.55%) was about five times greater than that in the root systems (0.12%) and this applies to both "B" and "C" seedlings.

In shoot parts, soil moisture stress caused a marked increase in sugar concentration. The concentration of shoot sugars in seedlings grown under moisture stress treatments (0.55% for both treatments B and C) was about twice as great as that of seedlings grown under the constant high moisture (0.28 % for treatment A). The effect of soil moisture stress on the concentration of shoot sugars of the teak seedlings is largely a reflection of changes in sugar concentration in leaves. When the concentrations of leaf and stem sugars of the test seedlings are compared, it is seen that under constant high soil moisture, sugar concentrations were the same in the leaves and stem (i.e. 0.28%). Under soil moisture stress treatments, the sugar concentration in the leaves was about three times that in the stems, that is 0.64% (leaves) : 0.18% (stem) for the "B" seedlings and 0.60% (leaves): 0.21% (stem) for the "C" seedlings. The concentration of sugars in the seedling leaves increased markedly with reduction of soil water supply. The concentration of leaf sugars of seedlings grown under treatments B and C was twice as great as that of seedlings grown under treatment A, that is 0.28% (A); 0.64% (B) and 0.60% (C). In contrast, restriction of soil water supply resulted in a small

TABLE 6.6 Effect of soil water stress on carbohydrate reserves in teak seedlings
(Data represent the mean of 2 x 4 extractions)

	Soil Moisture Regime					
	A		B		C	
A. Soluble sugars:	%*	mg**	%	mg	%	mg
Leaf	0.28	86.0	0.64	57.0	0.60	38.0
Stem	0.28	21.0	0.18	4.0	0.21	3.0
Tap-root	0.11	10.0	0.12	5.0	0.12	3.0
Lateral roots	0.07	4.0	0.13	6.0	0.12	2.0
Total shoot	0.28	107.0	0.55	61.0	0.55	41.0
Total root	0.10	14.0	0.12	11.0	0.12	5.0
Total plant	0.23	121.0	0.36	72.0	0.40	46.0
B. Starch:	%*	gm**	%	gm	%	gm
Leaf	25.7	7.9	24.0	2.1	23.1	1.4
Stem	27.4	2.0	27.8	0.6	28.7	0.4
Tap-root	30.6	2.9	33.8	1.4	33.9	0.9
Lateral roots	23.7	1.4	22.7	1.1	22.8	0.4
Total shoot	26.0	9.9	24.3	2.7	24.0	1.8
Total root	30.5	4.3	28.1	2.5	31.7	1.3
Total plant	27.2	14.2	26.0	5.2	26.7	3.1
C. Total CHO:	%*	gm**	%	gm	%	gm
Leaf	25.98	7.99	24.64	2.16	23.70	1.44
Stem	27.68	2.02	27.98	0.60	28.91	0.40
Tap-root	30.61	2.91	33.92	1.41	34.02	0.90
Lateral roots	23.77	1.40	22.83	1.11	22.92	0.40

* % of tissue dry weight

** total amounts content

decrease in the concentration of stem sugars of the seedlings. The concentrations of stem sugars of the "A", "B" and "C" seedlings were 0.28, 0.18 and 0.21% respectively.

In the root systems, there was a small overall increase in the concentration of root sugars as a result of soil moisture stress treatments. The concentration of root sugars increased from 0.10 (Treatment A) to 0.12 (Treatments B and C) %. This reflects a large increase in sugar concentration in the lateral roots of seedlings under stress treatments. From Table 6.6-A it is seen that the concentrations of sugars in the tap-roots of seedlings grown under Treatments A, B and C were at the same level, whereas the concentrations of sugars in the lateral roots of seedlings grown under Treatments B and C were almost twice as great as that of seedlings grown under Treatment A; that is 0.07% (A), 0.13% (B) and 0.12% (C). Within B and C treatments there was a substantial difference between total sugar content in the lateral roots, i.e. 6 mg (B) and 2 mg (C), reflecting the large amount of lateral roots produced by the "B" seedlings (Section 6.3.2.1). The total sugar content in laterals for the "B" seedlings (6 mg) was in fact greater than that of the "A" seedlings (4 mg) despite the greater dry weight of laterals in "A" seedlings (Table 6.5).

B. Starch Reserves: As noted above starch comprises the main fraction of the extractable carbohydrate reserve in the teak seedling, and is present in all parts of the seedling at a relatively high concentration (23 - 34% of tissue dry weight). A large fluctuation in the relative starch levels, as influenced by treatments, is not to be expected.

For all soil moisture treatments, the concentration of starch in the seedling shoot (24-26%) was significantly lower than that in the root system (28-32%). This indicates that teak seedlings channel a large proportion of the photosynthetic products to the root system.

Within the shoot parts, there was a slight difference in the concentrations of starch between the leaves and stem of the seedling, with a maximum for the stem parts. The ratios of the starch concentration in leaves and stems of the "A", "B" and "C" seedlings were 25.7 : 27.4, 24.0 : 27.8, and 23.1 : 28.7 respectively. Restriction of the supply of soil water caused a decrease in the concentration of the leaf starch and an increase in the stem starch, but there was a decrease in concentration of the starch in a whole shoot part (Table 6.6-B). The concentrations of starch in the shoots of seedlings grown under treatments A, B and C were 26.0, 24.3 an 24.0% respectively. A reduction of starch concentration accompanied by an increase in sugar concentration in the leaves of seedlings subjected to soil moisture stress might be due either to retardation of photosynthesis and growth of the seedlings or to a conversion of starch to sugars caused by an increase in the activity of the hydrolytic enzymes. This will be discussed in Section 6.4.

Within the seedling roots, there was a higher starch concentration in the tap-root than in the lateral root in all treatments. It is seen from Table 6.6-B that the concentration of starch in the tap-root is greater than that in any organ of the teak seedling. The tap-root of the teak seedling is believed to be the main storage organ for carbohydrate reserves. Reduction of soil water supply caused an increase in starch concentration in the seedling tap-root and a decrease in the starch concentration in the lateral roots. The concentrations of starch in the tap-roots of the "A", "B" and "C" seedlings were 30.6, 33.8 and 33.9% respectively.

In summary, it is clear that soil water stress caused some change in sugar and starch levels in various organs of the teak seedlings, with a tendency for concentrations of sugars to increase and starch to decrease in the seedling shoot. The tap-root of the seedling appeared to be the main storage organ for carbohydrate reserves; soil water stress caused an increase in starch concentration in the tap-root but did not affect the concentration of sugars. However, there was an increase in the concentration of soluble sugars with the lateral roots as a result of the water stress and a comparable decrease in the starch concentration. The total amount of both starch and sugar produced decreased progressively with more severe soil moisture regime from treatment A, to B, to C respectively.

6.3.2.3 Stump Sprouting

It has now been shown that (i) availability of soil water has an important influence on growth and development of teak seedlings, that is, growth is strongly restricted by soil water deficits; and (ii) a restriction of soil water supply caused an increase in the sugar concentration and a small decrease in starch concentration in the shoots of seedlings, and an increase in starch concentration but not the sugar in tap-roots. It remains to be seen what influence these changes may have on the subsequent sprouting vigour of the seedling stump. The production of stump sprouts of seedlings which had been subjected to the three soil moisture treatments is described in this section.

TABLE 6.7 Effect of the pre-stumping soil moisture regime on the subsequent production of stump sprouts (Data represent the mean of 7 stump sprouts taken 10 weeks after stumping)

Growth Parameters Measured of Sprouts	Soil Moisture Regime			L.S.D.	
	A	B	C	.05	.01
Sprouting Stump (%)	100	100	100		
Height (cm)	11.3 ± 1.2	5.7 ± 0.9	13.0 ± 1.9	4.3	5.8
Diameter (mm)	10.6 ± 0.4	9.6 ± 0.4	10.5 ± 0.2	0.9	
Leaf area (dm^2)	27.4 ± 1.6	18.6 ± 1.7	30.7 ± 2.1	5.4	7.3
No. leaf (pair)	6	6	6		
Leaf dry weight (gm)	14.7 ± 0.7	9.3 ± 0.9	16.6 ± 1.2	2.9	3.9
Stem dry weight (gm)	1.9 ± 0.1	0.8 ± 0.1	2.2 ± 0.3	0.7	0.9
Total shoot dry weight	16.6 ± 0.8	10.4 ± 1.0	18.8 ± 1.5	3.6	5.0
Lateral roots dry weight	3.4 ± 0.4	1.5 ± 0.1	3.3 ± 0.3		1.1

Ten weeks after stump-replanting, restriction of soil water supply prior to stump-replanting did not have a significant effect on the subsequent survival of stumps. All stumps from the three soil moisture treatments produced sprouts. Stump size, measured as stump diameter and stump fresh weight, was a maximum for the "A" seedlings and least for the "C" seedlings (Table 6.5). This clearly suggests that within a range of size of stumps used for planting in this study, there was no significant effect of stump size on the survival after stump-replanting.

There was a marked effect of moisture stress conditioning of seedlings on the subsequent growth responses of sprouts produced by the seedling stumps (Table 6.7). For all growth parameters measured, sprouts produced by the "A" and "C" stumps were much bigger than those produced by the "B" stumps. Sprouts produced by the "A" and "C" stumps were not significantly different in any of the growth parameters measured. Because stumps of the "B" seedlings were greater in size than those of the "C" seedlings and yet "C" seedling stumps produced the more vigorous sprouts, it is once again clear that stump size is not the principal factor influencing the vigour of stump sprouts. In addition, it is apparent that sprout response, does not reflect any obvious difference in carbohydrate concentration in stumps. The concentration of sugars did not differ between stumps of the "A", "B" and "C" seedlings, and while the concentration of starch in stumps of the "A" seedlings was smaller than that in stumps of the "B" and "C" seedlings, there was no difference between the "B" and "C" seedlings stumps. Thus there is no positive correlation between the concentration of carbohydrate reserves in the parent stumps and the vigour of stump sprouts in teak.

In summary, stumps of seedlings which have been grown either under the constant high soil water, or under severe moisture stress were superior to stumps of seedlings grown under the moderate soil moisture stress in the production of sprouts after stump-replanting. This is not directly related to carbohydrate supply in the seedling stump. It is a finding which is difficult to interpret and will be discussed in more detail in the next section.

6.4 DISCUSSION

6.4.1 Effect of Soil Water Deficits on Seedling Growth

Teak seedlings, like most plants, require a relatively high soil water supply for rapid growth and development. Even moderate soil water deficits restrict growth and dry matter production of the seedlings of this species. For example, the height of seedlings grown under the constant high soil moisture (Treatment A) increased almost 175% during the treatment period of 60 days; whereas the height of seedlings grown under the moderate and severe moisture stress treatments (Treatments B and C) increased only 30 and 20%, respectively. In respect to dry matter production, the total dry weight of the "A" seedlings was about 3 and 5 times, respectively, greater than that of the "B" and "C" seedlings. Treatment B had almost as great a restrictive effect as the severe stress treatment C despite the fact that leaf water deficit under moderate stress (21.0%) was not as great as that under severe stress (38.2%) (Table 6.2).

Although the overall growth of the teak seedling is strongly restricted by soil water deficits there is some evidence that shoot

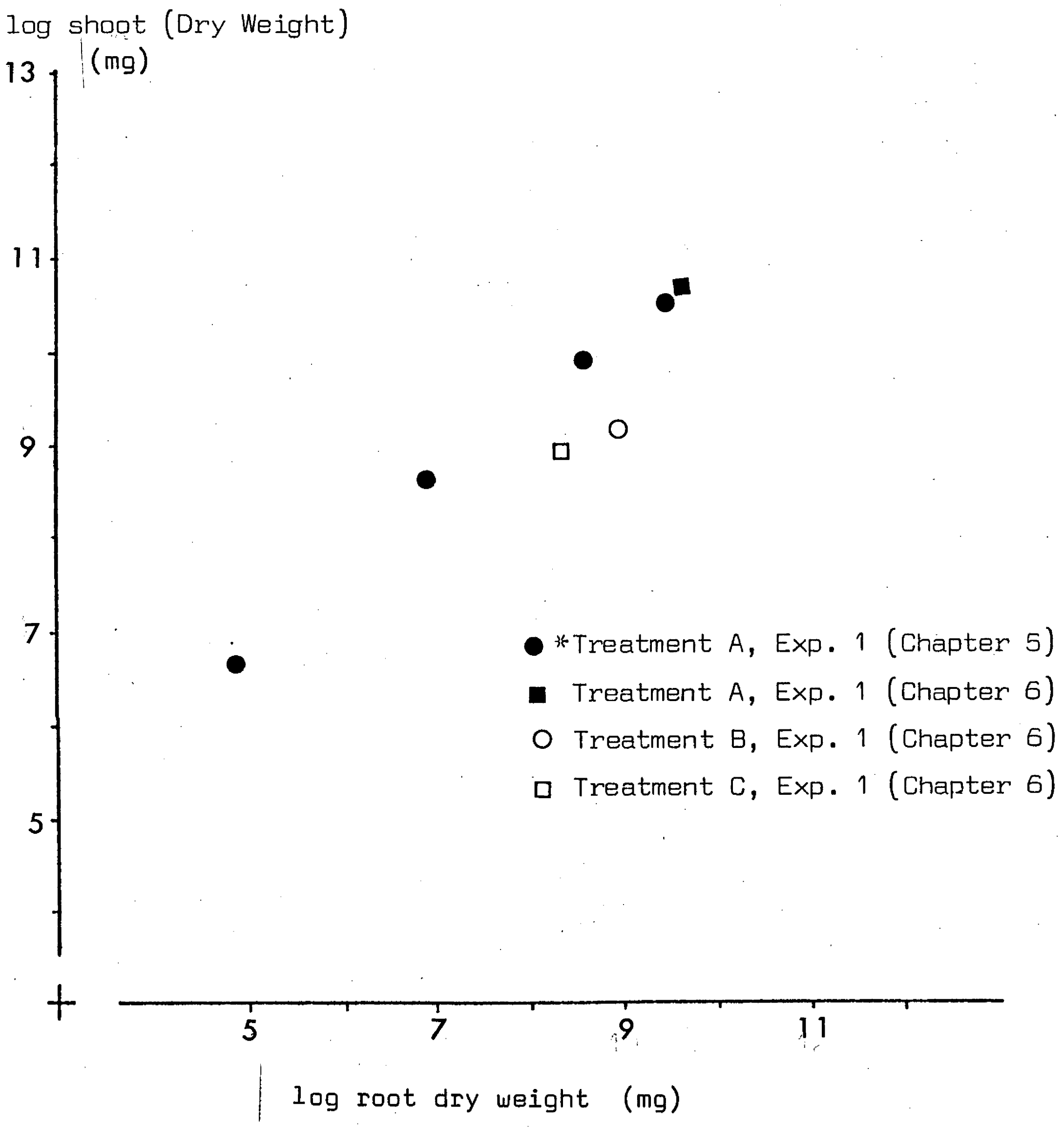


FIGURE 6.2 Effect of soil moisture deficits on the balance between root growth rate and shoot growth rate of teak seedlings

* Treatment A, Exp. 1 (Chapter 5) all seedlings were watered 3 times a day.

All seedlings were grown at 30/25°C controlled day/night temperature glasshouse.

growth is likely to be inhibited to a relatively greater degree than root growth. The root/shoot ratios of seedlings grown under the three soil moisture regimes were significantly different, with a maximum for the "B" seedlings and a minimum for the "A" seedlings. The root/shoot ratio values of seedlings grown under Treatments B and C were about twice those of seedlings grown abundant water in Treatment A. In Figure 6.2 the logarithm of shoot dry weight has been plotted against the logarithm of root dry weight, and this shows a fairly constant ratio between root and shoot growth of seedlings grown under the constant high soil moisture supply. Where the seedlings were grown under periodic soil moisture stress for 8 weeks, root/shoot ratios were altered; there was a substantial increase in root production per unit of shoot production. Many studies of plant-soil water relations have reported similar findings (Kramer and Kozlowski, 1960; Jarvis and Jarvis, 1963; Kramer, 1969; Ledig et al, 1970; Levitt, 1972; Borchert, 1973). Ledig and his co-workers (1970), for example, applied the allometric regression in a study of the effect of soil water deficits on growth of loblolly pine seedlings. They found that droughted seedlings tended to produce more roots than shoots and suggested that this phenomenon is likely to be an environmentally induced adaptation to drought. Similarly, Borchert (1973) reported that plants grown under constant conditions tend to maintain a constant ratio between the growth of their root and shoot systems; and where the plants are transferred from one environment to another, a different ratio of root growth to shoot growth will be established. This concept is supported by the work of Brouwer (1963), Wareing (1970), and Thornley (1972). Borchert also proposed that growth of various plant organs, including root and shoot parts, is a function of available water.

TABLE 6.8 Transpiration rate of teak seedlings under the unlimited soil moisture supply in relation to the ratios of absorbing surface and transpiring surface (root/shoot and root/leaf)
(Data represent the mean of 10 seedlings)

Time of Day (after rewatering)	Treatment A	Treatment B	Treatment C
	water loss (gm/dm^2 of leaf area)		
6 - 8 am	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.0
8 - 10 am	0.8 ± 0.1	1.2 ± 0.1	1.0 ± 0.1
10 - 12 am	0.8 ± 0.1	1.9 ± 0.3	1.6 ± 0.2
12 - 2 pm	0.8 ± 0.1	1.4 ± 0.2	1.9 ± 0.2
2 - 4 pm	0.6 ± 0.0	0.7 ± 0.0	1.0 ± 0.1
4 - 6 pm	0.1 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
6 - 6 am	1.0 ± 0.1	1.3 ± 0.1	1.3 ± 0.2
Total (gm/dm^2/day)	4.5	7.1	7.4
Root/Leaf (mg/gm)	0.4	1.1	0.8
Root/Leaf (gm/dm^2)	0.3	0.8	0.5
Root/Shoot (gm/gm)	0.4	0.9	0.7

If the root surface is inadequate to supply the water lost by the shoot, an internal plant water deficit will develop and this will stop shoot and leaf growth until enough roots are produced to re-establish a balance and reduce the plant water deficit.

One interpretation of the findings in the present study is that the development of a relatively high root/shoot ratio under moisture stress treatments is an adaptation for drought avoidance, that is, teak seedlings tend to increase the root surface for water uptake, and reduce the growth of transpiring surfaces. In this way a reduction of plant water deficit during droughting is achieved. This suggestion is also supported by measurement of the transpiration rates for seedlings from all three treatments immediately after watering to field capacity (Table 6.8). The transpiration rate of the "B" and "C" seedlings was much higher than that of the "A" seedlings. Over a period of 24 hours the "A" seedlings transpired 4.5 gm of water per square decimetre of leaf area, while the "B" and "C" seedlings transpired 7.1 and 7.4 gm of water per square decimetre, respectively. The higher rate of transpiration per unit leaf area may be associated with the higher root/shoot ratio of the droughted seedlings.

Levitt (1972) stated that the root/shoot ratio is one of the most important factors contributing to the high transpiration rates of "water spenders", that is an increase in root/shoot ratio increases the transpiration rate per unit leaf area. He also explained that the plant with the larger root system will explore a larger volume of soil and will tap more soil water to supply the shoot system. Working with red cedar and loblolly pine seedlings, Parker (1949) has similarly reported that the transpiration rate of seedlings of these species, grown with unlimited water supply, increased as a ratio of the root to shoot surface increased. The findings for teak is also in agreement with the results obtained with a variety of woody plants (Bialoglowski, 1936; Forwells and Kierk, 1945; Jarvis and Kramer, 1956 and Jarvis, 1963).

From this study, it can be concluded that teak seedlings require a relatively high soil water supply for rapid growth and development, and when subject to water stress, there is a marked reduction in both growth and dry matter production. Within the plant, the growth responses to water stress differ markedly between the shoot and the root systems. The growth of the seedling shoot is more inhibited by soil water stress than growth of the root system, and this is presumed to be an adaptation to drought avoidance of the teak seedling.

6.4.2 Effect of Water Deficits on Carbohydrate Reserves

The findings obtained in this study have clearly shown that there is a significant role of soil water availability in the balance of stored carbohydrates in teak seedlings. When subjected to soil water stress the seedling of this species exhibited:

(a) an increase in sugar concentrations associated with a decrease in starch concentrations in the actively growing tissues, i.e. leaves and lateral roots;

(b) a small decrease in sugar concentrations associated with a small increase in starch concentrations in the stems;

(c) an increase in starch concentrations in the tap-roots; and

(d) a marked reduction in the total amount of stored carbohydrates (i.e. sugars and starch) in both shoot and root system, and this is due primarily to a marked reduction in seedling size.

The increase in sugar concentrations and a corresponding decrease in starch concentrations especially in the actively growing tissues of the teak seedling as a result of water stress observed in this study are in agreement with those obtained in a number of studies (Eaton and Ergle, 1948; Hodges and Lorio, 1969; Maraville and Paulsen, 1970; Parker, 1970; Stewart, 1971; Levitt, 1972; Parker and Patton, 1975). This evidence might be due either to an increase in the activities of some hydrolytic enzymes which convert the stored starch into sugars during the period of water stress (Spocehr and Milner, 1939; Iljin, 1957; Vaadia et al, 1961; Maranville and Paulsen, 1970; Stewart, 1971), or to the changes of some metabolic activities which result in a decrease in both the amount and rate of utilization of carbohydrates especially sugars or seedling growth (Iljin, 1957; Hodges and Lorio, 1969; Levitt, 1972; Hsiao, 1973).

In the study of the effect of water stress on the changes of stored carbohydrates in corn plants Maranville and Paulsen (1970) found that water stress caused a marked increase in sugar concentrations and a corresponding decrease in starch concentrations in this species. This author also noted that this change of the balance of stored carbohydrates during water stress was a result of an increase in enzymatic hydrolysis of stored starch to sugars (i.e. alpha-amylase and beta-amylase). Similarly, Stewart (1971) reported that water stress caused a marked increase in the activity of the α-amylase, accompanied by an increase in sugar concentrations and a decrease in starch concentrations in the bean leaves. He suggested that the decrease in starch concentrations in the leaves of this plant during water stress might be due to starch hydrolysis catalyzed by α-amylase, rather than to reduced photosynthesis. The hydrolysis of starch to sugars during water stress has been suggested as an adaptation for drought avoidance in plants, in which the high concentration of sugars in cell sap might protect the protoplasm from coagulation and desiccation or might prevent visible wilting for a long time by an increase in osmotic pressure which enables plants to absorb water from the drying soil and reduce water loss (Parker, 1956, 1968; Iljin, 1957; Maraville and Paulsen, 1970; Levitt, 1972).

In contrast to the above suggestion, the increase in sugar concentrations in plants subjected to water stress was found to be the result of the decrease in plant growth rather than the hydrolysis of starch to sugars; that the use of sugars for growth in the droughted plants was less than in the well-watered plants (Hodges and Lorio, 1969). Levitt (1972) suggested that water stress stops or at least reduces plant growth without having as much effect on photosynthesis, therefore, a large accumulation of photosynthetic products occurs. This author also showed that water stress caused a marked increase in sugar concentrations without any increase in other carbohydrate fractions. Many studies on plant-water relationships have provided evidence to oppose the above suggestion that the amounts and forms of carbohydrate fractions in plants subjected to water stress were altered through the inhibitory effects of water stress on photosynthesis (Woodhams and Kozlowski, 1954; Kramer and Kozlowski, 1960; Brix, 1962;

Kozlowski, 1964; Kramer 1969). Brix (1962), for example, showed that net photosynthesis of loblolly pine seedlings was progressively reduced by water stress, and respiration exceeded photosynthesis when water stress was severe. The change of the balance between photosynthesis and respiration under water stress led to a decrease especially in starch and total carbohydrate concentrations particularly in the shoots of many plants (Woodhams and Kozlowski, 1954).

According to the results reported with teak seedlings in this study, the reduction of starch concentrations in the leaves of seedlings from the two stress treatments might be associated with their increase in both the stems and tap-roots. This suggests that water stress caused a hydrolysis of starch in the leaves, accompanied by a stimulation of the rate and amount of export of these products of starch hydrolysis from the leaves to accumulate in stems and tap-roots of the seedlings. This is in agreement with the study reported by Eaton and Ergle (1948) and Iljin (1957). Eaton and Ergle (1948), for example, showed that water stress caused a marked reduction in starch concentrations in the leaves of cotton plants, and a corresponding increase in starch concentrations in both the stem and root systems. These authors also suggested that soil moisture stress did not inhibit the rate and amount of translocation of photosynthetic products from shoot to root system in this plant.

One of the remarkable features obtained in the present study was that seedlings subjected to moderate soil water stress (Treatment B) tended to export a relatively larger amount of their photosynthetic products (in terms of sugars and starch) to the lateral roots, when compared with those subjected to constant high soil water (Treatment A) and severe soil water stress (Treatment C) (Table 6.9).

TABLE 6.9 Effect of soil moisture availability on the rate and amount of sugars and starch transported to and accumulated in the lateral roots of teak seedlings (Data represent the results extracted from Tables 6.5 and 6.6)

Carbohydrates in Seedling Lateral Roots	Soil Moisture Regime		
	A	B	C
A. Percentage of total products in the seedling (%):			
sugars	3.3	8.3	4.3
starch	9.9	21.2	12.9
Total	9.8	21.0	12.7
B. Percentage of total products in the root system (%):			
sugars	28.6	54.6	40.0
starch	32.6	44.0	30.8
Total	32.5	44.0	30.8

$$\text{A.} \quad \% = \frac{\text{CHO in lateral roots}}{\text{CHO in total seedling}} \times 100$$

$$\text{B.} \quad \% = \frac{\text{CHO in lateral roots}}{\text{CHO in total root system}} \times 100$$

The results summarized in Table 6.9 clearly show that the proportions of both total sugars and total starch in the lateral roots of seedlings grown under Treatment B were about twice as great as those of seedlings from Treatments A and C. Similarly, the proportions of both total root sugars and total root starch in the lateral roots of seedlings from Treatment B were much greater than those of seedlings from Treatments A and C. These findings suggest that the requirement for the products of photosynthesis, presumably for growth and development, of the lateral roots of seedlings grown under Treatment B was relatively higher than that of seedlings grown under Treatment A and C. These findings are also consistent with the results observed in the early study (Experiment 1), where the high proportion of total dry weight in the lateral roots was associated with seedlings grown under Treatment B (20.5%) as compared with that in the lateral roots of seedlings grown under Treatments A (11.1%) and C (13.6%).

6.4.3 Effect of Water Deficits on Subsequent Stump Sprouting

The experiment reported in the present study has clearly shown the effect of soil moisture stress on the ability of sprouting of teak seedlings after stump-replanting. There was evidence that stumps of seedlings grown under Treatment B (the moderate moisture stress) had a relatively poorer sprouting ability (in term of the vigour of sprouts produced) than stumps of seedlings grown under Treatments A and C (the constant high soil moisture and the severe soil moisture stress). Since the vigour of stump sprouting was not correlated with the degree of water stress or the level of soil moisture availability, the sprouting phenomenon of teak stumps observed in this study is difficult to interpret. In addition, there was no correlation between the ability of stump sprouting and the size of stumps or the amount of carbohydrate reserves in the planted stumps. Evidence was provided that both the size of stumps and the amount of carbohydrate reserves in stumps of seedlings grown under Treatments A and B were much greater than those of seedlings grown under Treatment C, but the ability of sprouting of both "A" and "B" stumps did not appear to be superior to that of the "C" stumps (Tables 6.5 and 6.6). Instead, the ability of sprouting of the "B" stumps was inferior to that of the "C" stumps. This suggests that the amount of stored carbohydrates in teak planting stumps is not the major factor governing their sprouting ability after planting. These findings are in agreement with those of a number of observations showing that there was no positive correlation between the ability of stump sprouting and the amount of stored reserves in the stumps (see for example in Section 2.2.1.2).

