

GERMINATION AND GROWTH STUDIES IN
EUPATORIUM ODORATUM FROM THE NEW AND OLD
WORLD TROPICS

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ALEXANDER AYODEJI EDWARDS
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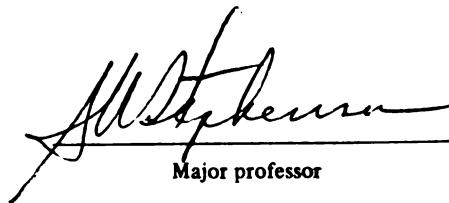


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ABSTRACT

GERMINATION AND GROWTH STUDIES IN EUPATORIUM ODORATUM FROM THE NEW AND OLD WORLD TROPICS

By

Alexander Ayodeji Edwards

Selected characteristics of Eupatorium odoratum L. from seven localities in the New and Old World Tropics were investigated. Germinability, dormancy, leaf area ratio, root weight ratio, relative growth and net assimilation rates were examined under uniformly controlled environmental conditions. The effects of moisture, nitrogen and density on growth were observed among the plants from the seven localities.

Significant differences were found among the plants from different localities in the rates and percentages of germination, and in time to reach maximum germination in response to soaking, moisture stress and light. The inhibitory effect of darkness on germination was reversible in seeds from six areas. Generally, germination occurred readily in the species under the experimental conditions in this investigation.

Variations and differences between plants in total dry weight, total nitrogen, root/shoot ratio, root weight

ratio, and leaf area ratio were found to be significant at all samplings and treatments. The plants also differed in relative growth rate and net assimilation rate. Plants from the Paleotropics were found to have significantly lower leaf area ratio and higher root weight ratio and net assimilation rate than those from the Neotropics.

Differences and variations in the characteristic germination behavior and growth functions among the plants observed in this investigation suggest that these characteristic features may be adaptive in this species. Significant correlation of germination and some growth functions with mean annual precipitation of locality of origin as well as differences in response to moisture stress suggest that plants from the seven localities may be climatic ecotypes.

This study suggests that the ecological success of Eupatorium odoratum as an introduction to the Old World Tropics is in part due to its characteristic ability to germinate readily under various conditions of the environment; also, due to the characteristic efficiency of the root system, or, of the photosynthetic apparatus. It is also possible that its success is due to the plastic nature of the species, or its competitive ability in the absence of predators.

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NEW AND OLD WORLD TROPICS

By

Alexander Ayodeji Edwards

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INTRODUCTION

Plant species found in a diversity of habitats, particularly those species differentiated by regionally expressed and geographically conditioned differences in climate, frequently consist of numerous ecotypes. Ecotypes are derived as a result of genotypical responses and adaptations to particular habitats. Variations occurring within species invading a new habitat may be morphological, physiological or both. The success of a species occurring in habitats other than its center of origin or geographic range may be due to the following: (1) the genotype, (2) ability to find an open niche, (3) lack of predation and (4) competition (Allard, 1965; Baker, 1965, 1967; Harper, 1965; Sakai, 1961, 1965; Stebbins, 1965).

Many plant species that have become abundant or widespread in new or disturbed habitats are usually referred to as weeds. Disturbed habitats may be agricultural, waste places or roadsides. Ecologically, weedy species may be referred to as pioneers in a secondary successional sere. What makes a plant species weedy or non-weedy is a question that has not been fully resolved, however, species that are non-weedy in one habitat may become weedy if introduced into

a new habitat. Weedy species have been shown, in general, to possess such characteristics as selfcompatibility, ability to flower quickly, high seed production, and neutral photoperiodism (Allard, 1965; Baker, 1965, 1967; Mulligan, 1965; Stebbins, 1965).

Baker (1967) has shown that tolerance to environmental extremes such as light, shading, drought, and waterlogging of the soil, have contributed to the success of Eupatorium microstemon as a weedy species. Harper and Chancellor (1960) have shown that the success of weedy Rumex species was not only due to the number, size and reproductive capacity of individuals, but also tolerance to variation in water table conditions and soil type.

Eupatorium odoratum L. is a recent introduction from tropical America to the flora of India, South East Asia, and Africa in the Old World Tropics (Adams, 1964; Bennett and Rao, 1968; Biswas, 1934; Moni and George, 1959). Introduction of this plant into areas of the Old World Tropics was accidental. It has become abundant and widespread within the last fifty years. The rapidity with which the species has spread has caused concern and stimulated investigation into possible eradication or biological control methods in India and Nigeria (Crutwell, 1968, 1969, 1971; Mohan Lal, 1960; Sheldrick, 1968).

In Nigeria, observation of E. odoratum in a number of habitats has revealed differences in leaf area, petiole length, and internodes to be significant among eleven

populations growing in different soil moisture conditions (Edwards, 1969, 1969a; Odukwe, 1965; Sheldrick, 1968). Observations over the two year period of 1967 and 1968 suggested that the spread of this species in Nigeria has reached its limit (Edwards, 1968). As suggested by the morphological variations found, the success of E. odoratum in this region of the Paleotropics appears to be related to some adaptations to the selective forces.

In order to understand fully a plant species' successful establishment in a new habitat, either by natural or accidental introduction, one must examine such features of the life history as germination, seedling establishment, and growth in several populations. Results obtained from this type of approach may be useful in examining evolutionary trends in widespread species. Evolutionary trends may be morphological, physiological, reproductive, or combinations of all three. Variations or differences occurring in these attributes are more or less accentuated by the selective forces of the habitat.

Germination and seedling establishment represent two of several critical stages in the life history of a plant species invading a new habitat. Modifications of the basic genotype program are expressed in a range of phenotypes (Bradshaw, 1965; Harper, 1965). Turesson (1922, 1925), noted that the point of primary importance in plant species is the genotypic constitution. He assigned the term 'ecotype' as

an 'ecological unit' to cover the products arising as a result of the genotypical response of a plant species (ecospecies), to a particular habitat. The genetic program of the species which allows it to survive during the critical stages of development may include a range of possible developmental pathways. The pathway selected or the direction followed by the species will depend upon the environmental conditions to which the organism is exposed.

Germination responses to factors of the environment such as moisture, light and temperature vary among and within populations of plant species. Seeds of many species have evolved ways to prevent desiccation of the embryo due to the moisture regime in the habitat. Harper and Benton (1966), also Harper and Sagar (1963) have shown that the failure of seeds of some plant species to germinate was the result of delayed or insufficient hydration of the seeds, a condition brought about by level of water table in the soil. Water uptake and available water (Lazenby, 1955; Toole et al., 1956) have been shown to be two important aspects of moisture requirements of many plant species. Uptake of water by seeds of Atriplex canescens (Springfield, 1966), Polygonum (Timson, 1965), and Iva annua (Ungar and Hogan, 1970) has been shown to be related to soil moisture stress, or any combinations of physical factors of the habitat.

In many weedy species, particularly those occurring in temperate climates, the presence of nitrates in the soil has been shown to increase germinability (Steinbauer and Grigsby, 1957, 1957a; Steinbauer et al., 1955; Williams and Harper, 1965). The effect of nitrates in breaking dormancy may be dependent on other factors of the environment such as light (Steinbauer and Grigsby, 1957), temperature and moisture (Steinbauer and Grigsby, 1957, 1957a; Williams and Harper, 1965).

The importance of light and its effect on germination of seeds has received much attention. When seeds are dispersed, they are either half or completely buried in the soil, or lie on the surface and covered with litter, or occupy cracks or crevices in the soil, or are completely exposed on the soil surface. They are thus exposed to light for some duration or not exposed at all. Germination of seeds in response to light revealed that variations occur on the inter- and intraspecific as well as inter- and intrapopulation levels (Caver and Harper, 1966; Cole, 1967; Shontz and Oosting, 1970; Toole et al., 1956; Thurling, 1966).

The effects of the factors of the environment on plant species cannot be over-emphasized. Bradshaw (1959) showed that differences in vegetative heights, inflorescence heights, basal and aerial tillers, and the mode of spread of underground stems in populations of Agrostis tenuis Sibth. were due to the environment in which the populations grew.

McWhorter (1971) in his study of populations of Sorghum halepense (L.) Pers. has shown that variations in growth habits were due to high fertility and adequate soil moisture. Robertson and Ward (1970) have concluded from their study of populations of Koeleria cristata (L.) Pers. that variations in phenological and morphological attributes were due primarily to the moisture regime of the habitat. McKell et al, (1962) studied populations of medusahead, Taeniatherum asperum (Simonkai) Nevski, an introduced annual grass to the United States, and concluded that the ecotypes differentiated mostly on phenological grounds. The study also showed rapid evolution in the species which has about an eighty-year history in the United States. The suggested reasons for the rapid evolution were, open niches in an almost closed community, high reproductive ability, and penetration of limited individuals of the species across a 'migration barrier' between the Old and the New World. The first two reasons given above may be applied to E. odoratum in the Old World Tropics.

In a series of studies of Eupatorium rugosum Houtt., Kucera (1958, 1962) noted that differences in flowering response would suggest physiological variations in populations within the range of the species. He concluded that variations in the natural populations were the result of genotypic responses to varying climatic conditions within the broad range of the species. Although E. rugosum

is not a weedy species, it is however widespread. It was also shown that differences in photoperiodic response were adaptations related to latitudinal distribution of E. rugosum (Cohen and Kucera, 1969). McMillan (1969, 1970) found that diverse photoperiodic responses in Xanthium strumarium L. were correlated with habitat and latitude. The study showed that a combination of critical night-length and maturity response formed the basis for reproductive adaptation in different climatic regimes of X. strumarium. Investigations of populations of several species of Amaranthus, Ulex europaeus L., and Cardamine indicated that differences in response to photoperiodism significantly correlated with date of flowering, habitat, and latitude (McWilliams et al., 1966; Millener, 1962; Thurling, 1966).

In order to understand fully how an invading species (introduced or otherwise) has become successful in a new habitat, it would perhaps be profitable to examine intrinsic physiological attributes such as accumulation of dry matter (biomass), root/shoot ratio, relative growth rate, leaf area ratio, and net assimilation rate. Also, the processes of respiration and photosynthesis must be included since they too contribute directly to growth functions. That differences in growth functions occur among populations have been clearly demonstrated with some field crops (Watson, 1947, 1952), and some annual and perennial species (Monk, 1966). In addition, Harper and Ogden (1970) have shown that

allocation of energy varied during the life cycle of Senecio vulgaris L. They concluded that the reproductive effort was not affected by gross variations in individual plants.

The idea of allocation of energy during the life cycle of the plant species, particularly at the seedling level, coupled with intrinsic growth functions, offer the prospect of utilizing them in interpreting the behavior of weedy species that have become successful in diverse habitats.

Among the early investigators who used growth functions to explain the behavior of plant species was Watson (1947). He showed that there were variations in net assimilation rate, leaf area ratio and leaf area between species and varieties, and within years in field crops. The aim of Watson's investigation was to find a better method of assessing or predicting behavior of field crops under selection. Björkman and Holmgren (1961) showed that there were differences in respiratory rate among ecotypes of Solidago virgaurea. In an earlier work, they showed that differences in photosynthesis also occurred among populations of S. virgaurea. They concluded that maximum respiration and photosynthesis took place at different temperatures for the ecotypes studied.

In recent years, growth functions have been utilized to assess the yield in the genus Lolium (Wilson and Cooper,

1969) in Dactylis glomerata L. (Eagles, 1969), and in Festuca arundinacea Schreb. (Chatterjee, 1961). These workers were particularly interested in being able to assess the potential for improvement of field crops under selection. The application of growth functions to the study of weedy species was made by Hammerton (1965), and Hammerton and Stone (1966). They concluded that populations of Polygonum periscaria L., and P. lapathifolium L. represented distinct ecotypes on the basis of correlation of growth functions with latitude of origin.

It is evident that the success of an invading species hinges on: (1) the genotype; (2) modifications of the basic genotype patterns; (3) influence of the factors or features of the environment; (4) physical manifestations of the genotype (phenotypes); (5) manipulations of internal processes (respiration, photosynthesis, and reproduction); and (6) growth functions and attributes which are manifestations of the internal processes. The idea has been suggested that examination and investigation of morphological variation within species is "like inspecting the 'tip of the iceberg', whereas the main complexity lies at the physiological level of the vital processes" (Briggs and Walters, 1969). It would appear therefore, that physiological approaches to the study of weedy species and, in particular, those that are widely distributed and have become abundant in areas of similar or varied environmental factors and habitats may yield useful

information and allow for greater understanding of the behavior of weedy species.

There are many facets of the behavior of a plant species, particularly a successfully established migrant species, that must be examined in order to understand fully the mechanisms by which the species manipulates available materials, energy and space. In order to obtain useful and meaningful information, a physiological approach to the study of plant species appears to be a realistic one. The importance of physiological attributes, particularly growth functions as relative growth rate, net assimilation, rate, root weight ratio, root/shoot ratio, and leaf area ratio, and their probable application in interpreting relationships among populations of plant species, has motivated the present study of Eupatorium odoratum.

The statement can be made that upon introduction, a species may undergo physiological changes sometime during its life history in order to survive in a new habitat. There are many facets to the physiological changes a species may undergo. It is difficult to examine all of the facets because the rate, or time, or type of changes depend upon the genetic program of the species. It would be logical perhaps to examine such sensitive characteristics as growth rate, assimilation rate, root weight, or leaf area ratios during the early growth phase of the species, in order to determine whether changes in some or all of these are adaptive characteristics. Evaluation of these physiological characteristics

may also indicate the strategy associated with the genotype under varying conditions of the environment. The objective of this study therefore is to determine the strategy and adaptations of some physiological attributes in populations of E. odoratum that have contributed to its rapid spread within a relatively short period of time.

MATERIALS AND METHODS

Characteristics and Distribution of *Eupatorium odoratum*

Morphological Characteristics

Eupatorium odoratum is a member of the family Compositae (Asteraceae) in the tribe Eupatorieae. It is a straggling or somewhat scandent herb or shrub. The stems are pubescent and round, or sometimes angular at the nodes. The opposite and decussate, or sometimes whorled leaves are three-nerved at or near the base, sparsely to moderately pubescent beneath, velvety or hirsute and copiously yellow glandular above. The leaves, which are generally rhombic-ovate to lanceolate with long acuminate apices and cuneate bases, have margins that are serrate to dentate, or the upper leaves may be nearly entire. The flower heads or capitula are arranged in a terminal, trichotomous, convex corymb. The green-tipped involucre bracts are imbricate and enclose 12 - 35 purple, pale lavender, or whitish flowers. The styles are exerted, as long as the corolla, and of the same color. The pappus is whitish and approximately the same length as the dark brown to black, angular, barbed achene (Adams, 1964; Cheeseman, 1940; Hutchinson and Dalziel, 1963; Long and Lakela, 1971).

Geographical Distribution

Eupatorium odoratum is an example of a tropical species that has become recently established in new habitata far from its geographic range. This species is now widespread in the Old World Tropics and has been described as an "aggressive weed" (Bennett and Rao, 1968; Simmonds, 1965).

Eupatorium odoratum is native to the West Indies and continental America from southern Florida to Paraguay in South America (Figure 1). It is abundant, but not widespread, in Trinidad and Tobago, Jamaica and Barbados. The continental range of the species extends from latitude 18°S in Bolivia and Paraguay in the south, through Costa Rica, Guatemala, Honduras and southern Mexico, and into southern United States in the north, where it occurs mainly in Dade and Monroe Counties in Florida (Cheeseman, 1928; Crutwell, 1969, 1970, 1971; Grashoff, 1969; Long and Lakela, 1971).

The species was accidentally introduced into the Old World Tropics where it is now abundant and widespread. It was first recorded in India, Burma, Singapore, and Thailand by Biswas (1934), and subsequently in Ceylon and Malaya by Moni and George (1959), and Salgado (1963). From Tropical Asia, the species was introduced into Africa and was first described as a new species in Ghana and Nigeria by Adams (1964). Further observations of the spread of

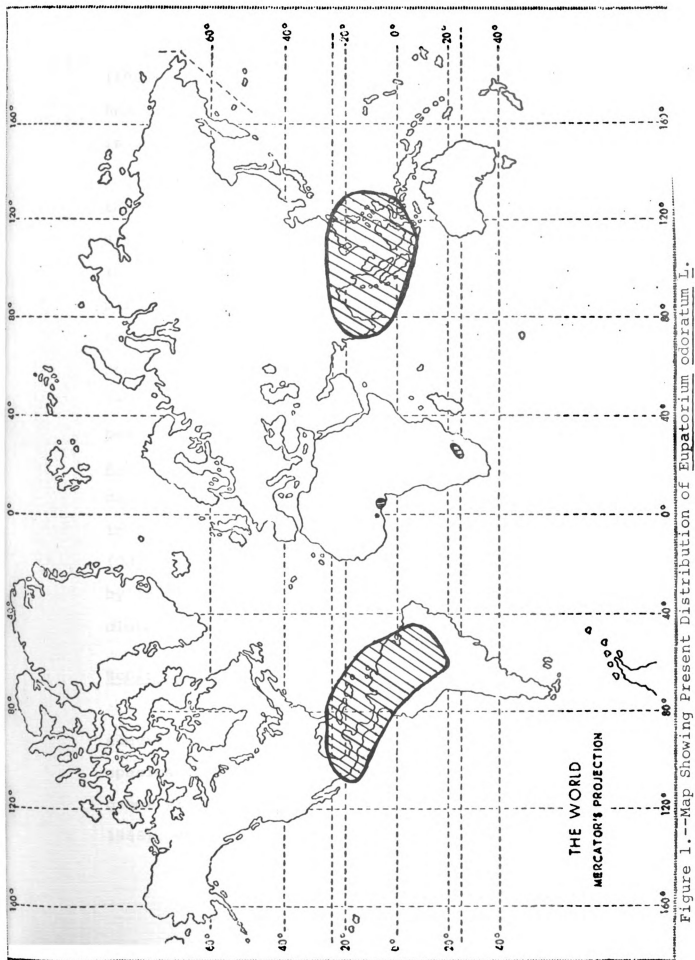


Figure 1.--Map Showing Present Distribution of Eupatorium odoratum L.

the species in Nigeria was made by Odukwe (1965) and Simmonds (1965), and in South Africa as reported by Bennett and Rao (1968). The present world distribution of the species is shown in Figure 1.

Eupatorium odoratum was apparently introduced from the West Indies in the ballasts of cargo boats into Singapore from whence it spread into Malaya, and Burma (Biswas, 1934). The introduction of the species in other parts of tropical Asia occurred by adherence of the seeds to the clothing of plantation workers returning to their homes (Moni and George, 1959). The first accidental introduction of E. odoratum into Nigeria was probably between 1937 and 1945, adhering to the seed of Gmelina arborea which was sent from Ceylon (Odukwe, 1965), or carried on the clothing of Nigerian soldiers who fought in Burma and Malaysia during the Second World War (Odukwe, 1965). Further spread throughout southern Nigeria by 1960 was probably through farm produce, goods, and clothing of traders (Edwards, 1968; Sheldrick, 1968).

Ecological Characteristics

In Neotropical regions, E. odoratum is found at elevations to 1500 meters, but is generally a valley species (Crutwell, 1969, 1970, 1971). Although the species grows vigorously in well drained soils (Bennett and Rao, 1968), where it reaches a height of 3 meters, it occurs

in a variety of habitats under a range of soil conditions. Cheeseman (1940) reported its occurrence on roadside banks, waste lands, and open fields in Trinidad and Tobago; Bennett and Rao (1968) and Crutwell (1969, 1970, 1971) found it growing under shade, and in fields or openings on plantations in Trinidad, Brazil, and Yucatan.

In the Old World Tropics, E. odoratum is also found primarily on well drained soils. However, the species has also been reported from poorly drained and dry soils in India (Bennett and Rao, 1968), and in Nigeria (Edwards, 1968). In Nigeria in particular, the species is found at elevations to approximately 600 meters, and has been observed growing on flood plains, at the margin of estuaries, and in swamps (Edwards, 1968, 1969) (Figure 2). Plant heights of over 6 meters have been reported from India (Bennett and Rao, 1968), and Nigeria (Edwards, 1969a) (Figure 3).

Dispersal

It has been stated that once the plant is established, spreading is chiefly by wind-borne seed (Bennett and Rao, 1968; Crutwell, 1969; Sheldrick, 1968). There is no evidence that this is indeed the mechanism for dispersal. The achenes and pappuses have very short bristle-like curved barbs (Figure 4); and, in addition, the achenes remain attached to the receptacle for a long period of time (Figure 5). Unlike many wind-borne seeds the achenes do

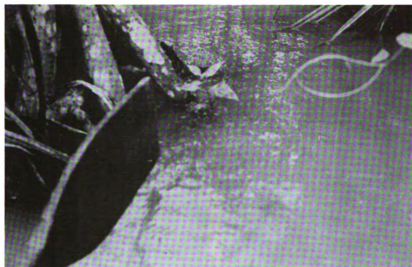


Figure 2.--Regeneration of E. odoratum in
3' of water in the flood plains
of River Ogun in Nigeria.



Figure 3.--E. odoratum growing on roadside in
Nigeria.

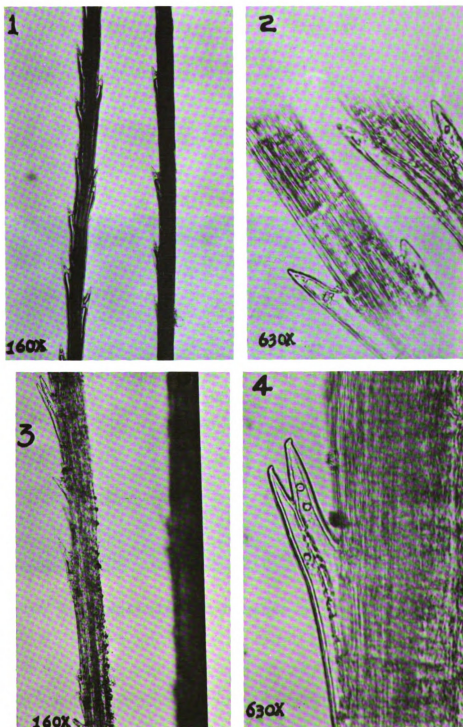


Figure 4.--Pappus and achene of *E. odoratum* showing bristle-like curved barbs. 1 and 2: pappus, 3 and 4: achene.

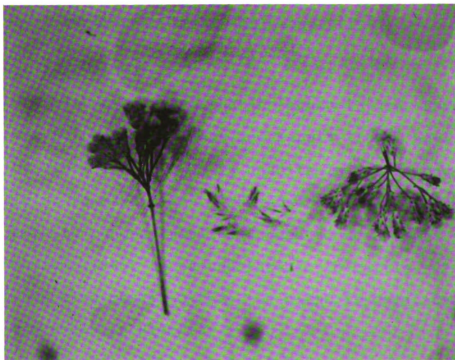


Figure 5.--Capitula and achenes of E. odoratum.

not float in air. It is suggested here that dispersal in E. odoratum is most likely to be by animal or other mechanical means. The problem of dispersal and dispersal mechanisms is a future project to be carried out in the field. The assumption of wind-borne dispersal was probably made because the achenes of many members of the Compositae are wind dispersed. The assumption is also in contradiction to the method of introduction and spread of the species as reported by Moni and George (1959).

Economic Importance

It is unfortunate that no economic uses have been found for E. odoratum. Bhat and Karnik (1954) have shown that the fiber in the stem is unsuitable for cordage or for pulping to make paper. The essential oil that gives the plant its pungent smell has been found by Moni and Subranmoniam (1960) to be unpalatable to cattle. Edwards (1968) has also observed that the plant is unpalatable to goats and sheep in Nigeria.

Mohan Lal (1960) has reported that the people of Khasi in Assam, India, use it as a fallow cover in their arable farming and burn it off when they wish to farm. In Cambodia, Litzenberger and Ho Tong Lip (1960) have reported its use as a green manure in paddy fields, or as a mulch for the growing of black pepper. They found that there was an increase in yield of black pepper which they attributed to perhaps reduced activity of nematodes caused

by the odor of E. odoratum. Wycherley (1960, 1963, 1965) and Wycherley and Chandapilla (1969) have reported attempts to use E. odoratum as a cover crop in rubber plantations in Malaya. In some areas of South America, Crutwell (1969) reported the use of leaves as a beverage for treatments of colds and fevers.

Few insects (larvae or adults) have been observed to feed on E. odoratum in Nigeria (Edwards, 1968). Several insects have been found feeding on the species in Trinidad (Bennett and Crutwell, 1969; Crutwell, 1968, 1970) in Central America and southern Mexico (Crutwell, 1969) and in South America (Crutwell, 1971). It appears therefore, that the absence of insect predation may be partly responsible for the rapid spread of E. odoratum in the Old World Tropics.

Seed Source

Seeds (achenes) of E. odoratum from eight localities from the New and Old World Tropics were used throughout this investigation; one locality each from Guatemala, Trinidad, and Florida in the New World Tropics, and three localities from Nigeria (Agege, Sango Otta, and Ifako), and two localities from the Far East (Thailand and Malaya) in the Old World Tropics. Table 1 gives a detailed summary of the localities with respect to latitude, longitude, mean annual rainfall, and mean annual temperature. All seeds were collected during 1970 and 1971.

TABLE 1.--Localities of origin of seeds of *Eupatorium odoratum* with approximate latitude, longitude, mean annual rainfall, mean annual temperature, and code names.

