STUDIES ON THE BIOLOGY OF SOURGRASS [*Trichachne insularis* (L.) Nees] AND OF ITS COMPETITION WITH BUFFELGRASS (*Cenchrus ciliaris* L.) AND GUINEAGRASS (*Panicum maximum* Jacq.)

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ABSTRACT

Sourgrass (Trichachne insularis (L.) Nees) is one of the most serious pasture weeds in Hawaii. It has ruined many good dryland pastures on Maui, Molokai, and Oahu.

Studies were conducted on its distribution, seed germination, seedling emergence and growth and development under natural and controlled conditions and on its competition with the improved pasture species, buffelgrass (Cenchrus ciliaris L.) and guineagrass (Panicum maximum Jacq.).

Field surveys showed that sourgrass was most abundant below 540 meters elevation, in dry zones of 120 to 760 mm of annual rainfall. Sourgrass occurred on hillsides or on gentle basal slopes where Prosopis pallida (Humb. and Bonpl. ex Willd) HBK. or Leucaena latisiliqua (L.) Gillis and Stearn grew. Distribution of sourgrass corresponded to shade conditions. The soils of infested areas were commonly silt clay to silt clay loam with shallow soil profiles. Low rainfall, high temperatures, and shade were the more important factors in the distribution of sourgrass.

Optimum germination of sourgrass seed was obtained under light with alternating temperatures of 20-30 C or 25-35 C or with constant 30 C. Germination in complete darkness was very poor at most temperatures. Germination of sourgrass seed was best under 8 or 12 hour photoperiod but was reduced under 16 and 24 hour photoperiods. Gibberellic acid, kinetin, and thiourea were effective in enhancing germination at 22 C in the dark. Germination percentages of sourgrass, buffelgrass, and guineagrass decreased as moisture stress simulated with mannitol was

increased. Guineagrass and buffelgrass were more affected by moisture tension than was sourgrass. The capacity of sourgrass to germinate rapidly under low soil moisture could give it a competitive advantage over buffelgrass and guineagrass under semi-arid to arid conditions.

Sourgrass seedling emergence was greatest from seeds planted near the surface and decreased as the depth of planting increased. Sourgrass was capable of emerging from a maximum depth of 5 cm in the clay loam used in this study.

Plant height, dry weight, tillers per plant, and seed yield per plant were greatly decreased as the plant density was increased from 5 plants to 160 plants per pot. Intraspecific competition was probably a major factor affecting seedling development and survival of sourgrass.

Sourgrass flowering was found to be day-neutral in response to photoperiod. The plants under longer photoperiods flowered earlier than those grown under shorter photoperiods probably because floral development was slow in response to insufficient light energy under shorter photoperiods.

Plant height and dry matter production of shoots of sourgrass, buffelgrass, and guineagrass increased but dry weight of roots and tillers per plant decreased with increasing shade. In addition, flowering was delayed as shade increased. Nitrogen fertilization increased plant height, dry weights of shoots and roots, and tillers per plant for all species.

A pot study was conducted to evaluate the competitive ability of sourgrass, buffelgrass, and guineagrass under different levels of shade and nitrogen fertilization. The growth of sourgrass was severely suppressed when grown with buffelgrass, guineagrass or both. Highly

significant reductions in height, dry weight, and tillers per plant of sourgrass resulted from competition with associated grass species. Sourgrass was thus less competitive than buffelgrass and guineagrass.

It is evident from these results that sourgrass in pastures can be controlled through competition from buffelgrass and guineagrass under proper management of grazing and fertilization. Practices which would enhance the competitive advantage of buffelgrass and guineagrass over sourgrass would include the following: (1) ensuring adequate moisture for germination, (2) fertilization, and (3) prevention of over-grazing.

TABLE OF CONTENTS

Page

LIST OF TABLES

APPENDIX TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Sourgrass (Trichachne insularis (L.) Nees), a densely tufted perennial, is native to Florida and the West Indies (Britton, 1918). It is distributed throughout the tropical and subtropical Americas. In the United States it is found in Alabama, Arizona, Florida, Texas, and Hawaii. It also occurs in Mexico, Bermuda, Cuba, Jamaica, Puerto Rico, West Indies and south to Argentina (Silveus, 1933; Whitney et al., 1933; Johnston, 1943; Hitchcock, 1950; Urban, 1964). Egler (1947) reported that sourgrass was introduced into Hawaii for experimental purpose from Puerto Rico, although it was known to be unpalatable to stock. Hosaka (1953) reported that it was first collected in 1906 on Oahu but was not noticed in the adjacent regions until about 1933, when it was found all over Oahu. Within a few years it spread to all the other major islands; Hawaii, Kauai, Lanai, Maui, and Molokai (Hosaka, 1945). It has become especially abundant in the lower altitudes of Oahu in the relatively dry zones of 20 to 30 inches of rainfall.