Whatever other factors may be involved in the sprouting ability of teak planting stumps, there was evidence to suggest that the rate of growth and development of seedling lateral roots prior to stumping might play a significant role in the subsequent sprout production of the teak stumps. Seedlings which had a relatively higher rate of lateral root production had a relatively poorer sprouting ability after stump-replanting. For example, seedlings grown under the moderate soil moisture stress (Treatment B) distributed a relatively larger amount of their total dry weight to the lateral roots, compared with seedlings grown under the constant high soil moisture (Treatment A) and those grown under the severe soil moisture stress (Treatment C). But the growth potential of sprouts produced by stumps of seedlings from Treatment B was considerably poorer than that of seedlings from Treatment A and C. However, the physiological mechanism of teak stump sprouting in relation to the growth rate of the seedling lateral roots observed in this study is very difficult to interpret. One possible suggestion is that the increase in lateral root growth rate of the seedling might change some physiological processes, such as the balance of stored reserves and plant growth substances. Consequently, these physiological changes might somehow reduce the sprouting potential of the seedling after stump-replanting. More research on the influences of soil water availability on growth and development of seedling lateral roots and subsequent stump sprouting in teak is required to help understand the phenomenon of stump sprouting in this species.

CHAPTER 7

EFFECTS OF TEMPERATURE REGIME AND SOIL MOISTURE STRESS ON TRANSLOCATION OF ^{14}C PHOTOSYNTHATES IN TEAK SEEDLINGS

7.1 INTRODUCTION

It has been shown in the previous studies that both temperature regime and soil moisture stress have important influences on growth and development of teak seedlings. Moreover, these two environmental factors also show a marked influence on the subsequent sprouting of teak seedlings stumps. But the results obtained in those studies did not show any significant relationship between stump sprouting potential and the concentration or amount of the stored carbohydrates in the stumps. On this basis, the effects of these two environmental factors on translocation and distribution of carbohydrates to the stumps of teak seedlings have been further examined in the present Chapter, to clarify whether there is no relationship between the level of stored carbohydrates in the stumps and the ability of stumps to sprout.

It is well known that the translocation system for photosynthetic products in plants consist of three main parts: (a) the assimilating sources (mainly the leaves), (b) the translocation channels or the transport conduits, and (c) the sinks for assimilates (all non-green growing and actively transpiring tissues) (Crafts and Crisp, 1971; Peel, 1974). Therefore, any factor affecting the rate and pattern of translocation of assimilates will affect either the sources, the sinks, or the transport conduits, or all three parts of the system together.

In reviewing literature Wardlaw (1968) suggested that environmental factors may control the rate and pattern of translocation of assimilates through their effects on the growth rate of the sinks, the rate of photosynthesis and outflow of photosynthates from the sources, or through their direct effects on assimilate movement. Reduced growth rate due to extreme environmental conditions would be expected to reduce the rate of assimilate translocation.

7.2 STUDY 1: EFFECTS OF TEMPERATURE REGIME ON PHOTOSYNTHESIS AND TRANSLOCATION OF ^{14}C PHOTOSYNTHATES IN TEAK SEEDLINGS

7.2.1 Purpose of Study

The purpose of this study is to examine the effects of temperature on rates of leaf photosynthesis and respiration, and the rate and pattern of translocation of photosynthates from the leaves to the stems and roots of the teak seedlings.

Three experiments are described in this section. In Experiment 1, seedlings grown at 30/25°C day/night temperature were transferred abruptly to grow at 18/13°C. Rates of photosynthesis and respiration were measured daily for 1 week after transferring and were measured again at the end of the second week after transferring from the warm to cool conditions. In Experiment 2, seedlings grown at 30/25°C were exposed to $^{14}CO_2$ at 30°C and then transferred abruptly to a range of temperature extending from 18/13° to 36/31°C with 6°C intervals. The rate of export of ^{14}C photosynthates from the leaves at each temperature, and its distribution to the stems and roots of seedlings were examined over a 48-hour period. For the range of temperature regimes, the distribution of ^{14}C photosynthates to different leaf and stem positions on the plant was also examined. In Experiment 3, seedlings grown at 30/25°C were exposed to $^{14}CO_2$ at 30°C and then transferred abruptly to grow at 18/13°C for 30 days. The rate of export of ^{14}C photosynthates from the leaves and its distribution to the stems and roots were examined over a 30-day period at this low day/night temperature.

7.2.2 Materials and Methods

Teak seeds from Laos were sown and the seedlings were grown singly in the 11 cm diameter cylindrical pots containing a mixture of equal parts of vermiculite and perlite. All seedlings were grown initially at 30/25°C day/night temperature. The procedures used in preparing the seedlings for the experiment are described in detail in Section 4.2.3.

7.2.2.1 Experiment 1: (Leaf Photosynthesis)

Fourteen weeks after germination, 8 uniform seedlings were selected for the experiment. The seedlings were divided into 2 groups, each of 4 seedlings. Seedlings in the first group were transferred abruptly to the 18/13°C day/night temperature glasshouse, and those in the second group were retained at 30/25°C temperature. Subsequently the rates of leaf photosynthesis and dark respiration of all seedlings in the two groups were measured at 1, 2, 3, 4, 5, 6, 7 and 14 days, respectively. These measurements were carried out in an artificially lit (LBH) cabinet (Morse and Evans, 1962) set at 18°C for the first group, and 30°C for the second group, with a light intensity of 3,344 f.c.

In determining the rate of photosynthesis and respiration, one whole leaf at the middle leaf-pair position was enclosed in a perspex leaf chamber (18 cm wide, 55 cm long and 2 cm deep) connected with the air inlet and outlet tubes of the gas analyser circuit. The leaf temperature inside the chamber was measured by a platinum resistance thermometer, and adjusted close to 18° and 30°C respectively for the first and second group of the seedlings. The differential in CO_2 concentration of an air stream before and after passing over the leaf chamber was determined with an infra-red gas analyser (IRGA) and the data transferred to the multi-speed chart recorder. Air flow rate was adjusted constantly to 10 litres per minute.

The rate of CO_2 exchange was calculated using the formula modified from Sesta'k et al, (1971) as follows:-

$$CO_2 \text{ exchange } (\pm) = \frac{C.\ F.\ S.\ Ca}{L} \times \frac{273.15}{(T + 273.15)} \times 60$$

where CO_2 exchange is nett photosynthesis and respiration ($mg\ CO_2/dm^2/hr$);

C is the difference between "blank" and "plant" on the chart recorder (chart unit);

F is flow rate through leaf chamber (10 L /min);

S is IRGA sensitivity per chart unit (2.65 ppm CO_2/unit);

Ca is ambient CO_2 concentration (assumed to be 1.93×10^3 mg per litre);

L is leaf area (dm^2);

T is temperature of flow meter at time of measurement (25°C):

and 273.15 is an absolute temperature determined at 0°C.

7.2.2.2 Experiment 2: (Translocation of ^{14}C-assimilates)

Twelve weeks after germination 12 uniform seedlings, each with 5pairs of leaves, were selected for the experiment. The seedlings were divided into 4 groups of 3 for 4 temperature treatments, and the groups were allocated at random to one of the following day/night temperature treatments :- 36/31°, 30/25°, 24/19°, 18/13°C.

Before transferring to the temperature regimes, all seedlings were exposed singly to $^{14}CO_2$ generated by the action of 50% (v/v) lactic acid on 10 mg of $Ba^{14}CO_3$ with a specific activity of 1.06 mCi/m mol. The whole plant was exposed to $^{14}CO_2$ for 10 minutes in a perspex plant chamber in an artificially lit cabinet set at 30°C. The procedures used for exposure of teak seedlings to $^{14}CO_2$ are described in detail in Section 4.2.6.

Immediately after exposure to the $^{14}CO_2$ the seedlings were transferred to one of the day/night temperature regimes.

To detect the rate of export of ^{14}C-photosynthate from the leaves, all leaves on each seedling were punched using a 1 cm diameter tube at 5 and 30 minutes and 6, 12, 24, and 48 hours after exposure to $^{14}CO_2$. Two discs per leaf (or 4 discs per leaf-pair position) were punched at each time and all discs were immediately dried in an oven set at 80°C. The dry weight for each leaf disc was obtained.

All seedlings from each temperature regime were harvested 48 hours after exposure to $^{14}CO_2$ (see Section 4.2.4). The leaves were removed from the stem and separated into a number of leaf-pair positions to determine the concentration of ^{14}C-assimilate at different leaf positions. The stem was removed from the root system and divided into 3 sections of equal length. All seedling components were oven dried separately, and the dry weights were determined.

7.2.2.3 Experiment 3: (Translocation of ^{14}C-assimilates)

On the basis of the results from Experiment 2, the effect of low temperature (18/13°C) on the translocation and distribution of ^{14}C-photosynthate in teak seedlings was examined over a longer period.

Twelve weeks after germination, 18 uniform seedlings grown at 30/25°C were selected for the experiment. The seedlings were divided into 6 groups of 3 seedlings for 6 harvests. All seedlings were exposed singly to $^{14}CO_2$ generated by the action of 50% lactic acid on 0.1 ml of a solution of $Na_2{}^{14}CO_3$ with a specific activity of 1.0 mCi/m mol (or 5 mCi/2L). Exposure of a whole plant to $^{14}CO_2$ was for 10 minutes at 30°C; and the procedure used for exposure of teak seedling to $^{14}CO_2$ are described in detail in Section 4.2.6.

Immediately after exposure to $^{14}CO_2$ two leaf discs were punched from each leaf of each seedling, using a 1 cm diameter tube, and the seedlings were transferred abruptly to grow at 18/13°C temperature.

Three seedlings were harvested at 5, 10, 15, 20, 25 and 30 days, respectively, after expsoure to $^{14}CO_2$. At each harvest time 2 leaf discs were punched from each leaf of each seedling to examine the pattern of change in ^{14}C concentration from that detected immediately after exposure to $^{14}CO_2$. The second set of leaf discs were punched close to the initial holes. The procedures used for harvesting the ^{14}C-assimilated seedlings are described in Experiment 2.

Determination of ^{14}C-activity: With the exception of leaf discs, all seedlings components from Experiments 1 and 2 were oven dried and ground separately in a Wiley mill to pass a 1 mm mesh sieve. A 30 mg sample (see O'Brien and Wardlaw, 1961) of the ground material was taken from each component, placed in a 1cm diameter planchet and ^{14}C activity detected on a Tracerlab Omni/Guard Scaler Model SC 520 W set time at 10 minutes.

To determine the ^{14}C activity in the dry leaf discs, the discs were mounted singly in the aluminium planchets and detected on the Tracerlab Omni/Guard Scaler.

The results of these studies are expressed either as relative specific activity in counts per minute (cpm) or as percentage distribution.

7.2.3 Results

7.2.3.1 Experiment 1: (Leaf Photosynthesis)

Growing temperature had a marked effect on leaf photosynthesis and respiration of teak seedlings. Both photosynthetic and respiratory rates of seedling leaves declined sharply when the temperature was reduced abruptly from 30/25° to 18/13°C (Table 7.1). After one day at 18/13°C, the rate of photosynthesis was reduced by about 31% and the rate of respiration was reduced by about 50%. Under the continuing 18/13°C regime the photosynthetic rate decreased progressively with time, but after the first day the respiratory rate was constant over a period of 7 days. Because of this the ratio of photosynthesis to respiration (P : R) was maintained at an increased value for a period of 5 days after transferring to the low temperature. The reduction in photosynthesis under the influence of low temperature is compatible with the previously established pattern of growth response to an abrupt reduction in temperature (Chapter 5).

TABLE 7.1 Effects of a reduction in temperature on the rate of photosynthesis and dark respiration of teak seedlings. (Data represent the mean of 4 seedlings)

Temperature (day/night)	day	Photosynthesis (P) ($mg\ CO_2/dm^2/hr$)	Respiration (R) ($mg\ CO_2/dm^2/hr$)	P : R (range)
$30/25^o$	0	21.4 ± 1.8	1.4 ± 0.1	13.0 - 17.8
$18/13^o$	1	14.7 ± 0.4	0.7 ± 0.1	17.9 - 25.2
"	2	12.8 ± 0.5	0.6 ± 0.1	17.6 - 26.6
"	3	11.6 ± 0.2	0.6 ± 0.1	16.3 - 23.6
"	4	11.6 ± 0.2	0.6 ± 0.1	16.3 - 23.6
"	5	10.4 ± 0.3	0.6 ± 0.1	14.4 - 21.4
"	6	8.9 ± 0.2	0.6 ± 0.1	12.4 - 18.2
"	7	7.2 ± 0.2	0.6 ± 0.1	10.0 - 14.8
"	14	5.4 ± 0.7	0.4 ± 0.01	11.5 - 15.6

7.2.3.2 Experiment 2: (Translocation of ^{14}C Assimilates)

A. Effect of temperature on the export of ^{14}C assimilates from seedling leaves: Results presented in Table 7.2 and Figure 7.1 show the rate of export of ^{14}C assimilates from the leaves of teak seedlings as influenced by the four day/night temperature regimes. At the high temperature regimes the percentage of ^{14}C photosynthates remaining in the leaves decreased markedly with times after exposure to $^{14}CO_2$. Reduction of growing temperature from $30/25^o$ to $18/13^oC$ markedly inhibited the rate of export of ^{14}C photosynthates from the leaves of teak seedlings. These effects were evident within 6 hours

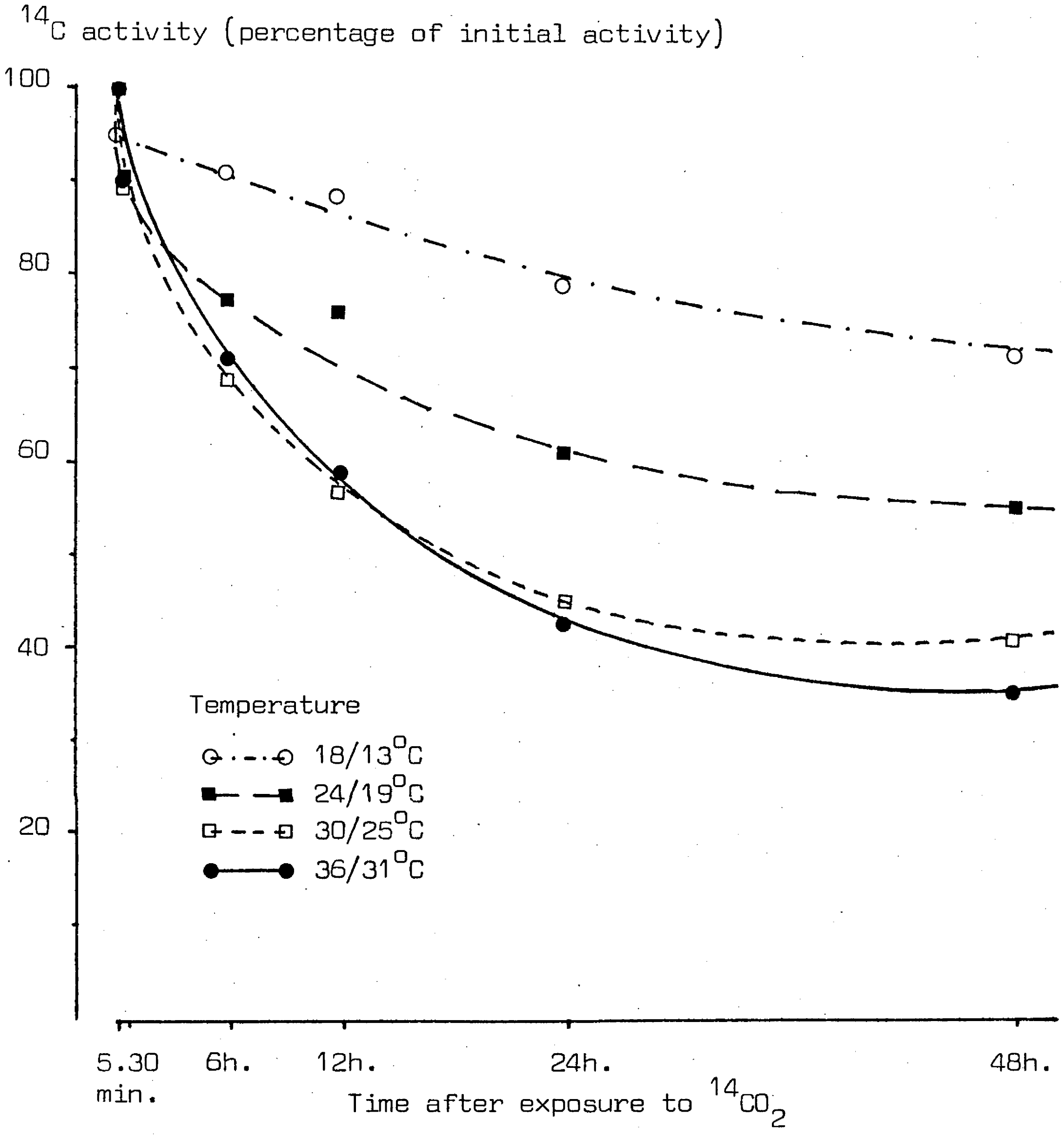


FIGURE 7.1 Time course for the loss of activity from whole leaves

TABLE 7.2 Effect of temperature regime on the loss of ^{14}C assimilate from leaves of teak seedlings (Data represent the mean of 3 plants)

Time after exposure to $^{14}CO_2$	Day/Night Temperature °C					
	36/31°	30/25°	24/19°	18/13°		
A. ^{14}C activity (cpm x 10^5/whole leaves)						
5 min.	82.3 ± 6.5	75.8 ± 6.5	70.4 ± 2.9	84.7 ± 5.2		
30 min.	75.9 ± 6.6	68.2 ± 5.5	62.8 ± 3.3	80.6 ± 5.9		
6 hr.	58.1 ± 4.0	51.8 ± 3.1	54.5 ± 2.6	77.4 ± 5.9		
12 hr.	48.8 ± 4.2	43.1 ± 2.1	53.9 ± 2.3	74.9 ± 4.8		
24 hr.	35.9 ± 3.9	34.6 ± 3.1	43.2 ± 3.7	67.1 ± 6.3		
48 hr.	29.3 ± 2.9	31.4 ± 3.0	38.8 ± 2.6	60.8 ± 6.1		
B. % ^{14}C remaining in the leaves						
					L.S.D. .05	.01
5 min.	100	100	100	100		
30 min.	92.1 ± 2.1	90.1 ± 1.6	89.2 ± 1.1	95.1 ± 2.3	ns	
6 hr.	70.7 ± 1.1	68.7 ± 2.5	77.4 ± 1.5	91.2 ± 2.7	6.7	9.7
12 hr.	59.3 ± 0.9	57.2 ± 2.0	76.6 ± 1.5	88.5 ± 2.0	5.4	7.8
24 hr.	43.5 ± 2.8	45.6 ± 1.0	61.3 ± 4.5	78.9 ± 2.6	9.8	14.3
48 hr.	35.6 ± 1.7	41.4 ± 1.3	55.0 ± 1.9	71.5 ± 2.9	6.6	9.6

of exposure to $^{14}CO_2$. At 30/25° and 36/31°C the percentage of ^{14}C photosynthates remaining in seedling leaves decreased rapidly during the first 24-hour period after exposure to $^{14}CO_2$. In the second 24-hour period the rate of decrease was much slower at the higher temperature, and was comparable to that of seedlings held at the lower temperature regimes. At 48 hours after exposure to $^{14}CO_2$, the amounts of ^{14}C photosynthates remaining in the whole leaves of seedlings held at 30/25° and 36/31°C were 41.4 ± 1.3 and 35.6 ± 1.7% respectively, of the amounts present 5 minutes after exposure to $^{14}CO_2$. At the same time, the percentage of ^{14}C photosynthates remaining in the leaves of seedlings held at 18/13° and 24/19°C were 71.5 ± 2.9 and 55.0 ± 1.9 respectively.

B. Effect of temperature on the distribution of ^{14}C assimilates: The distribution of ^{14}C photosynthates within leaves, stems, and roots of teak seedlings as influenced by the four day/night temperature regimes, 48 hours after exposure to $^{14}CO_2$, is presented in Table 7.3 and Figures 7.2a and 7.2b. Both concentration (cpm/mg dry tissue) and total amount (cpm) of ^{14}C photosynthates in the whole plant increased markedly with a reduction in the temperature regime. For example, the overall concentration of ^{14}C photosynthates in seedlings held at 36/31°C was 12.1±1.2 cpm/mg, at the same time that in seedlings held at 18/13°C was 16.5±0.6 cpm/mg. Similarly, the total amounts of ^{14}C photosynthates in seedlings held at 36/31°C and 18/13°C were 58.9 ± 5.8 and 81.4 ± 6.1 cpm × 10^4, respectively. The difference in the content of ^{14}C photosynthates between seedlings held at different day/night temperature regimes is presumably due to differences in respiration, that is, a larger amount of ^{14}C photosynthates was used in respiration at the higher temperatures regimes. This is in agreement with the patterns of respiration shown

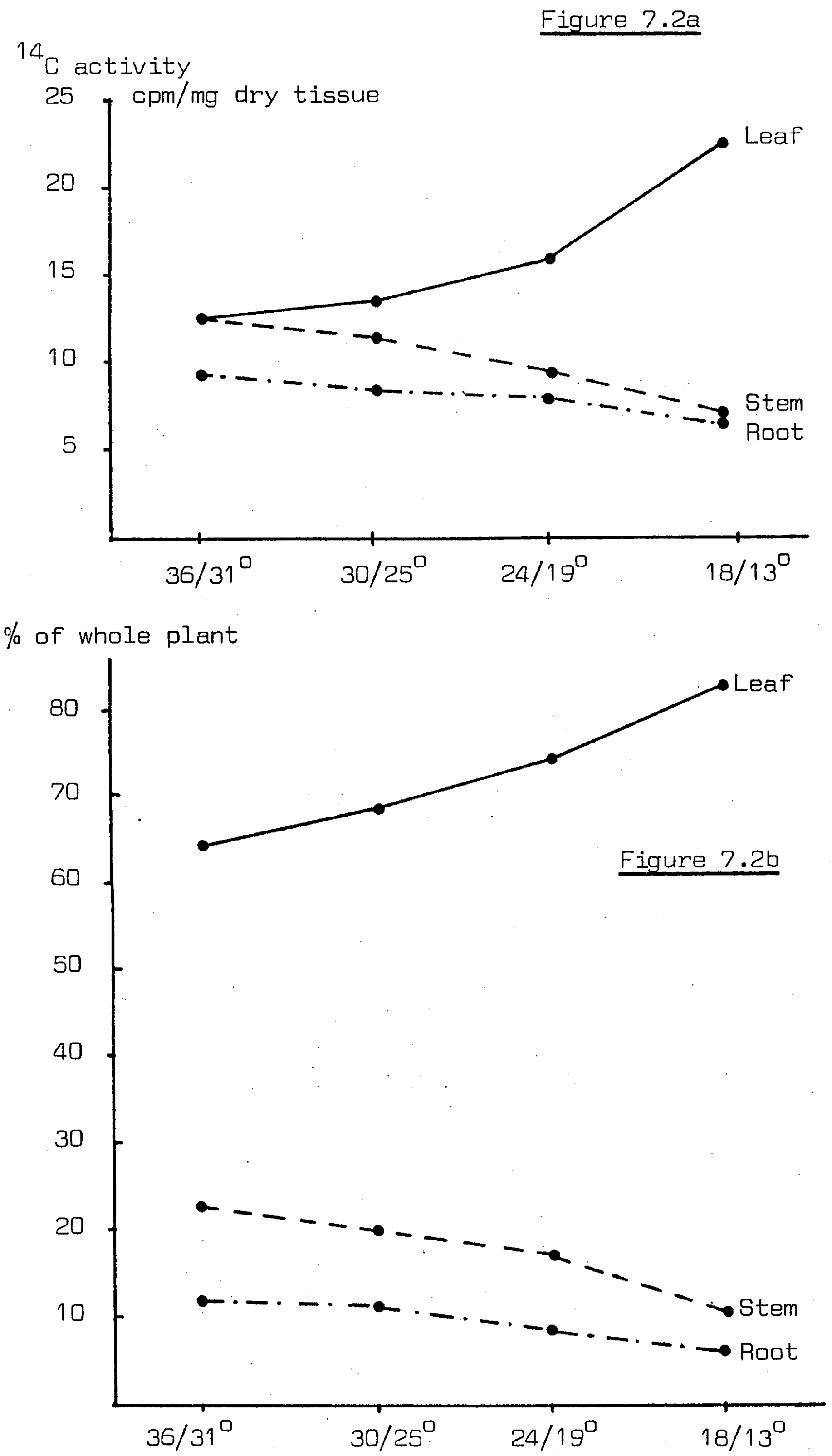


FIGURE 7.2 Effect of temperature regime on distribution of ^{14}C photosynthates in teak seedlings (48 hours after exposure to $^{14}CO_2$)

TABLE 7.3 Effect of temperature regime on distribution of ^{14}C assimilate in teak seedlings

(Data represent the mean of 3 seedlings at 48 hours after exposure to $^{14}CO_2$)

	Day/Night Temperature Regime			
	36/31°	30/25°	24/19°	18/13°
A. Relative specific activity (cpm/mg of dry matter weight)				
Leaf	12.6 ± 1.4	13.5 ± 1.1	15.8 ± 0.9	22.6 ± 1.9
Stem	12.6 ± 1.2	11.6 ± 1.0	9.6 ± 0.6	7.2 ± 1.4
Root	9.3 ± 0.9	8.4 ± 1.5	7.9 ± 0.2	6.6 ± 0.1
Whole plant	12.1 ± 1.2	12.2 ± 0.8	13.2 ± 0.6	16.5 ± 0.6
B. Total activity (cpm x 10^4)				
Leaf	37.9 ± 4.1	43.1 ± 2.8	54.1 ± 6.7	67.4 ± 3.5
Stem	13.7 ± 1.6	12.5 ± 1.4	12.5 ± 1.3	8.8 ± 1.6
Root	7.3 ± 1.3	7.3 ± 1.0	6.3 ± 1.3	5.2 ± 1.5
Whole plant	58.9 ± 5.8	62.9 ± 3.9	72.9 ± 9.2	81.4 ± 6.1
C. % distribution				
Leaf	64.2 ± 1.2	68.6 ± 1.8	74.2 ± 0.7	83.2 ± 2.1
Stem	23.2 ± 1.2	19.9 ± 2.4	17.3 ± 0.7	10.6 ± 1.3
Root	12.6 ± 2.4	11.5 ± 1.0	8.5 ± 0.8	6.2 ± 1.5
Whole plant	100	100	100	100

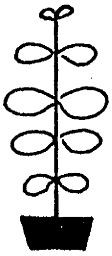
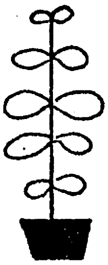
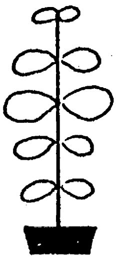
in Experiment 1, where the rate of respiration of seedlings held at the high temperature regime was much greater than that of seedlings held at the low temperature regime. This will be discussed in more detail in Section 7.2.4.

Within the teak seedling, the bulk of the ^{14}C photosynthates at 48 hours was still in the shoot, particularly in the leaves, and relatively little had been translocated to the root system (Table 7.3). This applies to seedlings held at all temperature regimes. Nevertheless, there were differences between temperature regimes in the distribution of ^{14}C photosynthates to the various plant organs.

Within the seedling, both the concentration and percentage distribution (% of whole plant) of ^{14}C photosynthates in the leaves increased with decrease in the temperature regime (Figure 7.2a and 7.2b). The highest concentration and percentage of ^{14}C photosynthates in seedling leaves were at the 18/13°C regime and the lowest at the 36/31°C regime. In contrast, both the concentration and percentage distribution of ^{14}C photosynthates in stems and roots of the seedlings decreased with the temperature regime. At the low temperature of 18/13°C there is clear evidence that the ^{14}C photosynthates produced during the short exposure to $^{14}CO_2$ have not been as effectively translocated to the stem, and certainly not to the roots as was the case at the warmer temperature regimes.