	Seed Source	Code	Latitude	Longitude	Mean Annual Temperature ($^{\circ}$ C)	Mean Annual Rainfall (mm)
1	Thailand near Sakarat	THLD	15 $^{\circ}$.00'N	102 $^{\circ}$.00'E	27.7	1350
2	Malaysia Kualar Lumpur	MLYA	3 $^{\circ}$.08'N	101 $^{\circ}$.42'E	27.7	2286
3	Nigeria Agege	NIAG	6 $^{\circ}$.37'N	3 $^{\circ}$.20'E	25.0	1850
4	Sango Otta	NISO	6 $^{\circ}$.42'N	3 $^{\circ}$.14'E	25.0	1850
5	Ifako	NIFA	6 $^{\circ}$.40'N	3.19'E	25.0	1850
6	Trinidad Curepe	TRND	10 $^{\circ}$.38'N	61 $^{\circ}$.31'W	26.0	1250
7	Guatemala near Antigua	GUAT	14 $^{\circ}$.33'N	90 $^{\circ}$.42W	27.7	1850
8	Florida Elliott Key Is.	FLRD	25 $^{\circ}$.25'N	80 $^{\circ}$.11W	25.0	1250

Germination Studies

The following procedure was used in all the germination studies. Modifications of this procedure and special treatments are described under each study.

Subsamples of twenty-five seeds were placed on moist #3 Whatman filter paper in glass petri dishes except in the moisture stress study, where fifty and twenty seeds were used. Distilled water was added periodically in order to maintain a moist condition. The dishes were placed on growth carts which were covered with black plastic material and maintained at $29^{\circ} \pm 1^{\circ}\text{C}$. Germination counts were made initially on the tenth day of incubation and every five days thereafter for the next thirty days. Seeds were regarded as having germinated if they had produced a radicle and a plumule; such seeds were counted and removed. At the end of each experimental period, ungerminated seeds were subjected to further treatment to induce germination. Treatment included incubation for an additional ten to fifteen days, or with concentrated sulfuric acid for one minute (chemical scarification). Finally, ungerminated seeds were examined under a binocular microscope in order to ascertain the condition of the embryos.

Effects of Moisture

As moisture is one of the critical factors affecting germination, studies of the effect of moisture on germination of seven seed populations of E. odoratum were

undertaken. The aims were: (1) to determine whether germination in the populations of E. odoratum differed with respect to water uptake and moisture stress; (2) to determine whether germination is delayed under moisture stress; and (3) to determine whether there were differences in the rate of germination by increased soaking time and moisture stress.

Soaking

Eight replicates of twenty-five seeds each were soaked in water for 0, 1, 4, 24, and 48 hours. These intervals were chosen on the basis of the fact that during the growing season, the amount of soil water available varies in the different localities, and also, on the result of preliminary experiments which indicated that there were no significant differences in percent germination when seeds were soaked in water for 1, 2, 4, 6 and 8 hours. Only seeds that were completely immersed were used. Floating seeds were considered not viable and therefore removed.

Moisture Stress

Two replicates of fifty seeds were placed on moist filter paper at the following moisture stresses: 0, 1, 3, 5, 8, and 10 atmospheres of pressure. Moisture stresses against the seeds were maintained by using solutions of mannitol. The amounts of mannitol needed to produce the required osmotic pressure were calculated from the following formula:

$P = gRT/mV$, where P = osmotic pressure in atmospheres,
 g = grams of solute, $R = 0.0082 \text{ l.atm./deg./mole}$
 T = absolute temperature, m = molecular
 weight of solute, and V = volume in liters
 (Knipe and Herbel, 1960; Shontz and Oosting,
 1970; Springfield, 1966; Uhvits, 1946).

The levels of imbitition and soil moisture stress were chosen because not only does the amount of soil water available vary in the different localities but also, that germination has been observed (Crutwell, 1969) in E. odoratum after intermittent rains during the dry season in Trinidad.

Effect of Nitrate

The effect of nitrogen as nitrate in the substrate was investigated in germination of E. odoratum. The purpose was to test the hypothesis that the presence of nitrogen as nitrate was not critical in breaking dormancy in the seeds of E. odoratum. Also, to examine whether germination responses differed among populations in the presence of nitrate.

Four replicates of twenty-five seeds each were placed in petri dishes containing filter paper which had been moistened with nitrate solutions whose concentrations were 0.00, 0.1, 10^{-2} , 10^{-3} , 10^{-4} , and 10^{-5} molar, using potassium nitrate as the source of nitrate. These concentration levels were assumed to represent approximate values of nitrate found in most tropical soils.

Effect of Light

The effect of light on germination in seeds of E. odoratum was examined. The aims were to determine the effect of light on germination; to examine variations in germination response among the seed sources; and to determine whether light is a prerequisite for germination in this tropical weed species.

The following light treatments were used in this experiment; (1) continuous light, (2) continuous dark, (3) 11 hours light - 13 hours dark period. At the end of the experimental period, those kept under continuous dark period were transferred to an 11 - 13 hour photoperiod. There were four replicates of twenty-five seeds. Photoperiods at all localities of the seed source are assumed to be uniform (Table 1, Figure 1).

Analyses of Results

Comparisons of total germination, percent germination, and rates of germination among populations were carried out by one and two-way analyses of variance, Duncan's Multiple Range Test, or Student's "t". Probability level for all tests of significance was 0.05 unless otherwise stated. Where variances did not appear to be homogeneous, square root transformation was made before analysis of variance was applied. Where percentages were used, arcsin transformation was employed.

Growth Studies

The experiments described below examined growth attributes as they relate to growth in E. odoratum. Effects of moisture, nitrogen and density were investigated. The growth attributes examined were: dry weight (W), leaf area, (LA), leaf area ratio (LAR), net assimilation rate (NAR), relative growth rate (RGR), root weight ratio (RWR), root/shoot ratio (R/S), total nitrogen (RN), height and number of leaves per plant.

Seeds of E. odoratum from seven localities were broadcast over greenhouse soil mixed with sand in plastic trays. The trays were covered with clear plastic material to prevent excessive evaporation. The seeds were allowed to germinate in the greenhouse at temperatures between 28° to 31°C. Four or eight seedlings were transplanted into 7" clay pots filled with greenhouse soil mixed with sand when the seedlings were five to six weeks old. The seedlings were watered regularly and dead plants were replaced until all the seedlings became established. At the end of twelve weeks, all pots contained three or six plants. The pots were rotated twice a week.

Plants were harvested for analysis on three two-week and two three-week intervals respectively. On each harvest day, samples of leaves were taken for leaf area determination. The plants were then carefully removed from the pots. Roots were thoroughly washed to remove

soil particles or any organic matter, and placed in plastic bags. In the laboratory, the plants were separated into root, leaf and stem. Each organ was put into a paper bag and dried at 95°C for 48 hours after which the samples were weighed. After tracing the leaf sample on Sub 20, Bond Paper, they were subsequently oven dried and weighed. For total nitrogen determination, the dry material was ground and analyzed by the Kjeldahl method.

Effect of Moisture

Growth of E. odoratum seems to depend to a large degree on the amount of available water in the soil. Crutwell (1968, 1971) stated that the 'only physical factor' which limits the growth of E. odoratum seems to be availability of moisture. Growth has been observed in water-logged areas in Nigeria (Edwards, 1968) and on irrigated land in India (Moni and George, 1959). The latter observations are contrary to those of Crutwell, who did not observe growth of E. odoratum in water-logged or poorly drained soils in Trinidad, Costa Rica, and Brazil. These observations also suggest that differences exist among the populations of E. odoratum growing in the New World Tropics. The investigation of the effect of moisture on growth of E. odoratum appears therefore to be relevant in ascertaining the variations occurring among the plants from the different localities.

Experiments were designed to examine growth response among seven populations of E. odoratum at soil moisture conditions kept at field capacity (0.33 - 1.0 atm.) and at two extremes of soil moisture (saturated soil condition, 0.00 - 0.05 atm., and soil condition at temporary wilting point, 10.0 - 15.0 atm.).

In the first part of this experiment, twelve pots containing three plants per pot were selected from each of the seven populations being investigated. They were randomly arranged in rows and columns. Once or twice a week, the pots were rotated and randomly rearranged such that all the plants had the same exposure to the environmental conditions of the greenhouse. The soil moisture stress was maintained at field capacity. The plants were watered twice a week. On each harvest day, four pots were selected at random and treated as described earlier. Soil samples were taken and soil moisture determined. Soil moisture was maintained at about 25 to 35 percent throughout the period of the experiment. There were four replicates per harvest.

In the second experiment, three levels of moisture stress were used: 0.00 atm.--representing saturated soil; 0.33 - 1 atm., representing soil moisture at field capacity; and 10.0 - 15 atm., representing soil moisture at temporary wilting point respectively. Twelve pots containing three plants per pot were each placed in plastic

bags. This was to prevent excessive evaporation, and to maintain approximate soil water stress in the pots. Three pots were prepared and placed in plastic bags as blanks. Soil moisture percent was determined once weekly throughout the experimental period. On each harvest day soil moisture percent was determined on the experimental pots to ascertain that the moisture stress was maintained. The percentage equivalents were 85 to 90 percent = 0.00 to 0.05 atm.; 25 to 35 percent = 0.33 to 1.0 atm.; and 5 to 10 percent = 10 to 15 atm. Soil moisture tension was maintained by periodic addition of water. The twelve pots were randomized by population for each treatment.

Effect of Nitrogen

The effect of nitrogen on growth of E. odoratum was investigated. The aim of this experiment was to examine the effect of nitrogen on total dry weight, leaf area, leaf area ratio, root/shoot ratio, and root weight ratio. Also to examine any morphological variations in plant height and number of leaves per plant.

Twenty four pots containing three plants per pot selected for uniformity from each locality were randomly placed on the greenhouse bench. During the first three weeks after selection, twelve pots received 200 mls of nutrient solution (modified Arnon nutrient solution) containing 0.1M nitrogen as potassium nitrate twice a week. Supply of nutrient solution was stopped one week before

the first harvest. At harvest time, the height and the number of leaves per plant were measured and counted. Harvested plants were treated as previously described.

Effect of Density

The purpose of investigating density effect was to find out the degree of interactions among the plants. It may be possible from the results obtained to explain the kind of strategies used in the establishment stage. The following growth parameters were specifically examined; dry weight, root/shoot ratio, leaf area ratio, and net assimilation rate.

Effect of density was investigated at two density levels: three plants and six plants per pot respectively were randomized on the greenhouse bench. The pots were rotated and randomly rearranged every week. There were two replicates for each level and two harvests were made. At each harvest, measurement of the height and the number of leaves per plant were taken. The harvested plants were treated for analysis as has previously been described.

Calculation of Growth Functions

Leaf area (LA), was determined by tracing out leaf samples on Sub 20, Bond Paper. The prints were cut out and weighed so that, knowing the area/weight ratio of the paper, the area of each sample was then determined, and hence the total area of the leaves (Watson, 1947).

The following growth parameters were calculated in the present investigation.

1. Leaf Area Ratio (LAR)

$$= \frac{(L_2 - L_1)(\log_e W_2 - \log_e W_1)}{(\log_e L_2 - \log_e L_1)(W_2 - W_1)} \text{ (cm}^2\text{/gm)}$$

Where L_1 is leaf area at initial harvest; L_2 is leaf area at final harvest; W_1 is dry weight at initial harvest and W_2 is dry weight at final harvest.

This growth function is the measure of the ability of the plant to produce and maintain leaf area, and hence of its whole opportunity for assimilation.

2. Net Assimilation Rate (NAR)

$$= \frac{(W_2 - W_1)(\log_e L_2 - \log_e L_1)}{(L_2 - L_1)(t_2 - t_1)} \text{ gm/cm}^2$$

where L_1 is leaf area at initial harvest; L_2 is leaf area at final harvest; W_1 is dry weight at initial harvest; W_2 is dry weight at final harvest; $t_2 - t_1$ is time interval between initial and final harvests.

NAR represents the rate of increase of dry matter per unit area of leaf surface and it is of significance because it is a measure of the rate of photosynthesis in the leaves, less the respiratory loss of dry matter in the whole plant.

3. Relative Growth Rate (RGR)

$$= \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \text{ (gm/gm/wk)}$$

where W_1 is dry weight at initial harvest, W_2 is dry weight at final harvest; $t_2 - t_1$ is the time interval between initial and final harvests.

RGR measures dry matter increase or what Blackman (1919) has referred to as the 'efficiency index' of dry weight production. It represents the efficiency of the plant as a producer of new material.

4. Root Weight Ratio (RWR)

$$= \frac{(Wr_1 - Wr_2)(\log_e W_2 - \log_e W_1)}{(\log_e Wr_2 - \log_e Wr_1)(W_2 - W_1)}$$

where W_1 is dry weight at initial harvest; W_2 is dry weight at final harvest; Wr_1 is root dry weight at initial harvest; and Wr_2 is root dry weight at final harvest.

This function measures dry matter increase per total dry weight in below ground organs. It also indicates the amount of assimilates allocated to below ground organs.

Since the increment of dry matter (RGR) added in any time interval is the integral of the product of net assimilation rate and leaf area, the progress of dry matter accumulation can therefore be described in terms of changes in the two attributes, NAR, which is a measure of the intensity of carbon assimilation, and, LA, which measures the size of the assimilating system. Thus in assessing the potential for growth, it is important to examine the relative contributions of rates of assimilation and expansion of the photosynthetic surface, as well as the expansion of the absorbing surface in determining dry matter increase, and perhaps the amount of genetic variations in these three components, (Hammerton, 1965; Hammerton and

Stone, 1966; Wareing and Phillips, 1970; Watson, 1957; Wilson and Cooper, 1969).

Analyses of Growth

One and two-way analyses of variance, comparison of means by Duncan Multiple Range Test, and Student's "t", were used as far as practicable. Probability level for all tests of significance was 0.05 unless otherwise stated.

RESULTS AND DISCUSSION

Germination Studies

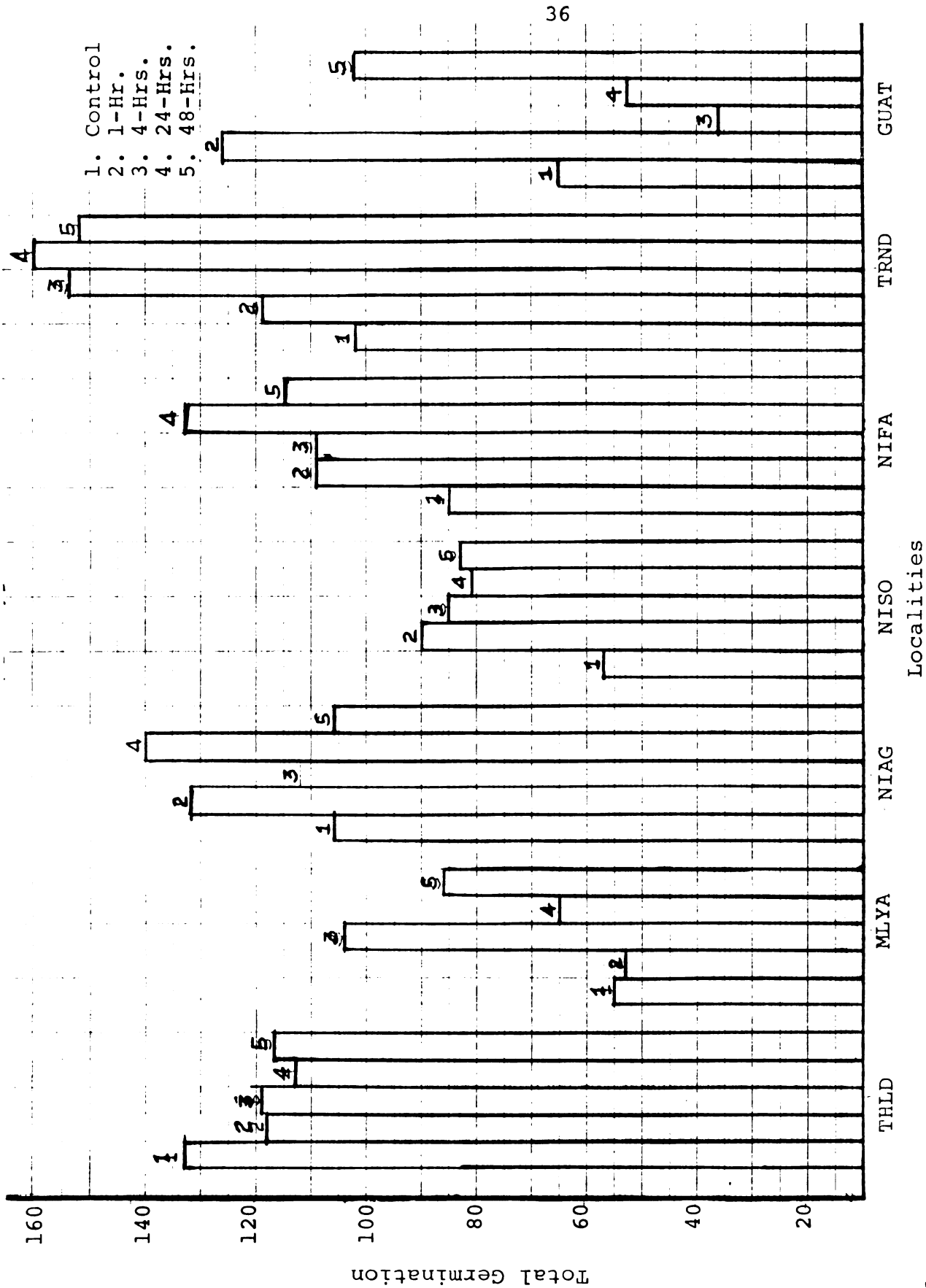
General Observations

The type of germination in E. odoratum is epigeal. The radicle emerges first and reaches about 20 - 25 mm in length before the emergence of the plumule.

Emergence of the radicle in seeds of E. odoratum from Trinidad and Nigeria occurred within 24 hours of incubation, but was delayed for an additional 12 - 24 hours in populations from Guatemala, Thailand, and Malaya. The plumule was completely out of the pericarp 4 - 6 days after the emergence of the radicle.

Effect of Soaking

Total germination in E. odoratum from seven localities is shown in Figure 6. There were significant differences in total germination at all levels of soaking among the seeds from the seven localities. Variations also occurred in germination of seeds from each locality. Maximum germination was attained at different levels of soaking; for example, after 1 hour, seeds from Sango Otta, and Guatemala gave maximum germination of 45 and 63%; after 4 hours, seeds from Malaya gave 52%; and after 24 hours,



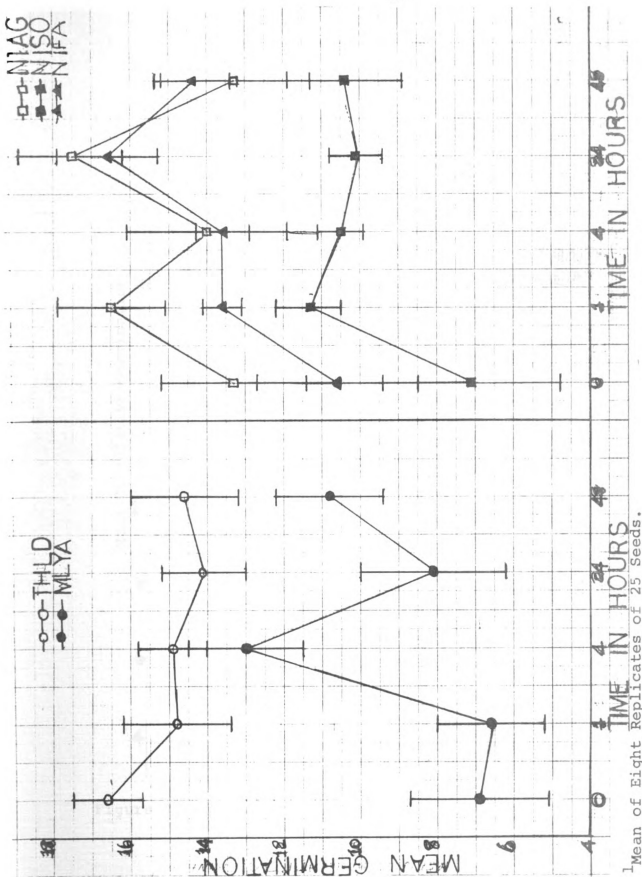
¹Total of Eight Replicates of 25 Seeds.

Figure 6.--¹Total Germination in Seeds of E. odoratum from Six Localities at Four Soaking Periods.

seeds from Ifako, Agege and Trinidad gave maximums of 66, 70, and 80%. There was no effect of soaking in the seeds from Thailand, where germination percent was lower at all treatment levels than the control which gave maximum germination of 66%. Differences in germination response at 1, 4, and 24 hours were significant for the seeds from Thailand, Malaya, Sango Otta, Trinidad, and Guatemala; however, no significant difference was observed among seeds from Ifako and Agege at 24 hours.

There were significant differences in germination among seeds from specific areas of the Old and the New World Tropics (Figure 7). Differences in germination response among the seeds from Thailand, Malaya (Far East), and Nigeria were significant, particularly at 24 hours. There was no significant difference in germination in seeds from two (Agege and Ifako) of three localities from Nigeria. The differences in germination in seeds from Nigeria and the New World Tropics were significant, particularly at 24 hours.

The rate of germination was uniform in seeds from the Old World Tropics but was different among seeds from the New World Tropics (Figure 8). The number of days to reach maximum and total percent germinated varied among the seed sources at each treatment level. The range was generally 15 - 30 days. About 50% of total germination was attained at all treatment levels in 10 days. In the



¹Mean of Eight Replicates of 25 Seeds.

Figure 7.--Mean¹ Germination and Standard Error in E. odoratum from Seven Localities at Four Soaking Periods.

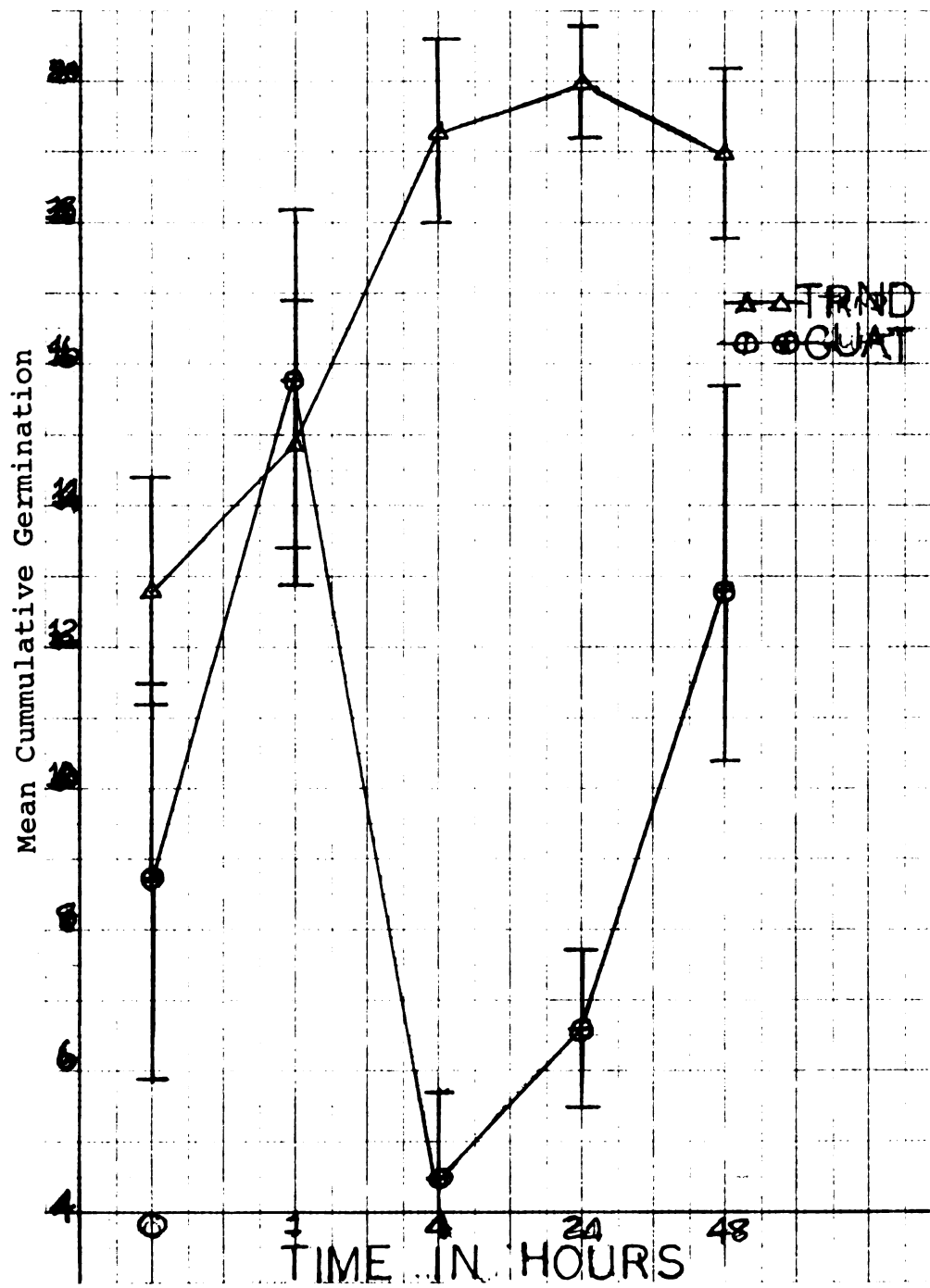


Figure 7.--Continued.