Of the total land area of Hawaii, about 18.4% or 667,380 acres is used for pasture and range, and livestock is the third largest agricultural enterprise in economic importance, second only to sugar and pineapple (Anon., 1972). Sourgrass has ruined many good dryland pastures in Maui, Molokai and Oahu. It was estimated that over 80,000 acres were infested with this pest (Anon., 1962) and is thus one of the most serious pasture pests in Hawaii. Sourgrass was also declared a

noxious weed for State land leases by Hawaii Board of Commissioners of Agriculture and Forestry in 1951.

The plant is highly unpalatable and consequently cattle preferentially graze other species, baring the soil, reducing competition, and favoring sourgrass. Once established, the land is essentially unsuitable for grazing. Partially dried sourgrass is often grazed, but green plants are very rarely touched unless other forage is not available.

Some work has been done on T. californica in Arizona where it is a fair forage because of its high palatibility at all seasons, its ability to produce green growth from axillary buds on older culms, and its wide adaptability to differing soils and climates (Cable, 1971). However, no comprehensive work has been done on the life cycle and characteristics of sourgrass and little is known about it.

In view of the lack of information concerning the life cycle, growth habits, and response of sourgrass to environmental factors, a series of studies was undertaken to gain this information. This information is essential for developing economical and effective programs for more successful control of this pest.

CHAPTER II

REVIEW OF LITERATURE

Description of Sourgrass

Trichachne is presently classified as a member of the Paniceae tribe, subfamily Panicoideae (Stebbins and Crampton, 1961). The genus Trichachne was formerly included in Panicum, Valota, or Andropogon (Britton, 1918; Small, 1933). Trichachne is closely related to Digitaria and Panicum, differing chiefly from the first in the acuminate fruit and silky spikelets, and from the latter by the cartilaginous fruit, being chartaceous-indurate in Panicum (Silveus, 1933). Gould et al. (1965) recognized Trichachne as a separate genus mainly on the presence of long silky hairs on the second glume and sterile lemma and the acute apex of the fertile lemma. However, since these differences are not consistent, he felt that the species of Trichachne group appeared best treated as a subgenus or section of Digitaria.

There are about 12 species in this genus which are found in the tropics and the warmer parts of the temperate regions (Small, 1933; Whitney et al., 1939). They are all tall perennial grasses with conspicuous whitish or brownish, silky flowering heads with slender, rather erect branches closely or rather distantly arranged along slender main axes. Silveus (1933) and Hitchcock (1950) classified Trichachne into four species in the United States. The key for identification of species of Trichachne by Hitchcock (1950) is as follows:

> "Fruit 4 mm. long; spikelets tawny-villous...1. T. insularis.
> Fruit 3 mm. or less long (rarely 3.5 mm.); spikelets whitevillous.
> Spikelets long-silky, the hairs exceeding the spikelet; fruit 3 to 3.5 mm. long.

Panicle branches stiffly ascending or spreading, comparatively few-flowered; fruit oblong-lanceolate, gradually pointed .... 3. T. patens.
Panicle branches appressed, densely flowered; fruit obovate, abruptly pointed, the point scarcely indurate .... 2. T. californica.
Spikelets short-silky, the hairs not exceeding the spikelet; fruit 2.4 mm. long ..... 4. T. hitchcockii."

Johnston (1943) reported that sourgrass is similar to T. californica, but readily distinguishable from it by its proportionately narrower, lanceolate spikelets, bearing sordid or tawny, rather than pure white or purplish, hairs. T. insularis and T. californica have 2n=36 chromosome number while T. patens has 2n=72 (Brown, 1951; Tateoka, 1962).