C. <u>Distribution of ^{14}C assimilates in seedling shoots as affected by leaf-pair and stem-section positions</u>: For all temperature regimes, both the concentration and distribution (% of whole plant) of ^{14}C photosynthates increased markedly from the base leaf pair (1) to the top leaf pair (5) (Table 7.4). The concentration of ^{14}C

TABLE 7.4 Distribution of ^{14}C assimilate in seedling leaves as affected by temperature regime
(Data represent the mean of 3 seedlings)

Leaf-pair position			Day/Night Temperature Regime			
			36/31°	30/25°	24/19°	18/13°
A. Leaf dry weight (gm):						
Top	5		9.8 ± 0.8	5.9 ± 1.9	8.0 ± 0.5	12.0 ± 4.0
	4		9.3 ± 1.5	10.5 ± 0.5	11.1 ± 0.9	15.1 ± 5.3
Middle	3		7.9 ± 1.7	9.1 ± 0.8	9.9 ± 2.9	6.2 ± 0.6
	2		2.6 ± 0.3	5.2 ± 0.7	3.8 ± 0.3	3.6 ± 1.2
Base	1		1.2 ± 0.9	1.8 ± 0.8	1.3 ± 0.2	0.7 ± 0.1
B. Relative specific activity (cpm/30 mg x 10)						
Top	5		58.8 ± 10.8	90.1 ± 14.5	83.0 ± 14.8	74.8 ± 11.7
	4		33.9 ± 1.8	39.2 ± 5.8	43.5 ± 1.8	53.6 ± 10.5
Middle	3		24.2 ± 1.0	28.5 ± 3.2	33.3 ± 1.8	45.1 ± 6.7
	2		24.2 ± 4.6	23.6 ± 2.5	33.8 ± 7.0	46.5 ± 6.5
Base	1		19.7 ± 0.8	23.1 ± 6.5	31.0 ± 7.0	33.2 ± 8.8
C. *% Distribution (% of whole plant)						
Top	5		31.7 ± 4.7	33.3 ± 2.8	31.1 ± 4.4	31.8 ± 5.1
	4		17.0 ± 0.5	17.2 ± 1.1	21.4 ± 1.3	26.3 ± 2.7
Middle	3		8.5 ± 1.2	11.5 ± 1.7	10.7 ± 0.8	14.3 ± 1.4
	2		4.9 ± 1.2	6.2 ± 0.6	8.2 ± 0.5	7.1 ± 0.9
Base	1		2.1 ± 0.6	1.4 ± 0.0	2.8 ± 0.7	3.7 ± 0.2
Total leaf			64.2 ± 1.2	68.6 ± 1.8	74.2 ± 0.7	83.2 ± 2.1

* $C = \dfrac{A \times B}{\text{Total activity in plant}} \times 100$

TABLE 7.5 Effect of temperature regime on the distribution of ^{14}C assimilate in seedling stems (stem positions) (Data represent the mean of 3 seedlings)

Stem Position	Day/Night Temperature Regime			
	36/31°	30/25°	24/19°	18/13°
A. Stem dry weight (gm)				
Top	2.1 ± 0.1	2.1 ± 0.2	2.5 ± 0.2	2.3 ± 0.5
Middle	3.8 ± 0.5	3.6 ± 0.1	4.5 ± 0.4	4.0 ± 0.9
Base	6.2 ± 0.9	6.1 ± 0.4	7.4 ± 1.1	7.6 ± 1.9
B. Relative specific activity (cpm/30 gm dry tissue) × 10				
Top	52.0 ± 6.3	57.7 ± 2.7	39.7 ± 3.7	35.1 ± 5.3
Middle	43.1 ± 5.1	39.1 ± 5.2	30.5 ± 3.0	24.3 ± 5.9
Base	32.4 ± 1.8	27.0 ± 3.2	27.0 ± 1.0	18.9 ± 3.2
C. % of whole plant*				
Top	5.3 ± 0.6	5.3 ± 0.2	4.0 ± 0.2	2.8 ± 0.4
Middle	8.0 ± 0.7	6.7 ± 1.0	5.8 ± 0.1	3.1 ± 0.5
Base	9.9 ± 0.2	7.9 ± 1.4	7.5 ± 0.1	4.7 ± 0.4
Total	23.2 ± 1.2	19.9 ± 2.4	17.3 ± 0.7	10.5 ± 1.3

$$* \quad C = \frac{A \times B}{\text{total activity in plant}} \times 100$$

photosynthates in leaf pairs at comparable positions increased with a reduction in temperature regime for positions 1 to 4. This suggests that the amount of ^{14}C photosynthates exported from leaves in positions 1 to 4 was greater at the higher temperature regime than at the lower temperature regimes, emphasising results given in Figure 7.1. However, there was a different pattern in apical leaf pair position (5). The concentration of ^{14}C photosynthates was lowest at 36/31°C (588 cpm/30 mg) and highest at 30/25°C (901 cpm/30 mg) then declined progressively to 830 cpm/30 mg at 24/19°C and 748 cpm/30 mg at 18/13°C. This suggests that the apical leaf pair could be a nett importer of photosynthates. On this basis a higher concentration of photosynthates at 30/25°C could be expected relative to that at 24/19° and 18/13°C, but the very much lower concentration of ^{14}C photosynthates in the apical leaf pair of plants at 36/31°C is difficult to interpret. One possible cause could be much accelerated respiration losses. Alternatively, and more likely, the apical leaves in this treatment are relatively larger (Table 7.4-A) and hence could be physiologically more mature, and thus nett exporters or, at most, not nett importers of photosynthates.

Within the seedling stem, the results presented in Table 7.5 show that the concentration of ^{14}C photosynthates increased markedly from the base segment to the top segment, and this applies to seedlings held at all temperature regimes. For each stem segment, the concentration of ^{14}C photosynthates decreased from the high to the low temperature regimes. The lowest concentrations of ^{14}C photosynthates were associated with the 18/13°C treated seedlings, and the highest with the 36/31°C and 30/25°C treated seedlings.

From these results, it is clear that temperature has a marked influence on the re-distribution of photosynthetic products from leaves to stems and subsequently to the root system. During the first 48 hours after exposure to the different temperature regimes, the rate of export of photosynthetic products from the leaves to the stems and subsequently to the root system was favoured under the warmer conditions. The upper leaves of the seedlings seem to be photosynthetically the most active. These leaves are, therefore, exporting the greatest quantities of the ^{14}C photosynthates, resulting in the high concentration of the ^{14}C photosynthates located in the upper stem segments.

7.2.3.3 Experiment 3: (Effect of low temperature on Translocation of ^{14}C photosynthates)

As shown earlier an abrupt reduction of temperature from 30/25° to 18/13°C for 4 weeks causes a marked reduction in growth of teak seedlings and an increase in sprouting potential of seedling stumps. The general results observed in those studies also showed that there was no obvious relationship between the subsequent growth potential of stump sprouts and the level of reserve carbohydrate content in seedling stumps. However, seedlings held for 4 weeks at 18/13°C exhibited a marked increase in the concentration of stump sugars. In the last Experiment (Section 7.2.3.2), there was evidence that the low temperature of 18/13°C caused a marked retardation in the rate of export of the products of photosynthesis from the leaves to the stems, and subsequently to the root system of teak seedlings. However, this result was recorded only 48 hours after the seedlings had been exposed to $^{14}CO_2$ and transferred to 18/13°C. On this basis, the inhibitory effect of the low temperature on translocation and redistribution of the products of photosynthesis in teak seedlings has been examined over an extended time period.

A. Time loss of ^{14}C photosynthates from leaves: The results presented in Table 7.6 show the rate of loss or export of ^{14}C photosynthates from the leaves of teak seedlings held at 18/13°C for a period of 30 days. It also shows the percentage of ^{14}C photosynthate activity remaining in the leaves of seedlings held at 18/13°C for 48 hours (2 days) after exposure to $^{14}CO_2$ as established in Experiment 2 (Section 7.2.3.2). There was apparently a striking decline in the % activity remaining in the leaves between day 2 and day 5, i.e. from 71.5% at day 2 (Experiment 2) to 33.9% at day 5 (Table 7.6). Subsequently the percentage of initial activity of ^{14}C photosynthates remaining in the leaves of seedlings was remarkably stable over the period day 5 to day 15. The percentage of initial activity of ^{14}C photosynthates remaining in the leaves then decreased rapidly again between day 15 and day 20. From day 20 there was no further decline in the percentage of initial activity of ^{14}C photosynthates.

B. Distribution of ^{14}C photosynthates: In Experiment 2 (Section 7.2.3.2) it was shown that there was a relatively large amount of the total activity of ^{14}C photosynthates remaining in the leaves of seedlings held at 18/13°C, 2 days after exposure to $^{14}CO_2$ (i.e. 83.2% of initial total activity). Alternatively, there was a relatively small amount of the total activity of ^{14}C photosynthates exported from the leaves to the stems (10.6%) and subsequently to the root system (6.2%). From these results it was suggested that an abrupt reduction of temperature from 30/25° to 18/13°C causes strong retardation of the transport of the products of photosynthesis from the leaves to the stems and subsequently to the roots of teak seedlings.

TABLE 7.6 Time loss of ^{14}C photosynthetic products from the leaves of teak seedlings held at 18/13°C temperature for 30 days. (Data represent the mean of 3 seedlings)

Day after Exposure to $^{14}CO_2$		Initial Activity	Final activity	% Activity remaining in the leaves
		(in each set of seedlings)		
		(cpm/leaf disc x 10^2)		
2	(Exp. 2)			71.5 ± 2.9
5		53.7 ± 4.6	18.6 ± 4.3	33.9 ± 4.9
10		58.7 ± 5.2	18.5 ± 1.7	31.7 ± 1.9
15		53.7 ± 7.1	18.9 ± 1.3	35.6 ± 2.0
20		26.0 ± 3.5	8.5 ± 1.3	23.2 ± 2.1
25		37.9 ± 1.8	9.1 ± 0.9	24.1 ± 2.1
30		45.7 ± 3.2	10.6 ± 2.8	22.6 ± 4.9

However, in the present study (Experiment 3) where teak seedlings grown at 30/25°C were exposed to $^{14}CO_2$ and then transferred abruptly to 18/13°C for 30 days, the amount of ^{14}C photosynthates in the roots was as great as 31.4% of the total activity within 5 days after exposure to $^{14}CO_2$ and only 55.6% of the total activity was still remaining in the leaves (Table 7.7). When compared with the results obtained in Experiment 2, it is seen that there was a substantial loss of ^{14}C photosynthate activity from the leaves (i.e. from 83.2 to 55.6% of the total), accompanied by a substantial increase in the activity of ^{14}C photosynthates in the root system (i.e. from 6.2 to 31.4%) from day 2 to day 5 after exposure to $^{14}CO_2$. This suggests that the inhibitory effect of the low day/night temperature of 18/13°C on the translocation of the products of photosynthesis from the shoot to the root system in the teak seedling is transient; and it occurs distinctively only within the first 2 days after the seedling is exposed to $^{14}CO_2$ and transferred abruptly from 30/25°C to 18/13°C.

TABLE 7.7 Distribution of ^{14}C photosynthates with time in different organs of teak seedlings held at 18/13°C for 30 days. (Data represent the mean of 3 seedlings)

Days after exposure to $^{14}CO_2$	^{14}C Activity (% of Whole Plant)				
	Leaves	Stem	Tap-root	Lateral roots	Total roots
2 (Exp. 2)	83.2 ± 2.1	10.6 ± 1.3	6.2 ± 1.5		6.2
5	55.6 ± 6.4	13.0 ± 1.0	21.8 ± 4.2	9.6 ± 1.4	31.4
10	51.5 ± 5.3	15.0 ± 3.7	25.0 ± 2.5	8.5 ± 1.4	33.5
15	58.3 ± 1.8	9.2 ± 0.6	24.7 ± 3.0	7.8 ± 0.7	32.5
20	43.0 ± 4.8	15.5 ± 1.1	27.5 ± 2.6	14.0 ± 3.0	41.5
25	44.7 ± 4.3	16.0 ± 1,3	28.1 ± 2.3	11.2 ± 3.4	39.2
30	44.3 ± 7.0	14.1 ± 1.3	29.6 ± 4.8	12.0 ± 3.3	41.4

Note: The statement at the top of page 215 "..... the inhibitory effect of low day/night temperature of 18/13° C on the translocation of the products of photosynthesis from the shoot to the root system in the teak seedling is transient: ....." can be differently interpreted. On the basis of data presented in Table 7.7, if the ^{14}C activity of leaves (as % of the whole plant) is plotted against time (days), the plot is linear from day 0, through day 2, to day 5. Thus, there is a continuing translocation of photosynthates from day 0 to day 5. The concept of inhibited translocation from day 0 to day 2 is not valid.

The amount of ^{14}C photosynthates in seedling leaves, expressed as a percentage of activity in the whole plant, tended not to change from day 5 to day 15 after exposure to $^{14}CO_2$ (Table 7.7); it declined markedly from day 15 to day 20 (i.e. from 58.3 to 43.0%), and then remained constant again from day 20 to day 30 after exposure to $^{14}CO_2$.

In the root system, the amount of ^{14}C photosynthates remained constant from day 5 to day 15 (i.e. between 31.4 and 33.5%); and about two-third of this activity was in the tap-root and one-third in the lateral roots during this period (Table 7.7). A corresponding but inverse change in the ^{14}C photosynthate activity occurred in roots as in leaves between day 15 and day 20 when the activity in the roots increased from 32.5 to 41.5%. It remained at this value until day 30. The proportion of the total root activity tended to remain at about the same proportion between tap-root and laterals, i.e. about 60 : 40.

7.2.4 Discussion

7.2.4.1 Effects of Temperature on Photosynthesis and Respiration:

It has been clearly shown in Experiment 1 that temperature has a marked effect on photosynthesis and respiration in the teak seedling. Both photosynthetic and respiratory rates in the seedling declined sharply when the growing temperature was abruptly reduced from warm to cool (i.e. from 30/25° to 18/13°C). This reduction in photosynthetic efficiency is compatible with the previous established pattern of response of teak seedlings to an abrupt reduction of temperature (Chapter 5), that is, both RGR and NAR of the seedlings declined sharply when the growing temperature was abruptly reduced from 30/25° to 18/13°C. These findings are also consistent with the results obtained in the work of Kanchanaburangura (1976), in which the rate of leaf photosynthesis in teak seedlings grown at 30/25°C was almost twice that in seedlings maintained at 24/19°C. Within the range of temperature in his study (i.e. from 24/19° to 36/31°C with 3°C intervals), Kanchanaburangura noted that the maximum rate of photosynthesis was associated with seedlings maintained at 30/25°C and the minimum was at 24/19°C.

There are many internal factors controlling plant photosynthesis and the degree of assimilate accumulation in the leaf has been suggested to be one of these factors (Kramer and Kozlowski, 1960; Warren Wilson, 1966; Neales and Incoll, 1968). A negative correlation has frequently been found between the level of assimilates (or carbohydrates) accumulated in the leaf and the rate of leaf photosynthesis. Neales and Incoll (1968), for example, demonstrated that the rate of leaf photosynthesis in many plants could be reduced by the following treatments which increased the level of carbohydrate concentration in the leaves:-

(a) an inhibition of the translocation of photosynthates from the sources to the sinks of photosynthates such as by phloem removal or ring-barking and by phloem chilling;

(b) an inhibition of sink growth and a complete or partial removal of some sinks so that the demand for photosynthates of the sinks is reduced; and

(c) a depression of respiratory rates so that the photosynthates are utilized only slowly.

In a study of the effect of temperature on net assimilation rate in Oxyria digyna plants, Warren Wilson (1966) reported that plants grown under cold conditions exhibited a marked reduction in their RGR and NAR, accompanied by an increase in leaf carbohydrate content. This author suggested that low temperatures depress respiration and new growth of the plants so that carbohydrates are only utilized slowly. As a result carbohydrates (especially sugars) accumulate, and their concentration in the leaves rises to a level at which they depress assimilation to a rate, that for a daily or longer period, roughly balances the rate of utilization of carbohydrates. Similar results have been reported in the works of Mooney and Billings (1961) and Beevers and Cooper (1964a, 1964b).

In the study reported for teak, the response to an abrupt reduction of temperature from 30/25° to 18/13°C has been characterized by marked reduction in growth of the seedlings (Chapter 5), an immediate reduction in respiratory rate (Section 7.2.3.1), and an initial reduction in both rate and amount of photosynthates translocated out of the leaves of the seedlings (Section 7.2.3.2). On the basis of these findings the level of carbohydrate concentration in the seedling leaves would be expected to increase; and this increase in carbohydrate level might somehow reduce the photosynthetic activity of the seedlings as suggested by Warren Wilson (1966) and Neales and Incoll (1968).

7.2.4.2 Effects of Temperature on Translocation of Photosynthates

The studies of ^{14}C assimilation clearly show that temperature has an important effect on translocation of photosynthates in the teak seedling. An abrupt reduction of growing temperature from 30/25°C to either 24/19°C or 18/13°C (day/night temperature) caused an immediate and a marked reduction in the rate and amount of ^{14}C

photosynthates exported from the leaves, limiting the amount of ^{14}C photosynthates in both stems and roots of the seedlings. In contrast, an abrupt increase of growing temperature from 30/25° to 36/31°C tended to accelerate translocation of ^{14}C photosynthates from the leaves to the stems and root system. A similar response of translocation of photosynthates to the changes of growing temperature has been reported in various plants (Hewitt and Curtis, 1948; Hartt, 1965; Hofstra and Nelson, 1969). Hewitt and Curtis (1948), for example, showed that when the whole bean plants (*Phaseolus vulgaris*) were subjected to a range of temperatures extending from 5° to 40°C the optimum temperature range for translocation of assimilates from the leaves was between 20° and 30°C. These authors also showed that the amount of assimilates moved out of the leaves increased progressively with increased temperatures to a maximum and then declined due to the detrimental effects of high temperature. Hartt (1965) studied the effect of temperature on translocation of photosynthates in sugar-cane plants (*Saccharum officinarum*) and found that a reduction of shoot temperature from 34° to 20°C caused a marked decrease in the amount of photosynthates exported from the leaves.

According to the results obtained in this study, it is evident that both the amount of ^{14}C photosynthates translocated out of the leaves and the amount of these products of photosynthesis translocated to the stems and root system of seedlings maintained at 36/31°C did not differ significantly from those of seedlings maintained at 30/25°C. This suggests that within the limitations of temperature studied the optimum temperature range for translocation of the products of photosynthesis in teak seedlings would be between 30/25° and 36/31°C. On the other hand, the lower temperatures from this range could inhibit the translocation of photosynthetic products out of the leaves to the stems and root system of the seedlings. This suggestion is, however, based on the results obtained in Experiment 2 in which the seedlings were maintained at this range of temperatures only for 2 days (i.e. 2 days after exposure to $^{14}CO_2$).

Where the translocation of ^{14}C photosynthates was examined over a longer period, that is from 2 to 30 days (Experiment 3), a substantial export of ^{14}C photosynthates from the leaves was recorded between days 2 and 5 following transference of seedlings from 30/25° to 18/13°C, resulting in a substantial increase in the accumulation of photosynthates in the root system. A secondary translocation of ^{14}C photosynthates out of seedling leaves also occurred between day 15 and day 20 after cooling. These findings clearly suggest that the inhibitory effect of low temperatures on the translocation of photosynthetic products in the teak seedling might be transient; the seedling will exhibit an initial inhibition of translocation at low temperatures but recovery of translocation will take place within a few days after the seedling has acclimatized at low temperatures.

It has been widely accepted that low temperatures have little or no direct effect in inhibiting translocation of photosynthates in plants, or that the effect of low temperature on translocation of photosynthetic products in plants is transient (Webb, 1966; 1971; Swanson and Geiger, 1967; Bowling, 1968; Geiger and Sonvonick, 1970; Wardlaw, 1968, 1972, 1974a, 1974b). Swanson and Geiger (1967), for example, showed that cooling a 2 cm zone of the petiole of sugar beet plants (Beta vulgaris) from 30° to 1°C caused an immediate inhibition of transport of photosynthates from the leaf blade through the cooled portion of the petiole. However, after a suitable thermal adaptation period (i.e. about 2 hours) recovery of translocation from inhibition to the pre-cooling rate occurred. Similarly, Wardlaw (1974a) reported that translocation of photosynthates in wheat plants (Triticum aestivum) is well adapted to a wide range of temperature condition; in that the translocation of photosynthates through a 1.0 cm controlled temperature zone of the peduncle was unaffected by temperature changes ranging from 1° to 40°C, while the rest of the plant was maintained at 21°C. The recovery of translocation under low temperatures has been suggested to be the result of an increase in the level of carbohydrate concentration within the source side of the cooled portion; turgor pressure will increase enough to overcome the viscous resistance caused by cooling, and translocation is resumed (Whittle, 1964; Wardlaw, 1968; Craft and Crisp, 1971). Wardlaw (1968) also suggested that the primary effect of temperature on translocation of assimilates in plants is associated with growth rather than the conducting system. Temperature will affect the translocation of photosynthates in plants largely through its effect on the organ with a greater demand for photosynthates, such that reduced growth due to low temperatures would be expected to reduce both the rate and amount of photosynthates translocated out of the sources to the sinks.

Based on the above evidence, the pattern of translocation of photosynthates within the teak seedling as affected by temperature might be interpreted in terms of the effects of temperature on physiological activities of the source and the sinks for photosynthates, rather than in terms of the direct effect of temperature on the translocation. As shown previously, all growth parameters of the seedlings were markedly reduced when the growing temperature was abruptly reduced from 30/25° to 18/13°C. This reduction in growth of the seedling would be expected to reduce the demand for photosynthates by the sinks (including the young leaves, stems and roots) for their metabolic activities, resulting in retarded translocation of photosynthates out of the sources to the sinks. This has been shown by an increase in a retention of ^{14}C activity in the leaves associated with a decrease in ^{14}C activity in the stems and root system of the seedlings. Under this circumstance, the products of photosynthesis in the leaves will be increased with time after the reduction of temperatures up to the level where their concentration is higher than that in the stems and root system; as a result a turgor pressure gradient develops which causes translocation of these products of photosynthesis from the leaves toward the region of lower concentration and lower turgor pressure in the stems and roots. This explanation is based on the Munch's (1930) hypothesis of mass or pressure flow as described by Zimmermann (1969). It has been shown earlier that an abrupt reduction of growing temperature from 30/25° to 18/13°C caused an immediate inhibition of leaf photosynthesis (Experiment 1). This evidence might affect a build-up of sugars in the leaves of seedlings after the first substantial translocation of photosynthates from the leaves (i.e. between day 2 and day 5), and subsequently result in the retardation of translocation of photosynthates from the leaves to the stems and root system between day 5 and 15 and between day 20 and 30, following the transference of seedlings from 30/25° to 18/13°C. It is believed that a relatively larger amount of the leaf exported photosynthates will be accumulated in the roots (mainly in the tap-root) as the stored reserves rather than for use in growth and development of the root system under this cool temperature condition (18/13°C). This suggestion is supported by the findings of the earlier study (Chapter 5) where the concentration of sugars and starch in the tap-roots of seedlings maintained at 18/13°C for 4 weeks is significantly higher than that in the tap-roots of seedlings maintained continuously at 30/25°C.

7.3 STUDY 2: EFFECT OF SOIL MOISTURE STRESS ON TRANSLOCATION OF ^{14}C PHOTOSYNTHATES IN TEAK SEEDLINGS

7.3.1 Purposes of Study

The teak seedling is very sensitive to soil moisture stress, growth being reduced markedly when the available soil moisture falls below about 60% of the soil's field capacity (Chapter 6). However, conditioning seedlings for about 4 weeks prior to stump-replanting by restricting soil water supply produces changes in carbohydrate levels in seedling organs, and also leads to changes in the sprouting ability of seedling stumps. The influence of soil moisture stress on stump sprouting ability varies with the degree of stress. While the change in the carbohydrate level of seedling stump could be a factor in improved sprouting ability, it does not appear to be the only factor operating (Chapter 6).

Because of the influence of soil drying and moisture stress on subsequent stump performance, a further study has been made of the effect of soil moisture availability on the transport and distribution of photosynthates within the teak seedling. The purpose of this study is to re-examine whether the influence of soil moisture on seedling growth and stump sprouting might be associated with the translocation and accumulation of photosynthates particularly in the seedling stumps. Teak seedlings were grown under the same range of soil moisture conditions for the same period as applied to the previous studies (Chapter 6), and were then exposed to $^{14}CO_2$. The subsequent distribution of ^{14}C photosynthates was monitored over a 3-day period after exposure to the $^{14}CO_2$.

7.3.2 Materials and Methods

A. Experimental Treatments:

Eight week old teak seedlings grown in the 30/25°C controlled day/night temperature glasshouse were allocated to one of the following soil moisture treatments:

a. the constant high soil moisture;

b. moderate soil moisture stress; and

c. the severe soil moisture stress.

The experimental treatments and procedures are as described in Experiments 1 and 2 in Chapter 6.

B. $^{14}CO_2$ Assimilation:

Eight weeks after the experimental treatments had been initiated, 3 uniform seedlings from each treatment were exposed singly to $^{14}CO_2$ for 10 minutes at 30°C temperature. The $^{14}CO_2$ was generated by the action of 50% (v/v) lactic acid on 10 mg of $Ba^{14}CO_3$ with a specific activity of 1.06 mCi/m mol. The exposure of seedlings to $^{14}CO_2$ was carried out when the soil moisture content in all treatments were held at field capacity. The procedures used for exposure of teak seedlings to $^{14}CO_2$ are described in Section 4.2.6.

C. Plant Harvesting and Determination of ^{14}C Activity:

Three days after exposure to $^{14}CO_2$ seedlings from all treatments were harvested (see Section 4.2.4). Leaves, stems, taproots, and lateral roots were oven-dried and ground separately in a Wiley mill to pass a 1 mm mesh sieve.

A 30 mg sample of the ground material was taken from each seedling organ and counted for the activity of ^{14}C on a Tracerlab Omni/Guard Scaler using the method described in Section 4.2.6.

7.3.3 Results

7.3.3.1 Seedling Growth

The results presented in Table 7.8 summarized the growth of teak seedlings under the influences of the three soil moisture treatments. **Since similar** results have already been presented and discussed in Chapter 6 (Experiment 2) in terms of the effects of soil moisture availability on growth and dry matter production of teak seedlings, a discussion of the results in these respects will not be repeated here.

TABLE 7.8 Growth characteristics of teak seedlings grown under the three soil moisture treatments (Data representing the mean of 3 seedlings)

Item	Soil Moisture Regime		
	A	B (see text)	C
Height (cm)	18.1 ± 1.1	11.4 ± 0.4	10.2 ± 1.1
Leaf area (dm^2)	42.3 ± 1.7	12.7 ± 0.4	8.5 ± 1.0
Dry matter weight (gm)			
Leaf	30.8 ± 2.0	8.9 ± 0.8	6.1 ± 0.7
Stem	7.3 ± 0.8	2.2 ± 0.04	1.4 ± 0.04
Tap-root	9.4 ± 1.1	4.1 ± 0.4	2.5 ± 0.2
Lateral root	5.7 ± 0.6	4.8 ± 0.9	1.6 ± 0.2
Shoot	38.1 ± 2.5	11.1 ± 0.9	7.5 ± 0.2
Root	14.4 ± 1.8	8.9 ± 1.2	4.1 ± 0.1
Total	52.5	20.0	11.6
R : S	0.38	0.80	0.55

7.3.3.2 Distribution of ^{14}C Photosynthates

Results presented in Table 7.9 show the pattern of ^{14}C photosynthate distribution within the teak seedling 3 days after watering and exposure to $^{14}CO_2$. These results are presented in terms of relative specific activity (cpm/mg), total amount of ^{14}C activity (cpm), and the percentage distribution (% of the whole plant).

A. Relative Specific Activity

On the basis of averaging the specific activity or the concentration of activity of ^{14}C in leaves, stems, tap-roots and lateral roots, there were no differences between treatments A, B and C in the specific activity of ^{14}C either in the shoot part, in the root part, or in the whole plant (Table 7.9-A). This clearly suggests that during the first 3 days after watering there were no differences between treatments in the ability of the seedlings (per unit dry weight) to photosynthesize $^{14}CO_2$ and subsequently to redistribute the ^{14}C products of photosynthesis from the shoot to the root part. Within the seedling, the specific activity of ^{14}C was significantly greater in the shoot part than in the root part, with a maximum in the leaves. This applies to all treatments.