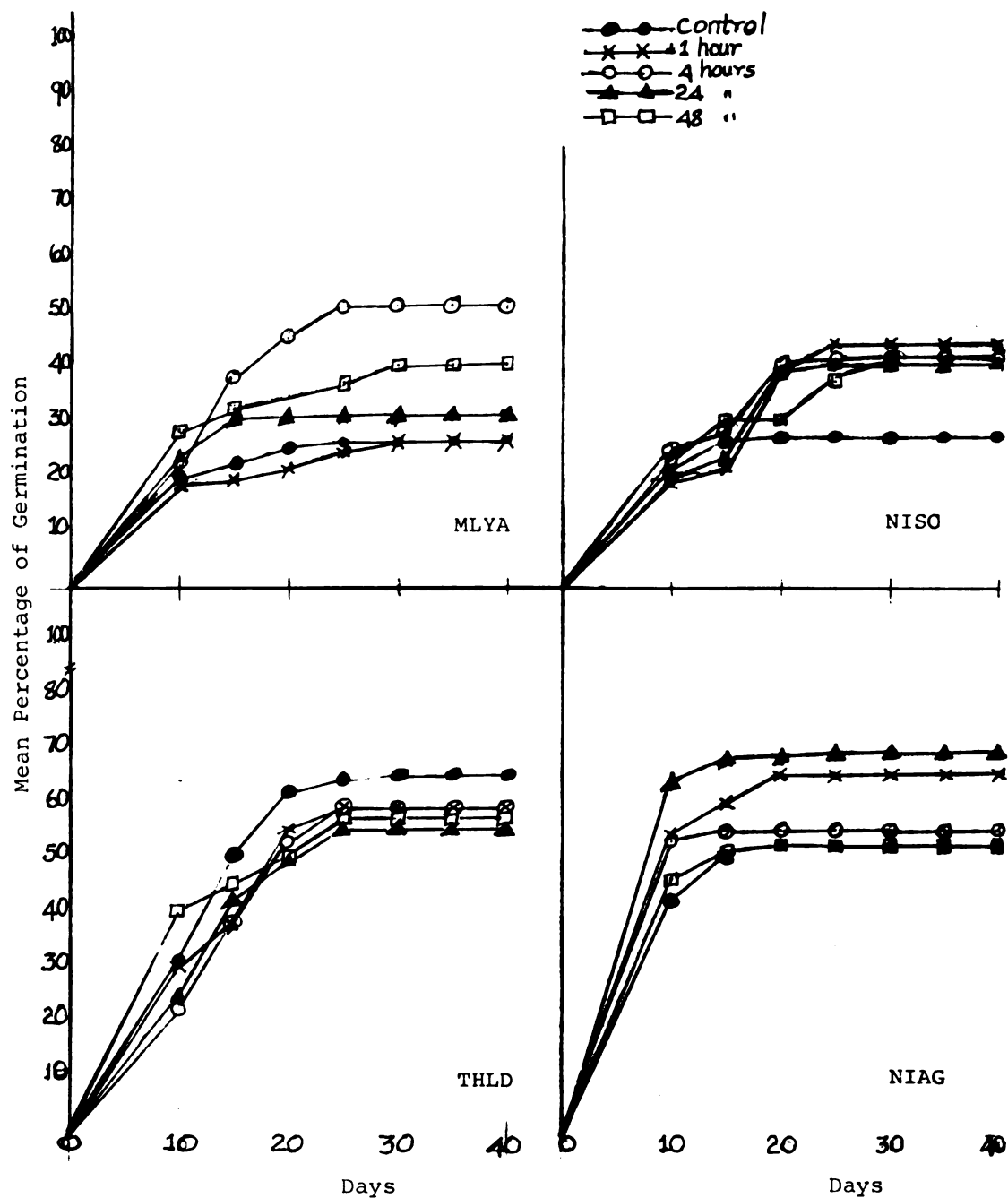


Figure 8.--Rate of Germination in *E. odoratum* from Seven Localities at Four Levels of Soaking After 40 Days.

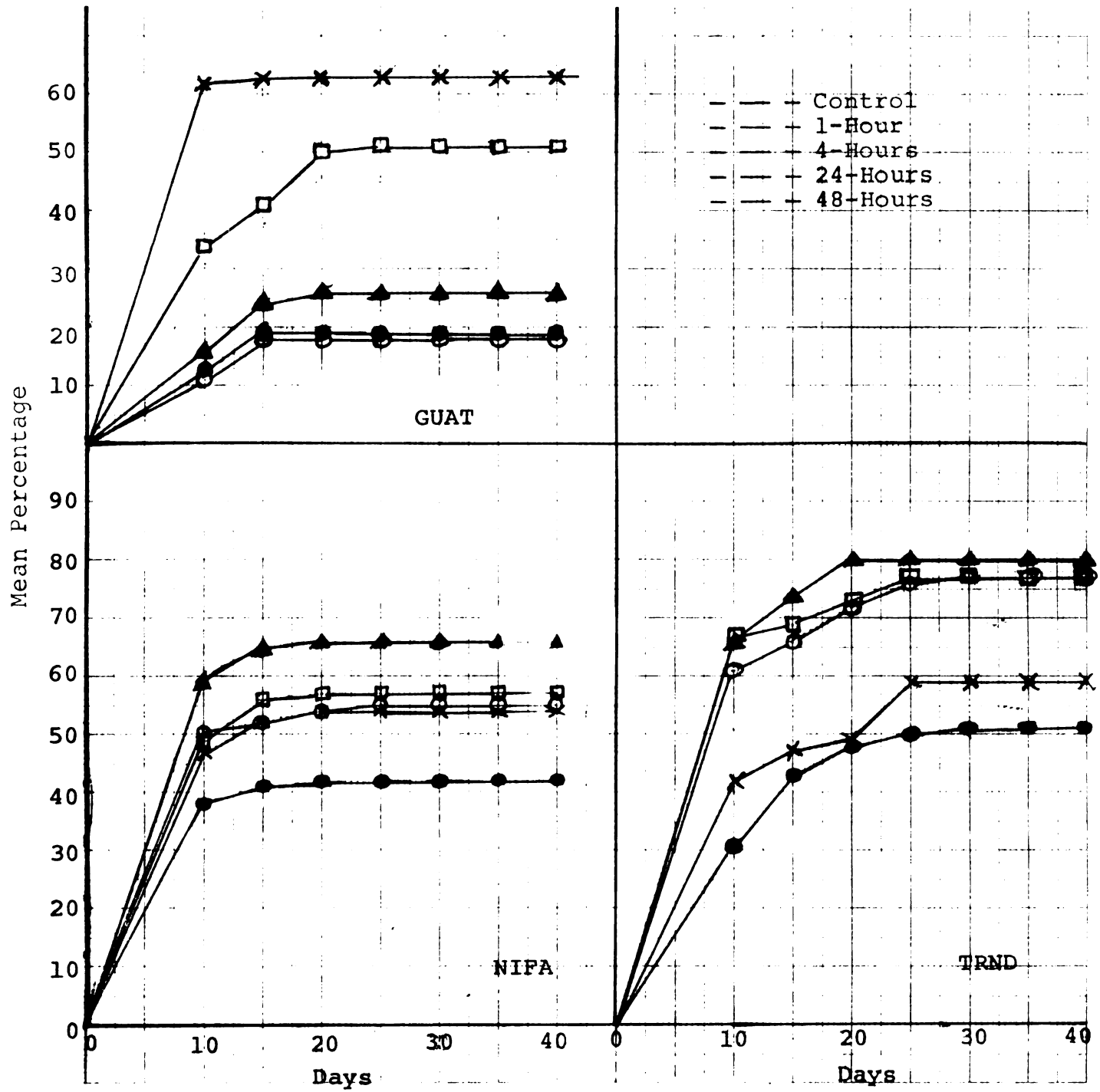


Figure 8.--Continued.

case of seeds from Agege, Ifako, and Trinidad, more than 65% of germination was reached in 10 days at 4, 24, and 48 hours. Ninety percent was reached in 10 days after 1 hour in seeds from Guatemala.

There were significant differences in the rate of germination among the seven seeds from localities at the 1, 4, and 24 hours of soaking after 10 days. For example, at 1 hour, seeds from Agege, Ifako, and Guatemala had 62% of total germination, seeds from Trinidad and Thailand had 23%, and seeds from Sango Otta and Malaya had 15%. At 4 hours, seeds from Agege, Ifako, and Trinidad attained 65% followed by seeds from Sango Otta, Malaya, and Thailand with 30%, and Guatemala had 5%. At 24 hours, seeds from Agege and Ifako gave 60% of total germination, and the rest 40%. No significant differences were evident in the rate of germination in 10 days at 48 hours. In 20 days, however, significant differences occurred among seeds from Agege, Ifao, Thailand, and Guatemala with 66%, Malaya and Sango Otta with 17%, and Trinidad alone about 17% of the total germination (Figure 9).

Germination in seeds from all localities was examined by a one-way analysis of variance using total germination for all levels of treatment. There were significant differences at $P < 0.05$. The pattern of differences was the same as using the results of the control alone. Seeds from the following localities did

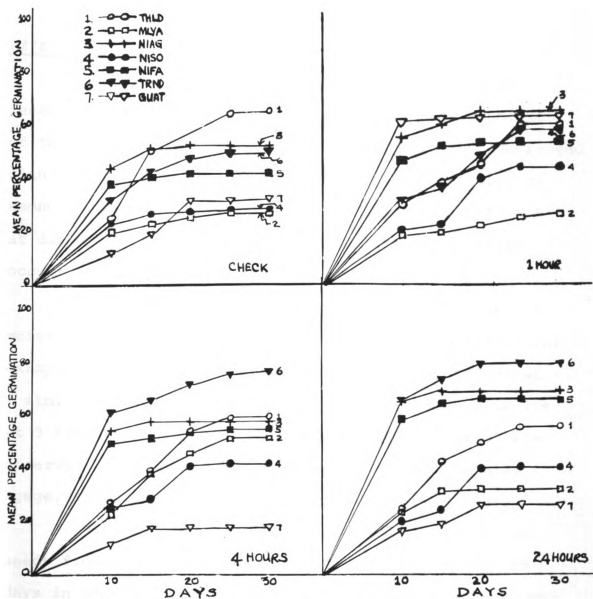


Figure 9.--Effect of Soaking on Germination Rate in Seven Populations of *E. odoratum*.

not show any significant differences; Agege and Ifako, Malaya and Guatemala, Sango Otta and Malaya, using Student's "t". Differences among seeds from other localities were significant at $P < 0.05$.

Effect of Moisture Tension

Available moisture in the soil is a critical factor in seed germination and subsequent establishment of the seedling. Results showed that germination decreased with increasing moisture tension. Germination response among the seeds from the six localities was significant at different moisture tension levels. No germination occurred at 10 atm.

In seeds from Trinidad and Guatemala, increased moisture tension appears to have induced germination. For example, seeds from Trinidad gave germination of 68% at 5 atm., and 74% at 3 atm.; seeds from Guatemala gave 12% at 5 atm. Fifty percent germination of the control was observed at 1, 3, and 5 atm. in seeds from Guatemala, Agege, Sango Otta, Malaya, and Trinidad (Figure 10).

Maximum germination was attained in 15 days in seeds from Agege, Guatemala, and Trinidad, and 20 - 25 days in seeds from Thailand, Malaya, and Sango Otta. The range in which at least 30% germination was reached was 15 - 25 days; whereas in the soaking treatment, it took generally 20 - 30 days to reach maximum germination

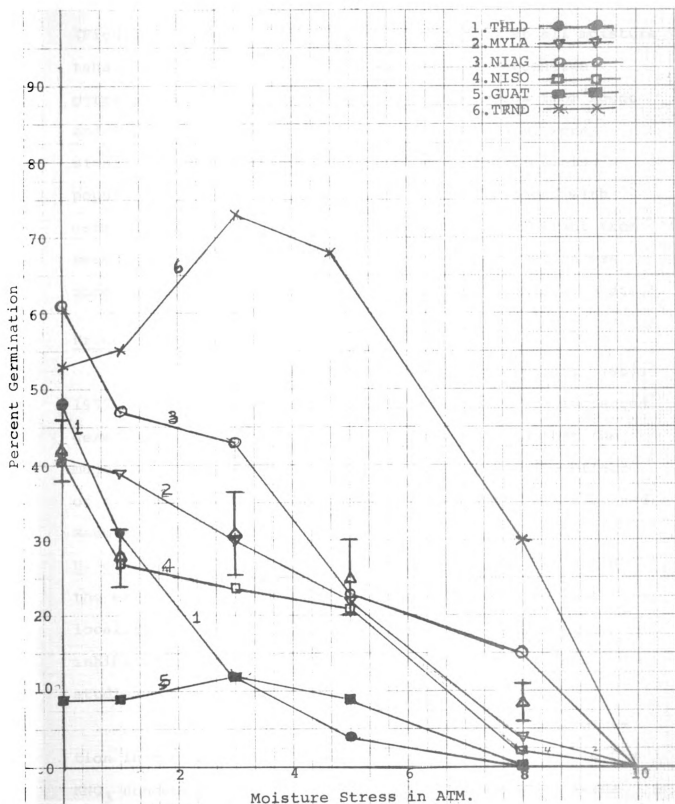


Figure 10.--Percentage Germination in *E. odoratum* from Six Localities at Varied Moisture Tension and their Weighted Means $\pm 5_x$.

(Figures 9 and 11). The rate of germination at all moisture tension levels was compared in Figure 11. Percentage germination of 43 and 47% observed in the seeds from Agege and Trinidad at moisture tension of 1 and 3 atm. were significantly different at $P < 0.05$ from the remaining populations. At 5 and 8 atm., seeds from Trinidad with germination of 30 and 65% was significantly different from seeds from the remaining localities. No germination was observed in the seeds from Thailand and Guatemala at 8 atm.

Effect of Nitrate

It has been observed (Steinbauer and Grigsby, 1957, 1957a) that nitrates in the germination substrate increased germinability in seeds of some weed species and that the major activity was that of breaking dormancy. The effect of nitrate on breaking dormancy in E. odoratum was examined. Results indicated that nitrate did not break dormancy in E. odoratum. The presence of nitrate, however, affected the emergence of the primary leaves in seeds from five localities (Figure 12). Concentration of 10^{-1}M KNO_3 inhibited the growth of roots in all the seed sources studies. The general effect is shown in Figure 13.

There were no significant differences in germination in the control and treated seeds except at the 10^{-1}M KNO_3 concentration level. Germination response in seeds from each locality varied at the different levels of

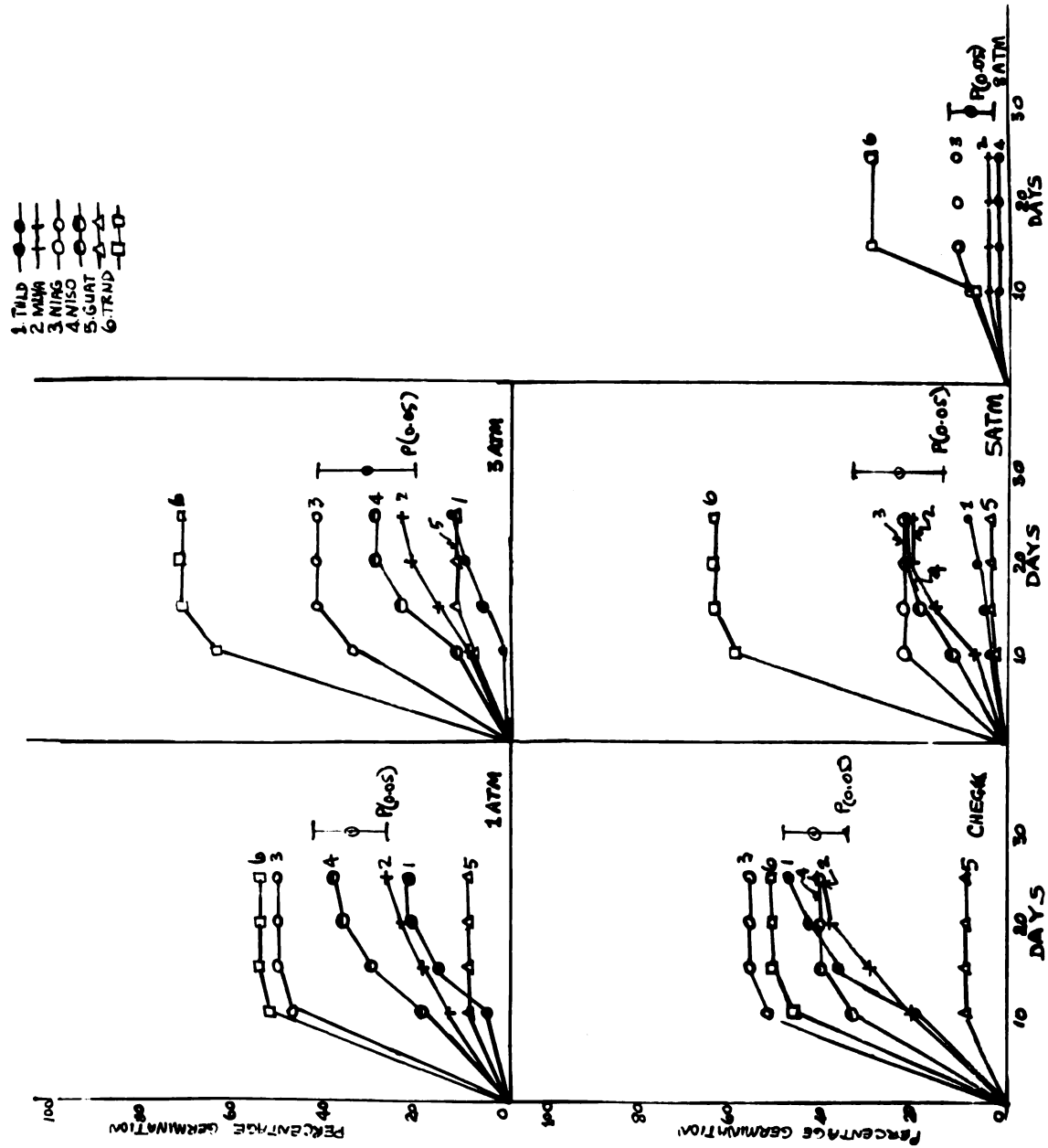


Figure 11.--Germination Rate in Six Populations of *E. odoratum* at Five Moisture Tension.

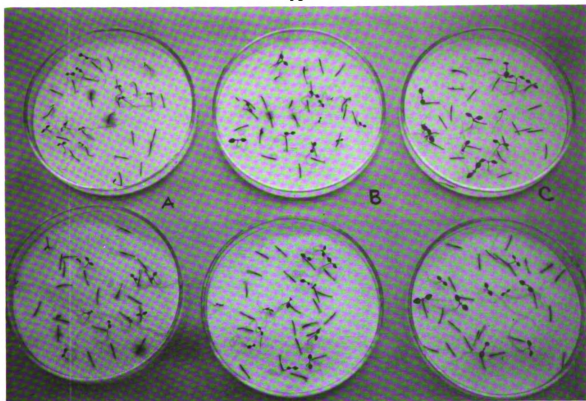


Figure 12.--Effect of nitrate on germination of *E. odoratum*
 A: Control; B: $1 \times 10^{-5}M$; C: $1 \times 10^{-3}M$ KNO_3 .
 Row 1. NISO; Row 2. NIFA; Row 3. TRND;
 Row 4. NIAG; Row 5. MLYA.

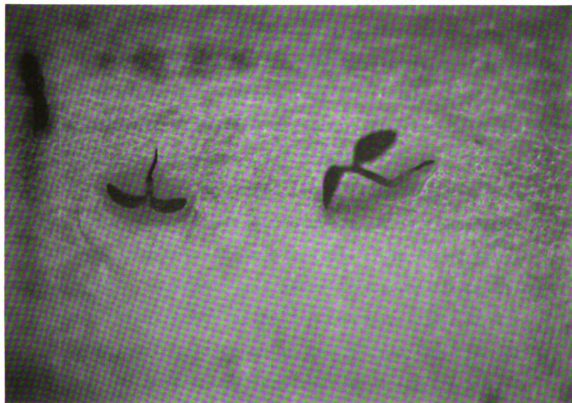


Figure 13.--Effect of 1×10^{-1} M KNO_3 on germination of E. odoratum.

nitrate concentrations (Figure 14). Total germination of 60% and above was observed in seeds from Thailand, Agege, and Trinidad; and less than 60% in the rest. This pattern of germination response to nitrate treatments was comparable to that of soaking where seeds from the same localities had more than 60% germination. Also, seeds from Trinidad had the highest percent germination among seeds examined.

Comparison of mean cumulative germination showed differences in response to nitrate treatment, for example, germination response in seeds from Thailand, Agege, and Trinidad were significantly different from seeds from Ifako, Sango Otta, and Malaya at 10^{-5} M KNO_3 . At 10^{-4} M, differences in germination in seeds from Malaya and Sango Otta were not significant; but differences among other seed sources were significant at $P < 0.05$. The differences in the seeds from Guatemala and seeds from other localities were highly significant at 10^{-3} M concentration of KNO_3 .

Germination response in seeds from the Old World Tropics varied from those from the New World Tropics. Differences in germination among seeds from the seven localities could not be attributed to the effect of nitrate alone. Germination, for example, differed in seeds from the Far East (Thailand and Malaya), in seeds from Agege

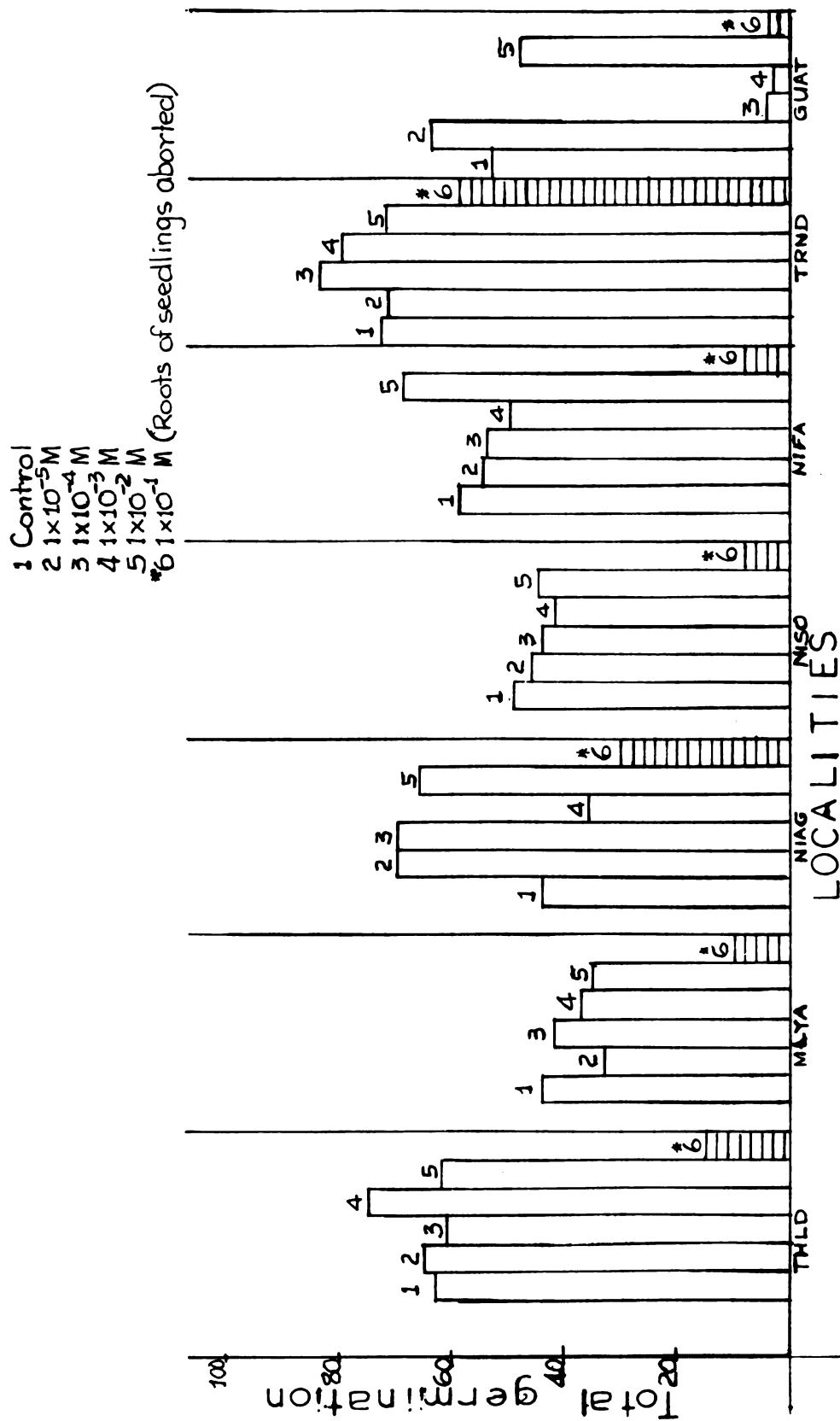


Figure 14.--Total Germination in E. odoratum from Seven Localities at Five Molar Concentrations of KNO_3 .