There is only one species of the genus Trichachne in the Hawaiian islands, T. insularis (Whitney et al., 1939). Silveus (1933) described sourgrass as follows:

"Culms 2-4 feet tall, tufted, erect or spreading, branching from swollen base; blades 3-12' long, 4-10 mm. (4-20) wide, flat, rough; sheaths longer than the internodes, glabrous or the lowermost pubescent; ligule membranaceous, ciliate, decurrent, about 2 mm. long; panicle excerted, 4-10' long, narrow, erect or nodding, silky tawny-white or purplish-tinged, shining, the appressed or ascending branches 1.5-4' long, often drooping, the spikelets usually in pairs, the pedicels 1-4 mm. long, one longer than the other, arranged along a narrow 3-angled scabrous rachis; spikelets about 4 mm. (4-5) long, including the hairs 6-7 mm. long, acuminate, clothed with numerous soft light tawny to purplish hairs 2-4 mm. long; glumes, the first minute, acute or truncate, the second and sterile lemma about equal, acuminate, the second glume 3-nerved, hairy over the back and along the margins, the sterile lemma 5-7-nerved, often slightly longer than the second blume, the middle portion being sparsely-hairy and the margins hairy as on the second glume, the hairs being 2.5-4 mm. much exceeding the spikelets, less copious than in T. californica; fruit brown, about 4 mm. long, about 1 mm. wide, lanceolate-acuminate, striateroughened."

Johnston (1943) reported that sourgrass is a tall coarse plant in the tropics, becoming less coarse and small in stature in northern Mexico. Individual plants increase in diameter by stooling at the base. Reproduction is by seeds and vegetative propagules. The plant

produces large quantities of viable hairy seeds which are carried by wind for considerable distances (Hosaka, 1945; Haselwood and Motter, 1966; Cardenas et al., 1972). Gould et al. (1965) reported that sourgrass does not develop creeping rhizomes.

Sourgrass is tough and has a bitter, acrid taste. Reid (1973) noted that unpalatable plants are often bitter and suggested that they may contain high levels of alkaloids (Williams et al., 1970), or saponins (Ender, 1960). Ribeiro and Machado (1952) isolated a new alkaloid, trichachnine, from the juice of Trichachne vestita. Hovin (1975)[1] analyzed indole alkaloid contents of sourgrass to determine the relationship between alkaloids and palatability. They contained 0.01 - 0.02% indole alkaloid for immature plants and 0.01% for plants in the boot stage. He suggested that these concentrations were too low to affect palatability of sourgrass.

Control of Sourgrass

Weed control in pastures is still largely achieved by cultural methods rather than by herbicides. Hosaka (1953) reported that it may be possible to eradicate small infestations of sourgrass by digging them out or burning them but the ready dispersal of seed by wind makes eradication impossible in well established stands.

Competition may involve the crowding out of a weaker cultivar or species by a more vigorous cultivar or species. Many perennial pasture grasses are strong competitors once they are established. Competitive

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[1] Hovin, A. W. (Dept. of Agronomy and Plant Genetics, University of Minnesota) Personal communication.

crops are frequently employed against weed infestations. On pastures and ranges the introduction of suitable forage species that compete effectively with weeds is a widely employed method of habitat management (Anon., 1972). Heinrich (1944) reported that weed competition might be reduced by planting stronger plants or by choking out the weeds with more crop plants. Hosaka (1953) suggested the possibility that sourgrass can be crowded out by planting such hardy plants as guineagrass (Panicum maximum Jacq.) and koa haole (Leucaena latisiliqua (L.) Gillis and Stearn) in stands of sourgrass because guineagrass can tolerate shade much better than sourgrass.

Many attempts have been made to re-establish the more valuable grass species by artificial reseeding on ranges heavily infested by weedy grasses. Hull and Stewart (1948) conducted an experiment to replace cheatgrass (Bromus tectorum L.) with seeded grass in Idaho. They recommended crested wheatgrass (Agropyron cristatum (L.) Gaertn.) and bulbous bluegrass (Poa bulbosa L.) on cheatgrass areas. Oakes (1968) conducted an experiment to determine the suitability of five grass species as replacements for hurricane grass (Bothriochloa pertusa (L.) A. Camus), a pasture weed. Pangolagrass with its aggressive, nutritious, and drought-resistant sward was outstanding in its ability to replace hurricane grass. Peters and Lowance (1974) also reported that tall fescue (Festuca arundinacea Schreb, Kentucky 31') drilled into a pasture infested with broomsedge (Andropogon virginicus L.), a perennial grass of low palatability, and fertilized with N, P, and K, eliminated broomsedge after 4 years. He also found that broomsedge died at a more rapid rate when subjected to mowing.