B. Total Amount of ^{14}C Activity

The total amount of ^{14}C activity remaining in all parts of the seedling 3 days after watering and exposure to $^{14}CO_2$ declined progressively from Treatment A to Treatment C (Table 7.9-B). For example, the total amount of ^{14}C activity in the "A" seedling (65.9×10^4 cpm) was about 2.5 and 4 times, respectively, greater than that in the "B" and "C" seedlings (i.e. 26.3×10^4 cpm for the "B" seedling and 15.9×10^4 cpm for the "C" seedling). As there is no difference between treatments in the ability of plants to assimilate $^{14}CO_2$ per unit dry weight, the difference between treatments in total amount of ^{14}C activity would be a function of plant size. As shown in Table 7.8, the total dry weight of the "A", "B" and "C" seedlings were 52.5, 20.0 and 11.6 gm, respectively, that is, the total dry weight of the "A" seedling was about 2.5 and 4.5 times greater than that of the "B" and "C" seedlings, respectively. This demonstrates the very close relationship between seedling size and the total amount of ^{14}C assimilated by the seedling.

C. Percentage Distribution of ^{14}C Photosynthates

In terms of the percentage of total activity in the whole seedling, the amount of ^{14}C activity in seedling shoots was much greater than that in the root system. This applies to all treatments (Table 7.9-C). Nevertheless, there was a marked treatment effect on the percentage distribution of ^{14}C photosynthates from seedling shoots to the root system. The results presented in Table 7.9-C show that the percentage of ^{14}C photosynthates remaining in the shoot of seedling from Treatment A (79.8%) was significantly greater than that in the shoots of seedlings from Treatments B (65.4%) and C (72.9%). Conversely, the percentage of ^{14}C photosynthates translocated to the root system of seedling from Treatment A (20.2%) was considerably smaller than that of seedlings from Treatments B (34.6%) and C (27.1%).

Whatever other factors may be involved in the translocation and distribution of photosynthates in the teak seedling, the results obtained in this study suggest that the balance between root and shoot growth of the seedling plays a significant role in controlling the pattern or direction of translocation of photosynthates. It has been shown earlier (Table 7.8) that seedlings grown under Treatments B and C exhibited a greater proportion of root to shoot dry weight than seedlings grown under Treatment A. These proportions were 0.38, 0.80 and 0.55 for seedlings grown under Treatments A, B and C respectively. Moreover, the percentage translocation of photosynthates to root systems in seedlings grown under Treatments B and C was significantly greater than that of seedlings grown under Treatment A. This could mean that under the periodic soil moisture stress, the teak seedling tends to develop a large root system probably to overcome internal water stress during the period of soil water stress, resulting in a relatively greater percentage of the products of photosynthesis being translocated to the root system of this seedling. In contrast, the relatively smaller percentage translocation of photosynthates to the root system of the seedling grown under constant high soil moisture would be due to the greater demand for photosynthates for rapid growth of its shoot part (Table 7.8).

Within the seedling shoot, the percentage of ^{14}C photosynthates in leaves was much greater than that in stems; and this applies to all treatments. There were significant treatment effects on the patterns of translocation and distribution of photosynthates to seedling leaves and stems in teak. The percentage distribution of ^{14}C photosynthates in the leaves of seedlings grown under Treatment A (69.0%) was considerably greater than that in the leaves of seedlings grown under Treatments B (58.7%) and C (61.9). There was no significant difference in the percentage distribution of ^{14}C photosynthates to the stems between seedlings grown under Treatment A and C, that is 10.9% for Treatment A and 11.0% for Treatment C. But the percentage

TABLE 7.9 Effect of soil moisture regime on distribution of ^{14}C photosynthates in teak seedlings
(Data representing the mean of 3 seedlings)

^{14}C Activity	Soil Moisture Regime		
	A	B (see text)	C
A. Relative Specific Activity (cpm/mg dry tissue):			
Leaf	15.0 ± 1.0	17.0 ± 2.0	17.0 ± 3.0
Stem	10.0 ± 1.0	8.0 ± 2.0	13.0 ± 1.0
Tap-root	10.0 ± 2.0	11.0 ± 2.0	9.0 ± 1.0
Lateral roots	9.0 ± 3.0	9.0 ± 1.0	13.0 ± 0.4
Whole shoot	14.0 ± 1.0	15.0 ± 1.0	16.0 ± 2.0
Whole roots	10.0 ± 2.0	10.0 ± 2.0	11.0 ± 1.0
Whole plant	13.0 ± 1.0	13.0 ± 1.0	14.0 ± 2.0
B. Total Activity (cpm x 10^4)			
Leaf	45.1 ± 1.8	15.4 ± 3.1	9.9 ± 1.1
Stem	7.3 ± 1.3	1.7 ± 0.3	1.7 ± 0.1
Tap-root	8.5 ± 2.3	4.6 ± 1.4	2.3 ± 0.3
Lateral roots	5.0 ± 1.0	4.6 ± 1.4	2.0 ± 0.2
Whole shoot	52.4 ± 2.7	17.1 ± 2.7	11.6 ± 0.9
Whole roots	13.5 ± 2.7	9.2 ± 2.9	4.3 ± 0.1
Whole plant	65.9 ± 4.5	26.3 ± 2.0	15.9 ± 1.0
C. % Distribution (% of whole plant):			
Leaf	69.0 ± 4.4	58.7 ± 6.0	61.9 ± 3.0
Stem	10.9 ± 1.3	6.7 ± 0.9	11.0 ± 1.7
Tap-root	12.6 ± 3.2	17.1 ± 3.5	14.3 ± 1.3
Lateral roots	7.5 ± 1.0	17.5 ± 3.5	12.8 ± 2.4
Total shoot	79.8 ± 3.3	65.4 ± 4.8	72.9 ± 1.2
Total roots	20.2 ± 3.3	34.6 ± 4.8	27.1 ± 1.2
R/S	0.25 ± 0.05	0.53 ± 0.09	0.37 ± 0.02

of ^{14}C photosynthates in the stems of seedlings from these two treatments was significantly greater than that in the stems of seedlings from Treatment B (6.7%). These results clearly demonstrate that compared with seedlings grown under Treatments A and C, there was a more substantial export of photosynthates from the leaves and stem to the root system in seedlings grown under Treatment B.

Within the root system, there was a marked difference in the percentage of ^{14}C photosynthates between the tap-root and the laterals for the seedling grown under Treatment A, but there was no difference between the tap-roots and lateral roots for seedlings grown under Treatments B and C. The percentages of ^{14}C photosynthates in the tap-roots were 12.6, 17.1, and 14.3 for Treatments A, B and C respectively; the percentages of ^{14}C photosynthates in the lateral roots were 7.5, 17.5 and 12.8 for Treatments A, B and C respectively. These figures show a relatively higher requirement for photosynthates in the lateral roots of seedlings grown under Treatments B and C, compared with that in the lateral roots of seedling grown under Treatment A. In other words, under the periodic soil moisture stress, the teak seedling tends to direct a larger amount of its products of photosynthesis to the production of the root system, particularly the lateral roots, compared with the seedling grown under constant high soil moisture. This is probably to increase the absorbing surface to maintain internal water balance during the period of soil water stress. These results will be discussed further in the next section.

7.3.4 Discussion

A. The Capacity of Photosynthetic $^{14}CO_2$ Uptake

The results clearly show that there was no difference in the specific activity of ^{14}C content either in the shoot, in the root, or in the whole plant between the "A", "B" and "C" seedlings. This can be interpreted as showing that there was no difference in the capacity of photosynthetic $^{14}CO_2$ uptake per unit plant dry weight between the three treatments. However, this interpretation is based on the results obtained during the first 3 days after rewatering and exposure of the seedlings to $^{14}CO_2$ where the soil in Treatment B and C was rewatered to field capacity following a period of soil moisture stress. The net photosynthesis of seedlings from both Treatments B and C would be expected to decline as the soil dried out from field capacity, because the final dry matter production of these two seedlings (B and C) was much smaller than that of the "A" seedlings.

It is well known that net photosynthesis is progressively reduced by leaf/soil water stress (Kramer and Kozlowski, 1960; Kozlowski, 1964; **Crafts**, 1968; Kramer, 1969; Slavik, 1973). This is due partly to a limiting CO_2 transport to the chloroplasts in the gaseous phase and in the liquid phase, and partly to a direct effect of dehydration on the photosynthetic system of the plant (Kozlowski, 1964; **Crafts**, 1968; Hsiao, 1973; Slavik, 1973). It has also been widely reported that there is a recovery of photosynthesis after rewatering following a period of plant water stress. But the rate of recovery of photosynthesis varies, depending primarily on the degree of preceding water stress (Ashton, 1956; Clark, 1961; Brix, 1962; Boyer, 1971). Clark (1961), for example, showed that the rate of photosynthesis of white spruce (Picea glauca) and balsam fir (Abies balsamea) was reduced markedly as soil moisture was reduced from field capacity to permanent wilting percentage, but gradually returned to maximum again a few days after rewatering to field capacity. Similarly, Brix (1962) noted that there is a substantial increase in photosynthesis within one day after rewatering of stressed plants of loblolly pine (*Pinus taeda*) seedlings, but the subsequent recovery is slow and some irreversible damage occurs especially of the lower leaves. According to the results reported in this study, both the "B" and "C" seedlings were rewatered for about 16 hours (over night) and followed by an exposure to $^{14}CO_2$. It can be assumed that the rate of full recovery of photosynthesis from water stress of the teak seedling is very rapid.

B. Translocation of ^{14}C Photosynthates

As stated earlier, the system of translocation of assimilates in plants consists of the assimilating source (mainly the leaves), the transport conduits (sieve tubes), and the sinks for assimilates; any factor which changes the rate and pattern of translocation is, therefore believed to influence one or all of these three main parts of the system. It is known that the whole plant growth and the rate and pattern of translocation of carbohydrates are all affected by water stress. A number of studies have shown that there is a marked inhibitory effect of water stress on translocation in plants (Roberts, 1964; Plaut and Reinhold, 1965; Hartt, 1967). Plaut and Reinhold (1965), for example, showed that the bi-directional transport of ^{14}C labelled sucrose out of the applied leaves of bean plants was markedly retarded by moisture stress. Crafts (1968) explained that the retardation of translocation caused by water stress is due partly to a reduced water and assimilate movement into the phloem at the source and partly to a reduced velocity of the flow in the phloem caused by the increased viscoscity of the assimilate stream. Peel (1974) reviewed the effect of water stress on translocation of carbohydrates in plants and concluded that water stress changes the rate and pattern of carbohydrate distribution in plants by acting upon either the loading of assimilates at the source or the unloading at the sink tissues. This conclusion is supported by Nelson (1963) and Wardlaw (1967; 1969). Nelson (1963) showed that water stress affects translocation by changing the physiological state of the exporting leaves; but once material has been transported (out of the leaves) into conducting tissue, water stress has little effect on movement of assimilates to the sink organs. Working with wheat plants Wardlaw (1967) reported that water stress reduced the rate of photosynthesis, but did not affect the growth of the grain. He also showed that water stress retarded the movement of assimilates into the conducting tissue in the wilted leaves, but had little effect on the rate of translocation in the conducting tissue. Wardlaw concluded that water stress acts directly on leaf physiology, rather than indirectly through its effect on growth or on assimilate transport within the conducting tissue. Similar results have been reported by Wardlaw (1969), using ryegrass (Lolium temulentum). From above studies it may be seen that plants when subjected to water stress would exhibit an ordered sequence as follows:

(a) a reduction in extension growth;
(b) a reduction in photosynthesis;
(c) a retardation in movement of assimilates into conducting tissues at the leaf source; and
(d) a retardation in movement of assimilates from source to sinks due to an indirect effect of water stress.

According to the results reported in the present study, both growth and distribution pattern of photosynthetic products of teak seedlings grown under different soil moisture treatments were significantly different. There was evidence that all growth parameters of seedlings grown under the constant high soil moisture (Treatment A) were much greater than those of seedlings grown under the periodical soil moisture stress conditions (Treatments B and C), with minima for Treatment C. The amount of photosynthates translocated from the shoot into the root system of seedlings was greater under Treatments B and C than Treatment A, with a maximum for Treatment B, that is seedlings under Treatment A tended to retain a relatively large amount of their photosynthetic products in their shoots (leaves and stems), as compared with seedlings from Treatments B and C. It should be noted that these results were obtained during the first 3 days after rewatering and exposure to $^{14}CO_2$.

It has been demonstrated earlier that there was no significant difference in the photosynthetic capacity of seedlings between the treatments. This suggests that the activities of the source of photosynthates did not differ significantly between the treatments; and, hence, the difference in the pattern of translocation and distribution of photosynthates might be due primarily to the difference in the activities of the sink of photosynthates between the treatments. These findings clearly suggest that the requirement for photosynthates for shoot activities of the seedling from Treatment A was greater than that of seedlings from Treatments B and C. Conversely, the requirement for photosynthates for root activities of seedlings from Treatments B and C was significantly greater than that of seedling from Treatment A. It was demonstrated earlier (Chapter 6) that the teak seedling grown under constant high soil moisture exhibited a fairly constant balanced growth of the root and the shoot system; but the balanced growth of these two parts in the seedling was markedly altered as the supply of soil water was periodically reduced, with an increase in root growth and decrease in shoot growth. Moreover, the concentration of sugars in the root system of seedlings grown under

Treatments B and C was significantly greater than that in the root system of the seedling grown under Treatment A; and this applies particularly to the lateral roots of the seedling. The above evidence clearly suggests that there are close relationships among the amount of photosynthetic products translocated to the root system, the level of sugars in the root system, and the balanced growth between the root and shoot parts of the teak seedling. Under periodical soil moisture stress conditions (Treatments B and C), the seedlings exported a relatively larger amount of their products of photosynthesis to the root systems, resulting in an increase in sugar concentration in the roots and associated with an increase in the proportion of root to shoot growth. In other words, the greater export of photosynthates from shoots to root systems in seedlings grown under periodical moisture stress conditions was due primarily to an increase in root growth associated with a decrease in shoot growth, compared with seedlings grown under the constant high soil moisture.

CHAPTER 8

THE ROLE OF PLANT GROWTH SUBSTANCES IN CONTROLLING TEAK STUMP SPROUTING

8.1 STUDY 1: EFFECTS OF EXOGENOUS APPLICATION OF PLANT GROWTH SUBSTANCES ON STUMP SPROUTING

8.1.1 Introduction

It has been stated earlier (Chapter 2) that there are two main internal factors involved in governing the ability of sprout production in stumps or roots of woody plant species. Those factors are stored reserves and plant growth substances. The studies reported in this thesis so far have not established any clear relationships between the ability of teak planting stump to produce sprouts and the amount or concentration of the stored carbohydrates in the stump (Chapters 5, 6, and 7). It is evident that the sprouting potential of the teak stump was not positively correlated with the amount or concentration of the stored carbohydrates in the stump. Therefore, it is of interest to study the role of plant growth substances in controlling the production of sprouts in teak planting stumps.

As noted earlier, plants will produce sprouts when they are seriously damaged either by physical or by biotic agents, resulting in an interruption of the downward translocation within the plant. Thimann and Skoog (1933, 1934), who worked with pea plants, found that the inhibition of lateral bud sprouting in the "intact" plant of this species is due primarily to the action of auxin which is produced in the apical bud and the young rapidly growing leaves in the terminal shoot and translocated basipetally along the stem of the plant. When the plant is decapitated, thereby removing the source of auxin, the sprouting of lateral buds occurs below the cut surface of the decapitated stem. A similar phenomenon of plant sprouting has been reported in woody plants (Wenger, 1953; Eliasson, 1969, 1971a, 1971b; Phillips, 1969a; Schier, 1973). The effect of auxin (both endogenous and exogenous auxins) on the inhibition of stump sprouting and root suckering has been intensively investigated with various woody plant species. Several studies demonstrated a negative correlation between the ability of stumps and roots to sprout and the auxin content in these tissues (Farmer, 1962; Steerett and Chappell, 1967; Eliasson, 1969, 1971a, 1971b; Vogt and Cox, 1970; Schier, 1973). Conversely, the production of sprouts was stimulated by reducing the amount of auxin in the plant either by removal of the terminal shoot, or girdling the stem with an application of an auxin inhibitor, or by restricting shoot growth by environmental treatment, (Eliasson, 1971b; Smith, 1975). The physiological mechanism of auxin in inhibiting plant sprouting has been discussed in detail in Chapter 2.

Apart from auxins, gibberellins and cytokinins have been found to play a significant role in controlling the sprouting potential of various plants (Phillips, 1969a, 1975; Vogt and Cox, 1970; Blake, 1974; Smith, 1975). Cytokinins release the buds from inhibition and gibberellins also stimulate growth and development of the released buds, especially in the elongation of stem internodes (Phillips, 1969a, 1975; Bachelard, 1969b; Vogt and Cox, 1970; Blake, 1974).

There appears to be very little available information dealing with the effects of these three major plant growth substances on the sprouting potential of teak stumps. This chapter reports on an initial evaluation of the effect of auxin, gibberellin, and cytokinin on the formation and subsequent growth of sprouts in teak stumps.

8.1.2 Materials and Methods

Teak seeds from Laos were used for the experiments. The seeds were sown and the seedlings were grown singly in 11 cm diameter pots containing a mixture of equal parts of vermiculite and perlite in a controlled day/night temperature 30/25°C glasshouse.

8.1.2.1 Experiment 1

Fourteen weeks after germination, 48 uniform seedlings were divided into 6 groups of 8 seedlings. All seedlings were removed from the pots, stumped, and immediately replanted singly in the same pots containing the same standard growth media. Immediately after replanting, one of the following substances was applied to the cut surface of the stumps:

Treatments

A. pure lanolin paste (the control treatment)
B. IBA 1 % in lanolin (w/w)
C. GA_3 1 % "
D. BAP 1 % "
E. IBA (1 %) + GA_3 (1 %) + BAP (1%) in lanolin.
F. IBA (1 %) + MH (0.5 %) in lanolin.

where IBA (indolebutyric acid), GA_3 (gibberellic acid) and BAP (6-benzylamino purine) were used as auxin, giberellin and cytokinin sources respectively: and MH (maleic hydrazide) was used as an auxin inhibiting source.

The treated stumps were placed in the glasshouse, and well supplied with water and nutrient solution. During the first 30-day period after replanting the treatments were reapplied at 5 day intervals: this was done by scraping the old lanolin paste from the cut surface and capping with fresh lanolin.

Sprouts were harvested 30 days after replanting. The stumps were returned to the glasshouse for another 60-day period. During this second period only water and nutrient solution were supplied. The final harvest was made 60 days after the first harvest.

8.1.2.2 Experiment 2

On the basis of the results of Experiment 1 treatment B was repeated. Sixteen week-old seedlings were used for the experiment. Thirty two uniform seedlings (Table 8.1) were divided into 4 groups of 8 seedlings. Seedlings were removed from the pots, stumped, and immediately replanted singly in the same pots containing the same growth media. Immediately after replanting one of the following treatments was applied to the cut surface:

Treatments

A. pure lanolin (the control treatment)
B. IBA 1% in lanolin (w/w)
B_1. IBA 0.1% " "
B_2. IBA 0.01 % " "

Stumps from all treatments were placed in the glasshouse for 60 days. During this period after replanting the treatments were reapplied at 5 day intervals as before. Sprouts from all treatments were then harvested 60 days after replanting.

Parameters Measured

Sprout height growth and the number of sprouts per stump in both experiments were recorded at 5 day intervals from replanting to harvest. At harvest several growth parameters including dry matter production of the sprouts were recorded.

TABLE 8.1 Growth characteristics of seedlings used in Experiment 2 (Data representing the mean of 8 seedlings)

	Seedlings used in Treatment				
	A	B_2	B_1	B	L.S.D. 0.5
Height (cm)	57.7	57.9	57.8	57.8	ns
No. of leaf pairs	7	7	7	7	
Leaf dry weight (gm)	20.7	17.5	17.8	19.7	ns
Stem dry weight (gm)	10.2	8.5	8.3	9.6	ns

8.1.3 Results

8.1.3.1 Experiment 1: (Plates 8.1a, 8.1b)

A. First Harvest

An exogenous application of auxin at the 1% concentration to the cut surface of the teak stump caused a marked inhibition of stump sprouting (Figures 8.1a, 8.1b). In contrast, the gibberellin and the cytokinin at the same concentration tended to increase the sprouting potential of the teak stumps, as compared with the control treatment (Figure 8.1b). It has been observed that all stumps treated with lanolin, GA_3, or BAP alone produced sprouts within 10 days after replanting, whereas none of the stumps treated with IBA alone produced sprouts during the 30 day period after replanting. At harvest time, i.e. 30 days after replanting, the mean number of sprouts per stump was significantly greater for stumps treated with GA_3 alone (7 ± 1.5) and BAP alone (6 ± 0.7) than the stump treated with lanolin alone (4 ± 0.5). (Figure 8.1b). This clearly demonstrates the stimulatory influence of both the gibberellin and the cytokinin on the stump sprouting ability in teak. Where IBA (1 %) was applied together with GA_3 + BAP (1 + 1 %) or with MH (0.5 %) an auxin inhibitor , the sprouting potential of the teak stump was still reduced (Figures 8.1a and 8.1b). These findings suggest that IBA at the 1 % concentration had a stroung inhibitory effect on the sprouting of the teak stumps.

Gibberellin had a marked effect on the promotion of an internode elongation in stump sprouts (Figures 8.2a, and 8.2b). Under a variety of plant growth substances used in this study, the greatest sprout height was associated with the GA_3 treatment and the smallest was associated with the IBA + MH treatment. There was no significant difference in height growth among sprouts produced by stumps treated with lanolin alone, BAP alone, and a mixture of IBA + GA_3 + BAP; and the height growth of sprouts from these three treatments were much smaller than that of the sprout from the GA_3 treatment (Figures 8.2a and 8.2b). Thus, gibberellin alone strongly promotes the height growth of sprouts produced by the teak stump, but when applied in combination with the auxin and the cytokinin at the same concentration its promoting effect was greatly reduced. Since the BAP had no effect on sprout height or total length

Plate 8.1 Effects of plant growth substances on sprouting of teak planting stumps

(Plates 8.1a and 8.1b showing the results 30 days after treatments, plate 8.1c showing the results 20 days after treatments)

Figure 8.1a

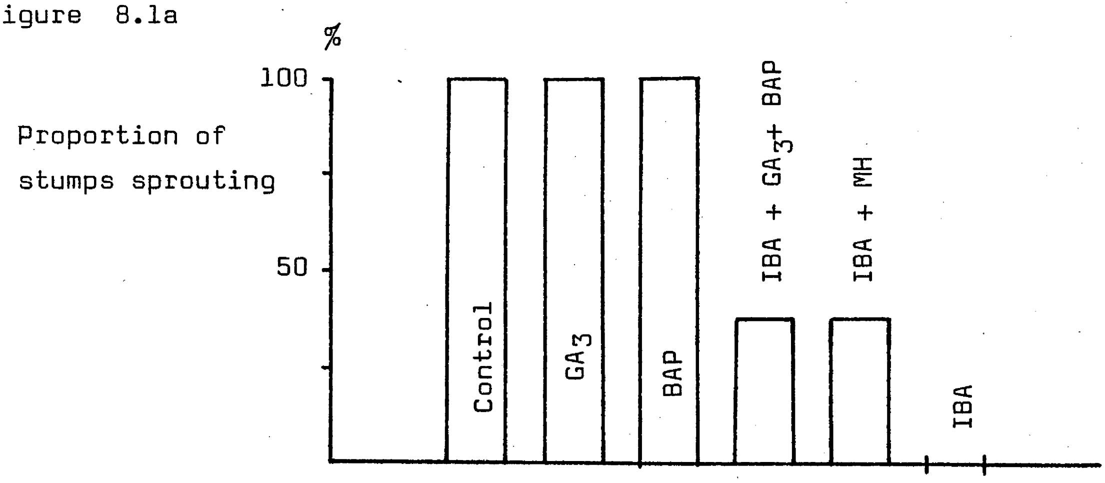
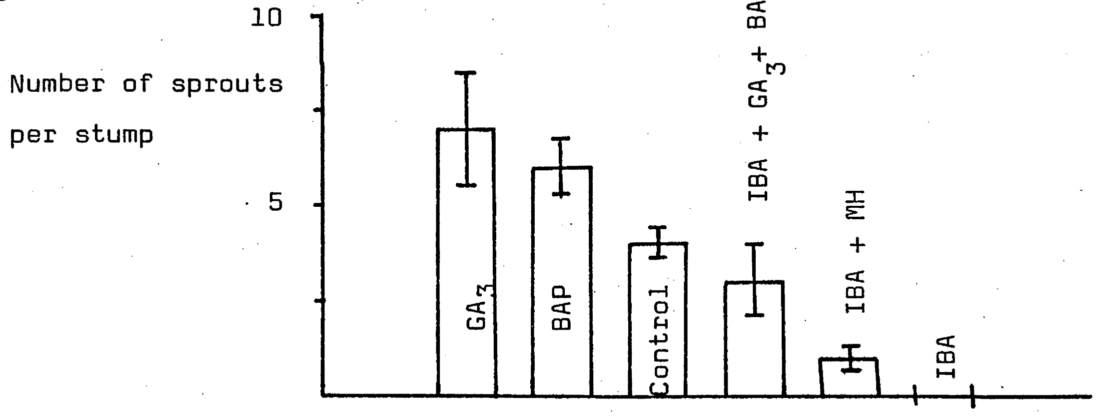