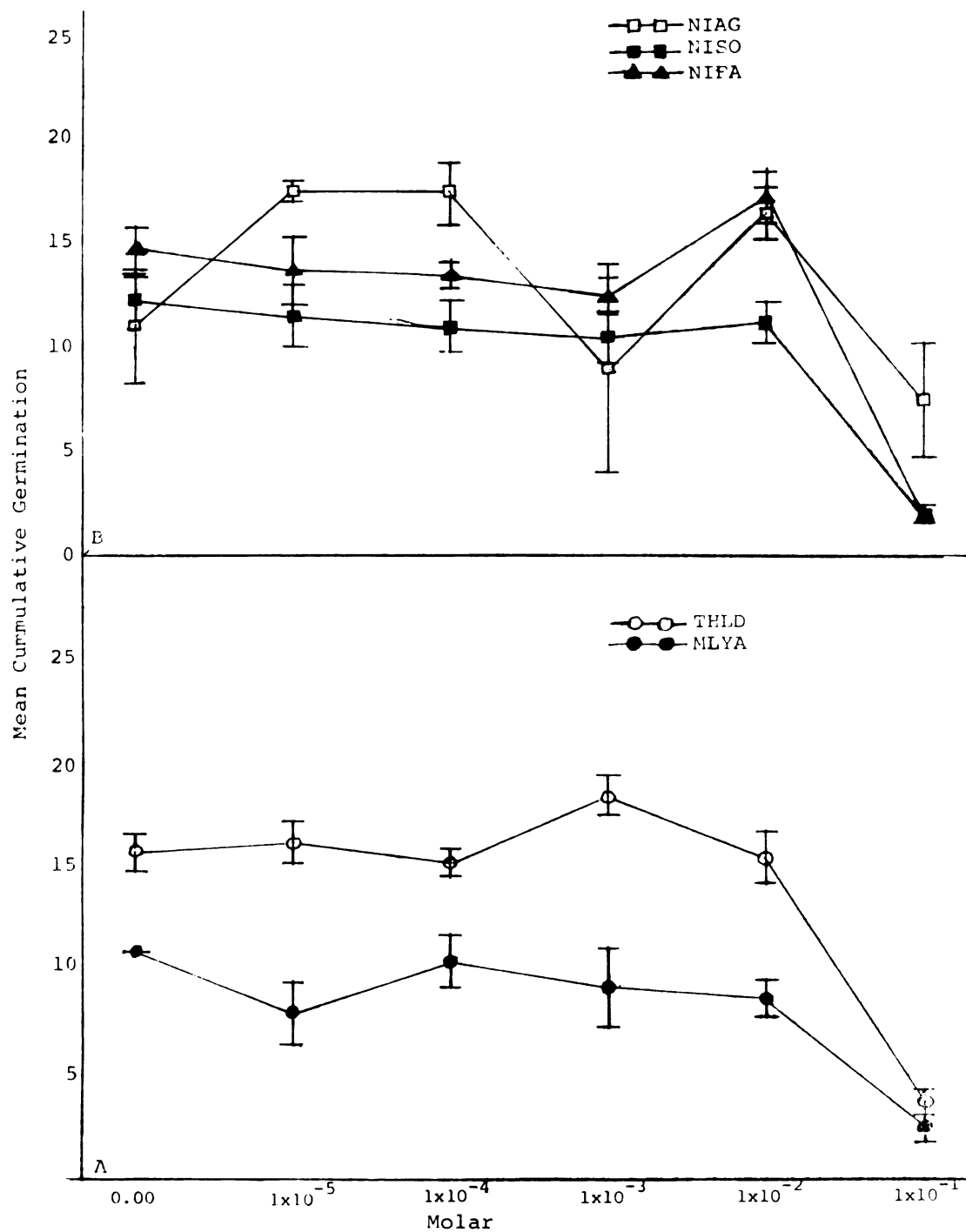
and Ifako, two of the three localities from Nigeria, and also in the two seed sources from the New World Tropics (Figure 15).

Effect of Light

The results of an experiment on the effect of light on germination in E. odoratum showed that light is an important factor in the germination of this species. Continuous darkness did not suppress germination in seeds from Trinidad and Agege which gave cumulative germination of 24 and 40, representing about 33% and 80% of those obtained for continuous light and 11 - 13 hour photoperiod respectively. The effect of continuous darkness inhibited germination in seeds from Guatemala. There were no significant differences in germination among seeds from Malaya, Agege, Ifako, and Trinidad, under continuous light and 11 - 13 hour photoperiods. Total germination ranged from 32 = 63% for continuous light, and 31 to 70% for 11 - 13 hour photoperiods. Here again, the seeds from Trinidad had the highest percent germination (Figure 16).

Discussion

The germination behavior of E. odoratum in response to soaking, moisture stress, nitrate and light treatments varied among seeds from seven localities investigated. Differences and variations in percent germination, and



¹Mean of Four Replicates of 25 Seeds.

Figure 15.--¹Mean Germination in *E. odoratum* from Seven Localities at Varied Molar Concentrations of KNO_3 and their Standard Error.

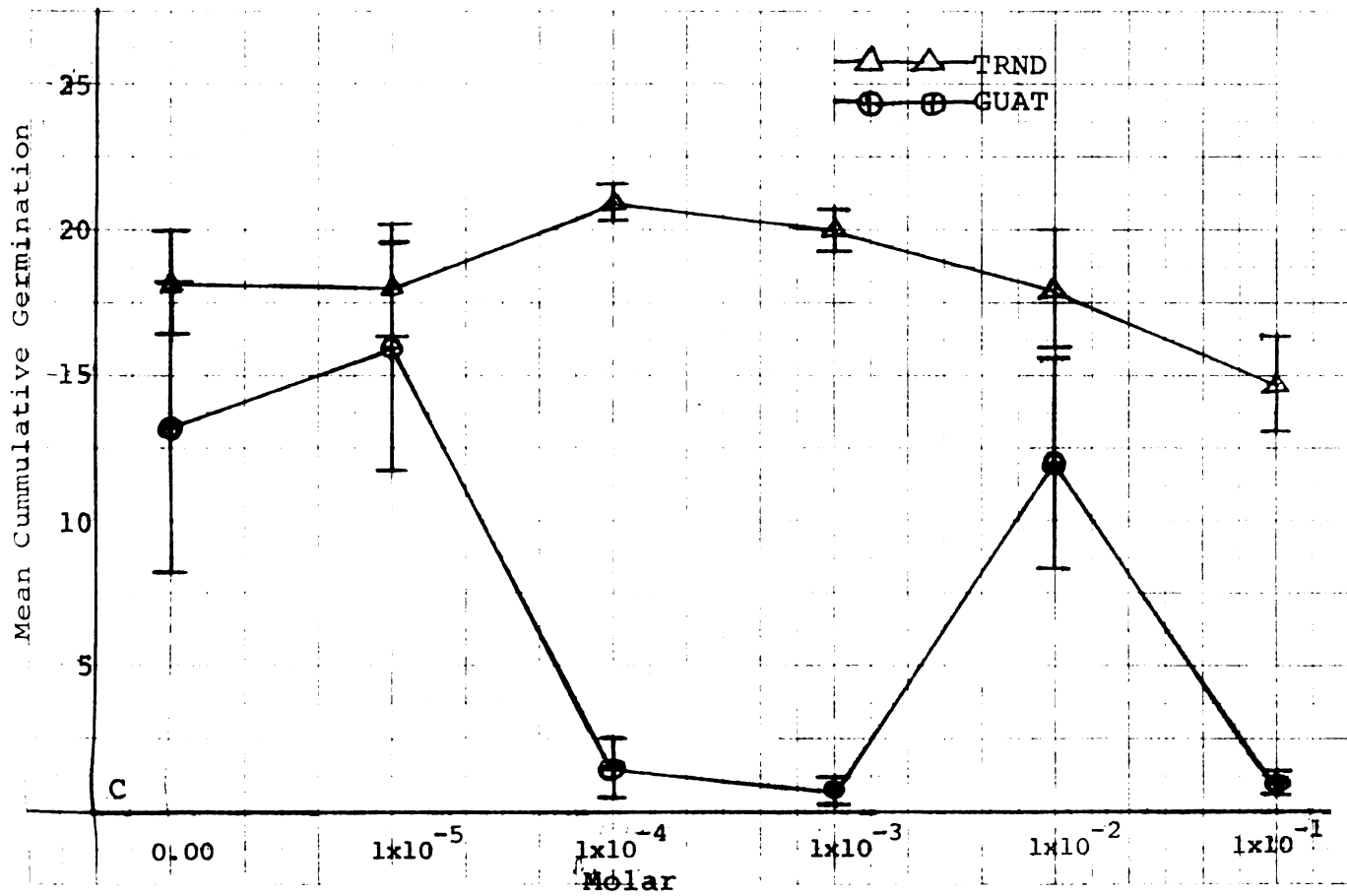
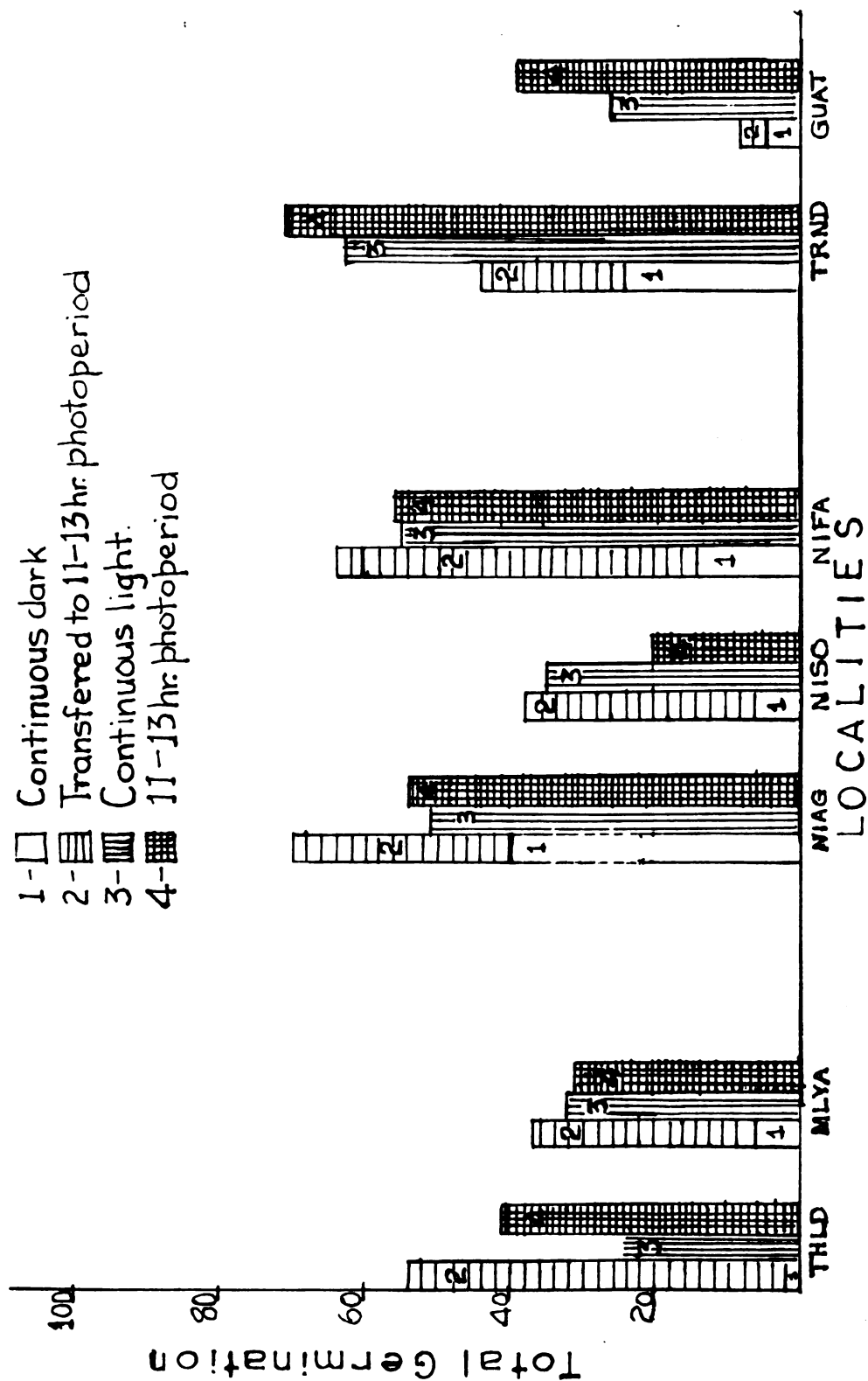


Figure 15.--Continued.



¹Total of 4 Replicates of 25 seeds.

Figure 16.--¹Total Germination in E. odoratum from Seven Localities at Three Light Treatments.

rates of germination observed under the four environmental conditions may be due to adaptations within the species.

Excluding seeds from Thailand, soaking time significantly affected germination in seeds from the remaining six localities investigated. For example, soaking for more than 1 hour did not significantly alter total germination in the seeds from Sango Otta. On the other hand, total germination after soaking for 1 hour and 48 hours was significantly different from the control in seeds from Guatemala. The response to soaking was highly correlated with precipitation of the localities from which the seeds originated ($r = +0.79$).

High osmotic pressure appears to reduce total germination in seeds from the Old World Tropics; yet, in the seeds from the New World Tropics, and in particular, the seeds from Trinidad, there were significant increases in percent germination at high osmotic pressure; 15% and 20% more germination were observed than in the control. It was observed also that seeds from Malaya, Agege, and Sango Otta had about 50% germination of the control at 5 atm.; while the seeds from Agege had about 25% germination of the control at 8 atm. Seeds from Thailand had 5% and 25% germination of the control at 3 and 5 atm.

Differences in germination among the seeds were found to be due to the effects of soaking and moisture

stress; by comparing percent germination of the controls in the two experiments, no significant differences were observed. In the case of the seeds from Sango Otta, collection site is usually water-logged; also, the mean annual precipitation of 2286 mm in Malaya suggests that the seeds from that area may be found in areas of low moisture tensions. The fact that more than 50% germination occurred at 3 and 5 atm. in seeds from Agege, Sango Otta, and Malaya may suggest the plastic nature of seeds from the Old World Tropics to variations in soil moisture conditions. Seeds from Agege perhaps showed a more plastic response than seeds from other areas of the Old World Tropics from the results obtained at the different moisture tensions.

The differences in the rate of germination and percent germination at increased soaking time, as well as at increased osmotic pressure may be an adaptive feature of the seeds to moisture conditions at the different localities. At 1, 3 and 5 atm., seeds of E. odoratum from Trinidad had a significantly higher rate of germination and percent germination than seeds from other localities; at 3 and 5 atm., it had a significantly higher rate and percent germination than at other treatment levels including the control. Although seeds from Agege had a significantly higher rate and percent germination at 1 and 3 atm.

than seeds from other areas of the Old World Tropics, there was a decrease in both the rate and percent germination at these two levels; and at 3 atm., the rate and the percent germinated were significantly lower than the control. Seeds from Trinidad and Guatemala had significantly higher rate and percent germination at 24 and 48 hours soaking time than at either 1 and 4 hours or the control; yet the rate was fairly uniform among the seeds from the Old World Tropics. It thus appears from the data that some modifications in the germination behavior of E. odoratum introduced into the Old World Tropics has occurred. These modifications may have been in the selection for genotypes adapted to moist conditions.

The presence of nitrate in the germination substrate did not appear to have any effect on germination in E. odoratum. Only the seeds from Agege showed significant differences at increased nitrate concentrations. High concentrations of nitrate in the germination substrate is likely to inhibit germination and subsequent seedling establishment. The effect of nitrate, however, may be that of accelerating development of the seedling, particularly in the early emergence and expansion of the primary leaves. There is much literature on the effect of nitrate in breaking dormancy in seeds. There was no evidence from the results obtained that prolonged dormancy exists in the seeds of E. odoratum. The lack of prolonged dormancy

perhaps is a characteristic of the seed that has contributed to the success of E. odoratum in the Old World Tropics; also, it may be a selective attribute that is basic in seeds from all the localities.

Light affected germination in the seven localities of E. odoratum. More than 40% germination was obtained when the seeds kept in continuous darkness were transferred to an 11 - 13 hour photoperiod. A dark period followed by light appeared to induce higher percentage germination in seeds from three areas. The data obtained may suggest that any buried viable seeds may germinate upon disturbance of the site, particularly those that are found on arable land. There is no evidence, however, to indicate whether longer periods of continuous darkness may eventually prevent germination.

The results of these experiments may be used to explain the ecological implications associated with germination behavior of introduced species in alien habitats. The data obtained may suggest also that variations and differences among the seeds from the seven localities may be due to adaptations in E. odoratum under the environmental factors investigated. The characteristic behavior of imbibition, or dormancy, or both appear to be similar in the seeds from the Old and New World Tropics. The number of seeds capable of germinating varied among the seed sources; seeds from Trinidad and Thailand had total

percent germination of 57% and 60%; seeds from Agege and Ifako had 50% and 52%; seeds from Malaya, Sango Otta, and Guatemala had 33% and 34%. By comparing percent germination under different treatments with the total percent germination, it was found that increase or decrease in total germination was due to the effect of soaking time, moisture stress, and light.

There seems to be sufficient evidence that the variability and differences in germination of seeds from seven localities investigated may be related to the features of the environment, particularly, precipitation, in the different localities. In order to understand fully the germination behavior of E. odoratum, further research is needed in the field and laboratory to verify the results obtained in this investigation; and, in addition, to determine light-moisture and temperature-moisture interactions on germination of E. odoratum as well as seeds of other weeds associated with it. It is also important to follow viability and germinability from the onset of seed production in order to determine what type of strategy has been utilized.

Growth Studies

General Observations on Growth and Development

Morphological differences and differences in the rate of growth were observed in the early stages of

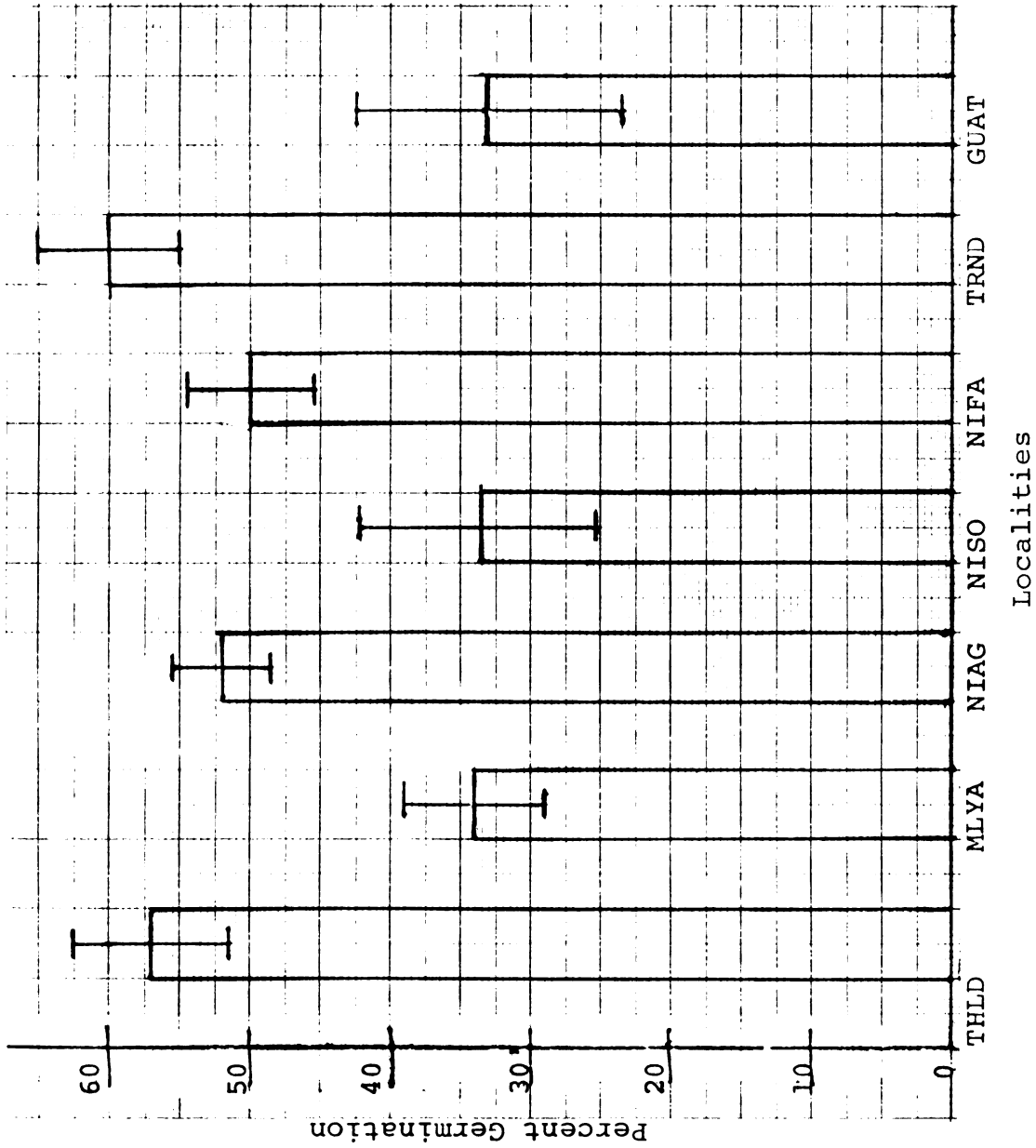


Figure 17.--Total Percent Germination in *E. odoratum* from Seven Localities.

development of E. odoratum. The plants from Guatemala were taller and weaker than plants from other areas. The leaves of plants from Florida were more or less glabrous and nearly entire. At twelve weeks, the internodes of plants from the Old World Tropics were short as compared to later formed internodes which were approximately three to four times as long. The first three pairs of leaves were seen to be generally smaller in surface area, length, and width than later developed ones. Occasionally, the plants from the Old World Tropics produced leaves that were orbiculate and nearly entire. The stems of plants from Florida and Guatemala were usually darker in color than in plants from other localities. Also, the young leaves are in general heavily pubescent except in young leaves of plants from Florida.

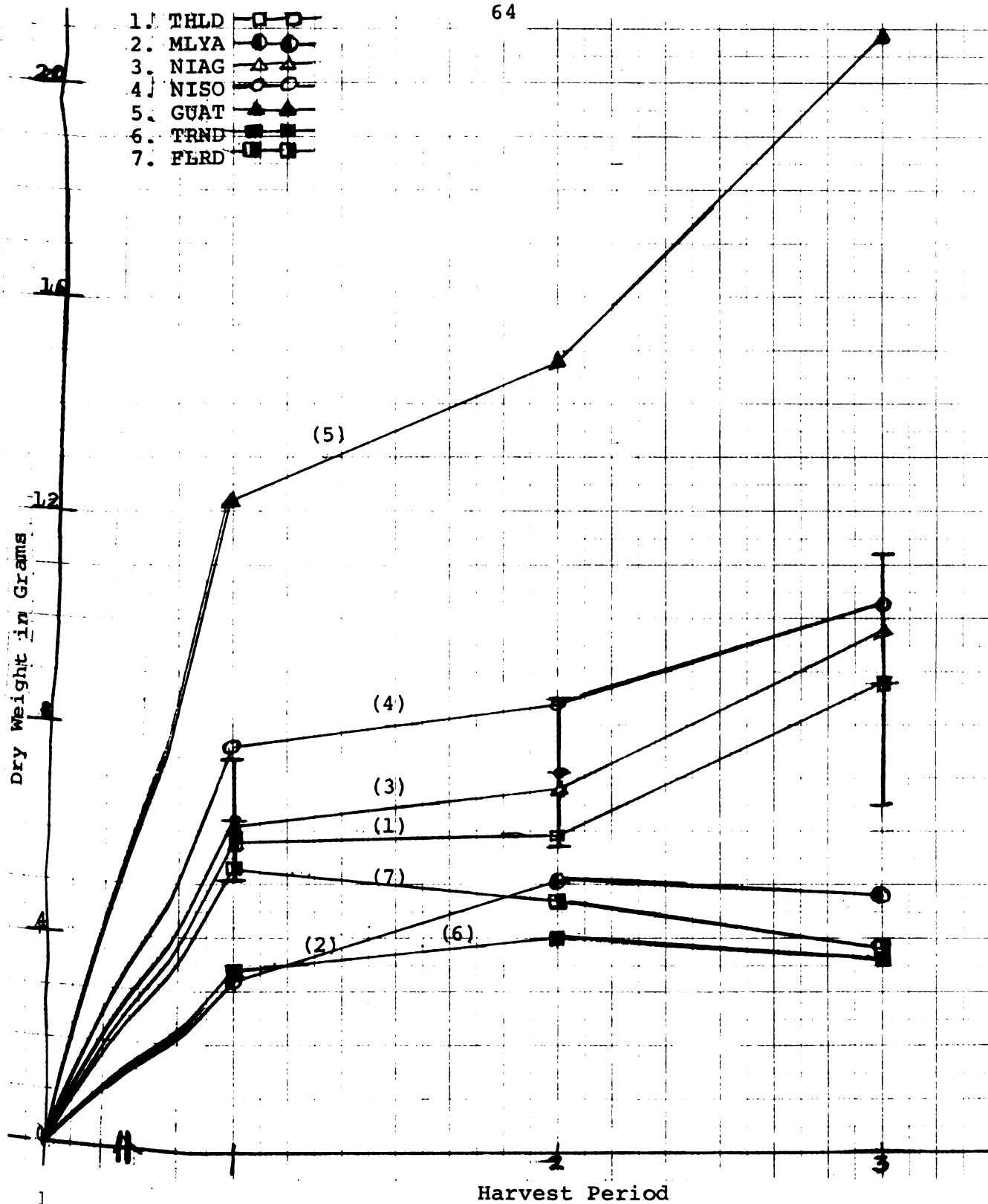
The hypocotyl and lower epicotyl tend to become woody very early in growth. This characteristic was especially noticed in plants growing in a water saturated environment. Secondary roots emerged at this point under conditions just described. Differences in growth among plants growing in different soil moisture conditions were also noticed. Plants growing in a water saturated and dry conditions tend to have broader or smaller and densely hairy leaves than those plants growing at field capacity.

Greenhouse Studies

The data presented here were from plants grown under uniform environmental conditions in the greenhouse to determine if there are variations in some physiological attributes within E. odoratum from Seven Localities.

Dry weight.--There were significant differences among the plants in total plant dry weight. There was an increase in total dry weight in plants from Guatemala, Agege, Sango Otta and Thailand at all sampling periods; there was an increase in total dry weight in the plants from Malaya and Trinidad between the first two samplings followed by a decrease in total dry weight between the second and third samplings; the population from Florida showed a decrease in total dry weight at all sampling periods (Figure 18). There were significant differences in plants from Guatemala and Malaya between the first two samplings, and in plants from Guatemala, Thailand, Agege, and Ifako between the second and third samplings. There were significant differences among the plants from seven areas in total dry weight over all sampling periods, except among plants from Malaya and Florida, and Agege and Sango Otta (Figure 19).

It appears that a definite trend in accumulation of organic matter (biomass) is seen among the plants from seven localities. As early as the first sampling period,



¹Mean of 4 Replicates.

Figure 18.--Mean Dry Weights of *E. odoratum* from Seven Localities on Three Harvest Periods and their Weighted Means $\pm S_{\bar{x}}$.