Chemical weed control has not been greatly exploited in pasture and range for economic reasons related to low value of the land involved. However, sodium TCA (trichloroacetic acid) applied to the basal area of sourgrass at a rate of 50 pounds dissolved in 150 gallons of water, and dalapon (2,2-dichloropropionic acid) have been used to kill sourgrass (Hosaka, 1954).

Requirements for Germination of Weed Seeds

Dormancy and irregular germination of weed seeds pose a major obstacle to effective weed control and eradication. Weed seeds often remain dormant in the soil for many years. Even periodic soil cultivation may fail to break dormancy in seeds of many species. It would be useful to obtain information on the factors that control longevity; and to determine the conditions that are most likely to induce dormancy, and the most effective methods of breaking it.

No literature was found concerning the influence of environment on germination of sourgrass seed. For seeds of many other species, rather specific requirements must be met, including temperature, light, and moisture conditions. Light quality, oxygen, and carbon dioxide also play decisive roles in determining whether or not certain seeds germinate. These combinations of factors and the mechanisms controlling the germination patterns of seeds play an important role in the ecology of plants and the persistence of weeds.

Temperature

Temperature is one of the primary factors influencing the germination of seeds. Temperature has a marked effect on the initiation of dormancy and on the after-ripening process. The great variability in

the optimum germination temperature for different species and within a species will depend on the age of the seed, storage conditions, and many other factors.

The effect of alternating temperatures on seed germination have also been widely studied (Anderson, 1947; Harrington, 1923; Morinaga, 1926; and Toole and Toole, 1956). The best alternating temperatures for maximum germination of red top (Agrostis alba L.), orchard grass (Dactylis glomerata L.), and Kentucky bluegrass (Poa pratensis L.) seeds was found to be: 20 C for 16 to 18 hours and 30 C for 8 to 6 hours daily. For the germination of bermuda grass (Cynodon dactylon L.) seed, a daily alternation of 20 C for 16 to 18 hours and 35 C for 8 to 6 hours was best. Generally an alternation from a temperature near the optimal constant value to some higher value which might be above the maximal is most effective (Tool et al., 1956). Harrington (1923) states that the beneficial effect of alternating temperatures on germination is due not to the specific effect of the extreme temperatures of alternation or to the mean temperature of the alternation but to the changes in the temperatures. Morinaga (1926) used more extreme temperatures in the alternation and found that a daily alternation of 10 to 38 C (6 hours in the high and 18 hours in the low temperature) in the dark was beneficial to the germination of the seed of bermuda grass. There are several theories on the effect of alternating temperatures on seed germination. Harrington (1923) stated that heat might be considered a stimulus to germination; and the advantage of an alternation between temperatures, the warmer of which lies either near the upper limit of endurance of a given seed or above the optimum for its germination, might lie in the fact that the seed is given the

temporary and recurring advantage of an elevation of temperature without being subjected to harmful effects of long-continued exposure to a high temperature. Davis (1939) suggested that alternating temperatures were particularly effective on seed types having membranes that restrict gaseous exchange. When alternating temperatures are employed there is a rise in both the respiratory intensity and the catalase activity throughout the period of germination. The time required at each temperature of the alternation depends upon the restriction of the membranes and the temperatures employed. Toole et al. (1956) suggested that the beneficial effects derived from varying temperatures may result from the formation of intermediate materials of respiration at the high temperature portion of the cycle. These intermediate products may promote germination at a lower temperature. Koller et al. (1962) suggested that there may be a plastic or adaptable macromolecular compound, such as an enzyme precursor, or a membrane-separating reactant, which is sufficiently modified by the temperature change to initiate the germination process. Koller concluded that neither the rate nor the duration of the temperature change determines whether germination will occur.