Figure 8.1b



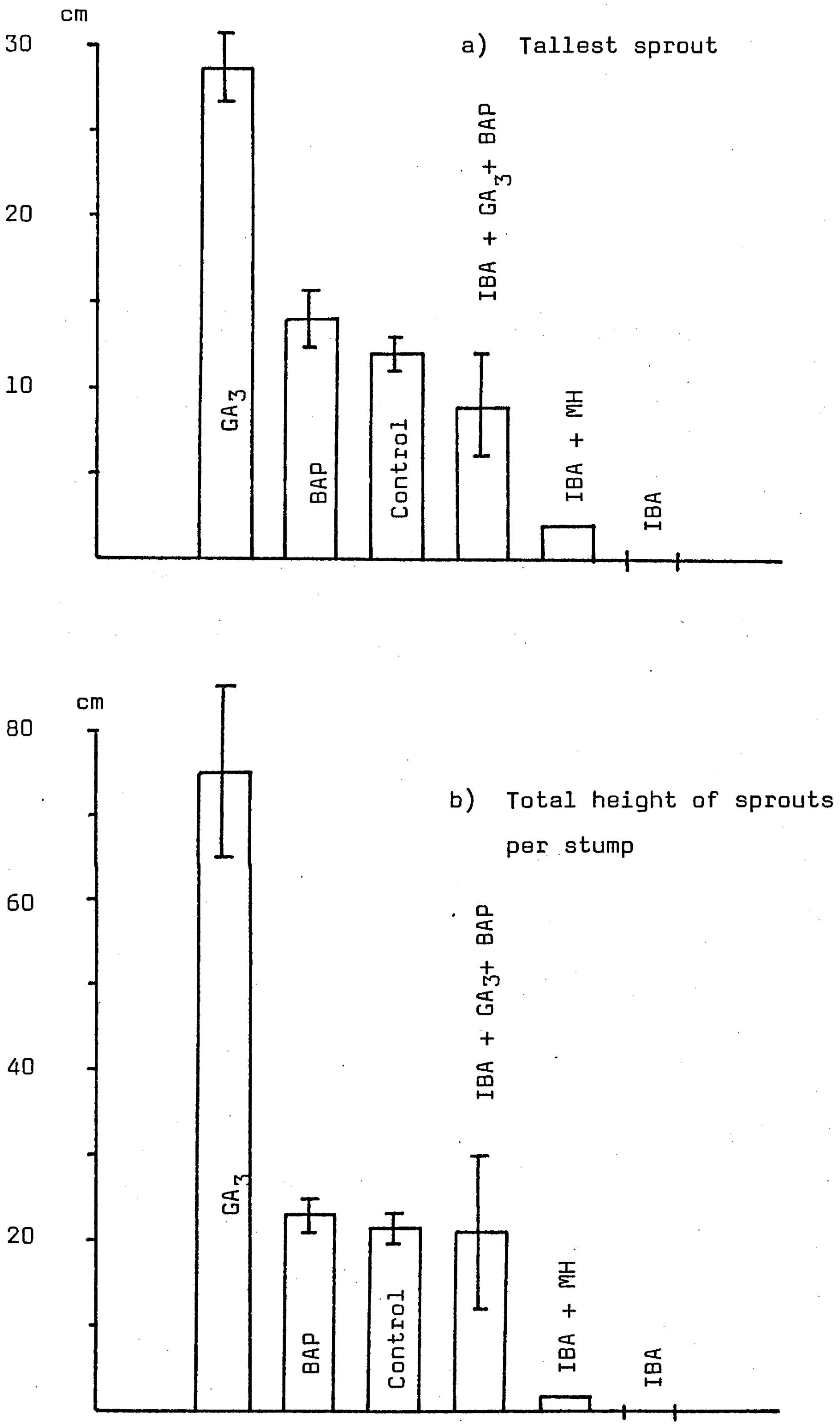


Figure 8.2 Height growth of stump sprouts

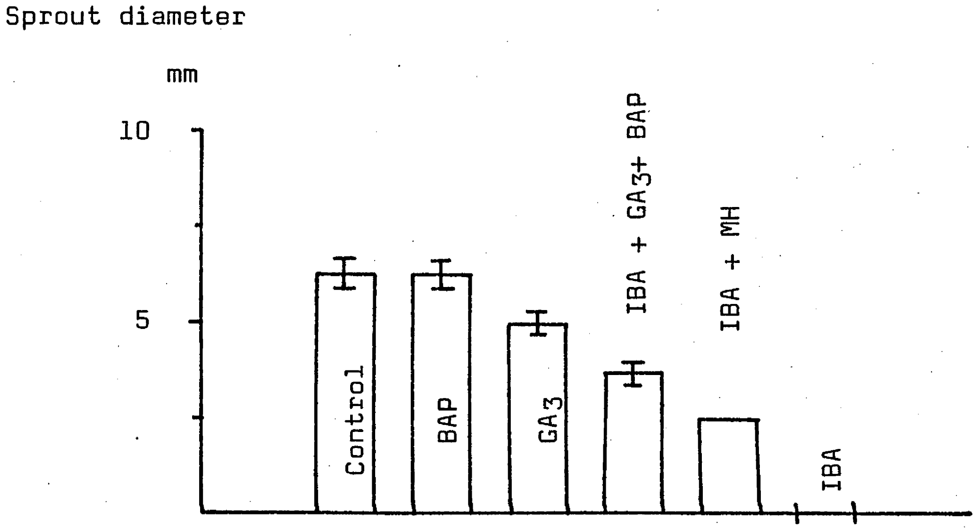


Figure 8.3 Sprout diameter

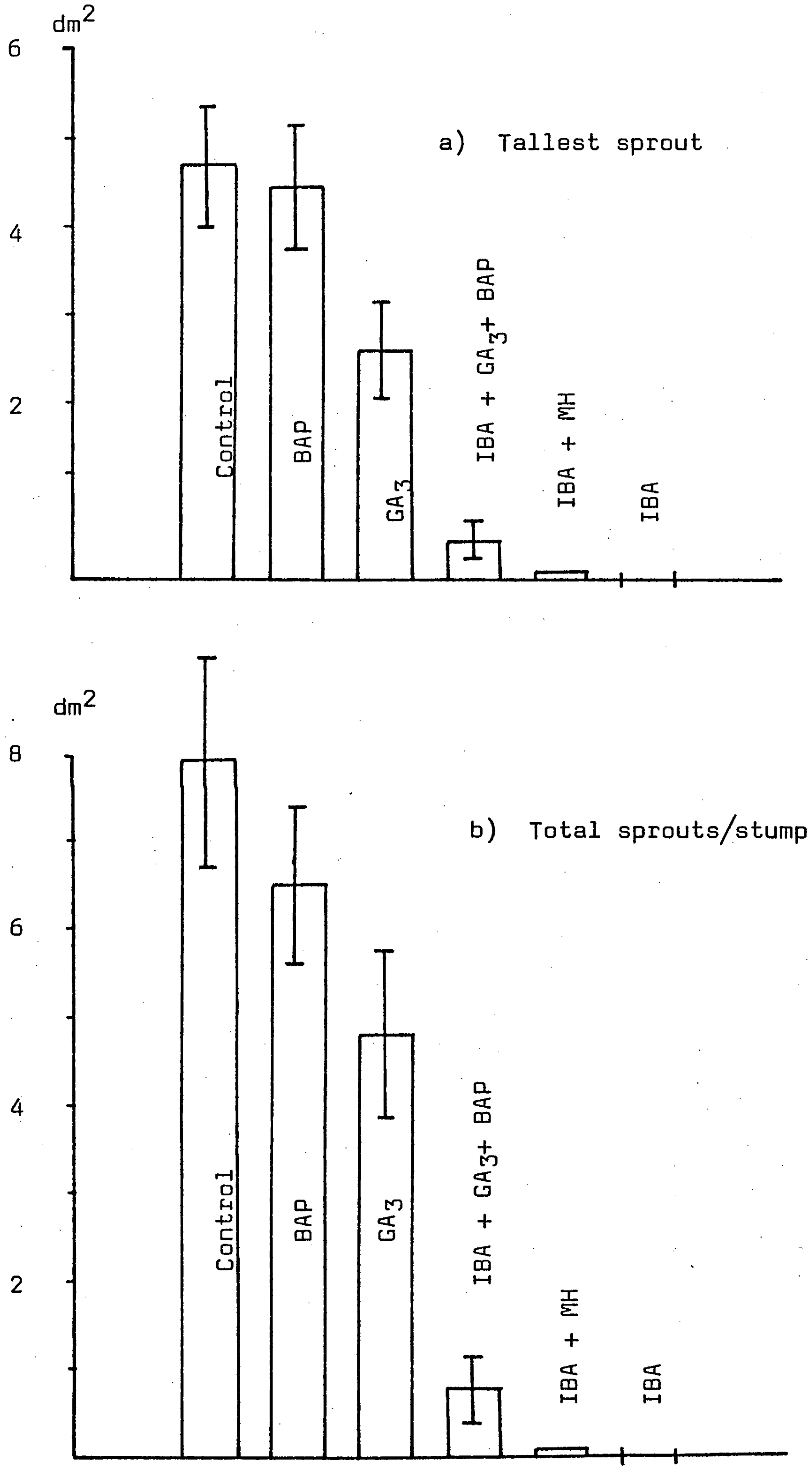
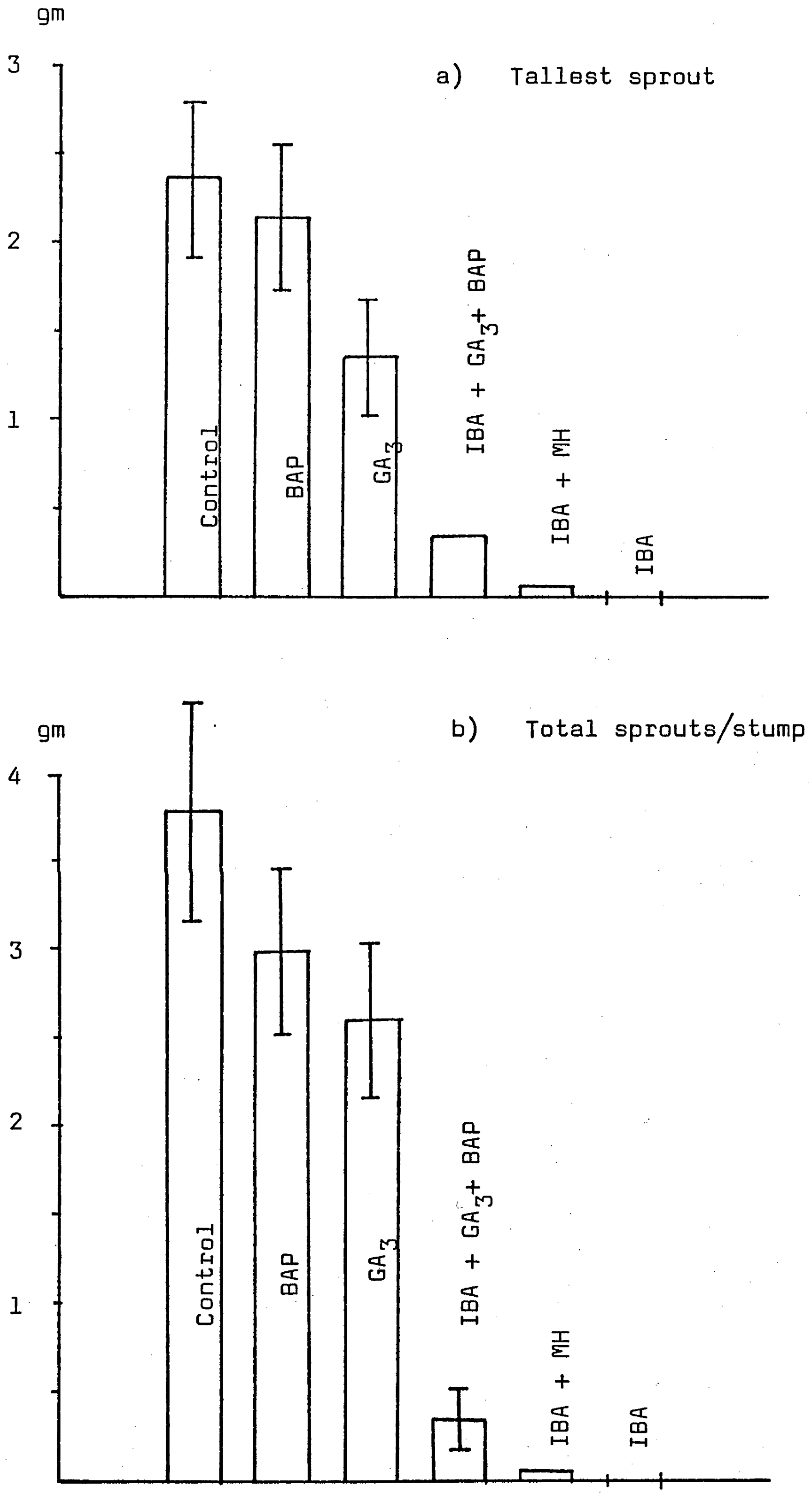


Figure 8.4 Leaf area of stump sprouts



a) Tallest sprout

b) Total sprouts/stump

Figure 8.5 Total dry weight of stump sprouts of sprouts per stump whereas the auxin strongly inhibited both, it is presumably the auxin in the combination which modified the effect of the gibberellin.

Although GA_3 had a marked promoting effect on the stem elongation of stump sprouts, this substance did not appear to promote the stem diameter growth (Figure 8.3) and leaf area production (Figure 8.4) of the stump sprout. Instead, the total leaf area of both the tallest sprout and all sprouts per stump in the GA_3 treatment were significantly smaller than in the control and BAP treatments (Figure 8.4). There was no significant difference in total leaf area between sprouts produced by the control and the BAP treated stumps, while stumps treated with GA_3 alone produced marginally less leaf area. All stumps treated with a mixture containing IBA produced little or no leaves. The same results were obtained for dry weight (Figure 8.5).

B. Second Harvest

After the first sprouts were harvested the stumps were replanted and maintained at 30/25°C for a further 60 days without any treatment. The residual effects of the treatments on the production of stump sprouts in teak are shown in Table 8.2.

All stumps from the control, GA_3, and BAP treatments produced sprouts, whereas only seventy five percent of stumps from the IBA, IBA + GA_3 + BAP, and IBA + MH treatments produced sprouts. Thus the inhibitory influence of IBA on the sprouting potential of stumps in the first harvest was markedly reduced.

TABLE 8.2 Residual effects of plant growth hormones on stump sprouting in teak. Sprouts produced in sixty days following cessation of hormone treatment

(Data representing the mean of the tallest sprout)

	Control	BAP	GA	IBA	IBA GA BAP	IBA + MH
Sprouting Stump (%)	100	100	100	75	75	75
No. sprouts/sprouting stump	3.0 ± 0.6	4.0 ± 0.4	9.0 ± 1.4	2.0 ± 0.3	5.0 ± 1.6	2.0 ± 0.4
Height (cm)	24.9 ± 2.3	21.0 ± 3.8	19.8 ± 2.0	18.5 ± 2.8	20.3 ± 2.2	15.0 ± 3.5
Diameter (mm)	6.2 ± 0.5	5.9 ± 0.6	4.0 ± 0.5	5.2 ± 0.6	5.3 ± 0.5	4.5 ± 0.1
Total shoot dry weight (gm)	6.0 ± 1.2	5.0 ± 1.0	2.2 ± 0.6	3.0 ± 1.1	3.3 ± 0.6	2.0 ± 0.7

GA_3 had a marked residual effect on the sprouting potential of the teak stump, that is, the greatest number of sprouts per stump was associated with stumps from the GA_3 treatment as compared with the control treatment (Table 8.2). There was no significant difference in the number of sprouts per stump between the control treatment and the treatments containing the residual effect of IBA (Table 8.2), and between the control and BAP treatments. These results clearly show that there was a marked reduction in the inhibitory effect of IBA after the first harvest and the cessation of IBA treatments for 60 days.

In terms of height, diameter growth and the total dry weight of sprouts, there was no significant difference between the control and BAP treatments. The total dry weight of sprouts per stump was significantly smaller for the GA_3 treatment than the control and BAP treatments. There were no significant differences in the growth parameters of sprouts produced by stumps formerly treated with GA_3, IBA, IBA + GA_3 + BAP, and IBA + MH. These findings will be discussed in detail in Section 8.4

8.1.3.1 Experiment 2 ((Plate 8.1c)

Similar to the results obtained in Experiment 1, IBA had a marked effect on the inhibition of stump sprouting in teak. The percentage of sprouting stumps decreased markedly with the increase of IBA concentration (Table 8.3). Within 15 days of replanting, all stumps treated with lanolin alone had produced sprouts while none of the stumps treated with the 1 % IBA produced sprouts during the 60 day period of replanting (Figure 8.6a).

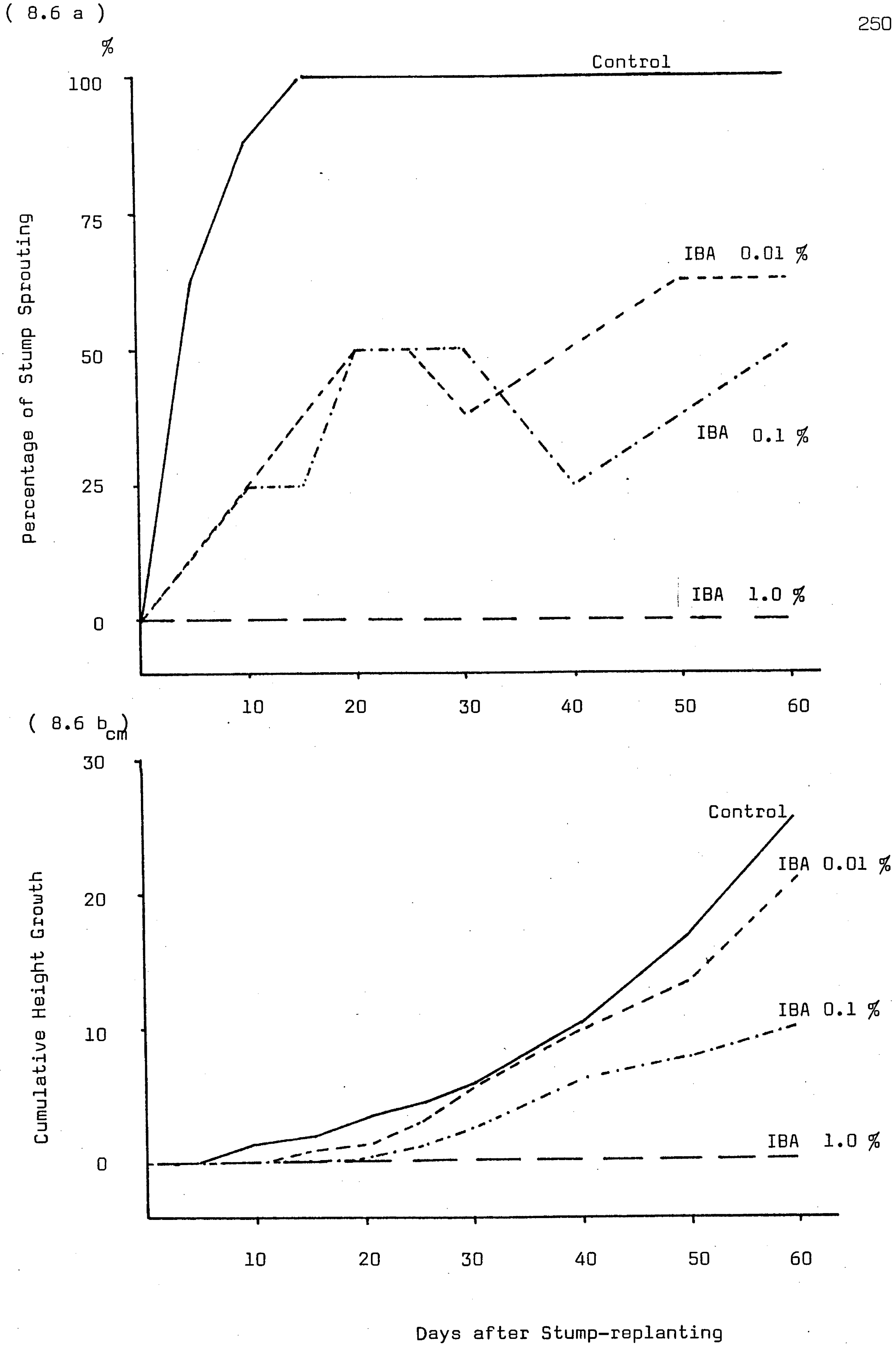


Figure 8.6 Effects of IBA on stump sprouting in teak

Height and diameter growth, leaf area production, and total shoot dry weight of sprouts decreased markedly with an increase of auxin concentration. These effects are well illustrated by height growth (Figure 8.6b, Plate 8.1c).

TABLE 8.3 Effect of IBA on the production of stump sprouts in teak (Sixty days after treatment)
(Data represents the growth of the tallest sprout)

	Lanolin Alone	IBA % Concentration			
		0.01	0.1	1.0	
Sprouting stump (%)	100	62.5	50.0	0	
Height growth (cm)	25.4 ± 2.8	21.0 ± 6.2	10.0 ± 3.7	0	*
Diameter (mm)	7.6 ± 0.4	6.1 ± 1.2	4.6 ± 1.6	-	*
Leaf area (dm^2)	14.2 ± 1.1	9.5 ± 3.5	5.4 ± 3.3	-	*
Leaf dry weight (gm)	6.9 ± 0.7	4.1 ± 1.9	2.6 ± 1.7	-	*
Stem dry weight (gm)	2.3 ± 0.3	1.6 ± 0.9	0.7 ± 0.5	-	*
Shoot dry weight (gm)	9.2 ± 1.0	5.7 ± 2.8	3.3 ± 2.2	-	*
Dead stumps (%)	0	37.5	50	100	

*Significant difference at 5% level.

8.1.4 Discussion

The formation and subsequent growth and development of sprouts produced in teak planting stumps were found to be largely influenced by the exogenous application of plant growth substances, particularly IBA and GA_3.

IBA had a strong inhibitory influence on the initiation of buds in the teak stump. Evidence indicates that the sprouting potential of the teak stump was negatively correlated with the concentration of IBA applied to the cut surface of the stump (Experiment 2). At a relatively high concentration of 1% (w/w), the IBA completely inhibited the production of stump sprouts and subsequently caused a deterioration of the planted stump, where the application of IBA (1%) was continued for a period of 60 days from replanting (Experiment 2). These findings suggest that IBA at a relatively high concentration might be toxic for teak planting stumps. The inhibition of stump sprouting induced by the action of the auxin-like substance (IBA) obtained in this study is consistent with the findings of a number of studies as reviewed in Section 2.2.2.

GA_3 when applied alone to the cut surface of the teak planting stump strongly promoted the initiation of buds in the stump and subsequently stimulated the stem alongation and height growth of the sprouts produced. Similar effects of GA_3 on the production and subsequent growth of stump sprouts has been reported with various plants by several workers (Brien et al, 1955; Seth and Mathanda, 1959; Nanda and Purohit, 1964a, 1964b; Nakamura, 1965; Bachelard, 1969b; Vogt and Cox, 1970; Blake, 1974). In contrast, Bachelard (1969a) reported the inhibitory effect of GA_3 (1 - 100 p.p.m.) on the epicormic shoot production in stem segments of <u>Eucalyptus polyanthemos</u>. Similar findings were also reported in the work of Smith (1975), who studied the effect of GA_3 on the epicormic shoot production in the stem of the girdled and decapitated seedlings of <u>Eucalyptus viminalis</u>. Both Bachelard (1969a) and Smith (1975) reported that the exogenous application of GA_3 to the cut surface of the eucalypt seedling-stumps caused a marked increase in the cambial activity in the plants.

They suggested that the GA_3 might inhibit the production of epicormic shoots in these plants through its stimulatory effect on the activity of cambium. In other words, there is a competative relationship between cambial activity and epicormic shoot production such that epicormic shoot formation is inhibited when the cambial activity is stimulated. The exogenous application of GA_3 to the shoot apex of the "intact" plant was also found to inhibit the lateral bud growth in various plants (Brian et al, 1955; Nakamura, 1965; Blake, 1974). This has been suggested to be due to an increase in shoot growth rate induced by the action of GA_3, resulting in an increased auxin level in the plant shoot and an inhibition of lateral bud growth (Phillips, 1969a, 1969b).

Unlike GA_3, BAP when applied alone to the cut surface of the teak planting stump increased the number of sprouts produced per stump, but did not stimulate the subsequent growth and development of the sprouts. That is, there was no significant difference in the sprout growth potential between the BAP treatment and the control treatment. This finding seems to be consistent with the theory that cytokinins have a significant effect on the release of buds from inhibition but have no influence on the subsequent growth and development of the released buds (Sachs and Thimann, 1964, 1967; Phillips, 1969a, 1975, Shein and Jackson, 1971; Smith, 1975). Phillips (1975) suggested that both gibberellins and auxins are required for continued growth and development of buds released from inhibition by the action of cytokinins. The effect of cytokinin-like substances on the stimulation of stump or lignotuber sprouting in eucalypt plants was also reported in the work of Blake (1974) and Smith (1975). In contrast, Bachelard (1969a) noted that the exogenous application of kinetin (5 p.p.m.) caused an inhibition of the sprouting in the stem segment of Eucalyptus polyanthemos, but stimulated the cambial activity in the treated stem segment. He suggested that kinetin inhibited the sprouting in the eucalypt stem segment through its influence on the stimulation of cambial activity.

From the above evidence it may be clearly seen that IBA has a strong inhibitory effect on the sprouting of teak planting stumps, whereas GA_3 has a marked stimulatory effect on the stump sprouting both in terms of the number of sprouts produced per stump and the sprout growth potential, and BAP seems to be of lesser importance on the sprouting of teak stumps. When these three substances at the same concentration (i.e. 1%) were applied in combination to the cut surface of the teak stumps, the sprouting potential of the treated stumps was markedly reduced, as compared with the "control" stumps. That is, only 37.5% of stumps from the "IBA + GA_3 + BAP" treatment produced sprouts. This suggests that the combination of GA_3 and BAP could overcome the inhibitory effect of the IBA in some stumps. On the other hand, it may be interpreted that IBA could overcome the stimulatory effect of the combination of GA_3 and BAP on the sprouting of teak stumps. The inhibitory effect of the combination of the auxin-, gibberellin- and cytokinin-like substances on the sprouting of plant stumps has also been reported by Woolley and Wareing (1972a) and Smith (1975). Smith (1975), for example, found that the application of IBA (1%) + GA_3 (1%) + BAP (1%) caused a marked inhibition of the formation of epicormic shoot in the girdled stem of eucalypt seedling. Woolley and Wareing (1972a) reported that both GA_3 and BAP when applied alone stimulated the sprouting of one-node cuttings of Solanum andigena, whereas NAA inhibited the sprouting. When these three substances (GA_3, BAP and NAA) were applied together to the cuttings at the concentrations of 1.0, 2.0 and 1.0 p.p.m. for GA_3, BAP and NAA, respectively, the inhibition of sprouting resulted. The mode of action of the combination of these three sustances on the inhibition of plant sprouting is not known. More research dealing with the effects of the combination of various concentrations of auxin-, gibberellin- and cytokinin-like substances on the sprouting of teak planting stumps is required to help understand the sprouting phenomenon.

Maleic hydrazide (MH) reduced the degree of inhibition of stump sprouting caused by the action of IBA, but did not stimulate the subsequent sprout growth and development. The effect of MH in antagonising the action of an auxin-like substance (IAA) has also been shown in the work of Vogt and Cox (1970) who found that this substance reduced the inhibitory effects of IAA on the sprouting of the oak seedling stump.

In summary, the results obtained in this study show that:-

a. IBA has a strong inhibitory effect on the sprouting of teak stumps, and the degree of the inhibitory effect decreases progressively with a decrease in concentration of the substance;

b. GA_3 has a marked promoting effect on the sprouting of teak stumps, (both number of sprouts produced per stump and an internode elongation of the sprout but not stem diameter was markedly promoted by the action of this substance);

c. BAP releases the buds from inhibition but has no effect on the subsequent growth and development of the released buds; and

d. MH (maleic hydrazide) has a marked effect on the reduction of the inhibitory effect of the auxin-like substance on the sprouting of teak stumps.

8.2 STUDY 2: EFFECT OF TEMPERATURE ON IAA LEVEL IN STEM AND TAP-ROOT TISSUES OF TEAK SEEDLINGS

8.2.1 Purposes of Study

According to the auxin theory of apical dominance, auxin is produced in the expanding terminal shoot and it translocated basipetally along the stem. This auxin is responsible for the inhibition of lateral bud development below the stem apex (Chapter 2). It was found earlier that growth and development of the teak seedling was markedly restricted when the growing temperature was reduced from 30/25° to 18/13°C. The production of stump sprouts was at the same time stimulated (Chapter 5). The studies reported in the earlier Sections of this Chapter have clearly demonstrated the effects of exogenous applications of a variety of plant growth substances on the sprouting potential of the teak planting stump. The findings obtained in these studies showed that an auxin (IBA) had a marked inhibitory effect on the sprouting potential of teak stumps, whereas the gibberellin (GA_3) and the cytokinin (BAP) had stimulatory effects on the production of stump sprouts in teak.

The above evidence suggests that it would be interesting to study the effect of temperature regime on endogenous auxin levels in teak seedlings. Does restricted growth of seedlings result in a lower level of auxin? In the present study, the seedlings of teak were grown under the warm temperature of 30/25°C for 12 weeks and then transferred to 18/13°C for 4 weeks. The amounts of IAA in the stem and tap-root of the control seedling (grown at 30/25°C) and those in the cool treated seedling were then determined using the fluorescence assay method.

8.2.2 Materials and Methods

A. Plant Materials

Teak seeds from Laos were used for the experiment. The seeds were sown and the seedlings were grown singly in 11 cm diameter pots containing a mixture of an equal part of vermiculite and perlite at 30/25°C day/night temperature.

Twelve weeks after germination, 8 uniform seedlings were selected for the experiment. The seedlings were divided into two groups of four, one group was transferred abruptly to grow at 18/13°C and the remaining group was maintained at 30/25°C.

B. Determination of IAA in Plant Tissues

Four weeks after treatment, seedlings from both groups were stripped of leaves and the stems were cut into 3 sections of equal length (top, middle, and base). The root systems were washed and all lateral roots were trimmed off from the main tap-roots. The three sections of stem and a whole tap-root of each seedling were then extracted separately to determine the IAA content. The procedure used for extraction, purification, and estimation of IAA in plant tissues were those of Jenkins and Shepherd (1972, 1974).