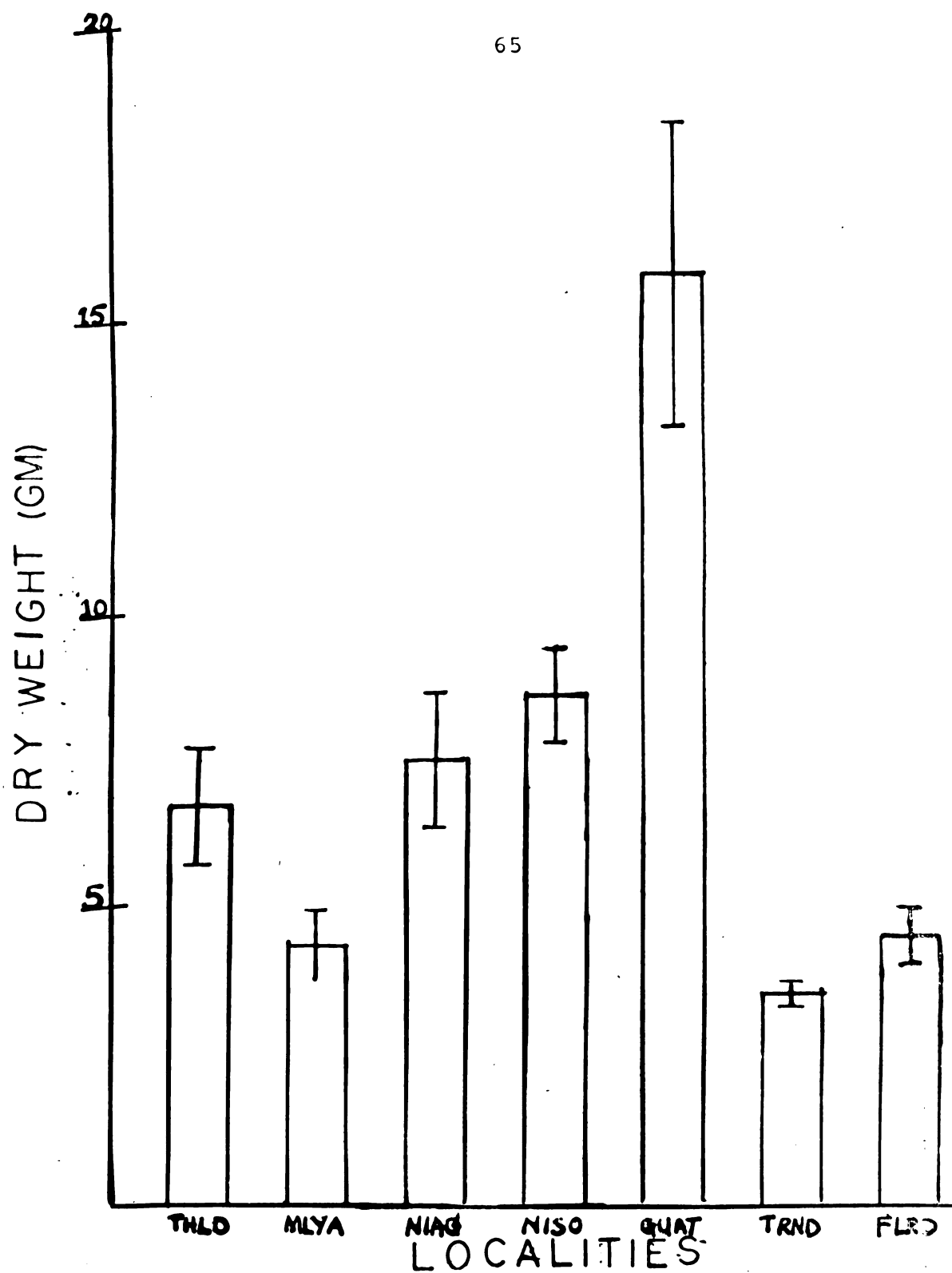
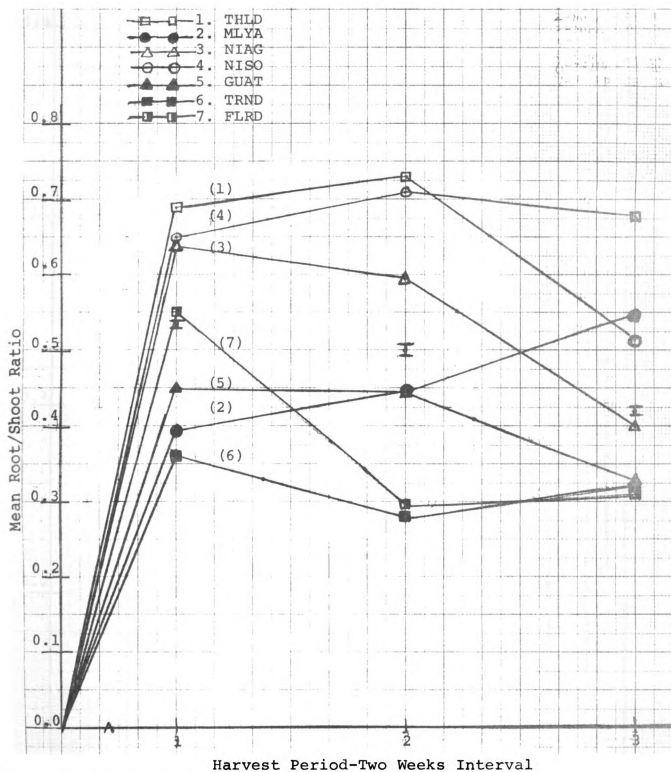


Figure 19.--Means of Dry Weights $\pm \bar{S}_x$ Over Three Sampling Periods in *E. odoratum* from Seven Localities.

plants from Guatemala had the greatest biomass; this trend was maintained throughout the sampling periods. In a period of four weeks from the first sampling, four distinct groups are seen: (1) plants from Guatemala, (2) the group of plants from Agege and Sango Otta, (3) those from Malaya and Florida, and (4) those from Trinidad (Figure 20).

Root/shoot ratio.--Figure 20 shows the pattern of root/shoot ratio among plants from the seven areas investigated. Plants from Thailand and Sango Otta had a higher root/shoot ratio at the second sampling than at the first or the third sampling periods. Plants from Agege and Guatemala had lower root/shoot ratio at the second and third sampling periods than at the first. Plants from Malaya continued to increase in root/shoot ratio at second and third samplings. A lower root/shoot ratio was obtained for plants from Florida and Trinidad at the second sampling than at either the first or the third. All differences were significant among and between samplings at $P < 0.05$.

An examination of root/shoot ratio over all sampling periods showed that plants from the Old World Tropics had higher root/shoot ratio than plants from the New World Tropics. Plants from Thailand had the highest ratio of 6.81 ± 0.14 , and plants from Trinidad had the lowest ratio of 3.99 ± 0.26 . All differences were significant at $P < 0.05$.



¹Mean of 4 Replicates.

Figure 20.--¹Mean Root/Shoot Ratio of *E. odoratum* from Seven Localities Calculated from Mean D_r and Mean D_x and their Weighted Means $\pm$ SX on Three Harvest Periods.

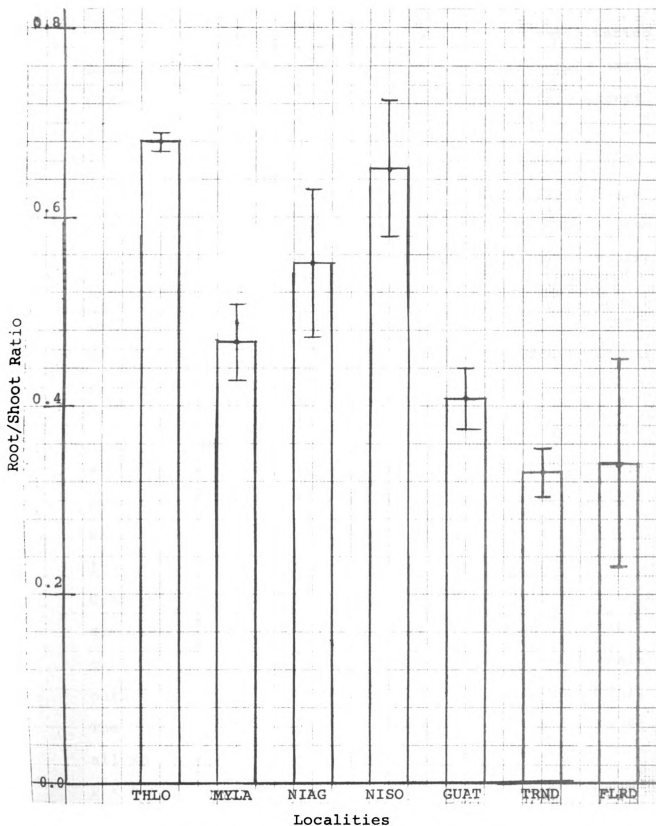


Figure 21.--Means of Root/Shoot Ratio $\pm$ SE Over Three Sampling Periods in *E. odoratum* from Seven Localities.

Root weight ratio (RWR).--Root weight ratio varied among plants from the seven localities. Differences among plants were significant at both sampling intervals except in plants from Thailand and Sango Otta. Plants from Thailand had the highest ratio (0.405), and those from Trinidad had the lowest ratio (0.237) (Figure 22). There was no apparent change in root weight ratio in plants from Thailand, Malaya, and Trinidad at both sampling intervals; the others showed significant decrease in root weight ratios at the second sampling interval. Plants from the Old World Tropics had higher root weight ratio than plants from the New World Tropics.

Leaf area (LA) and leaf area ratio (LAR).--Leaf area increased in plants from Thailand, Agege, and Guatemala at all sampling periods; however, plants from Malaya, Sango Otta, Trinidad, and Florida showed a decrease in leaf area at the third sampling period. Plants from Guatemala had the largest leaf area and differences between sampling periods and among the other plants were significant. Increase in leaf area in the plants from Guatemala parallels the increase in dry weight (Figures 23 and 24). The correlation between total dry weight and leaf area at all samplings was found to be highly significant at $P < 0.01$; $r = 0.907$ ($n = 21$). There were no significant differences among plants from the other areas except

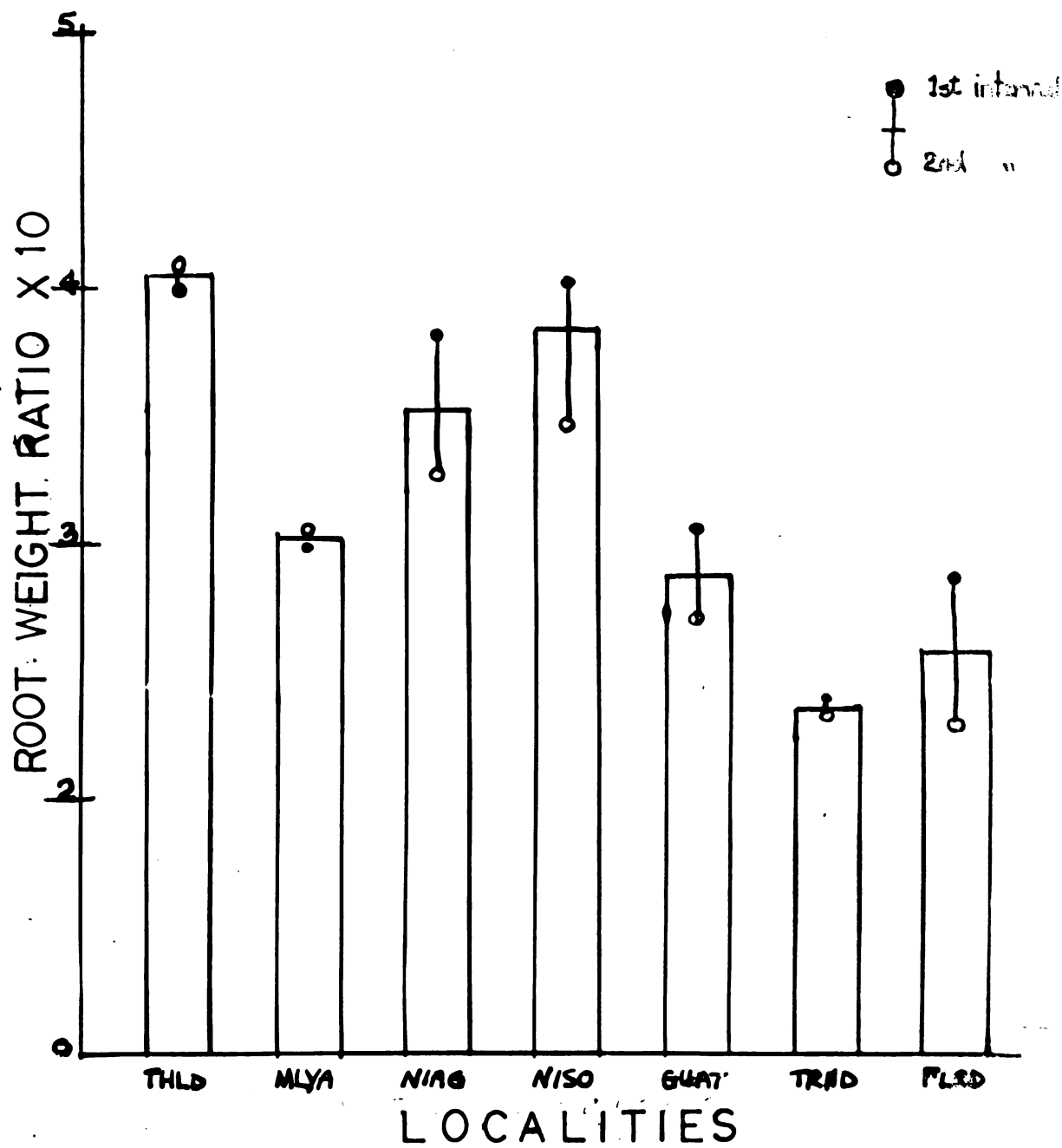
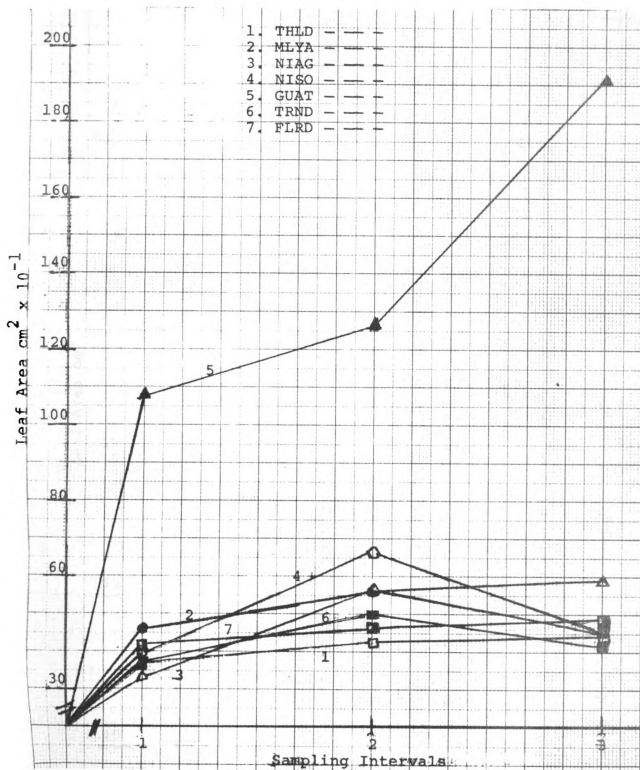


Figure 22.--Means of Root Weight Ratio of E. odoratum Localities over Two Sampling Intervals.

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¹Mean of 4 Replicates.

Figure 23.--¹Mean Leaf Area (cm^2) of *E. odoratum* from Seven Localities Over Three Sampling Periods.

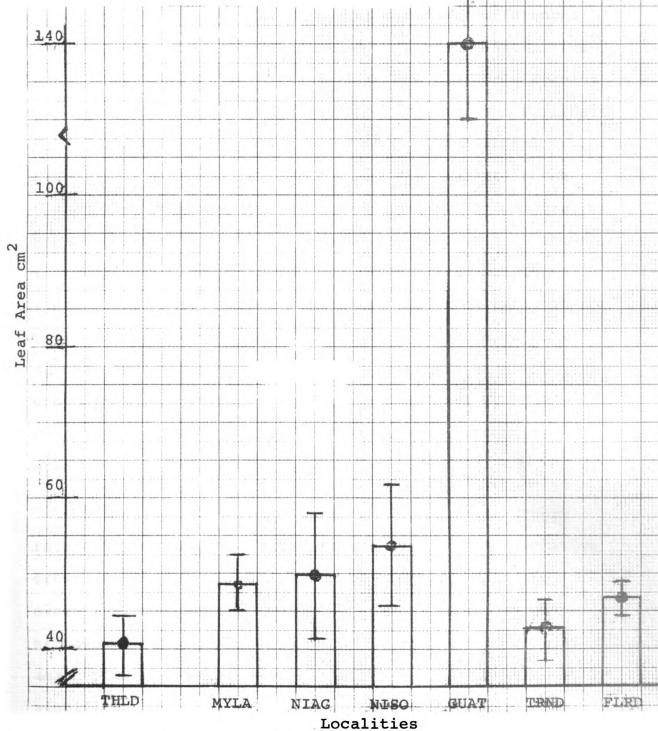


Figure 24.--Means of Leaf Area (cm²) of *E. odoratum* from Seven Localities over Three Sampling Periods.

Sango Otta, at the second sampling period, and Agege, at the third sampling period.

Weighted means over three sampling periods is presented in Figure 24. There were significant differences among plants from all the areas investigated. Except for the plants from Thailand, those from the Old World Tropics had larger leaf area than those from Trinidad and Florida.

Leaf area ratio varied between plants at all sampling intervals. Leaf area ratio was highest in the plants from Trinidad and least in those from Sango Otta. Mean leaf area ratio over two sampling intervals is shown in Figure 25. Except in the plants from Malaya, plants from the Old World Tropics had lower leaf area ratio than those from the New World Tropics. All differences were significant at $P < 0.05$. There were little or no differences in the plants from Agege and Sango Otta at both sampling intervals; differences among plants from other areas were however significant.

Net assimilation rate (NAR) and relative growth rate (RGR).--Results of net assimilation rate and relative growth rates are summarized in Table 2. There was no overall significance between sampling intervals in both net assimilation and relative growth rates. Differences among plants from the seven localities were however significant. Plants from Thailand had the highest net

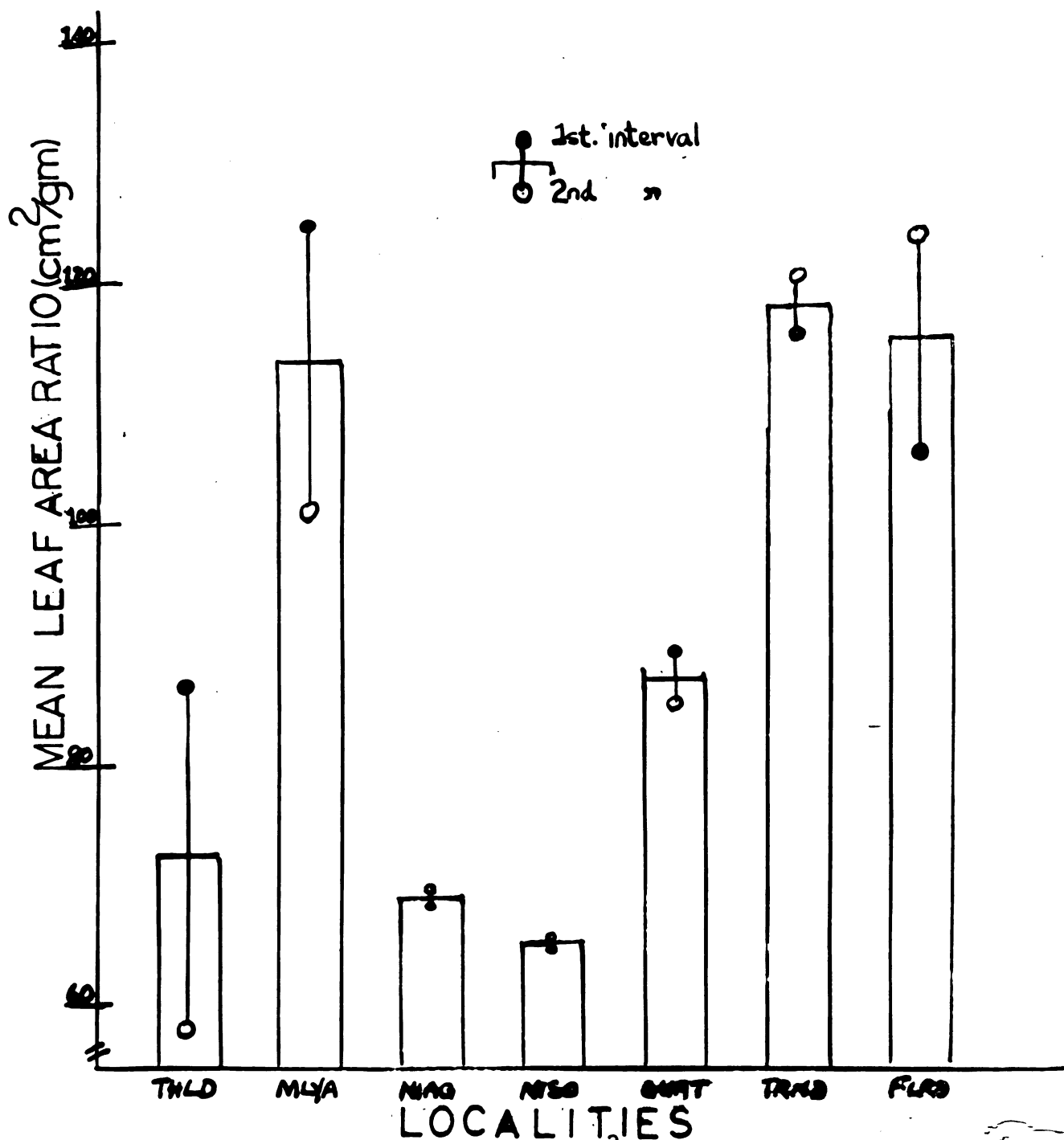


Figure 25.--Mean Leaf Area Ratio (cm²/gm) Over Two Sampling Intervals and their Range in E. odoratum from Seven Localities.

TABLE 2.--Relative growth rate gm/gm/wk, and net assimilation rate (cm^2/gm), in E. odoratum from seven localities over two sampling intervals.

Localities	GRG (gm/gm/wk)			NAR (cm^2/gm)		
	Sampling Interval		Mean	Sampling Interval		Mean
	1	2		1	2	
THLD	0.004	0.209	0.106	0.003	0.239	0.121
MLYA	0.229	-0.026	0.101	0.122	-0.017	0.052
NIAG	0.056	0.181	0.118	0.054	0.174	0.114
NISO	0.050	0.104	0.077	0.052	0.106	0.079
GUAT	0.093	0.173	0.133	0.069	0.136	0.102
TRND	0.075	-0.052	0.011	0.043	-0.029	0.007
FLRD	-0.034	-0.068	-0.051	-0.054	-0.128	-0.091

assimilation rate of $0.121 \text{ cm}^2/\text{gm}$, and those from Florida had the least net assimilation rate of $-0.128 \text{ cm}^2/\text{gm}$.

Increase in net assimilation rates was observed in plants from Thailand, Agege, Sango Otta and Guatemala over the sampling intervals.

There was an increase in relative growth rates in the plants from the Old World Tropics except those from Malaya. Increase in relative growth rate occurred only in plants from Guatemala in the New World Tropics. Differences between sampling intervals were significant in plants from all the localities investigated. There were significant differences also among plants from the seven localities by making use of the mean relative growth rate over two sampling intervals. Plants from Guatemala had the highest relative growth rate of 0.133 gm/gm/wk and those from Florida had the least of -0.051 gm/gm/wk .

Correlation with habitat factors.--A summary of simple correlations is shown in Table 3. Only RGR was significantly correlated with mean annual rainfall. It was expected that high correlations would be obtained with respect to latitude and longitude and perhaps temperature. It did confirm, however, that variations and differences among the plants may be due to available moisture in specific localities.

TABLE 3.--Simple correlation coefficient with climatic features of growth attributes of E. odoratum from seven localities.

	Lat.	Long.	Mean Ann. °C	Mean Ann. rainfall
LAR	+0.27	+0.53	+0.33	+0.35
NAR	+0.51	+0.18	+0.20	+0.60
RWR	+0.31	+0.30	+0.20	+0.47
RGR	+0.67	+0.08	+0.36	+0.75*

* significant at $P < 0.05$.

Effect of Moisture

Dry weight.--Results of the effect of soil moisture on total dry weight accumulation are summarized in Figure 26. There were significant differences between treatments and among plants from the seven localities investigated. Total dry weight accumulation among plants from these areas was less at temporary wilting point than at either field capacity or saturated point. At the two extremes of moisture conditions, plants from the Old World Tropics had larger total dry weights than those from the New World Tropics, excluding plants from Guatemala which had the largest total dry weight of 17.92g at saturated point and second largest total dry weight of 17.95g at temporary wilting point. Although no clear pattern was observed among plants from both the New and the Old World Tropics at the two extreme moisture conditions, plants from four localities--Thailand, Malaya, Guatemala, and Trinidad--however showed increase in total dry weight at saturated point, while there was a decrease in total dry weight in plants from all localities at temporary wilting point.