Light

In a study on the influence of light on grass seed germination, Stebler (1881) found that the seeds of a number of grass species germinated much better in light than in darkness. The lack of light may prevent the germination of some weed, while the presence of light may cause others to remain dormant. Seeds of the former type will not sprout if they are covered with soil to a depth which excludes all

light and seeds of the latter type remain dormant if a shallow planting allows too much light to reach them. Both the inhibition and the enhancement of germination by light were widely confirmed, and numerous examples of each have been reviewed (Crocker and Barton, 1957; Koller et al., 1962; Toole et al., 1962). Koller (1962) classifies the effect of light on germination as: (1) inhibition or promotion of germination, (2) photoperiodism, (3) temperature-light interactions. The reaction of light in germination is related to the deactivation of seed coat inhibitors. There are many indications that an inhibitor is formed during germination which can be destroyed by light or chemicals (Evenari, 1949). According to Evenari (1955) the photoblastic reaction, photosensitivity, and photo-requirement were greatly influenced by temperature, chemicals, and the gaseous atmosphere of the surrounding environment.

Much evidence would suggest that germination of certain seeds would be stimulated considerably if the seeds were subjected to proper photoperiod (Toole et al., 1956). The photoperiodic control of seed germination has been reported in a number of photoblastic seed by Ishikawa (1954). He indicated that many of the "light-favored seeds" were "short-day seeds" the germination of which was promoted in the presence of the dark period, which is analogous to the flowering of short day plants. Black and Wareing (1957) have investigated the response in short-day seed, and demonstrated that the response is markedly photoperiodic, a high germination percentage being obtained under short days. Betula pubescens Ehr seeds required long photoperiod for germination (Black and Wareing, 1955). Borthwick et al. (1952) reported that the action spectrum for germination of light-sensitive

lettuce seed is the same as that for the photoperiodic control of flowering. They concluded that the same photoreaction is involved both in the photoperiodic control of flowering and in the light-sensitivity of seeds.

The Effects of Chemical Treatments on Seed Germination

The use of chemicals to break dormancy and to induce germination of seeds has been extensive. Seed germination in many instances can be controlled or influenced by exogenous plant hormones.

Exogenous gibberellins have been shown to stimulate germination or break seed dormancy in a wide range of species. Gibberellins will cause germination of many light-requiring seeds in darkness and thereby substitute for the effect of light (Anderson, 1968; Evenari et al., 1958; Khan, 1960; Khan et al., 1957). Trelawny and Ballantyne (1963) and Tager and Clarke (1961) found that seeds which normally require alternating temperatures would germinate under constant temperature if gibberellin was supplied. Many other investigators including Bradbeer (1968), Corn (1960), Junttila (1970), Kallio and Piroinen (1959), Khan and Waters (1969), Stowe et al. (1957), and Thompson (1969) have demonstrated a germination response to gibberellin. Gibberellic acid (GA_3) is the most readily available, and hence the most commonly used gibberellin. However, there is evidence that other gibberellins, primarily GA_4 and GA_7, are far more active in seed germination (Brian et al., 1962; Hashimoto and Yamaki, 1959; Ikuma and Thimann, 1963; Thompson, 1968). The role of gibberellin in the germination of barley seed is probably the best known of all plant hormone responses. Chrispells and Varner (1967) demonstrated

that the presence of gibberellin is required to stimulate the synthesis of hydrolytic enzymes in the aleurone layer. These enzymes then break down stored carbohydrates in the endosperm of the germinating barley seed which are then utilized by the developing seedling. Simpson and Naylor (1962) reported that dormancy in oats is imposed by a maltase block, but exogenous GA_3 activates or initiates maltase synthesis which provides glucose for germination. Amen (1968) suggested that gibberellin is probably a universal component of an inhibitor-promotor complex which constitutes the naturally occurring mechanism in the regulation of seed dormancy and germination. He also suggested two modes of action for breaking dormancy by gibberellins: (1) as a reductant for releasing latent hydrolytic enzymes; (2) as an initiator of enzyme synthesis via RNA control. Khan and Waters (1969) proposed a scheme for the hormonal control of seed dormancy and germination in which they suggested that the role of gibberellin is to provide the primary stimulus for germination. Khan (1971) reviewed the effects of gibberellins and cytokinins in seed dormancy and proposed that gibberellins play a major role and are essential, whereas the function of cytokinins is mainly to overcome endogenous growth inhibitors which may or may not be present.