The tissue was chopped into small pieces, homogenized in ice cold methanol in a blender, and extracted in methanol overnight in a dark cold room. The extracts were then filtered and washed through Whatmann No. 541 filter paper under reduced pressure and evaporated to an aqueous phase at 35^{o}C with a rotary vacuum evaporator. The separated solid material was oven dried and the dry weight was determined. The aqueous phase was centrifuged at 3,000 rev/min. for 30 minutes to remove cell debris and precipitated pigment material. Partitioning of the aqueous extracts was employed using the diethyl ether method as scheduled in Figure 8.7.

The acidic ether extracts were taken up in a small amount of methanol and strip loaded onto chromatograms (acid washed Whatmann No. 3 MM paper) and dried under a stream of warm air. Chromatograms were equilibrated overnight in a solvent (isopropanal:ammonia: water, 10:1:1) saturated atmosphere in a chromatography tank, and then developed with the solvent using descending chromatography. IAA marker strips were run with all chromatograms. When chromatograms had run to about 20 cm from the application line, they were removed from the tank. The position of the front was marked, they were dried and stored in a freezer. IAA markers were identified under shortwave ultra violet light, indicating the probable Rf of endogenous IAA in chromatographed extracts.

A section of IAA zones (usually from Rf 0.2 to 0.4) was cut from the paper chromatogram, eluted by cutting the paper into small pieces and shaking these for 30 minutes in each of three changes of methanol. The washings were bulked, dried in the rotary vacuum evaporator at 35^{o}C, and taken up again in a small amount of methanol.

The extract was then applied, as a band, to acid washed Whatmann No. 3 MM chromatography paper for electrophoresis. Electrophoretograms were dipped carefully into an ammonium acetate buffer solution (0.05 M, pH 7.5) to wet all but not the application lines and blotted. The application lines were then dampened by adding the buffer from a small pipette.

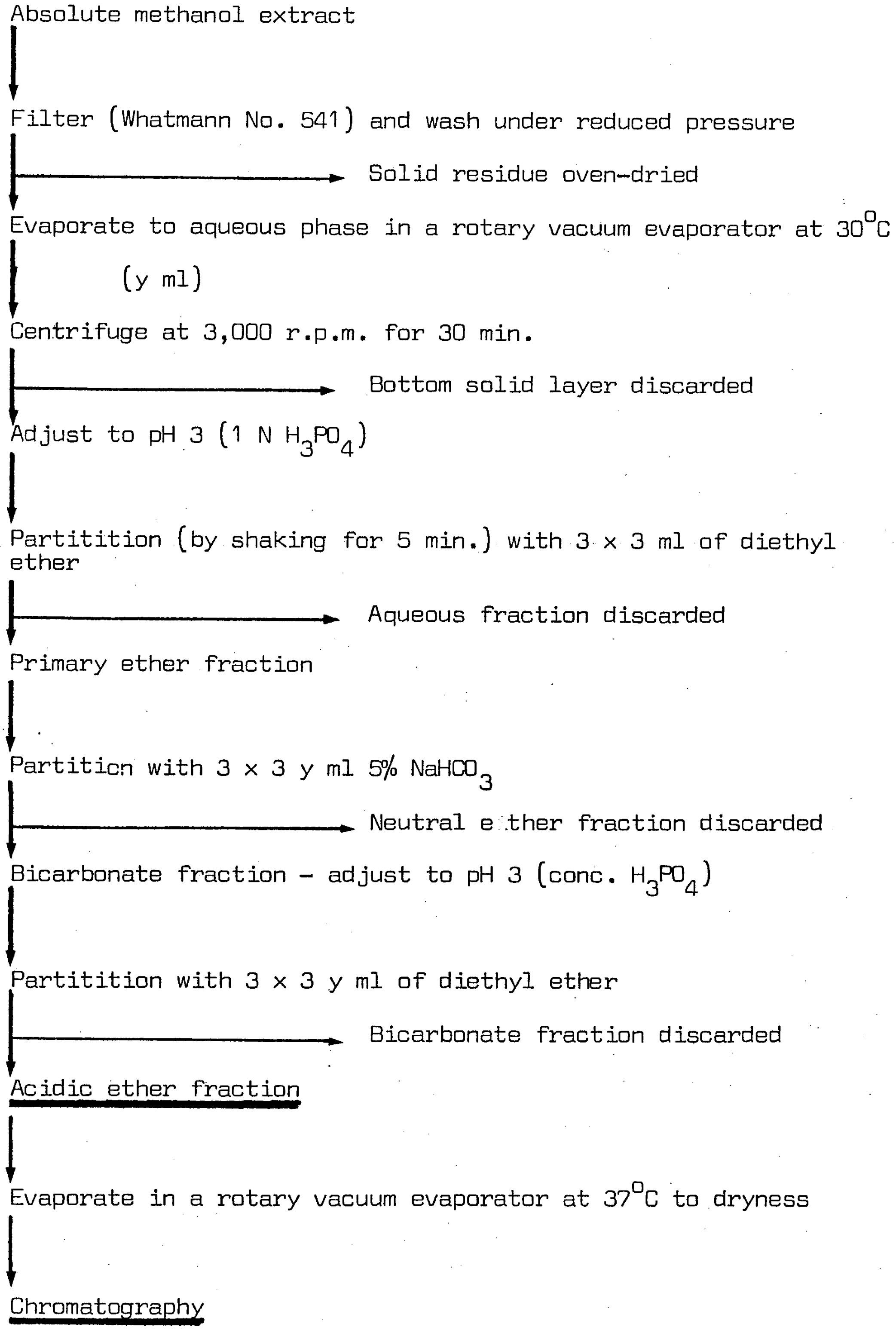


FIGURE 8.7 Diethyl ether partitioning schedule modified from West (1969) and Jenkins and Shepherd (1972, 1974).

Electrophoresis was carried out in acetate buffer on a Shandon high voltage electrophoresis unit. Electrophoretograms were run for 45 minutes at 3,500 volts, 45 - 65 milli-amps. Each run consisted of two electrophoretograms, one (10 cm wide) loaded the extract and one (2.5 cm wide) loaded IAA marker. The IAA marker electrophoretogram was used to indicate the probable position of IAA on sample electrophoretogram. After running, the electrophoretograms were air dried.

A 2 cm segment centered on the probable position of IAA on the sample electrophoretogram was eluted by shaking with 5 ml of citrate-phosphate buffer pH 5.4 for 30 minutes. Another segment was taken from each side of the first segment and eluted individually. The eluate from each segment was assayed with a Farrand Spectrophotofluorimeter Mark I. The intensity of fluorescence was recorded at the excitation/emission wavelength of 280/360 mμ. These wavelengths gave maximum fluorescence from IAA in the instrument used (Figure 8.8a). The IAA level was calculated from a standard curve (Figure 8.8b).

IAA level represented either the total amount (μg) or relative concentration (μg/10 gm dry weight of the extracted tissues including wood, cambial, and bark tissues). Since the main purpose of this study was to look at the relative levels of auxin content and not the exact amount of auxin content, the level of IAA content in the plant tissue was not adjusted for losses which occurred during extraction and purification as reported in the work of Shepherd (1965) and West (1969).

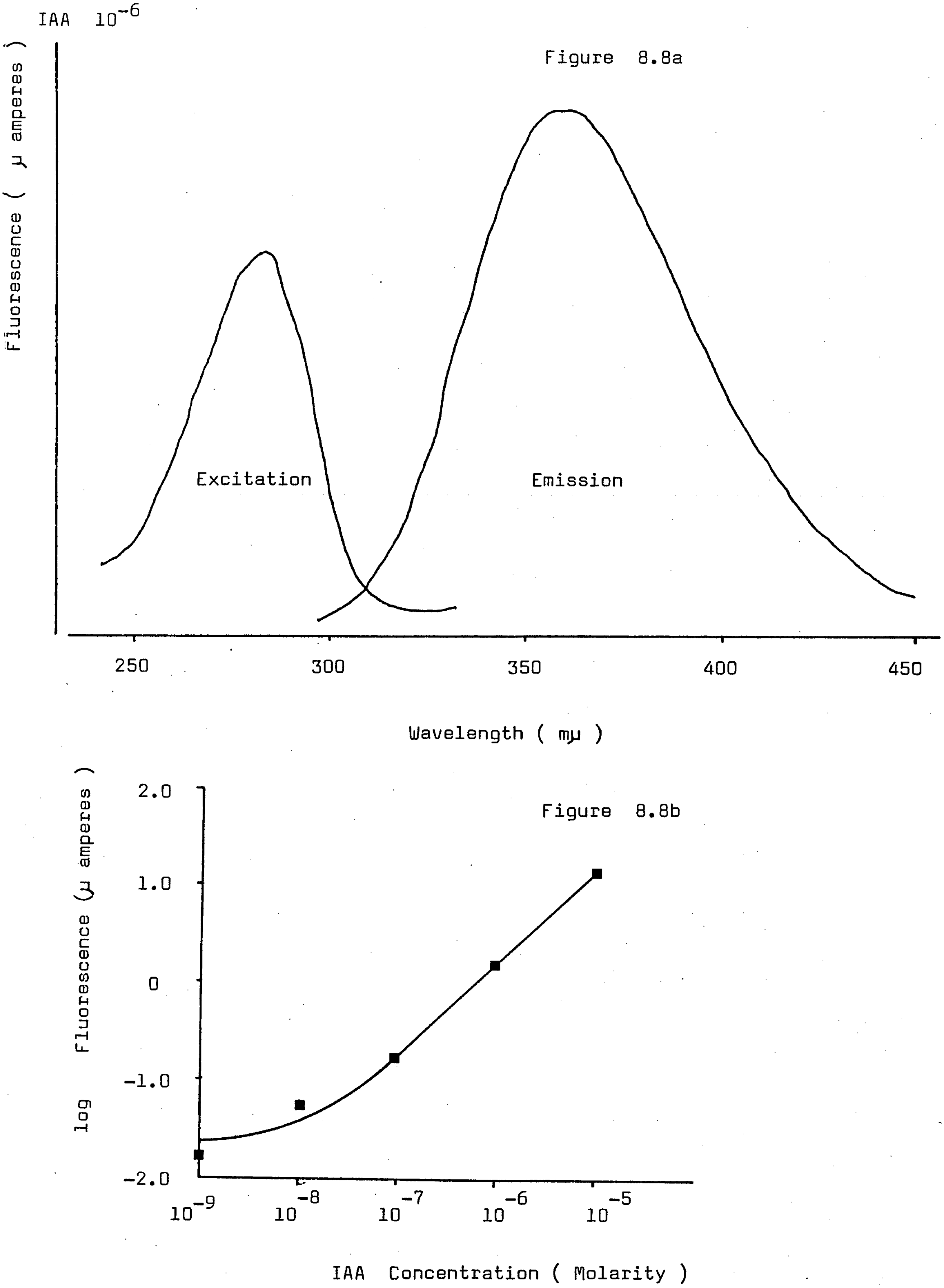

IAA 10^{-6}
Fluorescence (µ amperes)
Figure 8.8a
Excitation
Emission
250
300
350
400
450
Wavelength (mµ)
log Fluorescence (µ amperes)
2.0
1.0
0
-1.0
-2.0
Figure 8.8b
10^{-9}
10^{-8}
10^{-7}
10^{-6}
10^{-5}
IAA Concentration (Molarity)

Figure 8.8

8.2.3 Results and Discussion

The results obtained in this study may be summarized as follows:

a. Dry weights of all stem sections (top, middle and base) and the total stem tissue of seedlings grown at 30/25°C were significantly greater than those of seedlings subjected to the cool temperature of 18/13°C (Table 8.4).

b. The amount of IAA in all stem sections and total stem tissue was significantly greater for seedlings grown under 30/25°C than those grown under 18/13°C.

c. There was no significant difference in either the tap-root dry weight or total amount of IAA in the tap-root between the two groups of seedlings.

d. There were no significant differences in the relative concentration of IAA present in either stem sections or in the tap-root between the two groups of seedlings.

e. The concentration of IAA decreased from the top stem section through the mid and base stem sections to the tap-root of the seedling in both temperature treatments.

The above evidence suggests that for the stem part of the teak seedling, there were close relations among the growing temperature, the absolute amount of IAA present and the dry matter production of the seedling stem. That is, under the favourable warm temperature (30/25°C) there were relatively larger amounts of IAA present in the seedling stem (4.27 ± 0.16 μg) and a greater stem dry weight was observed (9.28 ± 0.62 gm). Conversely, where the growing temperature was reduced from 30/25° to 18/13°C the absolute amount of IAA in the seedling stem (2.52 ± 0.54 μg) was less and the stem dry weight of the seedling (4.69 ± 0.33 gm) was also markedly reduced. In contrast to the stem, the absolute amount of IAA present

TABLE 8.4 Effect of growing temperature on IAA level in stem and tap-root tissues of teak seedlings

(Data representing the mean of 4 seedlings)

	Oven dry weight (gm)	Total IAA (µg)	IAA Concentration (µg/10 gm dry matter weight)
30/25°			
Stem tissue			
Top stem	1.31 ± 0.10	1.51 ± 0.16	11.57 ± 1.15
Mid stem	3.04 ± 0.19	1.23 ± 0.05	4.25 ± 0.25
Base stem	4.93 ± 0.38	1.48 ± 0.08	3.11 ± 0.41
Total stem tissue	9.28 ± 0.62	4.27 ± 0.16	4.68 ± 0.42
Tap-root tissue	6.27 ± 0.61	1.37 ± 0.20	2.23 ± 0.33
18/13°			
Stem tissue			
Top stem	0.78 ± 0.08	0.68 ± 0.25	9.25 ± 3.81
Mid stem	1.46 ± 0.18	0.94 ± 0.18	6.82 ± 1.89
Base stem	2.46 ± 0.14	0.91 ± 0.28	3.74 ± 1.29
Total stem tissue	4.69 ± 0.33	2.52 ± 0.54	5.62 ± 1.54
Tap-root tissue	5.19 ± 0.70	1.13 ± 0.17	2.64 ± 0.77

in the tap-root and the tap-root dry weight of seedlings grown under the warm condition and those grown under the relatively cool condition were not significantly different (Table 8.4).

In terms of concentrations, the results obtained from the present study suggest that there was no significant difference in the IAA level, both in the stem and in the tap-root, between treatments. This suggests that a reduction of growing temperature from 30/25° to 18/13°C had no effect on the concentration of IAA in tissues of both stem and tap-root of the teak seedling. The difference in the absolute amounts of IAA between the treatments was due to the difference in plant size. The findings observed in this study are consistent with those of Jenkins (1971) who studied the effect of temperature regime on the concentration of IAA present in the stem tissue of the radiata pine seedling. Jenkins reported that there was no significant difference in the IAA concentration in the stem tissue between seedlings grown at 15/10°C and 30/25°C (day/night temperature), but the dry matter production of the former seedlings was much smaller than that of the latter seedlings. However, this author found that the optimum IAA concentration was associated with seedlings grown at 21/16°C, which is favourable for dry matter production and growth rate of the seedlings.

As discussed previously, cool temperature (18/13°C) appeared to have a stimulatory effect on the sprouting of the teak seedling following stump-replanting (Section 5.2), and IBA inhibited the stump sprouting in teak (Section 8.1). On this basis, it has been assumed that cool temperature might, somehow, reduce the auxin level in the teak stump, resulting in an increase in the stump sprouting ability. According to the results reported in this study, the above assumption could be eliminated. It now seems likely that the main cause of the difference in sprouting ability between stumps of the cool treated seedlings and those of seedlings grown at 30/25^{0}C (Section 5.2) was some other factor such as the mobilization of stored reserves and the balance of gibberellins and cytokinins in the seedling stumps as influenced by the growing temperature of the seedling. More studies dealing with the effect of cooling of the teak seedling on the levels of gibberellins and cytokinins in the seedling stump are required to help understanding the sprouting phenomenon of the teak stump.

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSIONS

9.1 GENERAL DISCUSSION

9.1.1 Occurrence and Habits of Teak

Teak is a deciduous tropical tree species. It occurs naturally only in India, Burma, Thailand and Laos, within the range of latitude of 9^{o} – $25^{o}30'$ N. and longitude of 73^{o} – $104^{o}30'$ E. The species has been introduced and established successfully in many countries in the tropical and sub-tropical regions.

Teak requires relatively warm-moist climatic conditions with a marked dry season of 3 to 5 months for growth and development. Within its distribution range, annual rainfall is between 1,270 and 3,800 mm.; and the average minimum and maximum temperatures throughout the year are 13^{o} and 40^{o} C, respectively. Experiments reported in Chapters 5 and 6 in this study show that teak seedlings require relatively warm temperatures (about $30/25^{o}$ C day/night temperature) and a high soil water content for maximum growth and development. These data on temperature for teak seedling growth are in agreement with KoKoGyi (1972) and Kanchanaburangura (1976).

Soil conditions appear also to be an important factor controlling growth and distribution of teak. In general, teak grows best and reaches its largest dimensions on soil derived from igneous rocks and river alluvia formed from these rocks. It has been suggested that relatively high amounts of exchangeable calcium and phosphorus in the soils derived from these rocks are responsible for this (Kulkarni, 1951; Bhatia, 1954; Puri, 1960). In addition to the amounts of these two major elements, soil acidity appears to play a significant role in controlling growth and distribution of the species. The optimum pH value of the soils which favour growth of teak is between 6.5 - 7.5 (Kulkarni, 1951; Bhatia, 1954). In areas where the soils are derived from conglomerate rocks or from sandstone, and the soil pH values are outside this range, the species may be absent or stunted.

Seedlings of teak in the forest are often burnt back and their aerial parts killed by severe fire during the hot-dry season. However, their buried parts normally survive and will produce new shoots in the following rainy season. It has been recorded that in some places it take about 7 to 29 years from the time of germination for the teak seedling to develop underground parts which will enable it to produce fire resistant shoots within one growing season before the fire season occurs (Kittinanda, 1963; Sono, 1964).

Stump planting is the most reliable and commonly used method in teak plantation establishment. In general, the planting stump of teak is prepared by root-shoot cutting of the 1- or 2-year-old nursery grown seedling. The optimum size of the teak planting stump for the production of sprouts with high survival and growth potential is about 1 to 2 cm in diameter at the collar level, and about 15 to 20 cm in length. Under favourable conditions for growth, the planted stump will produce sprouts within a week after out-planting, and the biggest sprout on the stump will eventually dominate the smaller sprouts and produce a vigorous erect shoot.

9.1.2 Physiological Bases of Teak Stump Sprouting :

It has been shown in Chapter 2 that there are many possible factors contributing to the sprouting ability of teak stumps ; the four main factors are :

a. the ability of stumps to form buds;

b. the presence of plant hormones which regulate the development of buds into sprouts;

c. stored reserves which enable sprouts to expand; and

d. environmental conditions which favour sprout growth.

Factors (a) and (d) seem to be of lesser importance on the control of teak stump sprouting in forest plantation establishment. Factors (b) and (c) are considered to play a more significant role in influencing the ability of teak stump sprouting, and these two factors and their effects were intensively examined in this study.

A. The role of plant growth hormones in teak stump sprouting :

The role of plant growth hormones in plant sprouting has been long recognized (Snow, 1925). Three main groups of plant growth hormones appear to be involved, that is, the auxins, cytokinins and gibberellins. Auxins which are substances produced in an actively growing shoot apex and transported basipetally along the stem are known to have a significant inhibitory effect on stump sprouting. Following on exogenous application of an auxin such as IBA or IAA to the cut surface of stumps, an inhibition of stump sprouting often results. With respect to teak, the study reported in Chapter 8 showed an inhibitory effect of IBA on stump sprouting. There was a negative relationship between the concentration of the IBA applied exogenously to the cut surface of the teak stump and its sprouting ability. Both the percentage of sprouting stumps and the sprouting vigor decreased progressively with an increase in the concentration of the IBA in this way. Moreover, the IBA, at a relatively high concentration of 1 %, appeared to be toxic to teak stumps, because no stump treated with IBA at this concentration sprouted, and at the end of the experiment some of these stumps died (Section 8.1).

In contrast to auxins, cytokinins produced in the roots are known to act as antagonists of auxins in the inhibition of plant sprouting. In other words, cytokinins play a significant role in the release of lateral buds from correlative inhibition or from apical dominance in the intact plants, this probably increasing the sprouting ability of plant stumps (Sachs and Thimann, 1967; Phillips, 1969a, 1975; Woolley and Wareing, 1972a,b,c). But the released buds still require the presence of auxins and gibberellins for their growth and development (Sachs and Thimann, 1967; Phillips, 1969a, 1975). In an experiment reported in Chapter 8, an exogenous application of the cytokinin-like BAP was made at 1 % concentration to the cut surface of teak stumps, but this failed to stimulate stump sprouting. There was no difference between treated and control stumps in the percentage of stump sprouting or in sprout vigor. This clearly suggests that under normal conditions the amount of the endogenous cytokinins in the teak stump is likely to be sufficient for stump sprouting. Moreover, the application of the BAP at 1 % concentration did not affect the subsequent growth and development of the stump sprouts as compared with the control, a finding consistent with results reported by Sachs and Thimann (1967), Shein and Jackson (1971), Smith (1975) and many others. The physiological mechanism of the cytokinins in releasing lateral buds from inhibition, particularly where the inhibition is associated with the action of auxins or apical dominance is discussed in the work of Woolley and Wareing, 1972a,b,c; and Skene, 1975.

Unlike cytokinins, gibberellins (root-shoot produced substances) are known to stimulate the elongation of stem internodes or the height growth of plants, and also to increase the potential for stump sprouting when applied to the cut surface of stumps (Nakamura, 1965; Bachelard, 1969b; Phillips, 1969b; Vogt and Cox, 1970; Shien and Jackson, 1971). But when these substances are applied alone to the shoot of the intact plants or applied together with auxins to the cut surface of plant stumps, inhibition of plant sprouting often results (Nakamura, 1965; Jacobs and Case, 1965; Scott et al, 1967; Smith, 1975). However, a number of workers have shown that the effect of gibberellins in inhibiting stump sprouting, when applied in combination with auxins, varied significantly with the growing conditions and the stage of development of the plants. In some cases an application of gibberellins caused a marked reduction in the inhibitory effect of auxins on stump sprouting (Kato, 1958; Phillips, 1969b, 1971a,b; Ali and Fletcher, 1970). In the present study it is shown that an exogenous application of the gibberellin-like GA_3 to the cut surface of the teak stump caused a marked increase in stump sprouting. Moreover, GA_3 also stimulated the expansion of stump sprouts, resulting in the production of relatively tall sprouts (Section 8.1). A similar effect of GA_3 on the elongation of internodes has been reported with several plants (Nakamura, 1965; Bachelard, 1969b; Vogt and Cox, 1970; Shein and

Jackson, 1971; and many others). Bachelard (1969b), for example, reported that the major response of <u>Eucalyptus camaldulensis</u> seedlings and stump sprouts to GA_3 is an increase in transverse cell divisions, which are important in internode elongation growth of the plants. Likewise, the change in the balance of storage materials in the seed caused by the action of GA_3 has been suggested as one of the most important physiological mechanism by which the germination of the seed is stimulated (Paleg, 1960; Mayer and Poljakoff, 1975). With respect to teak stump sprouting, the stimulatory effect of GA_3 on the stump sprouting may be similar to that on the germination of the seed. That is, the exogenous application of GA_3 to the cut surface of the teak stump may stimulate the activities of some hydrolytic enzymes (or may stimulate the enzyme synthesis), resulting in a greater capacity for mobilizing of stored reserves, and a greater availability of assimilable substrates for utilization in stump sprouting. The excess applied-GA_3 may stimulate cell division and cell enlargement or elongation in the meristem of sprouts, as reported by Bachelard (1969b) for eucalypt stump sprouts, resulting in an increase in internode elongation or height growth of the sprout produced. More research dealing with the stimulatory effects of GA_3 on the change of the balance of stored reserves in the teak stump and on cell division and cell elongation of the sprout produced is required to help understand the sprouting phenomenon of the teak stump.

Although the above evidence suggests significant roles for both the auxin-like IBA and the gibberellin-like GA_3 in controlling the sprouting of teak stumps; it is apparent that the sprouting mechanism in this species cannot be explained simply by single direct effects of these substances. For example, while stumps treated with GA_3 at a 1 % concentration produced more and taller sprouts than stumps treated with lanolin (the control) and with the BAP at a 1 % concentration, the sprouts appeared to be abnormal in their growth and development. These sprouts were thin and tall and had long narrow and chloritic leaves (Plate 8.1b). The stem and leaf tissue of the sprouts produced by these GA_3-treated stumps was also soft and succulent. These findings suggest the loss of "balance" among the hormones both in the sprout produced and in the stumps. Similar responses of plant sprouting to the action of the gibberellin-like substances at a relatively high concentration have been reported by Woolley and Wareing (1972b) with *Solanum andigena* stem cuttings and Schier (1973) with aspen root cuttings.

In the present study an exogenous application of a combination of IBA, BAP and GA_3 at 1 % concentration also failed to improve the sprouting ability of the teak stump. Instead, the combinations of substances had a marked inhibitory effect on sprouting (Section 8.1). This suggests that the sprouting mechanism of the teak stump in relation to plant hormones is complex, probably depending upon the balance among these hormones in the stumps. More research is required to determine more precisely the role of specific growth hormones, and interaction among them on the ability of teak stump sprouting.

B. The role of stored reserves in teak stump sprouting :

The early stages of shoot expansion during spring growth, especially in deciduous tree species, must depend largely on the stored reserves accumulated during the previous season. Similarly, recovery of plants following the physiological damage such as cutting, stumping, girdling and severe defoliation would be expected to be dependent largely on the stored reserves in the remaining parts of the plants (Woods et al, 1959; Parker and Houston, 1971; Wargo, 1972; Wargo et al, 1972; Parker, 1974; Parker and Patton, 1975). For example, in a study of the effects of defoliation, girdling and cutting of sugar maple trees (Acer saccharum) on root starch and sugar levels, Parker (1974) showed that stored starch in the roots of these treated trees was substantially depleted 4 weeks after treatment, especially in the defoliated trees. Similarly, Wargo et al (1972) reported that refoliation following defoliation of sugar maple trees caused a severe depletion of the stored starch in the root system of treated trees. Other studies have similarly shown that cutting or defoliation of the plants causes a depletion of the stored reserves of the roots as a result of their utilization by the new growth which follows (see for example in Priestley, 1962,1970; Kozlowski and Keller, 1966; Kozlowski, 1971a).

Several attempts have been made to determine the effects of cutting, girdling and defoliation on changes in the balance of stored reserves in the remaining organs of the plants (especially in the root system). An artificial defoliation of sugar maple trees was found to cause a mobilization of the stored starch to labile sugars in the roots, that is defoliation caused a decrease in the stored starch accompanied by an increase in reducing sugars such as glucose and fructose (Parker and Houston, 1971; Wargo,1972). The mobilization of the stored starch to labile sugars in the lower stem and roots of the treated trees following defoliation or interuption of stem translocation may be a result of the change of the balance of a number of complex hormones, causing an increase in the activities of some hydrolytic enzymes which convert the stored starch to sugars, enabling plants to utilize the sugars in sprouting (Kozlowski, 1971b; Parker and Houston, 1971; Parker, 1974).

With respect to teak stump sprouting, the early stages of stump sprouting including the formation of buds, the expansion and elongation of sprouts and the regeneration of the lateral roots, would be expected to depend primarily on the stored reserves in stumps. Later, when the newly expanded leaves of the sprouts are actively photosynthetic and are able to supply photosynthetic products for growth of subtending internodes and other tissues, the subsequent growth and development of sprouts would be independent of the stored reserves. Several investigations on the spring growth of deciduous trees in relation to the utilization of the stored reserves have shown that the first growth flush of the season utilizes the stored reserves, but new shoots soon begin to utilize current photosynthetic products for growth (see for example in Priestley, 1962; Kozlowski and Keller, 1966; and Kozlowski, 1971a). In the present study, the relationship between sprout production and stored reserves (especially the stored carbohydrates) may be discussed in terms of both

a. the amount of stored reserves

and b. the mobilization or utilization of the stored reserves.