Root/shoot ratio.--Figure 27 shows the effect of moisture on root/shoot ratio in plants from seven areas investigated. There were significant differences in root/shoot ratio among the plants from all localities at three moisture conditions. Differences were due to the

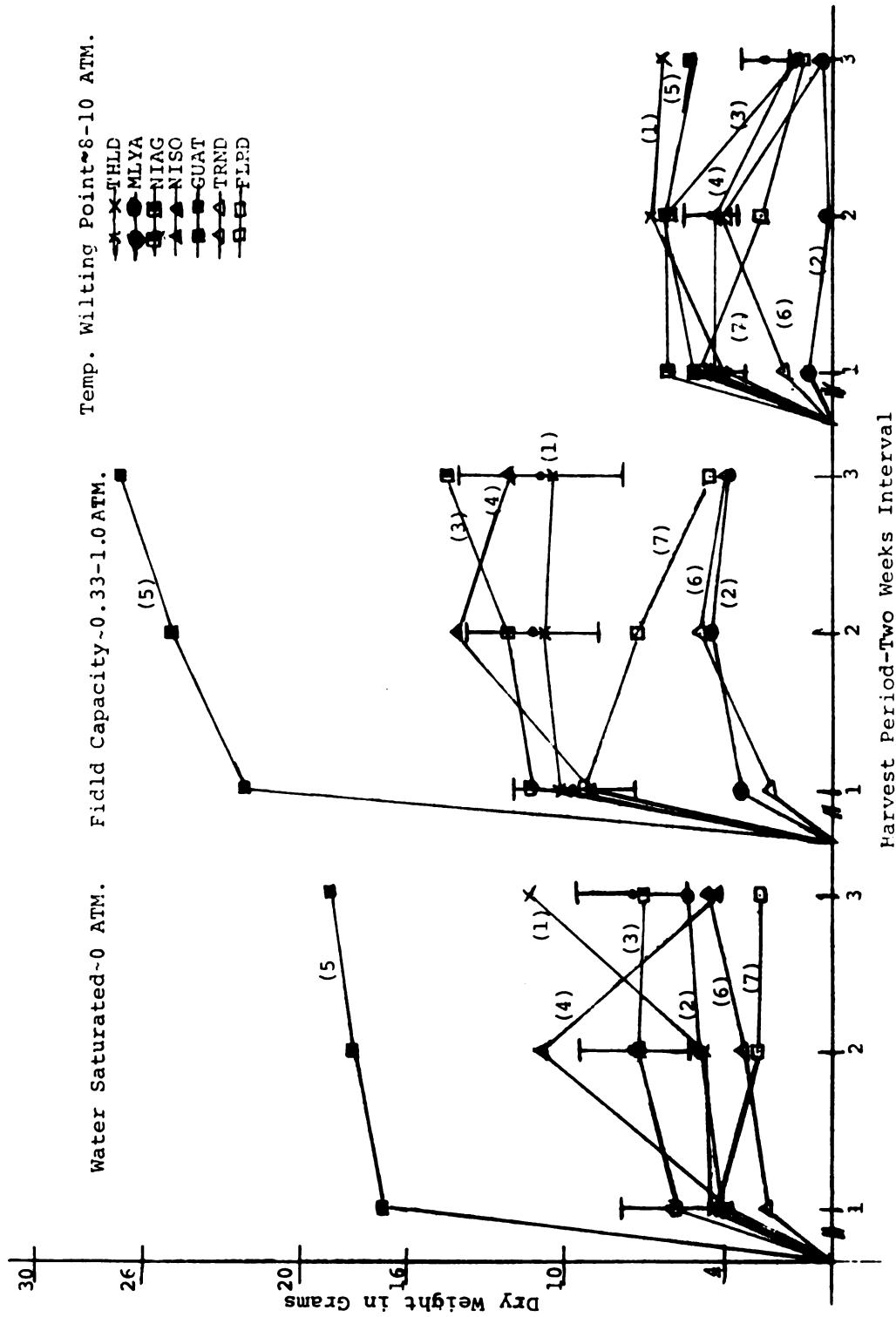


Figure 26.--Dry Weight of *E. odoratum* from Seven Localities at Three Moisture Levels and their Weighted Means $\pm$ SE at Three Sampling Periods.

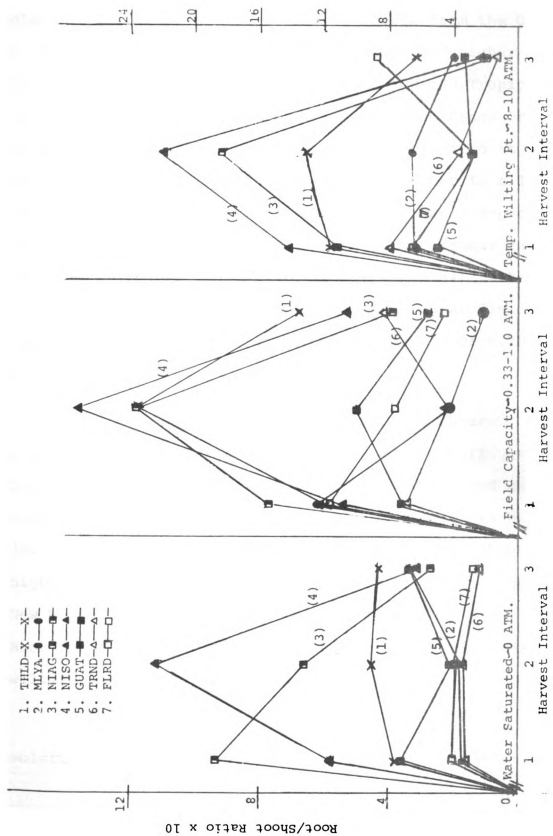


Figure 27.--Root/Shoot Ratio of E. odoratum from Seven Localities at Three Moisture Levels.

plants and treatment effects only. Plants from the Old World Tropics excluding those from Malaya had higher root/shoot ratio than those from the New World Tropics at all treatment levels. Plants from Agege and Sango Otta appear to have rapid decrease in root/shoot ratio at all treatment levels. Root/shoot ratio was higher in all plants at temporary wilting point than at field capacity or saturated point. For example, total root/shoot ratio at three samplings in plants from Agege (18.84) at temporary wilting point was about twice as high as at field capacity and saturated point which had totals of 6.70 and 8.08 respectively.

Root weight ratio.--Root weight ratio varied among plants and between treatments. There were significant differences among them at each treatment level and between sampling intervals. The results are summarized in Figure 28. Excluding plants from Malaya, root weight ratio was higher among those from the Old World Tropics than the New World Tropics at the different moisture conditions. Root weight ratio was higher among all plants at temporary wilting point than at saturated point.

Leaf area ratio.--Figure 28 shows the effect of moisture in leaf area ratio among plants from the seven

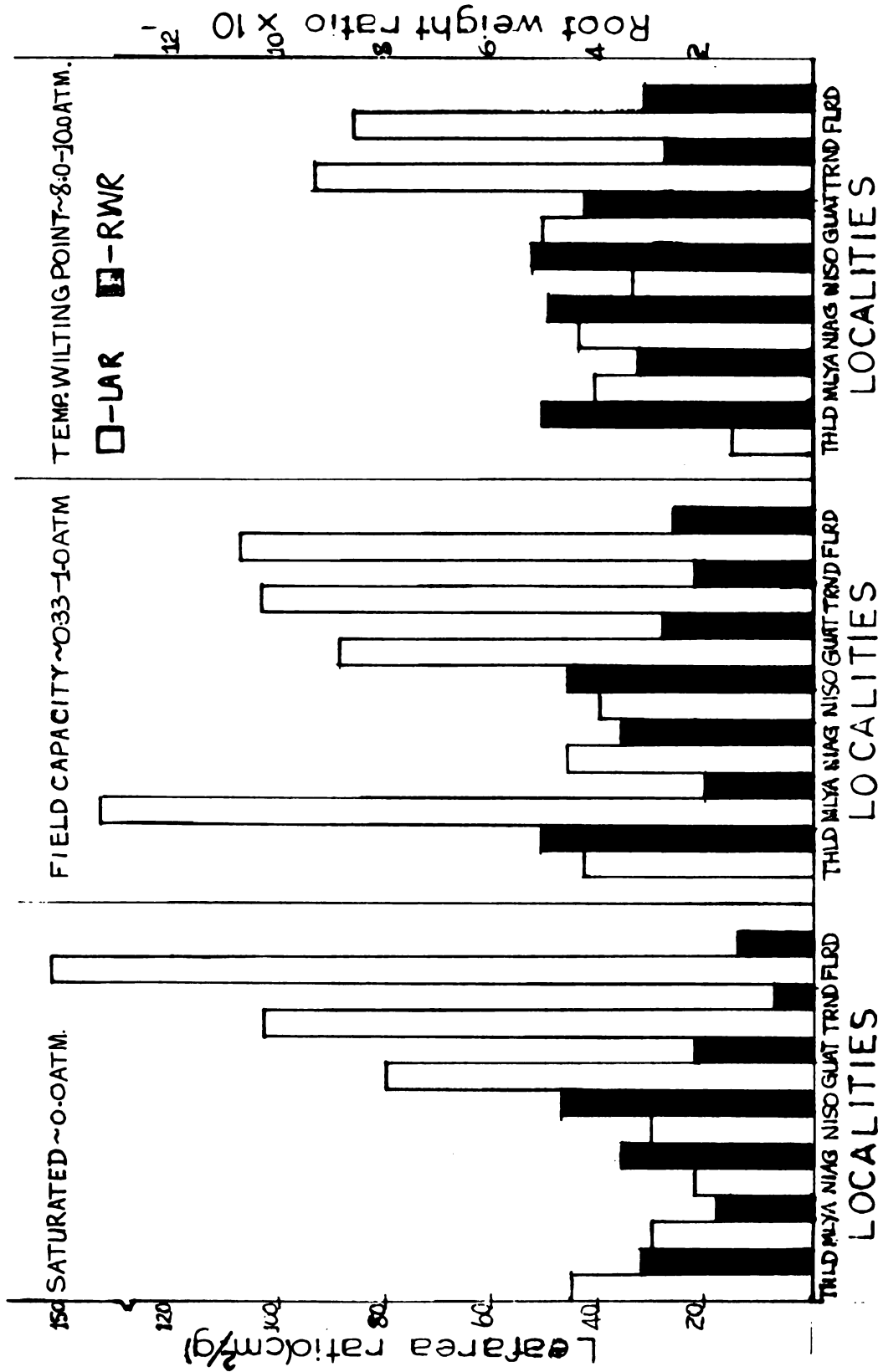


Figure 28.--Comparison Between LAR and RWR in *E. odoratum* from Seven Localities at Three Moisture Levels Over Two Sampling Intervals.

areas investigated. Leaf area ratio was higher in plants from the New World Tropics than those from Old World Tropics at the different moisture treatments excluding the plants from Malaya which had the highest leaf area ratios at temporary wilting point than at saturated point. Differences among plants from different areas and between treatments were highly significant at $P < 0.01$.

The trends in root weight and leaf area ratios at the different moisture levels showed that the roots were more sensitive than the leaves in response to the treatments in plants from the New World Tropics. Both the roots and the leaves, however, were sensitive to the treatments in plants from the Old World Tropics. In the plants from the Old World Tropics, both the roots and leaves contributed primarily to the total dry weight; in plants from the New World Tropics, the leaves contributed more to the total dry weight than the roots. It would appear, therefore, that the rate of development of either the leaves or the roots are adaptive features in the plants from the Old World Tropics.

Net Assimilation and relative growth rates.--The results of the effect of moisture stress on net assimilation rate and relative growth rate are summarized in Tables 4 and 5. There was no overall significance among the plants at all treatment levels. A one-way analysis of

TABLE 4.--Relative growth rate (gm/gm/wk) in E. odoratum from seven localities at three moisture stress localities.

Treatments	Sampling Interval	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD
¹ SP	1	0.043	0.089	0.115	0.531	0.031	0.210	-0.211
	2	0.430	0.048	-0.013	0.482	0.023	0.158	-0.009
	Mean	0.236	0.068	0.051	0.506	0.027	0.184	-0.110
² FC	1	0.028	0.151	0.038	0.213	0.062	0.388	-0.114
	2	-0.012	-0.082	0.090	-0.068	0.042	-0.099	-0.254
	Mean	0.008	0.034	0.064	0.072	0.052	0.144	-0.184
³ TWP	1	0.328	-0.899	0.102	-0.006	0.000	0.405	-0.317
	2	-0.327	-0.456	-0.824	-0.585	-0.082	-1.393	-0.285
	Mean	0.0005	-0.677	-0.361	-0.295	-0.041	-0.494	-0.301

¹SP = saturation point

²FC = field capacity

³TWP= temporary wilting point

TABLE 5.--Net assimilation rate ($\text{gm/cm}^2/\text{wk}$) in E. odoratum from seven localities at three moisture stress localities.

Treatment	Sampling Interval	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD
¹ SP	1	0.010	0.027	0.031	0.153	0.004	0.022	-0.014
	2	0.109	0.016	-0.022	-0.031	0.003	0.014	-0.001
	Mean	0.059	0.021	0.004	0.061	0.003	0.018	-0.007
² FC	1	0.007	0.014	0.010	0.056	0.007	0.039	-0.012
	2	-0.002	-0.005	0.017	-0.016	0.005	-0.009	-0.019
	Mean	0.002	0.004	0.013	0.020	0.006	0.015	-0.015
³ TWP	1	0.821	-0.535	0.026	0.003	0.000	0.051	-0.039
	2	-0.013	0.070	-0.171	0.116	-0.009	-0.125	-0.038
	Mean	0.104	-0.232	-0.072	0.059	-0.004	-0.037	-0.038

¹SP = saturation point

²FC = field capacity

³TWP= temporary wilting point

variance for each treatment showed that differences among plants from all areas were significant. Net assimilation rate varied among the plants at the two extremes of moisture treatment. The plants from Thailand had the highest net assimilation rate at temporary wilting point and second only to those from Sango Otta at saturated point. Relative growth rate varied also among plants from the seven areas investigated. Plants from Sango Otta had the highest relative growth rate at saturated point followed by those from Thailand (Table 4). All plants showed reduced growth rates at temporary wilting point.

Effect of Nitrogen

Results of the effect of nitrogen on plant height, number of leaves per plant, total dry weight, root/shoot ratio, leaf area, leaf area ratio and total nitrogen are presented here.

Plant height and number of leaves per plant.--There were no marked differences in height and number of leaves per plant among plants from the seven areas investigated in the control and nitrogen treated plants (Figures 29 and 30). Nitrogen appears to have no effect on plant height and number of leaves produced per plant under the conditions at which the investigation was carried out. Significant differences in plant height and number of leaves could not

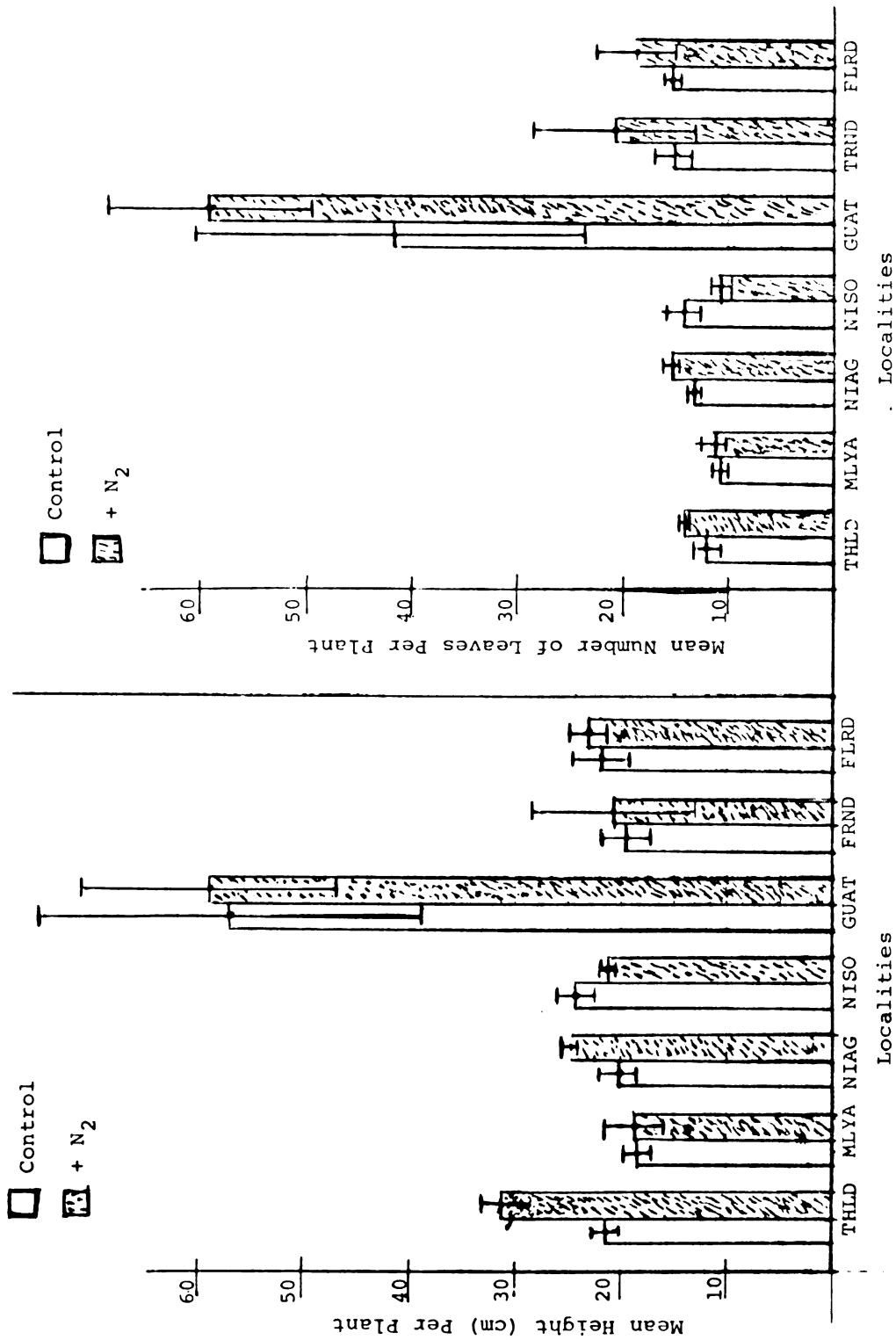


Figure 29.--Mean Height (cm) Per Plant of *E. odoratum* From Seven Localities Treated with Nitrogen Six.

Figure 30.--Mean Number of Leaves Per Plant of *E. odoratum* From Seven Localities Treated with Nitrogen Six.

be attributed to the effect of nitrogen. Variations within plants from each locality were evident in plant height and number of leaves.

That there were no significant differences between treatments may be due to either very low nitrogen concentrations in the soil as a result of leaching (application of nitrogen was stopped one week before harvest), or excess nitrogen assuming that the greenhouse soil already had a high nitrogen content, or the effect was not manifested in either the plant height or the number of leaves.

Dry weight.--Accumulation of dry matter appears to be uniform in both the control and treated plants. There was no significant differences that could however be attributed to the effect of nitrogen in total dry weight; for example, plants from an area that showed significant differences in the control were also significantly different in the nitrogen treated plants (Figure 31). Differences among plants from each locality may be assumed to be inherent in the species. It is noted that except for plants from Guatemala, those from the New World Tropics had lower total dry weights than plants from the Old World Tropics.

Root/shoot ratio.--Although there was no overall significant difference among plants from each area between

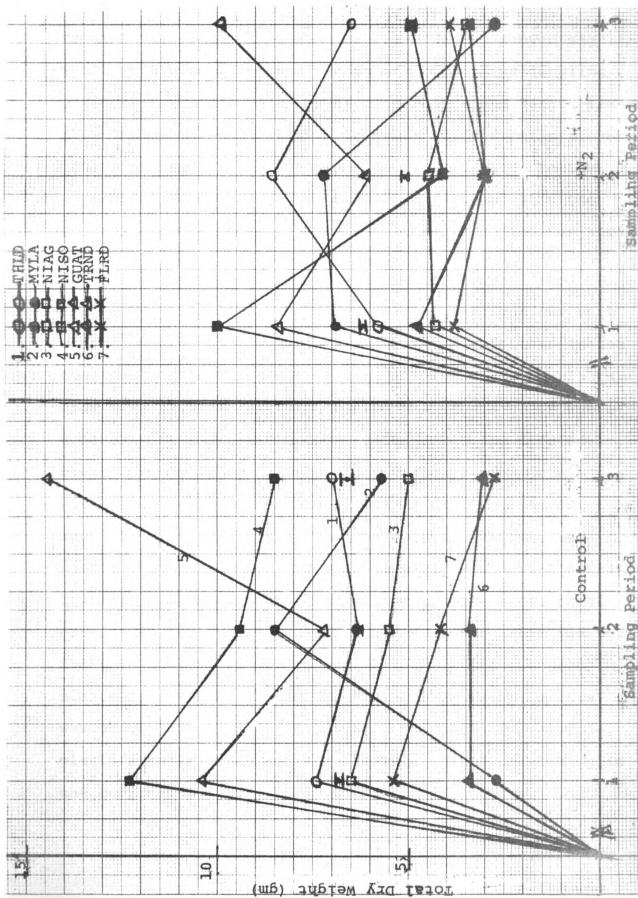


Figure 31.--Effect of Nitrogen on Total Dry Weight (gm) and Weighted Mean (W) in *E. odoratum* from Seven Localities at Three Sampling Periods.

treatments, plants from some areas, however, showed significant differences between treatments over three sampling periods. Excluding the plants from Malaya and Agege, plants from the others had lower root/shoot ratios under nitrogen treatment than in the control. Also, root/shoot ratios were higher in plants from the Old World Tropics in the control and treated plants than in those from the New World Tropics (Figure 32).

Total nitrogen.--Total Kjeldahl nitrogen per unit of dry weight was higher in the treated plants than in the control. There were significant differences among plants from each area and between treatments. While there was generally an increase in total nitrogen in the treated plants from some areas, there was a decrease in total nitrogen in the control plants from four of the seven localities (Figure 33). Total nitrogen in the treated plants over three sampling periods showed that plants from Trinidad and Florida had about twice as much nitrogen as present in those from the Old World Tropics. This was not the case however in the control. Also, total nitrogen in plants from the New World Tropics in the treated plants was about twice as high as in the controls. For example, plants from Trinidad had a total nitrogen of 169.6 mg/g in the control and 240.4 mg/g in the treated plants.

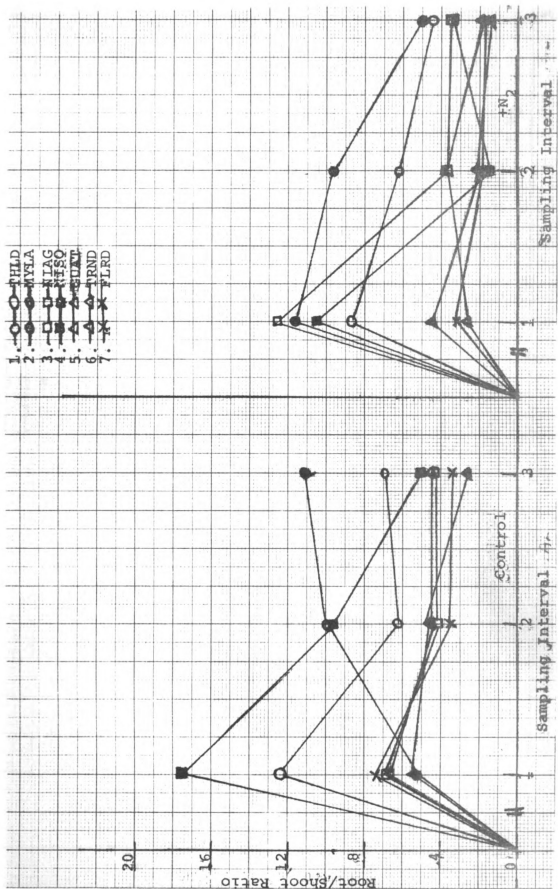


Figure 32.--Effect of Nitrogen on Root/Shoot Ratio in E. odoratum from Seven Localities at Three Sampling Periods.

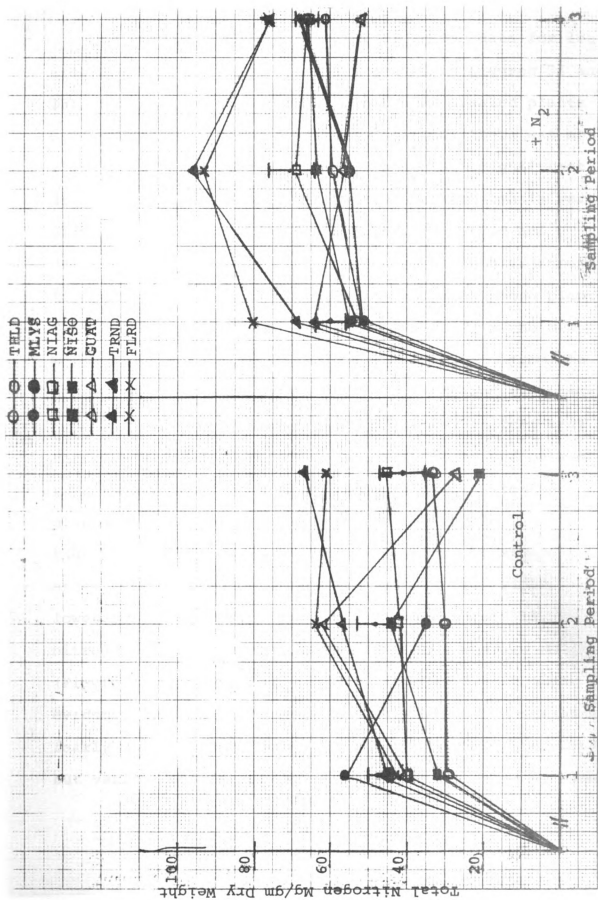


Figure 33.--Total Kjeldahl Nitrogen Mg/gm Dry Weight and Weighted Means $\pm Sx$ in *E. odoratum* from Seven Localities over Three Sampling Periods.