Miller (1956) found that kinetin greatly increased germination of lettuce seeds. An appreciable increase in rate of germination was observed in the case of carpet grass (Axonopus compressus Beauv.) after presoaking in several of the more active purine solutions (Skinner et al., 1958). Lang (1965) also reported that application of exogenous GA_3 and kinetin overcame dormancy in seeds of many species showing various types of dormancy. Kinetin can replace the light

required for germination in a wide range of species. Miller (1958) reported that kinetin sensitizes the light-requiring lettuce (Lactuca sativa L.) seeds so that they germinate with a smaller dose of light than is normally required for their germination. Increase in endogenous cytokinin levels following exposure to red light have been found in seeds of Rumex obtusifolius (van Stadem and Wareing, 1972). Ikuma and Thimann (1963) proposed that kinetin stimulates proteinase, pectinase, and cellulase activity in lettuce cotyledons which in turn reduce the endosperm-integument restrictions. In Xanthium seeds, coumarin and xanthatin are naturally occurring germination inhibitors, but exogenous kinetin and red light are effective in reversing this inhibition (Khan and Tolbert, 1965). Khan (1971) concluded that cytokinins, although not affecting germination directly, appear to be essential for completion of gibberellin-induced germinative processes when these processes are blocked by inhibitors.

A considerable number of studies has been carried out on the effects of exogenous growth regulators, particularly GA_3 and kinetin, on seed germination. These two substances stimulated germination in a wide variety of seeds. Sinner et al. (1958) reported that a combination of gibberellin and the purine derivatives synergistically stimulated the rate of lettuce seed germination. Overbeek (1966) proposed that gibberellins and kinins both regulate the synthesis of hydrolytic enzymes via RNA control. Amen (1968) suggested that the gibberellins may be the predominant germination agent early in the germination phase, whereas the cytokinins may exert greater influence later in germination process. He also noted that gibberellin activity is more closely associated with food reserve

degradation, and cytokinin activity with initiation of cell proliferation and expansion.

Thiourea stimulated the germination of lettuce seeds at higher temperatures (Thompson and Horn, 1944). Garman and Barton (1946) reported that lettuce seeds which were soaked in 0.5 and 1.0 per cent thiourea solutions and germinated immediately after treatment displayed a gradual increase in germination with the lengthening of the period of dry storage between harvest and treatment. Thiourea was also effective for increasing germination in seeds of kola [(Cola nitida (Ventenant) Schott and Endlicher) (Ashiru, 1969)] and in Chenopodium species (Yamada, 1954; Jordan and Jolliffe, 1969).

The Effects of Moisture Stress on Seed Germination

Lawrence (1960) defined moisture stress as the diffusion pressure deficit of the water in the medium supporting a plant. It can consist in whole or in part of osmotic pressure due to dissolved solutes in the water. The minimum levels of moisture required for successful seed germination have been found to differ considerably among species (Hunter and Erickson, 1952; Stiles, 1948) as well as varieties (Helmerick and Pfeifer, 1954; Powell and Pfeifer, 1956).

Doneen and MacGillivray (1943) concluded that seed germination was proportionately delayed as soil moisture was decreased. They also observed that germination percentages for some crops decreased as soil moisture approached the wilting coefficient. Seeds of most crops and grasses tend to germinate in a shorter time at high rather than at low soil moisture. McGinnies (1960) studied the effects of mannitol-induced osmotic stress and temperature on germination of six

range grasses and reported that as water stress increased, the rate as well as the total germination were reduced. Knipe and Herbel (1960), using mannitol as the osmotic substrate, found that the total germination of lovegrass (Eragrostis lehmanniana Nees) was significantly reduced by increasing the osmotic pressure from 0.3 to 7.0 atm.

With respect to the influence of salt solutions of varying osmotic concentrations upon water absorption by seeds, Rudolfs (1921) found that water absorption by seeds was decreased 9 percent within 15 hours when the osmotic pressure of the germinating solution was increased from 0 to 7 atm. Hadas (1969) reviewed and discussed the influence of external water-stress on germinating seed and concluded that water stress and rate of uptake of water may influence growth that follows imbibition. Manohar and Heydecker (1964) and Sedgley (1963) concluded that germination was affected not only by the moisture potential but also by the surface area of a seed in contact with liquid water for water transport to the seed.