Evidence provided in Chapters 5 and 6 demonstrates

a. there was no positive correlation between the amount

(or the concentration) of the stored carbohydrates in the planted stumps and the vigor of sprouts produced,

and b. there was no positive correlation between the size of stumps and the vigor of sprouts produced.

This clearly suggests that the production of sprouts and their subsequent growth was not limited by the amount of the stored carbohydrates in the stump. In a study of the effect of stump size on the field performance of teak stumps, Nwoboshi (1976) showed that stump sprouting, as determined by the number of sprouting stumps and sprout growth, decreased markedly with increasing size of stumps from >1 to 3 cm collar diameter. Since all stumps in his experiment were prepared from the same batch of seedlings, it may be assumed that the bigger stumps would contain more stored reserves than the smaller stumps. Nwoboshi's results, therefore, support the finding of the present study, that is, the amount of stored reserves in teak stumps is not likely to be the most important factor governing the sprouting potential of those stumps. Similar findings have been reported with a number of other plant species (Wenger, 1953; Priestley, 1964; Cremer, 1973). Priestley (1964), for example, compared the sprouting ability of young apple planting stock girdled at different stem levels before cutting and re-planting. This was done to prevent the autumn accumulation of carbohydrates in the lower stem of the planting stock. There was no significant treatment effect on the sprouting ability of the planting stock, and the amount of carbohydrate supply did not appear to be the main factor limiting growth and development of the sprouts produced in this species. The same author also demonstrated that only about one-third of the stored carbohydrates was utilized in the shoot growth of apple trees (Priestley, 1962). It is stated by Kozlowski (1969,1971a) that growth and development of tree shoots appear to be limited more by the lack of regulatory compounds which influence the rate of mobilization and conversion of foods to new tissues, rather than soely by a lack of foods. In other words, the supply of foods for shoot growth and development in trees is often adequate, but shoot growth is still inhibited because utilization of foods is controlled by other internal regulatory mechanisms.

As discussed above, the production of sprouts in teak stumps is likely to depend largely on the stored reserves. The amount of the stored reserves, however, does not appear to be the most important factor limiting the subsequent growth and development of the sprouts. What appears to be of greater importance is the stump capacity for mobilizing and utilizing stored reserves for the production and subsequent growth of stump sprouts. It is well known that the first stage in the utilization of stored reserves for plant growth or seed germination is the process of hydrolysis or mobilization of those reserves. In this process, the stored reserves are converted into assimilable and easily translocated substrates by the activities of some hydrolytic enzymes such as amylases, proteinases and lipases. The mobilization of the stored reserves, especially the stored starch, into assimilable substrates, or an increase in the activities of hydrolytic enzymes has been found to be stimulated by many factors. These include a rapid reduction of growing temperature (Siminovich et al, 1953; Parker, 1962; Sakai, 1966; Marvin and Morselli, 1971; Levitt, 1972), effects of water stress

(Spoehr and Malner, 1939; Eaton and Ergle, 1948; Iljin, 1957; Vaadia et al, 1961; Maranville and Paulsen, 1970; Stewart, 1971; Levitt, 1972), and a change in the balance of plant hormones. The balance of plant hormones may be altered due to a reduction of the sources of the shoot-produced hormones through defoliation, girdling and cutting (Parker and Houston, 1971; Parker, 1974), or by an exogenous application of plant hormones such as the gibberellin-like GA_3 (Paleg, 1960; Bachelard, 1969b; Cleland, 1969; Mayer and Pojakoff, 1975). Under favourable conditions for growth, plants which have a high capability for mobilizing and and utilizing their stored reserves often exhibit a high sprouting and growth potential of the sprouts produced. (Kozlowski, 1971 a).

From the present study, the following evidence supports the above concept in that :

a. An abrupt reduction of growing temperature from $30/25^0$ to $18/13^0$ C (for 4 weeks) caused a marked increase in the sugar level in the teak seedling tap-root, and this was associated with an increase in sprouting potential after stump-replanting.

b. Dry storage of stumps of seedlings subjected to cool temperature treatment ($18/13^0$ C) stimulated the hydrolysis of the stored starch into labile sugars in the stumps and also promoted the sprouting potential of these stored stumps.

c. The exogenous application of GA_3 to the cut surface of the teak planting stump stimulated the sprouting of the stump, and it has been suggested this was due partly to the break-down of the starch into sugars induced by the action of GA_3.

From the above evidence it may be inferred that any factor stimulating the mobilization of the stored starch into labile sugars has a significant effect on the promotion of teak stump sprouting. In other words, teak stump sprouting and the subsequent growth and development of sprouts may be largely governed by the potential for mobilizing and utilizing of stored reserves. Any factor increasing that potential may result in relatively greater stump sprouting.

9.1.3 Physiological Implications in Field Studies :

Teak is a deciduous tree species and occurs in the tropical regions where the climate is seasonal. The tree usually starts to shed its leaves towards the end of the cool season (about the end of January) and remains leafless throughout the hot-dry season (March-April) or until the break of the monsoon rains (about the end of April). Bud-break and leaf/shoot flushing occur fairly quickly thereafter.

In forest plantation establishment, teak-stump planting is usually started at the beginning of the rainy season (May-June), so that the teak seedling which is lifted for stumping and planting is at an actively growing stage; indeed, it may be at or even beyond the spring growth flush stage. Many changes in the physiological balance in the teak seedling would be expected during this period. For example, a large amount of stored reserve, especially that in the main storage organ, the tap-root, would be utilized for growth during the spring flush. The amount and rate of mobilization of these stored reserves would then decline as the new leaves expanded and were able to produce new products of photosynthesis for the growth of other tissues or even for accumulation. The balance of plant growth hormones in the teak seedling stump may also change as a result of the spring growth; probably the level of auxin raises due to an increase in the source of auxin production in the seedling shoot.

With regard to the sprouting potential of the teak planting stump, the field studies have clearly demonstrated the influence of lifting date of the planting stump (or the stage of phenological development of the seedling at the time of lifting) on the field survival of the stump and its subsequent height growth. It has been shown that when planted at the same time or the same site, the performance of stumps lifted between mid-October and mid-April (i.e. between the end of seedling shoot expansion and the beginning of bud-break period) was at least as great as, or significantly better than that of stumps lifted in June-July (i.e. during or after the period of spring flush growth). In these studies, stumps lifted between mid-October and mid-April had been kept in an underground store until the time of planting. Among the stored stumps, it is evident that the sprouting potential of the stumps increased progressively with lifting date, that is, from mid-October to mid-March and mid-April (Figure 3.9). In other words, the sprouting potential of the teak stump is relatively greater when the parent seedling is between the leaffall and early bud-break stage. Explanations of these phenomena were sought in controlled environment studies.

The studies reported in Chater 5 demonstrate the influence of growing temperature on the growth and development of the teak seedling, the subsequent sprouting potential of the teak stump and the accumulation of carbohydrate reserves in the seedling tap-root. It has been shown that a reduction of growing temperature from $30/25^{0}$ to $18/13^{0}$ C for about 4 weeks caused a marked reduction in growth of the seedling. However, following the cool temperature treatment, the sprouting potential of the stump, when returned to warm ($30/25^{0}$C) conditions, was markedly greater than that of seedlings and stumps grown continuously at $30/25^{0}$ C. This seems to correlate with the field observations where stumps of seedlings whose growth had been resticted by low temperature, had a greater sprouting potential than those of the stumps of actively growing seedlings. Under controlled conditions, storage of stumps of cool treated-seedlings did not reduce their sprouting potential after replanting under warm conditions. Instead, this storage treatment seemed to stimulate the growth of sprouts produced by these stored stumps. Alternatively, storage of stumps of the actively growing seedlings (i.e. seedlings grown at $30/25^{0}$C) caused a marked reduction in sprouting, that is, both the survival and sprouting of these stored stumps were very poor compared with those of the unstored stumps. This suggests that storage of teak stumps might be satisfactory only where the parent seedling is at a restricted growth or dormant stage. This finding again correlates with the field observations, where stumps lifted during the cool season (i.e. during the period of leaf-brown and leaf-fall) could be stored until the time of planting in the following rainy season without deterioration in their sprouting potential.

The studies reported in Chapter 6 demonstrate the influence of soil moisture availability on growth and development of the teak seedling, the sprouting potential of the seedling following stump-replanting and the accumulation of carbohydrate reserves in various parts of the seedling. It has been shown that severe droughting caused a marked reduction in growth of the teak seedling but did not affect the stump sprouting under favourable conditions. In contrast, moderate droughting caused a marked reduction in both seedling growth and the sprouting of the stump. It has been shown that there were no significant differences between the moderate and severe soil moisture treatments in the amount and rate of export of photosynthates from the shoot to the root, and the concentration of carbohydrates in the root system, especially in the tap-root. At this stage of our understanding of the physiology of the teak seedling stump it is not possible to interpret these differences in stump sprouting. Again, while it has been shown that droughting increases sugar concentration in teak seedlings, especially in leaves and lateral roots, it is not possible to correlate directly the results of the controlled droughting study and the effect of the hot-dry period in normal nursery operations. This is suggested because the condition of seedlings grown under periodic soil moisture stress (Chapter 6) was different from that of seedlings grown in the field during the hot-dry season (March-April). For example, the field grown seedling was fully dormant and remained leafless during this season, whereas seedlings grown under the controlled droughting were still functional, especially in processes of photosynthesis and translocation of photosynthates from shoots to root systems.

From the above evidence, it can be provisionally suggested that the growing temperature rather than the availability of soil moisture might be the most significant influence on the sprouting potential and the success of storage of the teak planting stump. Cooling of the teak seedling prior to stumping, somehow, increases the ability of the stump to produce sprouts and to survive to storage without deterioration. It might be inferred from the controlled environment studies that as the growing temperature declines during October to January, the following changes will be taking place in the nursery seedling :

a. reduction in net assimilation rate (NAR), photosynthesis, respiration, and hence the growth and development of the seedling;

b. an increase in the Photosynthesis : Respiration ratio value;

c. possibly a slowing down of the translocation of photosynthetic products from the shoot to the root system during the initial stage of cooling;

d. the export of a relatively large amount of the products of photosynthesis and its accumulation in the tap-root as the cooling process continues;

e. as a result a substantial increase in the starch and sugars levels of the tap-root by the end of the coolest period.

Thus a cooling temperature condition could be favouring translocation and accumulation of carbohydrate reserves as growth of the seedling slowed down, and eventually ceases, and leaf senescence takes place.

It has been suggested that the increase in sugar level in the seedling tap-root under cool temperature conditions might be due partly to an increase in the activity of some hydrolytic enzymes which convert the stored starch into labile sugars. The process of conversion of the stored starch into sugars in the tap-root continues even when the seedling is stumped and stored. This suggests that there may be no mechanism for"switching off" the conversion of starch to sugars in the teak stump, that is, enzyme activity, once induced, may continue to increase until the stored starch has been depleted from the storage cells, or until some other inhibitory factors affecting the enzyme activity are involved. Similarly, in the controlled droughting study it has been shown that droughting increased the sugar levels in the teak seedling, especially in the leaves and lateral roots, and this may be due to an increase in the activity of some hydrolytic enzymes induced by droughting. In other words, droughting does not limit the activity of hydrolytic enzymes or the conversion of stored starch into labile sugars. More studies on the influences of temperature and soil moisture on the conversion of starch into sugars or on the activity of hydrolytic enzymes in the teak seedling tap-roots are required. In extrapolating these findings in the field situation, it can be suggested that the conversion of the stored starch in the seedling tap-root into labile sugars is "switched on" during the cool season (November-February). This conversion process would be expected to continue and is possibly stimulated throughout the hot-dry season (March-April), providing the labile sugars for the sprouting and growth flushing of the seedling at the end of the hot-dry season or the beginning of the rainy season. Hence, stumps lifted following the coolest month (January) or during the hot-dry season (March-April) might contain a relatively high activity of the hydrolytic enzymes converting the stored starch into labile sugars. The success of stump storage and the relatively high sprouting potential of stored stumps may be related to the initiation of these processes.

The hormonal factor would also be expected to have a significant effect on the sprouting potential of the field-planted teak stumps. As shown earlier, the auxin-like IBA has a strong inhibitory effect on the sprouting of the teak stump (Chapter 8). This group of substances (auxins) is known to be produced in the actively growing shoot and transported downward along the plant stem, resulting in an inhibition of the lateral bud growth. In the field, it might be expected that stumps lifted between the period of leaf-fall and early bud-break (January-April) would contain auxins at a relatively lower concentration than those lifted after the spring flush growth or during the actively growing period of the seedling (May-July). The lower auxin level may contribute to the greater sprouting potential obtained for the former group of stumps than the latter or the "routine" stumps.

9.2 CONCLUSION

The field studies have clearly shown the important influence of lifting time on the sprouting potential of the teak planting stump, both in terms of survival and growth of the sprouts. Stumps lifted after the coolest month (January) and throughout the hot-dry months (March-April) have a relatively higher sprouting potential than those lifted during the early months of the rainy season. Results of controlled environment studies have suggested that temperature, and possibly soil moisture availability, play a significant role in controlling the sprouting potential of the teak stump. A reduction of growing temperature from optimum to cool temperature,and soil moisture supply changes some physiological processes in the seedling, resulting in an increased sprouting potential following stump-replanting. From the results of the controlled environment studies, it has been implied that climatic conditions during the cool season are primarily responsible for the developing condition within the plant which enhance its subsequent stump sprouting potential. In addition, the climatic conditions during the hot-dry season may further improve this sprouting potential. Since the favourable time for teak planting (mid-May) and the optimum time for lifting and stumping of the teak seedling (mid-January - mid-April) do not coincide, the teak planting stumps may be lifted and kept in a suitable dry underground store for some period until the time of planting.

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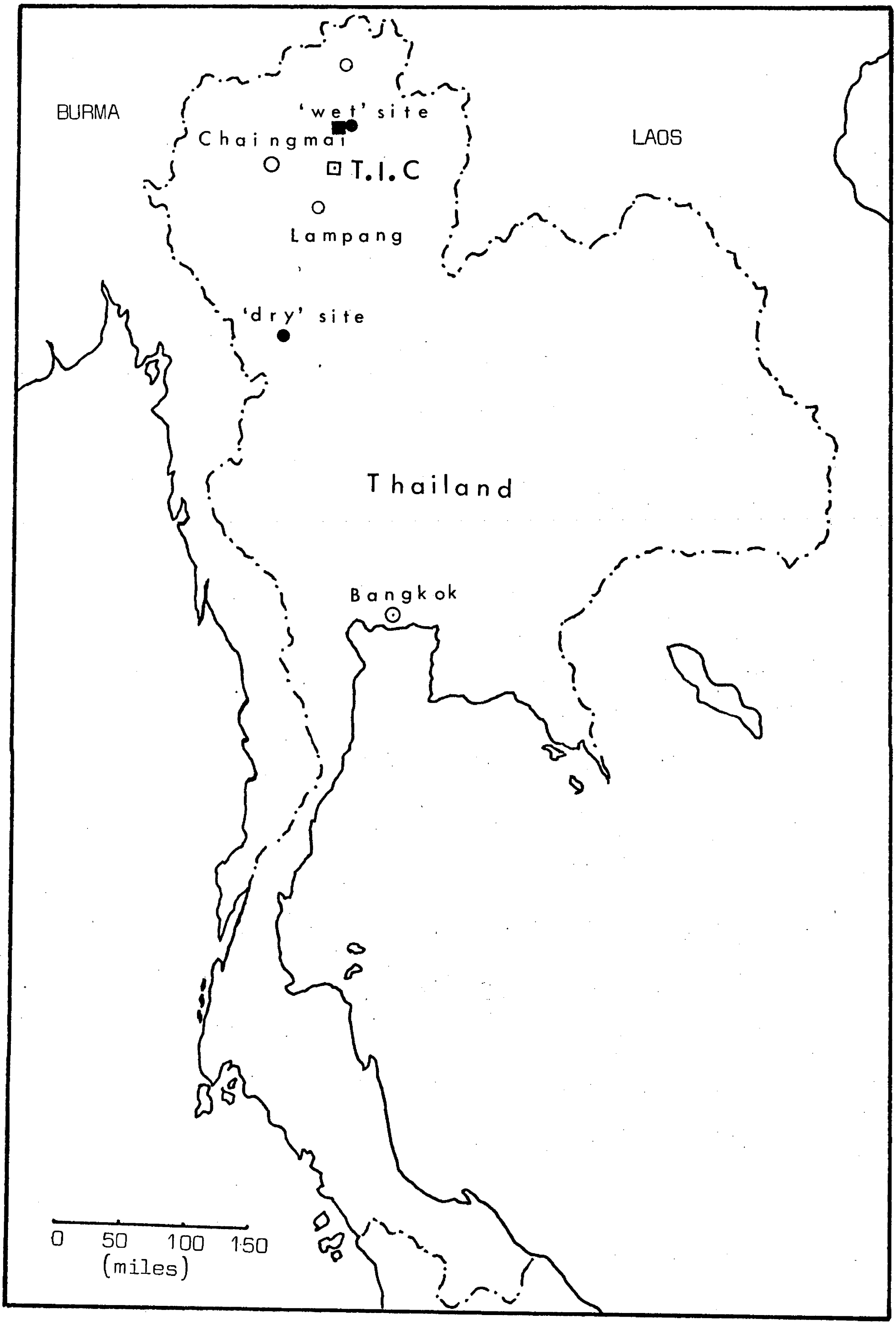
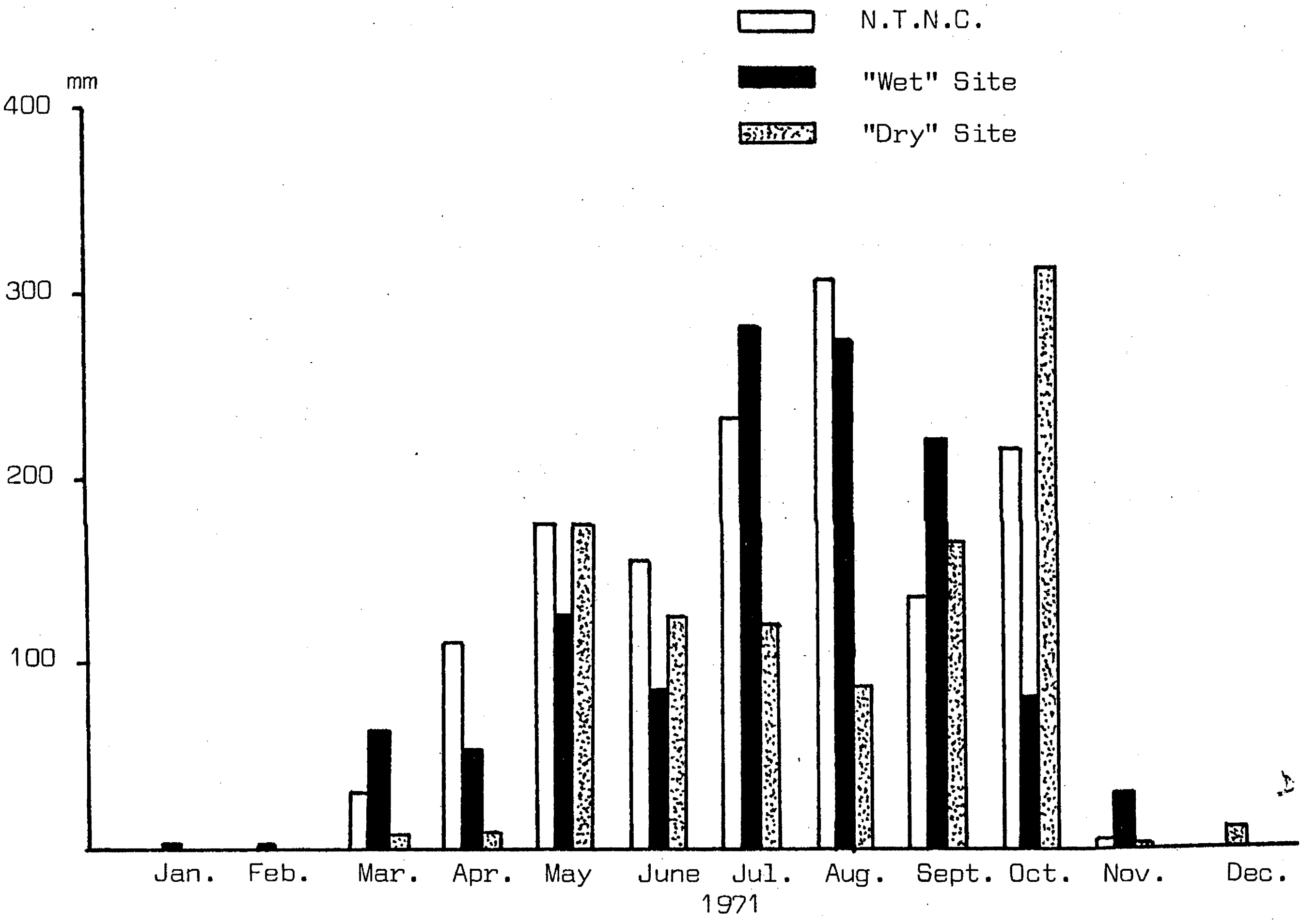
APPENDIX 1

Locations of Field Study



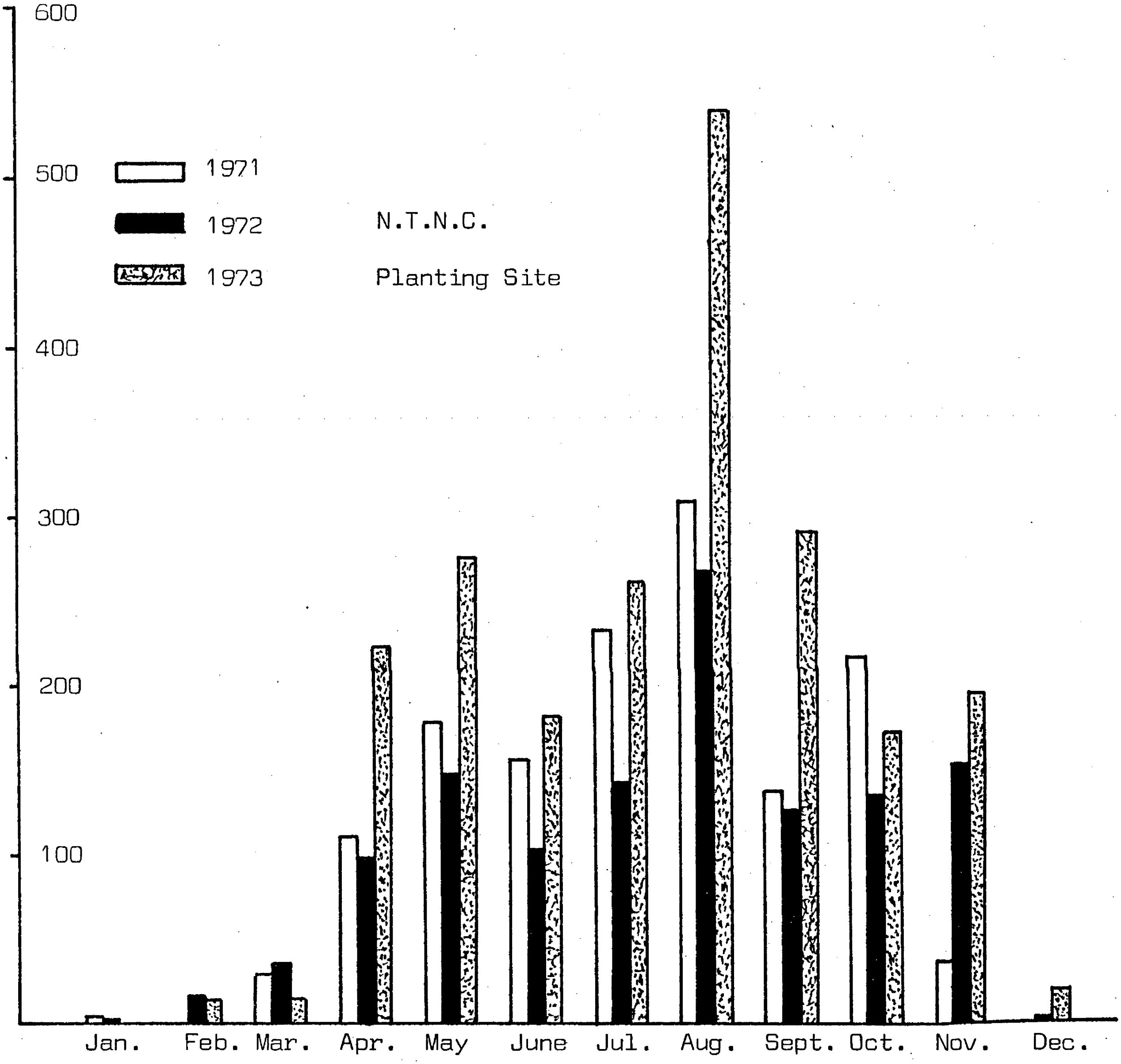
APPENDIX 2a (Study 1)

Monthly Rainfall



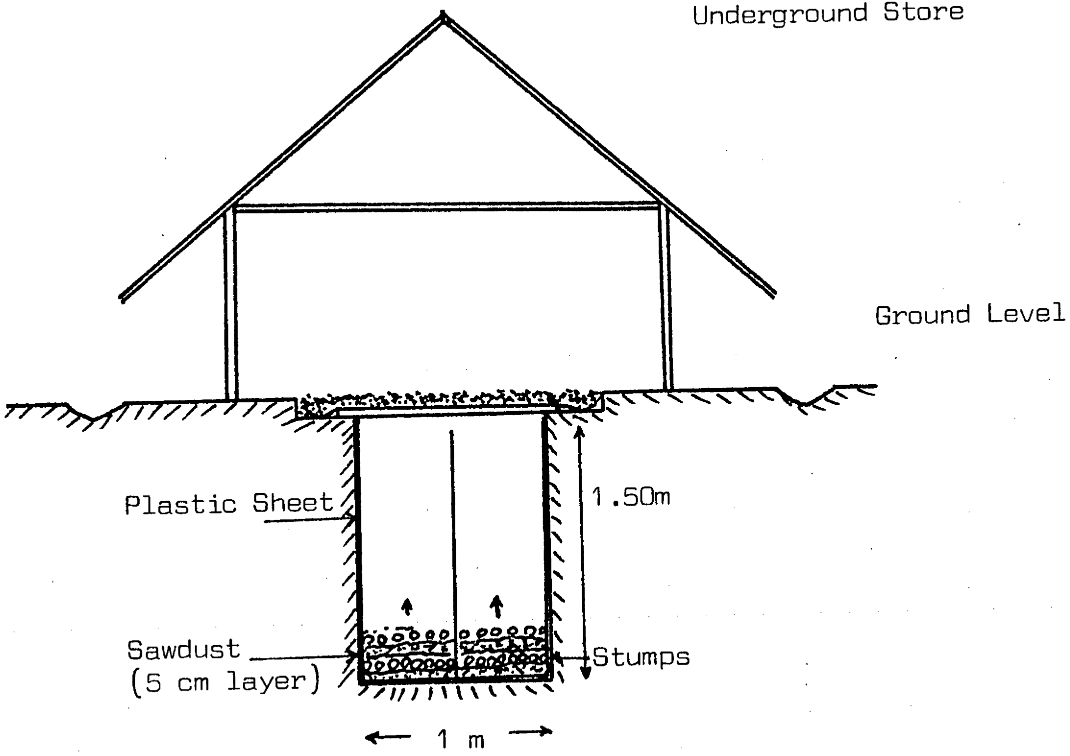
APPENDIX 2b (Study 2)