Leaf area and leaf area ratio.--The data for leaf area and leaf area ratio are summarized in Figures 34 and 35. Although leaf areas in the nitrogen treated plants were generally larger than in the control, there was no significant difference between treatments. Significant differences between sampling periods and treatments were observed however. Plants from Guatemala (867.7 and 941.7 cm²/g) had the largest leaf area at both treatment levels (Figure 34). Variations in leaf area among plants from each locality were observed. Plants from the New World Tropics had larger leaf area than plants from the Old World Tropics between sampling periods and treatments.

There were significant differences in leaf area ratio among plants from the seven localities and between treatments. Leaf area ratio in the nitrogen treated plants were higher in those from the New World Tropics than in those from the Old World Tropics. No apparent effect of nitrogen on plants from Malaya was evident as a lower leaf area ratio (59.6 cm²/g) was obtained in the nitrogen treated plants than in the control (73.2 cm²/g) (Figure 35). Variations in leaf area ratio were also evident. The range between the two sampling intervals was fairly uniform among some plants from areas in the control, but varied considerably among others in the treated plants.

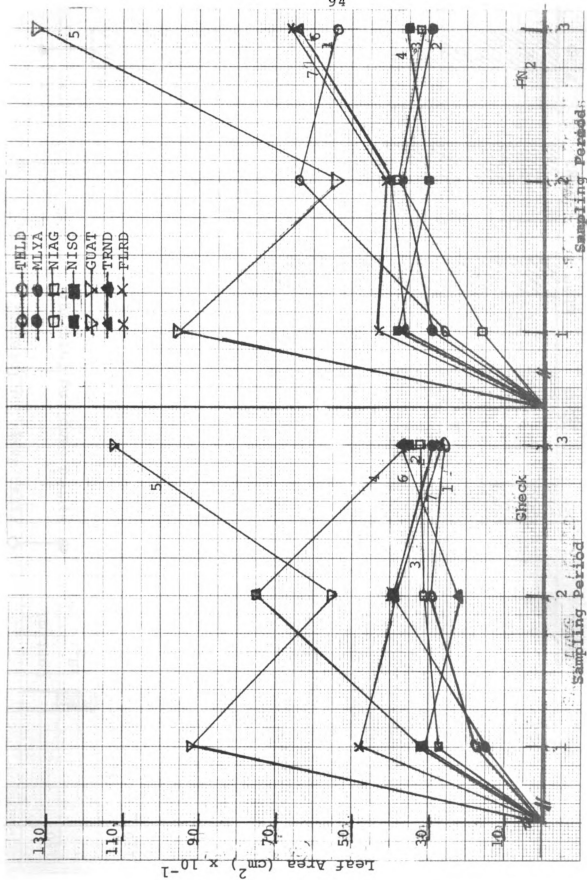


Figure 34.--Effect of Nitrogen on Leaf Area (cm²) in *E. odoratum* at Three Sampling Periods.

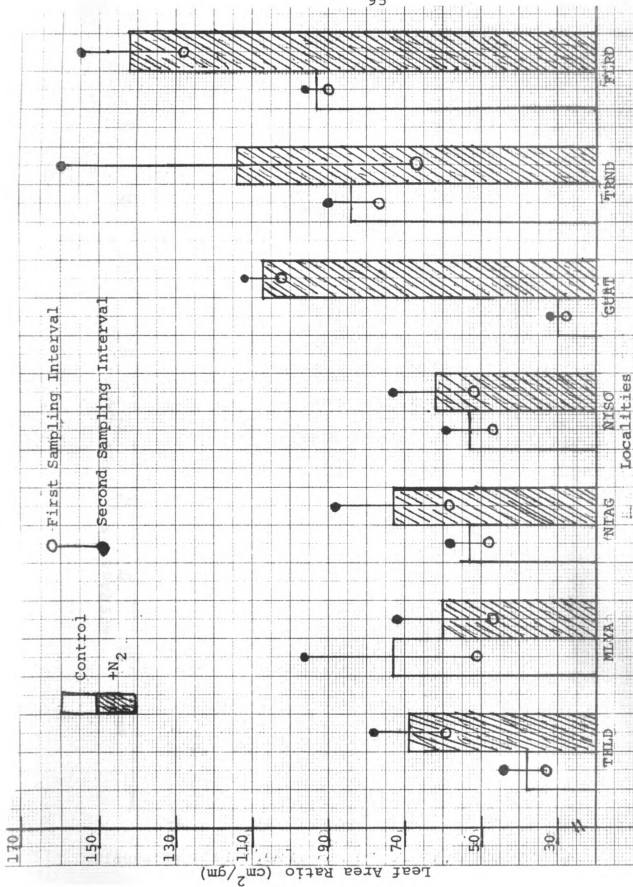


Figure 35.--Mean Leaf Area Ratio (cm^2/gm) in *E. odoratum* from Seven Localities over Two Sampling Intervals.

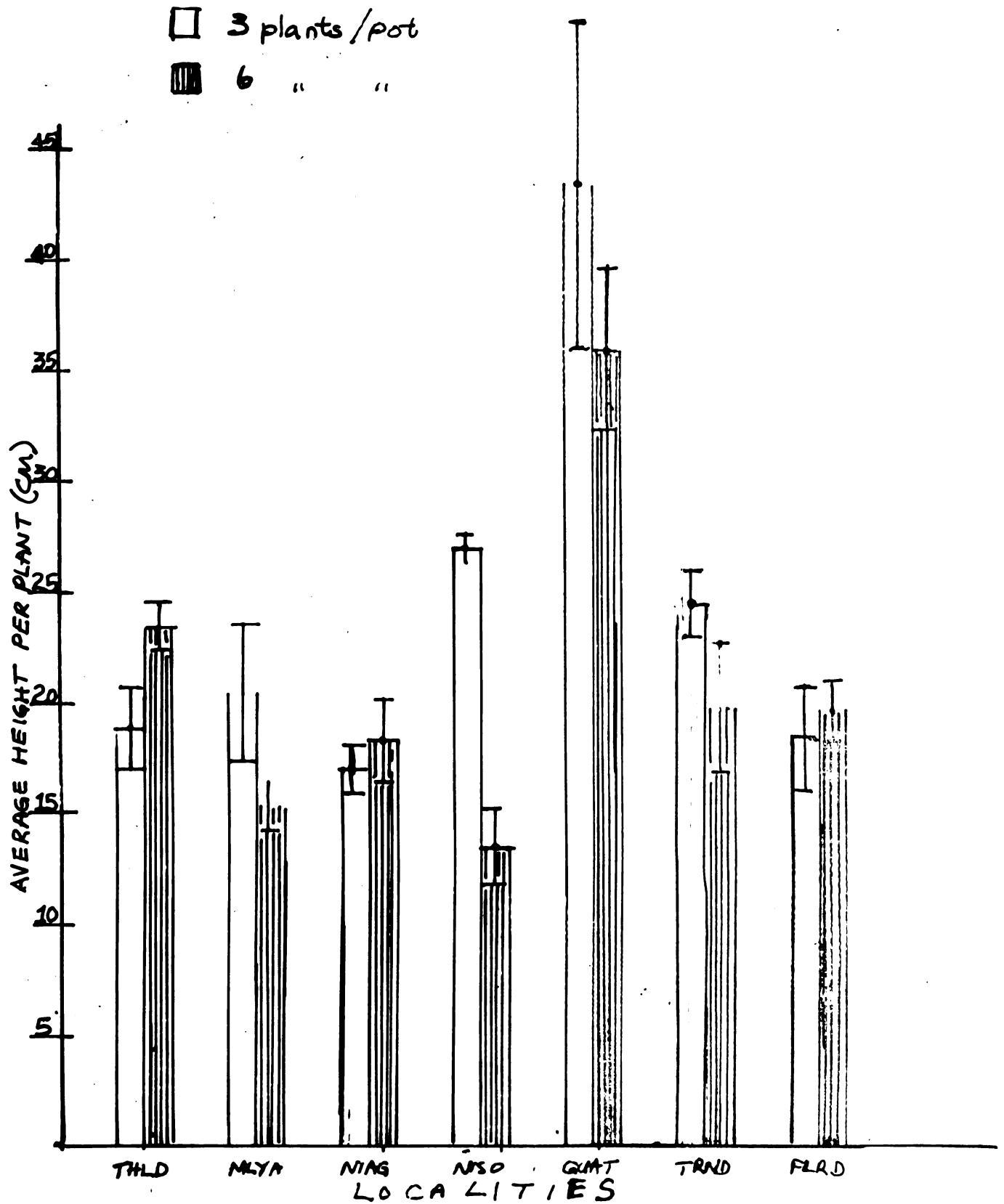


Figure 36:--Average Height Per Plant (cm) $\pm$ S $\bar{x}$ of *E. odoratum* from Seven Localities at Two Density Levels of Three and Six Plants Per Pot.

Nitrogen did not appear to have any definite effect on growth and development of E. odoratum. Increments and variations in leaf area, leaf area ratio may be due to nutritional effect only. Observation on the effect of nitrogen on germination supported the idea of nutritional effect. Increase in surface area of cotyledons and early development of the primary leaves with increasing nitrogen concentration were observed. Further investigation of the effect of nitrogen in the field may help confirm the nutritional role as well as any other role the nitrogen may play in the growth and development of E. odoratum. The early phases of seedling development may be considered also.

Effect of Density

Results of the effect of density on the behavior of E. odoratum are presented here. The response of plants from the seven localities was different in each of the growth attributes examined. Height and number of leaves per plant were significantly different among plants and between treatments. Total dry weight and net assimilation rate were much higher at low plant density level than at the high plant density level. Root weight ratio, however, was generally larger at the high plant density level than at the low plant density level.

Plant height and number of leaves per plant.--

Plant heights in four populations from Malaya, Sango Otta, Guatemala, and Trinidad were greater at the low plant density level than at the high plant density level. Plants from Thailand were taller at the high plant density level than at the low plant density level. Plant heights were slightly greater in those from Agege and Florida at the high plant density level than at the low plant density level (Figure 36); differences were not, however, significant. Variations within the plants from each area at both density levels were evident.

The average number of leaves per plant (Figure 37) was generally greater in plants at the low density level than at the high density level. Variations within the plants from Malaya (17.6 ± 2.35), and Guatemala (27.40 ± 5.79) were highly significant at the low density level. The average of leaves per plant was largest in plants from Guatemala at all samplings. Differences among plants from each area were significant at the two density levels.

The average number of leaves per plant appears to be related to the height. There was an inverse relationship between height and number of leaves in plants from Agege, Sango Otta, and Florida.

Dry weight.--Total dry weight was generally higher at the low density level than at the high density level;

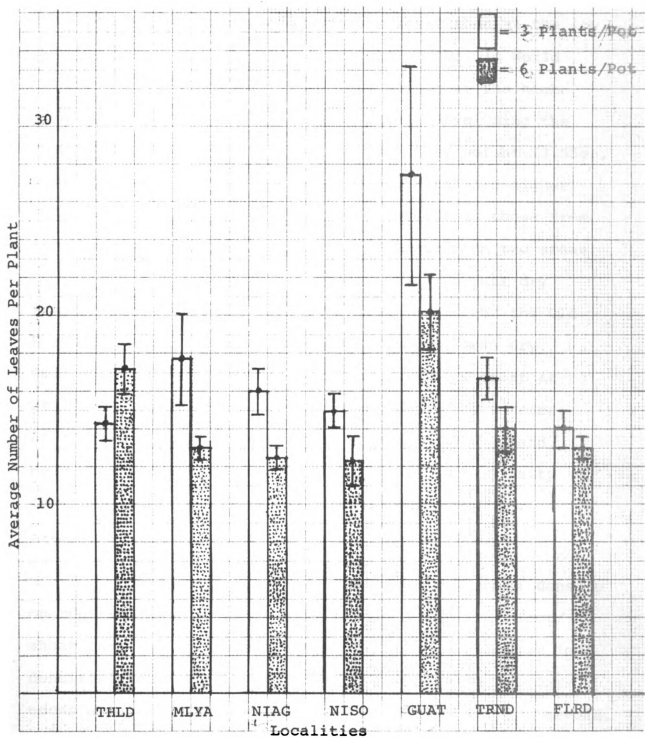


Figure 37.--Average Number of Leaves Per Plant $\pm$ Sx in *E. odoratum* from Seven Localities at Two Density Levels of Three and Six Plants Per Pot Respectively.

plants from Florida, however, had significantly higher total dry weight at the high density level than at the low density level. Plants from two areas of the Old World Tropics had significantly lower dry weight at the high density level than at low density level. Excluding the plants from Guatemala with highest mean dry weight (3.55g), plants from the Old World Tropics in general had higher total dry weight at the low density level than those from the New World Tropics (Figure 38). Plants from two areas of the New World Tropics had significantly higher dry weight at the high density level than those from the Old World Tropics. In plants from Florida, the mean dry weight at high density was more than twice as great as at low density level; whereas, there was no difference at the two density levels in the plants from Thailand. Mean dry weight was about twice as high at low density level as at high density level in plants from other areas.

Root/shoot ratio.--Results of the effect of density on root/shoot ratio are summarized in Figure 39. Root/shoot ratio was greater at high density level than at low density level. There was no overall significant differences among plants from each area at the two density levels. There were significant differences among plants from each locality, however, between samplings.

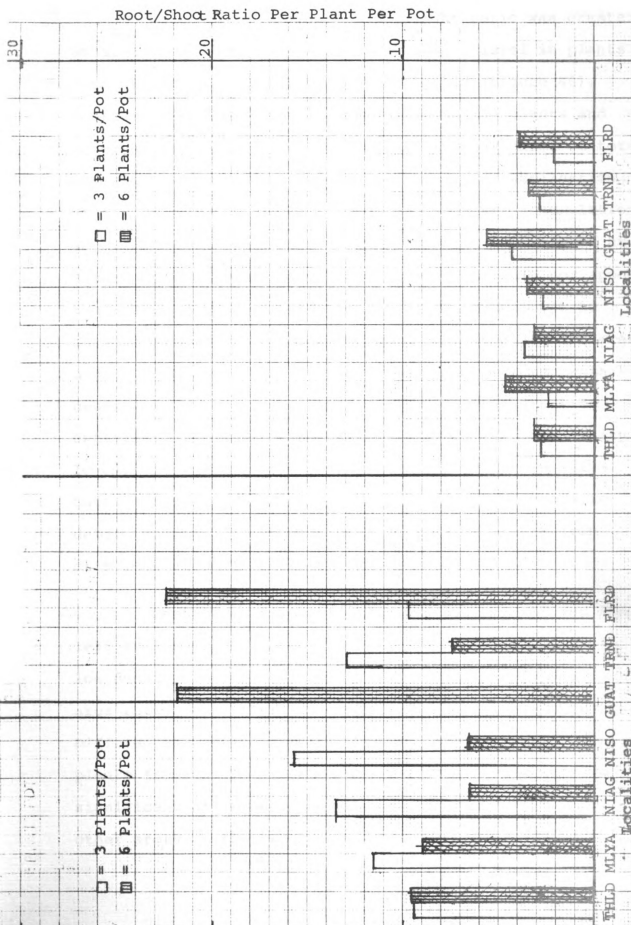


Figure 38.--Mean Dry Weight Per Plant Per Pot in *E. odoratum* from Seven Localities at Two Density Levels.

Figure 39.--Mean Root/Shoot Ratio Per Plant Per Pot in *E. odoratum* from Seven Localities at Two Density Levels.

Root/weight ratio. --Root weight ratio was greater at high density level than at low density level in plants from six of seven localities investigated (Figure 40). There were significant differences among the plants and between treatments. As root weight ratio is based on total dry weight, it appears to offer a meaningful explanation as to the behavior of the roots in dry matter accumulation in E. odoratum. Although root weight ratio was higher at higher density level than at low density, it did not appear that intraspecific competition is sufficiently high to inhibit growth and development in plants from the different areas. Interpretation of this result may be taken with caution in that two samplings may not be sufficient to explain the true behavior of this species at high density level. It is therefore suggested that further investigation of density levels be carried out in the field to determine the degree of interaction within plants from different areas as well as among other species.

Leaf area ratio.--In plants from Thailand and Agege leaf area ratio was higher at high density level than at low density level; in plants from Malaya and Florida, leaf area ratio was higher at low density than at high density. Differences between the two treatments were significant in plants from the four areas listed above. There were no significant differences in the rest of the plants from other areas at the two treatment levels (Figure 41).

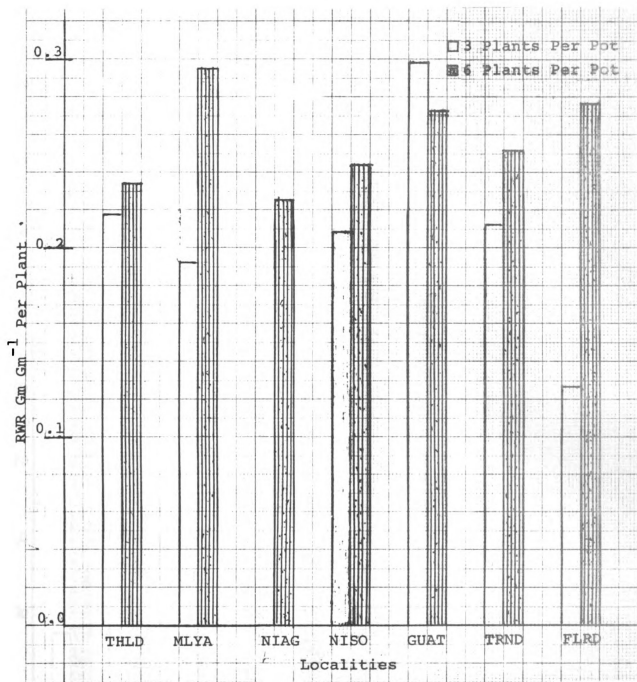


Figure 40.--Root Weight Ratio (Gm Gm^{-1}) Per Plant of *E. odoratum* from Seven Localities at Two Density Levels of Three and Six Plants Per Pot.

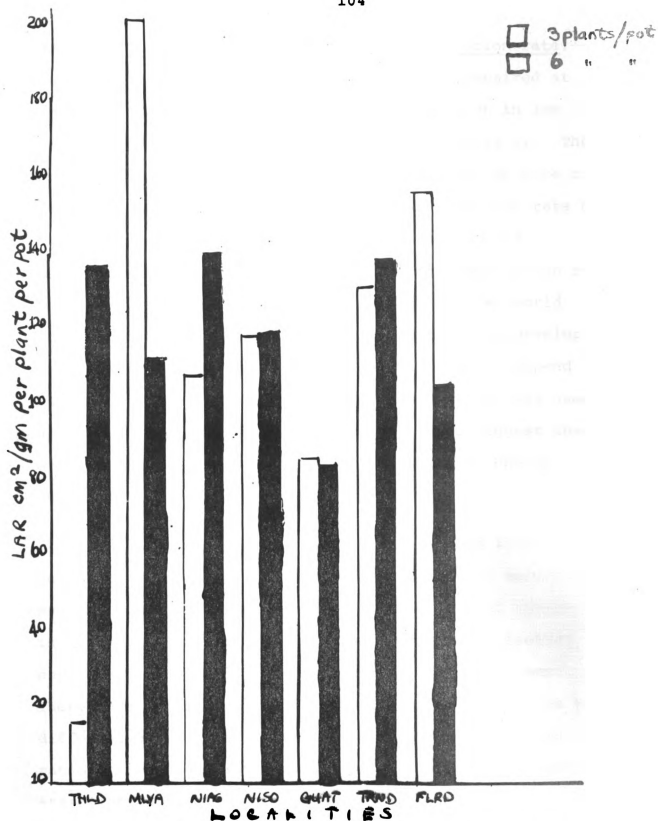


Figure 41.--Leaf Area Ratio cm²/gm Per Plant Per Pot of *E. odoratum* from Seven Localities at Two Density Levels of Three and Six Plants Per Pot Respectively.

Relative growth rate and net assimilation rate.--

The contribution of leaves to growth may be impaired at high density level. Evidence for this was seen in low relative growth and net assimilation rate (Table 6). The rate of carbon assimilation did not depend on the size of the photosynthetic apparatus. It appears that the rate of carbon assimilation was much less than the rate of respiration; consequently, a negative net assimilation rate and relative growth rate among plants of the New World Tropics particularly at high density level. The development and growth of the plants in general seem to depend on how much dry matter was accumulated and how much was used up in supplying energy for growth. The data suggest that at high density level, a much larger amount of energy was required for growth.

Discussion.--The data obtained in this investigation have shown the presence of physiological variations and also variations due possibly to experimental errors, etc., in Eupatorium odoratum grown under uniformly controlled environment and under some features of the environment. There were significant differences between plants from the different areas in dry matter accumulation, root/shoot ratio, root weight ratio, relative growth rate, and net assimilation rate. Marked differences were also seen

TABLE 6.--Total dry weight, root weight ratio, leaf area ratio, relative growth rate, and net assimilation rate of seven populations of E. odoratum at two density levels.

Population	l_w (gm)	RWR GM^{-1}	LAR GM^{-2}	GM. GM^{-1}	RGR $GM^{-1} WK^{-1}$	GM. $CM^{-2} WK^{-1}$	NAR $CM^{-2} WK^{-1}$
THLD	a 1.875	0.218	15.99		0.045		0.418
	b 1.908	0.234	136.39		-0.038		-0.043
MLYA	a 2.325	0.192	201.88		0.022		0.017
	b 1.775	0.295	116.86		-0.003		-0.005
NIAG	a 1.708	0.000	107.79		0.126		0.177
	b 1.292	0.225	140.33		0.091		0.097
NISO	a 3.142	0.208	118.24		0.034		0.043
	b 1.308	0.244	119.26		0.077		0.097
GUAT	a 7.108	0.298	86.26		0.163		0.284
	b 4.363	0.271	84.03		-0.002		-0.006
TRND	a 2.575	0.214	131.12		-0.019		-0.021
	b 1.471	0.251	138.06		-0.074		-0.081
FLRD	a 1.945	0.127	155.78		-0.071		-0.066
	b 1.483	0.276	115.11		-0.102		-0.133

a = 3 plants/pot b = 6 plants/pot

l_w = total dry weight/plant of two harvests.

among plants from these areas in response to some features of the environment and in particular to moisture.

Root weight ratio, leaf area ratio, and net assimilation appear to be genetically controlled in E. odoratum. The significant differences and variations observed among plants in these growth functions suggest that they may represent physiological adaptations to features of the environment. Correlations between net assimilation rate, leaf area ratio, and root weight ratio were significant among plants from the different areas. Relative growth rate and net assimilation rate were also highly correlated. Differences in net assimilation rate and leaf area ratio were also closely associated. In plants grown under uniform greenhouse environment, or, under extreme moisture conditions, high leaf area ratio was accompanied by low net assimilation rate, or vice versa. Generally, plants from the New World Tropics had high leaf area ratio and low net assimilation rate; plants from the Old World Tropics had low leaf area ratio and high net assimilation rate (Figures 42 and 43). No definite pattern was established under high density effect; some populations had high leaf area ratio and low net assimilation rate.

The inverse relationship between leaf area ratio and net assimilation rate observed in E. odoratum was similar to the findings of Watson (1947, 1952), and

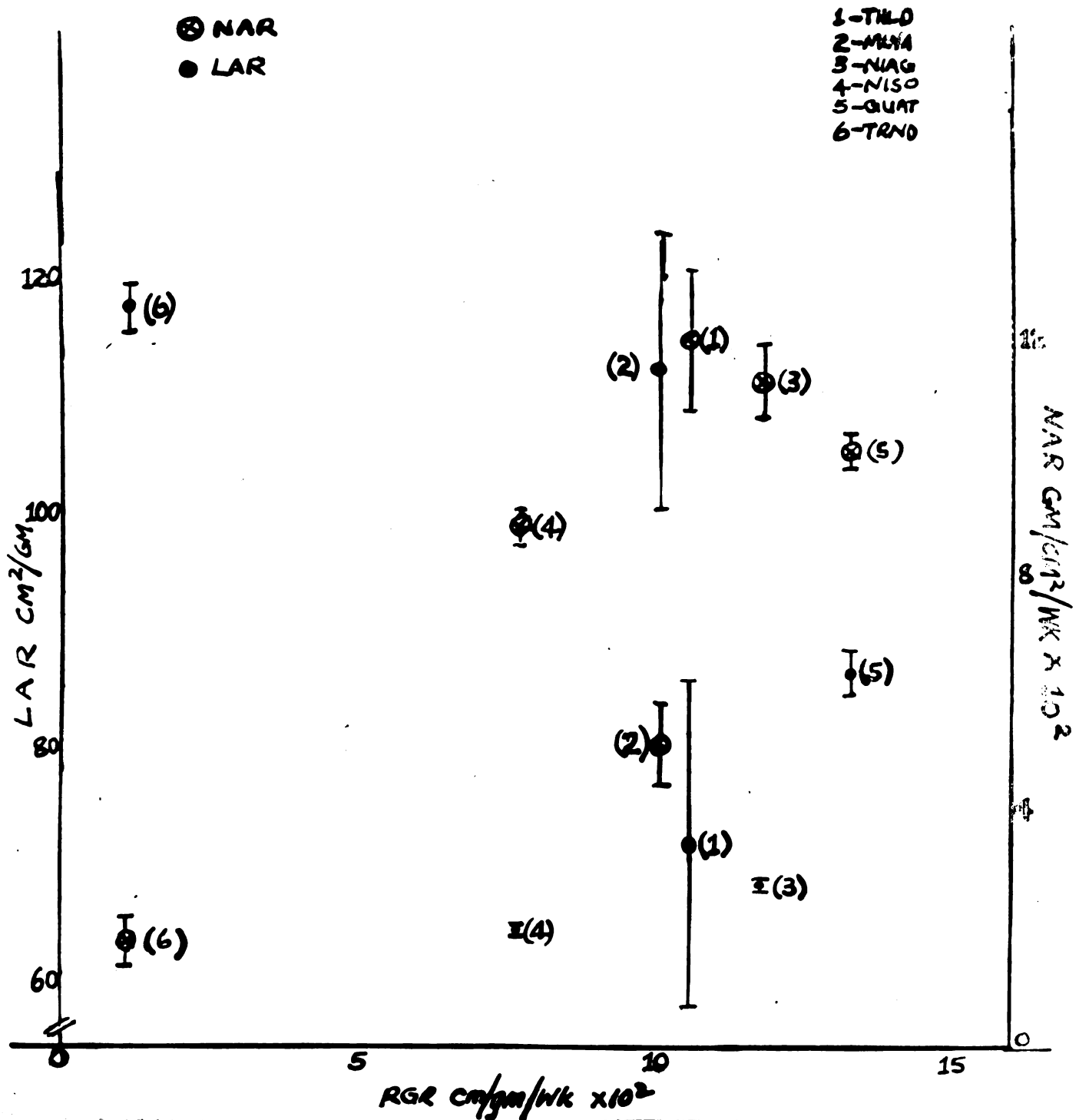


Figure 42.--Relationship Between Relative Growth Rate, Net Assimilation Rate, and Leaf Area Ratio in *E. odoratum* from Seven Localities (Means and their Range over Two Sampling Intervals).