The Effect of Depth of Planting on Emergence

Even though seeds germinate in the soil, they may not be able to develop into an established plant. The size of the seed and the depth of planting are very important factors in determining the ability of plants to become established from seed. Murphy and Arny (1939) studied the emergence of grass and legume seedlings planted at different depths in five different soil types. They found that seedling emergence of all the species tested was greatest at the soil surface and decreased with depth. Usually the larger and heavier seeds could emerge from greater depths. Moore (1943) found that with small seeded grasses

optimum emergence occurred between the one-fourth and one-half inch depths of planting. Seedlings that emerged from deeper plantings were much slower in emerging compared to these which emerged from the optimum depths. He stated that the lack of an adequate food supply probably accounted for the limited emergence of small seeds from depths of one and one-half inch or deeper. Dawson and Burns (1962) also found that there was a definite relationship between seed size and their ability to emerge from relatively greater depths presumably because greater seed size represented more stored food. Since the environment changes with differences in the soil profile, depth of planting will influence germination and emergence.

Photoperiodic Effect on Development of Plants

The term photoperiod indicates the number of hours of illumination per day to which a plant is exposed (Garner and Allard, 1920). They classified flowering plants in accordance with their response to day length. Long-day plants required 14 or more hours of light in a cycle of 24 hours and short-day plants required 10 or more hours of dark. The criteria to distinguish long-day and short-day plants has changed since this early characterization and has been explained by Hillman (1969):

> "Flowering in long-day plants, whatever the absolute value of their critical day lengths, requires an illumination longer than their critical day length, while short-day plants require illumination shorter than their critical day length in order to flower."

A third group of plants was described as being day neutral. The day neutral plants were characterized by an insensitivity to the duration of light as long as there was sufficient light to maintain the plant

above the compensation point. Plants with dual daylength requirements were also recognized; long-short-day plant and the short-long-day plants (Dostal, 1950; Sachs, 1956). In 1938 Allard described a type of intermediate sensitivity where floral induction is inhibited by extremes of natural photoperiod. Garner and Allard (1923) were able to show that the response to day length was a phenomenon distinct from temperature, water supply and light intensity. Furthermore, they were able to show that length of day affected vegetative growth, formation of bulbs and tubers, extent of branching, root growth, and dormancy. However, early research in photoperiodism was primarily directed towards discovering the photoperiodic responses of flowering in a number of species and varieties. The effect of photoperiod on vegetative growth is difficult to separate from intensity or total energy received and varies depending on the plant involved. According to Schwabe (1971), the daylength effects are not merely quantitative responses to the amount of light received (intensity x time), but rather in the regulatory action of the actual durations of the alternating light and dark periods.

Olmsted (1943), studying clones of side-oats gramagrass (Bouteloua curtipendula Torr.) from different latitudes, found that height of plants and yield increased with daylength. When Kentucky bluegrass and Canada bluegrass were subjected to short daylengths by Evans and Watkins (1939), short, decumbent stems resulted; under long daylengths, stems were taller and more erect. Evans and Allard (1934) found timothy (Phleum pratense L.) stems, growing under short daylengths, usually prostrate. Purvis (1934) noted that tillering was favored by exposure of winter barley, winter oats, and winter rye to short

day lengths. Increased tillering in Kentucky bluegrass under short photoperiods was reported by Peterson and Loomis (1949). Tinckner (1925) found that yield of herbage in orchardgrass was greater under long daylengths, but the ratio of leaf blade to leaf sheath was greater under a short 10-hour daylength. Allard and Evans (1941) reported that orchardgrass had decumbent stems under 12-hour daylengths and that the stems did not become fully erect with less than 14.5 hour daylengths.

The critical day length of strains of a species may vary considerably with latitude of origin or ecological niche (Cohn, 1969; Ray, 1966). Larson (1947) demonstrated photoperiodic strains of Andropogon scoparius Michx. Gall (1947), Dibbern (1947) and Evans and Wilsie (1946) showed that smooth bromegrass (Bromus inermis Leyes.) exhibited a series of photoperiodically sensitive strains. In all cases the short-day strains originated in the southern latitudes of the United States while the long-day strains originated in more northern latitudes. The northern (long-day) strains would not flower in the south, and the southern (short-day) strains would not flower in the north until very late summer.

The response to photoperiodism is an important factor in the natural distribution of plants. As suggested by Murneek (1948), a variety with a specific photoperiodic requirement cannot populate areas where the photoperiod is unfavorable for flowering and fruiting.