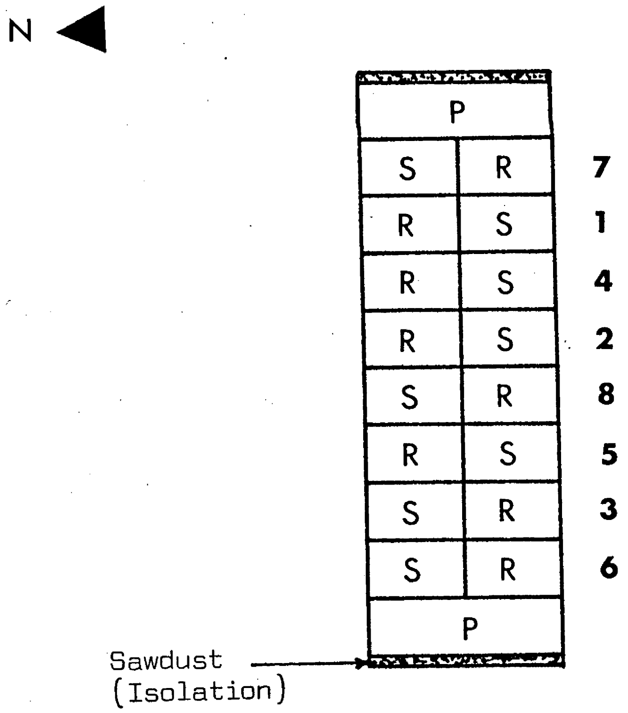
Monthly Rainfall



APPENDIX 3

(a) Cross Section of an Underground Store





P		
S	R	7
R	S	1
R	S	4
R	S	2
S	R	8
R	S	5
S	R	3
S	R	6
P		

Storage Medium

P = Plastic Wraps

S = Sawdust

R = Rice husk

Lifting/Storing Date (1971)

1 = Jan 18
2 = Feb 2
3 = Feb 17
4 = Mar 4
5 = Mar 19
6 = Apr 3
7 = Apr 19
8 = May 3

(b) Storing Layout

APPENDIX 4a

Experimental Layout
(Split-Plot Design)
"Wet" Site

Block 3

S	6	4	2	5	R	3	7	1	8
P	7	R	4	3	8	6	2	1	5
R	5	8	4	R	1	3	6	7	2

Block 5

4	2	7	1	5	8	R	6	3	**R**
2	8	5	7	R	3	4	1	6	**S**
8	4	3	6	1	5	R	7	2	**P**

Block 2

P	R	6	4	8	5	2	3	7	1
R	7	R	6	5	2	1	3	8	4
S	2	5	8	7	3	1	4	6	R

Block 1

8	4	5	7	3	1	6	2	R	**S**
6	5	3	7	4	2	8	R	1	**R**
8	4	7	5	3	1	R	6	2	**P**

7	5	2	8	R	1	3	4	6	**R**
8	R	3	4	2	5	6	1	7	**P**
1	6	8	7	R	4	2	5	3	**S**

Block 4

Lifting Date (1971)

R = Routine stumps

1 = Jan 18
2 = Feb 2
3 = Feb 17
4 = Mar 4
5 = Mar 19
6 = Apr 3
7 = Apr 19
8 = May 3

Storage Medium

S = Sawdust

R = Rice husk

P = Plastic wraps

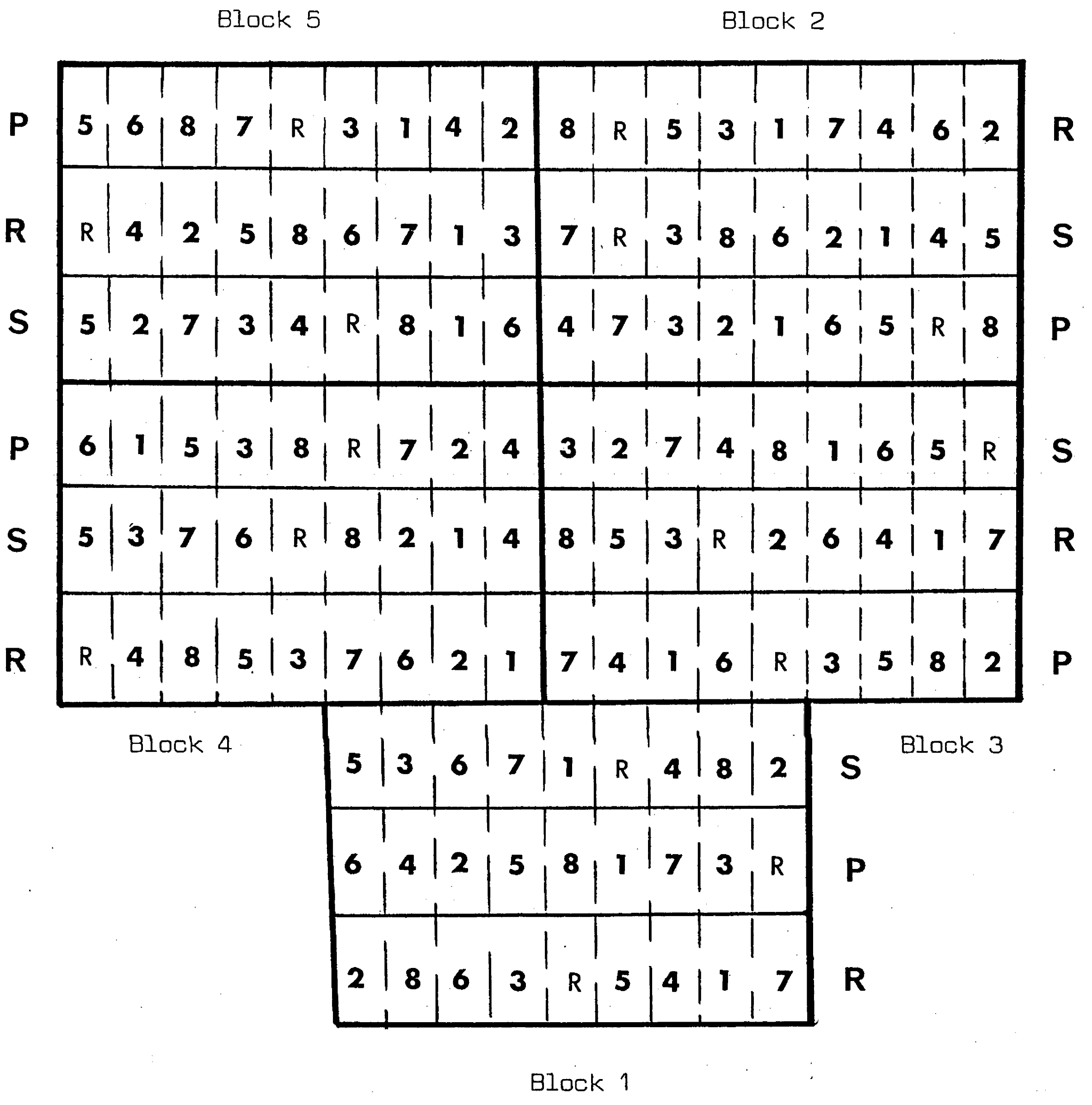
Planting date = June 15

Planting Espacement = 1 x 1 m

Number of stumps in each sub-plot = 8

APPENDIX 4b

Experimenta Layout
(Split-Plot Design)
"Dry" Site



Block 5

P	5	6	8	7	R	3	1	4	2
R	R	4	2	5	8	6	7	1	3
S	5	2	7	3	4	R	8	1	6

Block 2

8	R	5	3	1	7	4	6	2	R
7	R	3	8	6	2	1	4	5	S
4	7	3	2	1	6	5	R	8	P

Block 4

P	6	1	5	3	8	R	7	2	4
S	5	3	7	6	R	8	2	1	4
R	R	4	8	5	3	7	6	2	1

Block 3

3	2	7	4	8	1	6	5	R	S
8	5	3	R	2	6	4	1	7	R
7	4	1	6	R	3	5	8	2	P

Block 1

5	3	6	7	1	R	4	8	2	S
6	4	2	5	8	1	7	3	R	P
2	8	6	3	R	5	4	1	7	R

Lifting Date (1971)

R = Routine stumps
1 = Jan 18
2 = Feb 2
3 = Feb 17
4 = Mar 4
5 = Mar 19
6 = Apr 3
7 = Apr 19
8 = May 3

Storage Medium

S = Sawdust
R = Rice husk
P = Plastic wraps

Planting date = June 15 Planting espacement = 1 x 1 m

Number of stumps in each sub-plot = 8

APPENDIX 5

Storage Layout

(Field Study 2)

Store Layout

1	2	3	4
1	6	6	6
2	5	5	5
3	4	4	4
4	3	3	3
5	2	2	2
6	1	1	1
I	II	III	IV

Planting time

1 27 April 1972

2 22 May 1972

3 15 June 1972

4 11 July 1972

Lifting date

1 15 October 1971

2 15 November 1971

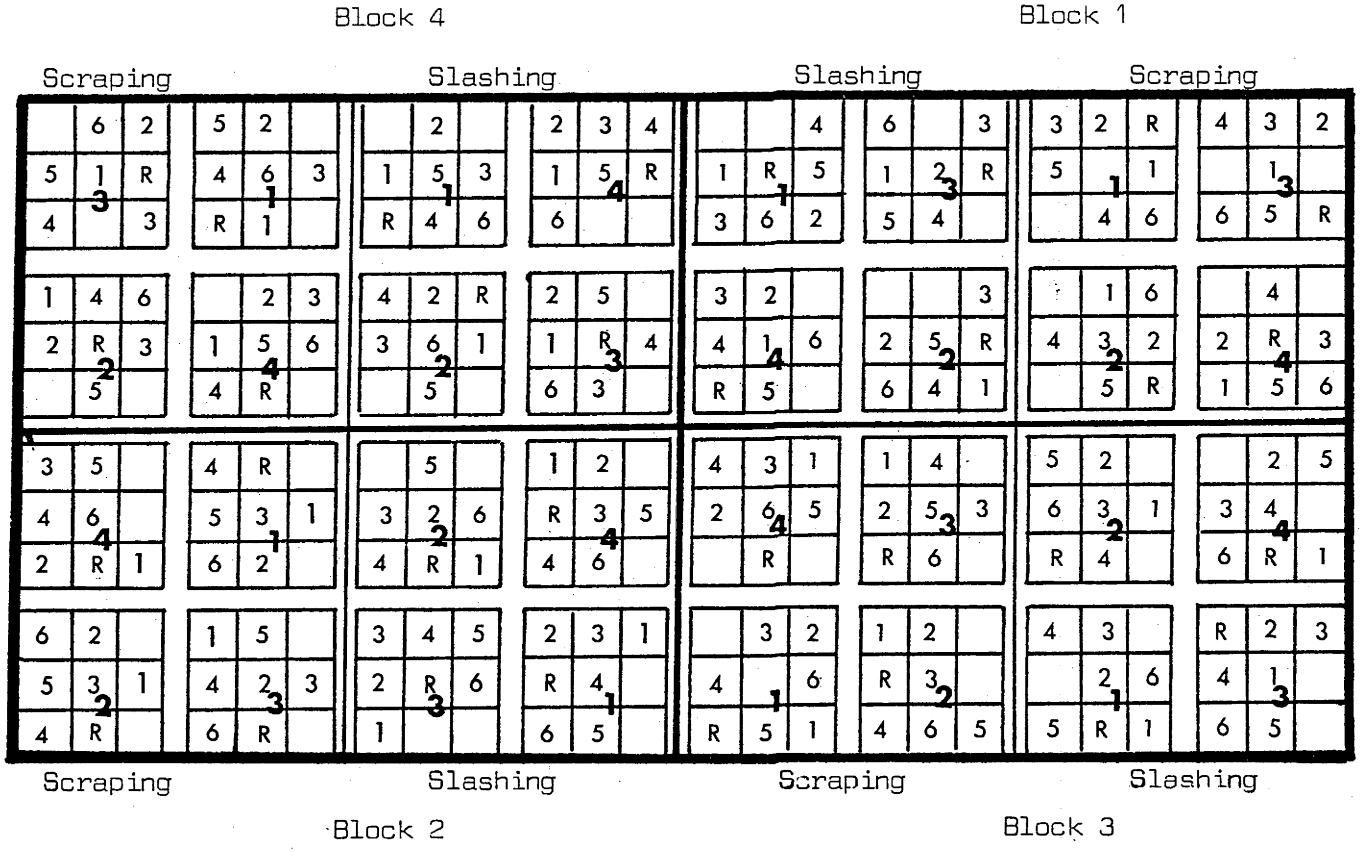
3 15 December 1971

4 15 January 1972

5 15 February 1972

6 15 March 1972

(Split-split plot Design)



<u>Lifting/Storing Date</u>

R = Routine Stumps*
1 = 15 October 1971
2 = 15 November 1971
3 = 15 December 1971
4 = 14 January 1972
5 = 15 February 1972
6 = 15 March 1972

<u>Planting Date</u>

1 = 27 April 1972

2 = 22 May 1972

3 = 15 June 1972

4 = 11 July 1972

APPENDIX 7

Phenological Development Stages of Teak Seedlings at Lifting

(Study I. Date presenting the percentage of leaf and dormant bud in each seedling)

(Study II. Data presenting the percentage of seedling with leaf and bud)

Lifting Date	Leaves Full Size	Leaves Brown	Leaves Fall	Buds Break	Leaves Development	Rainfall (mm)
1971	Study I (Leaf Brown and Fall)					(15 days before lifting)
Jan 18	9		55	23	13	0
Feb 2	11		72	13	4	3
Feb 17	6		84	7	3	1.5
Mar 4	3		90	5	2	0
Mar 19	1		91	6	2	20.5
Apr 3	0		55	40	5	9.5
Apr 19	0		51	43	6	2.1
May 3	0		45	40	15	109.0
1972	Study II					(15 days before lifting)
Oct 15	93	1	1	1	4	207.3
Nov 15	92	1	0	3	4	3.2
Dec 15	0	78	21	1	0	0
Jan 15	0	41	32	27	0	1.6
Feb 14	0	11	45	27	17	0
Mar 15	0	0	24	51	25	0
Routine Stumps						

APPENDIX 8

Experiment 1 (Field Study): Effects of lifting date, storage and storage medium, and planting site on subsequent survival (%) and height growth (cm) of teak planting stumps. (Data represent the mean of 5 blocks or 40 stumps)

Lifting Date (1971)	Storage Period (mongh)	Storage Medium					
		Sawdust		Rice Husk		Plastic Wraps	
		"Wet" Site (Jan 25, 1972)					
		%	cm	%	cm	%	cm
Stored Stumps:							
Jan 18	5.0	80.0	36.6	90.0	36.8	90.0	46.0
Feb 2	4.5	97.5	44.0	97.5	44.7	87.5	53.9
Feb 17	4.0	77.5	39.6	65.0	47.5	90.0	52.1
Mar 4	3.5	87.5	44.3	87.5	44.1	100.0	50.7
Mar 19	3.0	82.5	40.6	90.0	43.8	100.0	44.0
Apr 3	2.5	100.0	41.8	97.5	48.9	90.0	43.0
Apr 19	2.0	95.0	38.8	97.5	41.0	92.5	35.5
May 3	1.5	95.0	33.0	97.5	37.1	92.5	39.8
Routine Stumps:							
June 15	0	90.0	18.3	87.5	22.2	95.0	17.5
		"Dry" Site (Feb 25, 1972)					
		%	cm	%	cm	%	cm
Stored Stumps:							
Jan 18	5.0	62.5	55.4	87.5	68.6	77.5	52.4
Feb 2	4.5	90.0	66.0	87.5	69.0	92.5	60.5
Feb 17	4.0	72.5	48.3	82.5	47.5	75.0	63.0
Mar 4	3.5	95.0	66.7	87.5	64.1	95.0	62.9
Mar 19	3.0	87.5	56.6	80.0	75.8	90.0	41.2
Apr 3	2.5	90.0	54.9	85.0	45.5	82.5	37.3
Apr 19	2.0	90.0	53.3	85.0	51.1	90.0	54.3
May 3	1.5	72.5	41.4	82.5	40.9	82.5	37.0
Routine Stumps:							
June 15	0	47.5	24.9	52.5	20.2	52.5	26.1

APPENDIX 9

Experiment 2 (Field Study): Effects of lifting date, storage, planting time and weeding treatment on subsequent survival (%) and height growth (cm) of teak planting stumps (Data representing the mean of 4 blocks)

"Scrap Weeded" Plot:

Lifting/ Storing Date (1971-1972)	Planting Date (1972)							
	April 27		May 22		June 15		July 11	
	Surv. %	Height cm	Surv. %	Height cm	Surv. %	Height cm	Surv. %	Height cm
Stored Stumps:								
Oct 15	71.8	92.0	79.6	60.0	68.6	40.3	64.0	29.0
Nov 15	39.0	46.0	21.8	41.0	23.4	35.0	18.7	16.8
Dec 15	84.2	71.0	74.9	60.8	85.8	39.7	76.4	40.3
Jan 15	67.1	76.3	88.9	66.5	73.3	46.0	78.0	40.3
Feb 14	87.4	86.5	76.4	67.5	88.9	53.0	64.0	33.0
Mar 15	82.7	60.5	73.3	71.5	81.1	39.3	56.2	39.8
Routine Stumps	65.6	51.3	84.2	48.5	65.5	22.8	84.2	23.8
"Slash Weeded" Plot								
Stored Stumps:								
Oct 15	76.4	21.3	76.4	22.5	68.6	21.0	48.4	12.8
Nov 15	21.8	13.0	20.3	26.3	18.7	19.8	12.5	14.8
Dec 15	74.9	28.3	81.1	33.8	68.6	17.5	70.2	18.8
Jan 15	56.2	21.3	79.6	28.8	71.8	22.3	64.0	19.3
Feb 17	70.2	26.5	76.4	56.3	68.6	17.5	64.0	19.0
Mar 15	74.9	22.3	76.4	38.0	76.4	19.0	54.6	20.0
Routine Stumps	54.6	18.0	71.8	26.3	39.0	9.0	35.9	6.8

APPENDIX 10

Composition of Nutrient Solution

Nutrient solution, is a modified Hoagland solution in which the iron is present as chelate (sequestrene).

Reference : Went, F.H. 1957. The experimental control of plant growth. Chronica Botanica Co., pp.78–79.

The composition is as follows:

1.	$Ca(NO_3)_2.4H_2O$	95 gm/100 L.
2.	$(NH_4)H_2PO_4$	6 "
3.	KNO_3	61 "
4.	$MgSO_4.7H_2O$	49 "
5.	H_3BO_3	0.06 gm/100 L.
6.	$MnCl_2.4H_2O$	0.04 "
7.	$ZnSO_4.7H_2O$	0.009 gm/100 L.
8.	$CuSO_4.5H_2O$	0.005 "
9.	$H_2MoO_4.4H_2O$	0.002 "
10.	$Co(NO_3)_2.6H_2O$	0.0025 gm/100 L.
11.	$FeSO_4.7H_2O$	2.49 gm/100 L.
12.	EDTA	3.32 "
13.	NaOH	0.50 "

APPENDIX 11

Bartlett's Test of Homogeneity of Variances of Field Experimental Data (Chapter 3)

A. Effect of storage media on stump survival:

(Study 1, Chapter 3)

Storage medium	numbers of survive stumps I	II	III	IV	V	sum of squares	(s^2) mean square	log s^2
			"wet" site					
Sawdust	65	66	65	64	62	9.2	1.8	0.2648
Rice husk	66	66	69	66	57	82.8	16.6	1.2191
Plastic	70	60	67	70	68	68.0	13.6	1.1335
Total a = 3 treatments, n = 5 blocks							32.0	2.6174
Chi-square (2 df) = 4.3, corrected chi-square = 3.87 ns								
			"dry" site					
Sawdust	57	55	55	59	57	11.2	2.2	0.3502
Rice husk	58	57	60	63	54	45.2	9.0	0.9552
Plastic	62	63	55	60	55	58.0	11.6	1.0645
Total a = 3 treatments, n = 5 blocks,							22.8	2.3709
Chi-square (2df) = 2.5, corrected chi-square = 2.3 ns								

B. Effect of lifting date on stump survival:

(Study 1, Chapter 3)

Lifting date	numbers of survive stumps I	II	III	IV	V	sum of squares	(s^2) mean square	log s^2
Jan. 18	23	21	19	21	20	8.8	1.76	0.2455
Feb. 2	23	21	24	23	22	5.2	1.04	0.0170
Feb. 17	19	20	20	18	16	11.2	2.24	0.3502
Mar. 4	23	22	24	23	18	22.0	4.40	0.6434
Mar. 19	22	22	24	22	19	12.8	2.56	0.4082
Apr. 3	23	23	22	24	23	2.0	0.40	- 0.3979
Apr. 19	24	19	23	24	24	18.8	3.76	0.5752
May 3	23	22	23	22	24	2.8	0.56	- 0.2518
June 15	21	22	22	23	21	2.8	0.56	- 0.2518
Total a = 9 treatments, n = 5 blocks,							17.28	1.3380
Chi-square (8 df) = 11.16, corrected chi-square = 10.24 ns								
			"dry" site					
Jan. 18	20	16	18	21	16	20.8	4.16	0.6191
Feb. 2	22	18	24	24	20	27.2	5.44	0.7356
Feb. 17	16	20	19	18	19	9.2	1.84	0.2648
Mar. 4	22	24	24	21	20	12.8	2.56	0.4082
Mar. 19	23	22	16	24	18	47.2	9.44	0.9750
Apr. 3	21	23	20	19	20	9.2	1.84	0.2648
Apr. 19	23	20	23	21	19	12.8	2.56	0.4082
May 3	21	20	15	20	19	22.0	4.40	0.6434
June 15	7	12	11	14	15	38.8	7.76	0.8899
Total a = 9 treatments, n = 5 blocks,							40.00	5.2090
Chi-square (8 df) = 5.72, corrected chi-square = 5.24 ns								

APPENDIX 11 (Cont'd)

C. Effect of storage medium on height growth of stump sprouts:

(Study 1, Chapter 3)

Storage medium	Total height (cm) I	II	III	IV	V	sum of squares	(s^2) mean square	log s^2
				"wet" site				
Sawdust	292.9	462.0	265.0	355.0	320.7	20943.4	4188.7	3.6221
Rice husk	398.5	450.8	345.0	367.8	268.7	18158.7	3631.7	3.5601
Plastic	427.1	477.2	353.8	362.8	291.9	20377.4	4075.5	3.6102
Total	a = 3 treatments, n = 5 blocks,						11895.9	10.7924

Chi-square (2 df) = 0.02, corrected chi-square = 0.0199 ns

Storage medium	Total height (cm) I	II	III	IV	V	sum of squares	(s^2) mean square	log s^2
				"dry" site				
Sawdust	404.6	446.4	410.1	673.1	400.8	32554.4	6510.9	3.8136
Rice husk	527.3	404.1	384.4	485.3	513.1	16788.8	3357.8	3.5260
Plastic	464.3	404.3	470.2	449.2	405.3	4056.8	811.3	2.9092
Total	a = 3 treatments, n = 5 blocks,						10680.0	10.2488

Chi-square (2 df) = 3.73, corrected ch-square = 3.36 ns

D. Effect of lifting date on height growth of stump sprouts:

(Study 1, Chapter 3)

Lifting date (1971)	Total height (cm) I	II	III	IV	V	sum of squares	(s^2) mean square	log s^2
			"wet" site					
Jan. 18	108.5	161.5	109.7	112.3	105.1	2240.2	448.0	2.6513
Feb. 2	152.6	169.8	132.0	130.6	128.4	1297.8	259.6	2.4142
Feb. 17	141.2	180.5	109.0	139.7	126.0	2796.2	559.2	2.7476
Mar. 4	125.5	150.7	148.9	153.1	106.8	1986.8	397.4	2.5992
Mar. 19	144.9	157.8	107.6	138.6	93.6	2884.3	576.9	2.7611
Apr. 3	136.8	173.2	116.0	128.6	113.6	2305.2	461.0	2.6637
Apr. 19	123.8	157.3	94.8	115.1	85.9	3120.9	624.2	2.7953
May 3	124.4	145.4	95.5	107.3	77.1	2760.4	552.1	2.7420
June 15	60.8	53.1	50.3	60.3	44.6	189.6	37.7	1.5766
Total	a = 9 treatments, n = 5 blocks,						3916.1	22.9510

Chi-square (8 df) = 7.34, corrected chi-square = 6.71 ns

Lifting date (1971)	Total height (cm) I	II	III	IV	V	sum of squares	(s^2) mean square	log s^2
			"dry" site					
Jan. 18	174.7	180.1	136.1	232.3	158.7	5078.8	1015.7	3.0068
Feb. 2	226.8	184.1	185.0	173.8	207.2	1827.6	365.5	2.5629
Feb. 17	154.5	149.4	189.0	163.8	157.0	969.5	193.3	2.2876
Mar. 4	174.5	158.0	158.3	168.6	148.6	410.3	82.1	1.9141
Mar. 19	156.9	171.0	140.8	207.2	192.2	2836.4	567.3	2.7538
Apr. 3	137.4	116.3	120.3	213.2	101.1	7800.6	1560.1	3.1932
Apr. 19	142.0	130.1	185.2	186.5	149.8	2651.1	530.2	2.7245
May 3	152.6	86.7	90.2	128.6	138.1	3458.4	691.7	2.8399
June 15	76.8	79.1	59.7	73.6	66.5	253.8	50.7	1.7056
Total	a = 9 treatments, n = 5 blocks,						5057.2	22.9884

Chi-square (8 df) = 16.20, corrected chi-square = 14.82 ns

E. Effect of planting time on stump survival:

(Study 2, Chapter 3)

Planting date (1972)	numbers of survive stumps I	II	III	IV	sum of squares	(s^2) mean square	log s^2
Apr. 27	161	147	151	135	347.0	86.7	1.9383
May 22	174	152	143	160	518.8	129.7	2.1129
June 15	159	137	136	144	338.0	84.5	1.9269
July 11	137	120	141	99	1098.2	274.7	2.4388
Total	a = 4 treatments, n = 4 blocks,					575.6	8.4169

Chi-square (3 df) = 1.49, corrected chi-square = 1.34 ns

F. Effect of lifting date on stump survival:

(Study 2, Chapter 3)

Lifting date (1971-1972)	numbers of survive stumps I	II	III	IV	sum of squares	(s^2) mean square	log s^2
Oct. 15	89	93	93	80	112.8	28.2	1.4502
Nov. 15	26	24	27	36	84.8	21.2	1.3261
Dec. 15	112	101	102	80	542.8	135.7	2.1326
Jan. 15	106	90	83	92	278.8	69.7	1.8432
Feb. 14	101	100	97	84	185.0	46.2	1.6651
Mar. 15	105	91	90	83	254.8	63.7	1.8041
Routine stumps	92	67	79	83	322.8	80.7	1.9069
Total	a = 7 treatments, n = 4 blocks,					445.4	12.1282

Chi-square (6 df) = 3.44, corrected chi-square = 3.05 ns

G. Effect of planting time on height growth of stump sprouts:

(Study 2, Chapter 3)

Planting date	Total height (cm) I	II	III	IV	sum of squares	(s^2) mean square	log s^2
Apr. 27	608	601	722	605	10350.0	2587.5	3.4129
May 22	585	583	581	841	49931.0	12482.7	4.0963
June 15	326	451	377	454	11506.0	2876.5	3.4589
July 11	326	386	287	337	4986.0	1246.5	3.0957
Total	a = 4 treatments, n = 4 blocks,					19193.2	14.0638

Chi-square (3 df) = 4.56, corrected chi-square = 4.01 ns

H. Effect of lifting date on height growth of stump sprouts:

(Study 2, Chapter 3)

Lifting date (1971-1972)	Total height (cm) I	II	III	IV	sum of squares	(s^2) mean square	log s^2
Oct. 15	288	307	289	311	428.7	107.2	2.0301
Nov. 15	175	238	159	278	9290.0	2302.2	3.3621
Dec. 15	274	348	272	346	5480.0	1370.0	3.1367
Jan. 15	323	291	309	359	2491.0	622.7	2.7943
Feb. 14	292	379	401	365	6688.7	1672.2	3.2233
Mar. 15	298	299	213	331	714.7	178.5	2.2516
Routine stumps	195	159	224	247	4334.7	1083.7	3.0349
Total	a = 7 treatments, n = 4 blocks					7336.5	19.8330

Chi-square (6 df) = 9.05, corrected chi-square = 8.03 ns