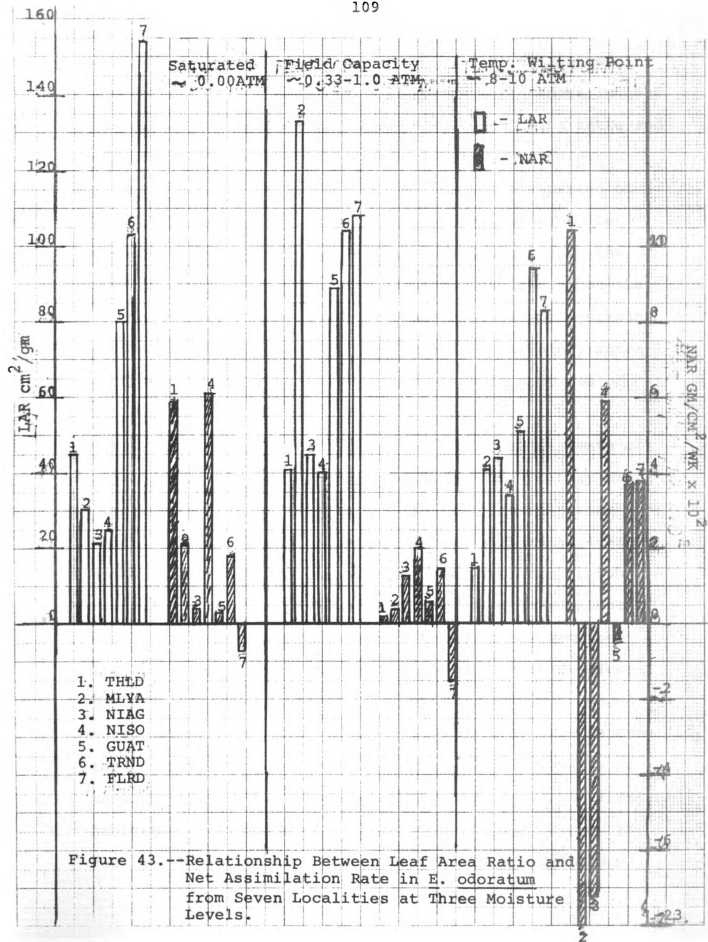


Figure 43.--Relationship Between Leaf Area Ratio and Net Assimilation Rate in *E. odoratum* from Seven Localities at Three Moisture Levels.

Wilson and Cooper (1969). Hammerton (1965) attributed differences in net assimilation rate to differences in leaf fall, which may affect the estimates of leaf area ratio and net assimilation rate in Polygonum persicaria. In E. odoratum, no leaf fall was observed during the period of investigation. Differences in net assimilation may be due to the size of the leaves, or to differences in the rate of respiration which may be higher or lower than the rate of photosynthesis. It has been reported by Björkman and Holmgren (1961) that differences in respiratory rates and the rates of photosynthesis occurred in ecotypes of Solidago virgaurea.

Root weight ratio as a function of an estimate of the contribution of root to growth was found to vary among plants from the different areas investigated. Increase in root weight ratio was accompanied by a decrease in leaf area ratio as seen in plants grown under uniform greenhouse environment or under extreme moisture conditions. Root weight ratio was generally higher among plants from the Old World Tropics than those from the New World Tropics. The fact that plants from the Old World Tropics produced more root in proportion to the dry weight than plants from the New World Tropics may suggest that this attribute is an adaptation of the plants in the Paleotropics to different habitats in which they grow. Significant differences in root weight ratio among the plants from the Old World

Tropics may perhaps reflect the plastic nature of the genotypes that have been produced in these areas. It appears that significantly higher root weight ratio in some plants may be in response to the effect of density; or, it may be due to the experimental techniques employed.

Correlation with habitat factors suggests that physiological differences may be associated with precipitation, consequently, the populations of E. odoratum may be thought of as representing climatic ecotypes. The lack of correlation of the growth functions with such features as longitude, latitude, and temperature did not imply that these factors have no effect on growth and development of E. odoratum. It may be that the behavior of the plants under uniformly controlled conditions was masked in such an environment.

The plants from Agege and Sango Otta differed in their response to the effects of moisture and density in some of the growth functions investigated. The affinity of the plants from Thailand to that from Agege may suggest that introduction of E. odoratum to Nigeria was from Thailand; also some similarities between plants from Malaya and Trinidad may indicate that introduction into Malaya was from Trinidad. It may be suggested that plants from the Old World Tropics represent separate introductions.

The introduction of E. odoratum in the Old World Tropics in recent years is seen in its physiological diversity which has helped it to be a successful species in a wide range of habitats. It is envisaged that further research will be carried out in the field to ascertain the results that have been obtained from the various greenhouse experiments. Such investigation must include seedling establishment, efficiency in the utilization of mineral nutrients, inter- and intraspecific competition, and reproductive biology.

GENERAL DISCUSSION

The results obtained from germination and growth studies of E. odoratum from the New and Old World Tropics suggest that several different genotypes are represented in these different areas. The conditions necessary for the evolution of ecotypes within a species have been summarized by Bradshaw (1959). The physiological variations observed in this investigation appear to be genetically controlled, because they were observed under uniformly controlled environmental conditions; it is reasonable to assume such variations to be adaptive.

Correlation of growth functions and percent germination with mean annual precipitation in locality of origin may lead one to conclude that moisture is perhaps one of the features of the habitat that has acted as a selective force to which adaptations have been made. Furthermore, significant differences have been found in some morphological characteristics in plants of E. odoratum from Nigeria growing along a moisture gradient (Edwards, 1969). That there is a correlation between a growth attribute and a habitat factor does not necessarily indicate a causal relationship, nor does it demonstrate the adaptive value of that particular attribute. As Bradshaw (1959) has

pointed out, a population may appear unrelated to its environment because our assessment of the environment is at fault, or the factor involved may no longer be operative.

When seeds are introduced into a new habitat, only those that are suited to the prevailing conditions will germinate and produce offspring. Suitability depends upon the adaptive features that have evolved within the species. Therefore, variations occurring in these adaptive features under changes in environmental conditions may indicate the degree of plasticity of these features. The characteristic ability of seeds of E. odoratum to germinate readily under varying moisture conditions suggests the plastic nature of the genotype in this respect; unlike some species of temperate climates whose seeds will not germinate unless at optimum conditions of particular environmental factors (Harper and Benton, 1966; Harper and Sagar, 1963; Harper et al., 1963). This characteristic ability to germinate readily is thus considered an asset in E. odoratum that enables it to compete with other species whose seeds do not have this adaptive value.

It is perhaps in the establishment and growth phases that the ultimate survival of the species depend. E. odoratum is a species that has been introduced into more or less stable or seral communities in the Old World Tropics. For a species to be successful in such a community, its genetic program must allow it to operate

within an array of environmental conditions. It has been argued (Cody, 1966; Harper, 1967; MacArthur and Connell, 1967) that the manner in which the resources of an organism are apportioned or manipulated may be important in establishment and success of plant species. This concept may be applied to examining the behavior of plant species introduced into stable or seral communities. It appears that in E. odoratum some physiological adaptations have contributed to the survival of the species in the Old World Tropics. These physiological adaptations are seen in the photosynthetic mechanisms and in the allocation of energy to root production at the expense of shoot growth or leaf expansion. These characteristic features have been shown to be sensitive to features of the environment (Björkman and Holmgren, 1963; Cooper, 1963) in a manner suggesting adaptive significance.

There is sufficient evidence to conclude that the physiological attributes and characteristic features observed in germination and growth of E. odoratum have contributed to the success and rapid distribution that have been observed in populations from the Old World Tropics. These physiological attributes may also have contributed to the aggressiveness of the species. The characteristic efficiency of the root system, the shoot system, and high net assimilation rate appear to have been a few of the pathways selected by the genotypes introduced

into the different habitats in the Old World Tropics. The variations observed in plants from the three localities from Nigeria suggest the influence of the microhabitats on the plants in which the species became established. Plants from each of these areas apparently are of different genotypes.

The ecological success of E. odoratum in becoming a widespread species in the Old World Tropics may be attributed in part to its characteristic germination and growth behavior in response to some factors of the environment. Perhaps of much significance is the characteristic behavior in allocation of energy and materials during the growth phase of the species. The absence of predators also may have enhanced the development of adaptive physiological features in approximately fifty years of the species' introduction into the Old World Tropics. Furthermore, these physiological adaptations and the absence of predators may have contributed to the species competitive capacity within the communities in which it is found.

SUMMARY

Physiological attributes of germination and growth response in E. odoratum from seven localities of the New and Old World Tropics have been investigated under uniformly controlled environmental conditions.

Significant differences were found among seeds from the seven localities in rate of germination, percent germination, and in time to reach maximum germination. Also, variations and differences in growth functions were found to be significant among plants from the areas investigated.

Ecological success of an introduced species in new and alien habitats is discussed.

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APPENDIX

TABLE A1.--Mean¹ germination and standard error in E. odoratum from seven localities at four imbibition levels.

Locality	Check	Time in Hours			
		1	4	24	48
THLD	16.62±0.92	14.75±1.42	14.87±0.93	14.12±1.09	14.62±1.35
MLYA	6.87±1.80	6.62±1.36	13.00±1.49	8.12±1.94	10.75±1.40
NIAG	13.25±1.87	16.50±1.38	14.00±2.12	17.50±1.08	13.25±1.89
NISO	7.72±2.32	11.25±0.82	10.62±0.60	10.12±0.74	10.37±1.50
NIFA	10.62±2.08	13.62±0.53	13.62±0.73	16.62±1.32	14.37±1.02
TRND	12.75±1.61	14.87±1.98	19.25±1.31	20.00±0.82	19.00±1.24
GUAT	8.72±2.80	15.75±2.41	4.50±1.15	6.62±1.07	12.75±2.39

¹Mean of eight replicates of 25 seeds.

TABLE A2.--Analysis of variance of mean germination in
E. odoratum from seven localities at four soaking
 levels.

Source	df	MS	F
Total	275	165.11	
Subgroups	34	1098.68	32.89**
Pops.	6	5191.09	155.40**
Trts.	4	576.01	17.24**
Pops. x Trts.	24	162.69	4.87**
Error	241	33.40	

** Significant at $P > 0.01$ level.

TABLE A3.--Number of days to reach maximum germination and percentage germination in E. odoratum from seven localities at four soaking levels.

Locality	Check	Time in Hours				Mean S.E. % gern
		1	4	24	48	
THLD	30(66.5)	25(59.0)	25(59.5)	25(56.5)	25(58.5)	60.0±1.39
MLYA	25(27.5)	25(26.5)	25(52.0)	20(32.5)	30(43.0)	36.3±4.89
NIAG	20(53.0)	20(66.0)	15(56.0)	15(70.0)	20(53.0)	59.6±2.88
NISO	20(28.5)	25(45.0)	25(42.5)	25(40.5)	25(41.5)	39.6±2.87
NIFA	15(42.5)	20(54.5)	25(54.5)	20(67.5)	20(57.5)	55.3±3.99
TRND	20(51.0)	15(59.5)	15(77.0)	20(80.0)	25(76.0)	68.7±5.69
GUAT	20(32.5)	20(63.0)	30(17.5)	20(26.5)	25(51.0)	38.1±8.29

TABLE A4.--Percentage¹ germination and number of days to reach maximum germination in parenthesis in *E. odoratum* from seven localities at varied moisture stress.

Locality	Check	Atmospheres				
		1	3	5	8	10
THLD	48(25)	32(20)	12(25)	9(25)	0	0
MLYA	41(25)	27(25)	24(25)	21(20)	4(10)	0
NIAG	61(15)	47(15)	43(15)	24(10)	15(15)	0
NISO	41(15)	39(25)	30(20)	22(20)	2(10)	0
GUAT	9(10)	9(10)	12(15)	4(15)	0	0
TRND	53(20)	55(15)	73(15)	68(15)	30(15)	0

¹Mean of two reciplicates of 50 seeds except TRND (40 seeds).

TABLE A5.--Analysis of variance of percentage germination arc sin transformation in *E. odoratum* from six localities at various moisture tensions.

Source	df	MS	F
Total	29	241.78	
Treatments	4	669.46	3.861*
Error	25	173.36	

*Significant at $P > 0.05$.

TABLE A6.--Mean¹ germination and standard error E. odoratum from seven localities at five molar concentrations of KNO₃.

Locality	Check	Molar Concentration				
		1x10 ⁻⁵	1x10 ⁻⁴	1x10 ⁻³	1x10 ⁻²	1x10 ⁻¹
THLD	15.7±0.85	16.2±1.11	15.2±0.63	18.7±1.11	15.5±1.26	3.7±0.63*
MLYA	11.0±0.00	8.2±1.49	10.5±1.26	9.2±1.80	8.7±0.85	2.5±0.64
NIAG	11.0±2.74	17.5±0.50	17.5±1.66	9.0±5.12	16.5±1.26	7.5±2.72*
NISO	12.2±1.18	11.5±1.55	11.0±1.47	10.5±1.26	11.2±1.11	2.0±0.41*
NIFA	14.7±1.03	13.7±1.55	13.5±0.64	12.5±0.87	17.2±1.25	2.0±0.41*
TRND	18.2±1.75	18.0±1.58	21.0±0.58	20.0±0.71	18.0±1.91	14.7±1.60*
GUAT	13.2±5.04	16.0±4.26	1.5±0.96	0.7±0.48	12.0±3.58	1.0±0.41*

* roots aborted at the appearance of shoots (Plate 2).

¹Mean of 4 replicates of 25 seeds.

TABLE A7.--Mean germination and standard error in *E. edentata* from seven localities under light treatment.

	Continuous Light	Continuous dark	11hrs L 13hrs D	Cont. dark Trt.Trfd TollL-13D
THLD	6.0±1.29	0.5±0.29	10.3±0.75	13.0±0.91
MLYA	8.0±1.00	1.5±0.50	7.5±1.85	7.7±0.75
NIAG	15.2±1.31	10.0±1.22	13.5±0.64	7.0±0.71
NISO	8.7±0.75	1.5±0.29	5.0±0.41	8.0±0.82
NIFA	13.7±1.31	3.5±1.19	14.0±1.47	12.5±0.50
TRND	15.7±2.29	6.0±1.78	17.7±0.25	6.5±1.85
GUAT	6.5±2.82	1.0±0.71	9.7±0.48	1.0±1.00

^aTransfer made after the first twenty days.

TABLE A8.--Mean¹ dry weight (g) at three sampling periods in E. odoratum from seven localities.

Sampling Periods	Populations							S.E.
	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD	
1	5.74	3.20	6.10	7.57	12.16	3.41	5.28	1.15
2	5.79	5.06	6.82	8.37	14.66	3.96	4.74	1.38
3	8.80	4.80	9.80	10.30	20.85	3.57	3.67	2.28
Mean	6.77	4.35	7.57	8.74	15.89	3.64	4.56	1.59

¹Mean of four replicates.

TABLE A9.--Analysis of variance of mean dry weight in E. odoratum from seven localities.

Source	df	MS	Fs
Total	20	18.925	
Populations	6	52.860	12.065**
Error	14	4.381	

** Significant at $P < 0.01$.

TABLE A10.--Mean¹ root/shoot ratio (x10) at three sampling periods in E. odoratum from seven localities
E. odoratum x 10.

Sampling Periods	Localities							
	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD	S.E.
1	6.51	3.97	6.44	6.92	4.48	3.64	5.80	0.51
2	7.08	4.46	5.97	7.31	4.44	2.77	2.94	0.69
3	6.84	5.48	4.00	5.15	3.33	3.47	1.79	0.52
Mean	6.81	4.64	5.47	6.46	4.08	3.29	3.40	0.53

¹Mean of four replicates.

TABLE A11.--Analysis of variance of mean root/shoot ratio in
E. odoratum from seven localities.

Source	df	MS	Fs
Total	20	20.421	
Populations	6	79.111	32.807**
Error	14	2.411	

**Significant at $P < 0.01$.

TABLE A12.--Root weight ratio (RWR) and leaf area ratio (LAR)
(cm²/gm) of *E. odoratum* over three sampling
periods from seven localities.

Locality	RWR			LAR		
	1	2	Mean	1	2	Mean
THLD	0.400	0.410	0.405	86.52	58.35	72.43
MLYA	0.302	0.304	0.303	125.14	101.52	113.33
NIAG	0.382	0.325	0.353	68.68	69.31	68.99
NISO	0.423	0.347	0.385	64.86	65.44	65.15
GUAT	0.307	0.272	0.289	89.37	85.12	87.24
TRND	0.239	0.236	0.237	116.20	120.42	118.31
FLRD	0.287	0.232	0.259	106.80	124.60	115.70

TABLE A13.--Dry weight (g) of E. odoratum from seven localities at three moisture levels.

Treatment	Sampling Period	THLD	MLYA	NIAG	NISO	GAUT	TRND	FLRD	S.E.
1 _{S.P.}	1	4.40	4.10	5.80	3.80	16.90	2.20	4.20	1.87
	2	4.80	4.90	7.30	11.00	18.00	3.25	2.75	2.05
	3	11.35	5.40	7.10	4.20	18.85	4.60	2.70	2.20
Mean		6.85	4.80	6.73	6.33	17.92	3.35	3.22	
2 _{F.C.}	1	10.30	3.40	11.30	9.10	22.10	2.30	9.30	2.44
	2	10.90	4.60	12.20	14.25	25.00	5.00	7.40	2.66
	3	10.65	3.90	14.60	12.15	27.20	4.10	4.60	3.14
Mean		10.62	3.97	12.70	11.83	24.77	3.80	7.10	
3 _{TWP}	1	4.10	0.85	5.30	4.40	6.30	1.80	5.00	0.73
	2	7.90	0.14	6.25	4.35	6.30	4.05	2.65	0.98
	3	7.40	0.35	1.25	1.35	5.35	0.40	1.50	1.03
Mean		6.47	0.45	4.27	3.37	5.98	2.08	3.05	

1_{S.P.} = Saturation Point (80-90%) ~0.00. Atm.2_{F.C.} = Field Capacity (45-55%) ~0.33-1.00 Atm.3_{TWP} = Temporary Wilting Point~(10-15%) 10.00-15.00 Atm.

TABLE A14.--Two-way analysis of variance of dry weight (gm)
in *E. odoratum* from seven localities at three
soil moisture levels.

Source	df	MS	Fs
Total	62	116.125	
Group	20	343.175	42.865**
Population	6	1040.237	129.934**
Treatments	2	260.359	32.521**
Pop. x Trts.	12	8.447	1.055ns.
Error	42	8.006	

** Significant at $P < 0.01$.

TABLE A15.--Root/shoot ratio in *E. odoratum* from seven localities at three soil moisture levels and three sampling periods x 10.

Treatment	Sampling Period	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD	S.E.
1 _{S.C.}	1	3.75	1.71	9.33	5.83	3.63	1.58	2.00	1.06
	2	5.48	1.78	6.59	11.15	2.08	1.75	1.96	1.35
	3	4.28	3.33	2.68	3.12	3.33	1.22	1.25	0.43
Mean		4.50	2.27	6.20	6.70	3.01	1.52	1.73	0.08
2 _{F.C.}	1	5.85	6.19	7.66	5.42	3.56	3.53	5.76	0.55
	2	11.80	2.10	11.78	13.55	4.97	2.19	3.80	1.89
	3	6.77	1.14	3.90	5.28	2.77	4.14	2.28	0.72
Mean		8.14	3.14	7.78	8.08	3.76	3.28	3.95	0.91
TWP	1	11.58	5.45	11.20	13.16	5.00	8.00	6.67	1.23
	2	13.23	5.55	18.41	23.08	2.86	3.73	2.93	3.13
	3	5.74	4.00	1.90	2.27	3.37	1.43	8.75	0.09
Mean		10.18	5.00	10.50	12.84	3.74	4.39	6.12	1.35

1_{S.P.} = Saturation Point

2_{F.C.} = Field Capacity

3_{TWP} = Temporary Wilting Point

TABLE A16.--Analysis of variance of root/shoot ratio in E. odoratum from seven localities at three soil moisture levels.

Source	df	MS	Fs
Total	62	19.143	
Groups	20	28.821	1.982 [*]
Population	6	63.679	4.381 ^{**}
Treatment	2	78.437	5.396 ^{**}
Pops. x Trt.	12	3.124	0.215
Error	42	14.533	

* Significant at $P > 0.05$.

** Significant at $P < 0.01$.

TABLE A17.--Root weight ratio in *E. odoratum* from seven localities at three moisture levels over two sampling intervals.

Treatment	Sampling Interval	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD	S.E.
¹ S.P.	1	3.12	1.56	4.37	4.57	2.15	1.43	1.54	0.51
	2	3.24	1.98	2.81	3.86	1.97	0.00	1.31	0.57
Mean		3.18	1.77	3.59	4.21	2.06	0.71	1.42	0.52
² F.C.	1	4.50	2.59	3.31	4.59	2.96	2.13	3.21	0.35
	2	5.64	1.36	3.93	4.55	2.70	2.30	1.86	0.59
Mean		5.07	1.97	3.62	4.57	2.83	2.21	2.58	0.45
³ TWP	1	5.50	3.54	5.87	6.26	6.69	3.40	3.15	0.57
	2	4.61	3.15	4.12	4.32	1.97	2.15	3.20	0.39
Mean		5.05	3.34	4.99	5.29	4.33	2.77	3.17	0.39

¹S.P. = Saturation Point

²F.C. = Field Capacity

³TWP = Temporary Wilting Point

TABLE A18.--Analysis of variance of root weight ratio x 10 on
E. odoratum from seven localities at three soil
 moisture levels at three sampling periods.

Source	df	MS	F's
Total	41	2.226	
Groups	20	3.514	3.515**
Populations	6	7.642	7.644**
Treatments	2	10.227	10.229**
Pops. x Trts.	12	0.332	0.332
Error	21	0.999	

** Significant at $P < 0.01$.

TABLE A19.--Leaf area ratio (cm^2/gm) in *E. odoratum* from seven localities at three moisture levels and two sampling intervals.

Treatment	Sampling Period	THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD	S.E.
¹ S.P.	1	49.99	32.21	36.83	34.70	79.60	93.43	152.43	16.615
	2	39.44	29.68	6.22	15.27	80.85	113.15	154.78	20.944
Mean		44.71	30.44	21.52	24.98	80.22	103.29	153.60	18.672
² F.C.	1	37.50	106.84	39.09	37.82	86.94	100.36	92.69	12.061
	2	47.68	159.37	52.51	41.86	90.36	108.16	124.11	16.772
Mean		42.59	133.10	45.80	39.84	88.65	104.26	108.40	14.201
³ TWP	1	3.99	16.82	39.19	16.51	0.00	78.80	89.99	13.644
	2	25.20	64.67	48.18	50.54	102.43	110.06	75.51	11.497
Mean		14.59	40.74	43.68	33.52	51.21	94.43	82.70	10.555

¹S.P. = Saturation Point

²F.C. = Field Capacity

³TWP = Temporary Wilting Point

TABLE A20.--Analysis of variance of leaf area ratio in *E. odoratum* from seven localities at three soil moisture levels at three sampling periods.

Source	df	MS	Fs
Total	41	2316.879	
Groups	20	4209.440	8.182 **
Populations	6	10361.331	20.141 *
Treatments	2	13143.368	25.549 **
Pops. x Trts.	12	355.493	0.691
Error	21	514.440	

** Significant at $P < 0.01$.

TABLE A21.--Mean dry weight (g) in E. odoratum from seven localities at two density levels over two sampling periods.

Density Level	Sampling Period	Localities						
		THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD
3 plants/pot	1	0.875	1.125	1.100	1.492	2.700	1.325	1.075
	2	1.000	1.200	1.650	1.650	4.408	1.250	0.870
	Mean	0.937	1.163	1.354	1.571	3.554	1.287	0.972
6 plants/pot	1	1.008	0.892	0.559	0.579	2.192	0.817	1.854
	2	0.900	0.883	0.733	0.729	2.171	0.654	2.629
	Mean	0.954	0.887	0.646	0.654	2.181	0.735	2.241

TABLE A22.--Mean root/shoot ratio E. odoratum from seven localities at two density levels over two sampling periods.

Density Level	Sampling Period	Populations						
		THLD	MLYA	NIAG	NISO	GUAT	TRND	FLRD
3 plants/pot	1	0.280	0.273	0.450	0.326	0.459	0.303	0.387
	2	0.276	0.210	0.270	0.215	0.399	0.250	0.040
	Mean	0.278	0.241	0.360	0.270	0.429	0.276	0.213
6 plants/pot	1	0.352	0.726	0.410	0.463	0.724	0.400	0.454
	2	0.263	0.204	0.214	0.232	0.404	0.287	0.313
	Mean	0.307	0.465	0.312	0.347	0.564	0.343	0.383

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