Hamner (1940) and Hamner and Bonner (1938) have shown that the photoperiodic stimulus is perceived by the leaves. Induction of flowering failed if the leaves were removed. Further, Hamner and Bonner (1938) state that mature leaves were more perceptive than young

leaves. Hamner and Bonner (1938) noted that the photo-inducted stimulus in cocklebur (Xanthium pennsylvanicum Wallr.) was translocated from one part of the plant to another. Gardner and Loomis (1953) reported that the stimulus is not transferred from inducted to non-inducted parts of the orchardgrass sods.

Promotive effects on initiation of short-day plants by applying anti-auxins have been obtained by several workers including Fisher and Loomis (1954) and Bonner and Thurlow (1949). Long-day plants have generally shown promotive responses to auxin application. Leopold and Thimann (1949) obtained promotion of flowering of winter barley by applying low auxin concentrations. Lang (1965) and Evans (1964) reported that GA promotes inflorescence initiation under noninductive conditions for many cold-requiring and long-day plants. Moreover endogenous gibberellin-like substances increased response to inductive conditions. Stoddart (1966) and Stoddart and Lang (1968) have shown that the proportional concentrations of three active gibberellins changed during long days. The GA-like component was present in highest amount in short days and decreased relative to the other two under long-day inductive conditions.

The Effect of Competition Between Plant Species on Growth and Development

Competition among plants is a widely observed phenomenon both in natural plant communities and in agricultural crops. Competition among plants occurs when the supply of light, water, and nutrients is less than that required for growth of each individual plant. Plants growing in association most commonly compete for light, water, and

nutrients, although competition for oxygen and carbon dioxide may also occur (Clements et al., 1929). Donald (1963) explained that most of the factors of competition can be thought of being in a pool from which competitors may draw. The plant which is the most successful competitor is the one which draws most rapidly from the pool and which continues to draw when the pool has been depleted to the extent that other plants cannot easily use its contents. Competition between root systems for nutrient and water commences in advance of shoot competition in establishing plants but competition for light becomes important in later stages (Weaver, 1926; Troughton, 1956; and Milthorpe, 1961). The intensity of competition depends on the severity of the deficit. The result of competition is a reduction in both the rate and total amount of growth and, in some cases, in the survival of the competing plants (Deschenes, 1973).

Yamada and Horiuchi (1961) stated that competitive ability is determined by quantitative differences with respect to characters governing the physiological processes involved in the uptake of water, nutrients, and light. Species with rapid germination and emergence have an immediate competitive advantage over slower ones. Blaser et al. (1956) pointed out that aggressiveness during establishment was associated with seedling emergence and survival and with the growth rate of seedling plants. Milthorpe (1961) also reported that the size of the plant at emergence and its subsequent relative growth rate influenced its early competitive ability, so that the plant with the initial competitive advantage became increasingly dominant during seedling growth. Rummel (1946) found that the competitive success

of two wheatgrass (Agropyron spp.) ecotypes in competition with cheatgrass attributed to their relative earliness of germination and subsequent growth rates.

Competition controls shifts in floristic composition in response to environmental manipulations (Evans and Young, 1972). Changes in floristic composition result from differential responses of species to added nutrients and from competition for various factors of the environment among the associated plants. A greenhouse study involving soft chess (Bromus mollis L.), foxtail fescue (Festuca megalura Nutt.), and prostrate stork's bill (Erodium botrys (Cav.) Bertol.) indicated that competition among these species resulted primarily from differences in nitrogen uptake (Evans, 1960). These differences were expressed as changes in growth rate in the presence of sufficient phosphorus and as changes in nitrogen content of the plants when phosphorus was limiting. Evans (1960) pointed out that the differential ability to take up and utilize soil nitrogen would be the effective mechanism in competition between grasses and differential shading of plants between grass and the broad leaf species, stork's bill. Lang (1934) stated that the encouragement given to the crop by fertilization enabled it to withstand weed invasion, and frequently even to outgrow and suppress existing stands of the weeds. McCown and Williams (1968) conducted experiments to study the effect of sulfur fertility on competition for light and nutrients between soft chess and stork's bill. They found that with competition under a low sulfur regime, stork's bill acquired a disproportionate share of the available sulfur because of its more rapid root extension, but at high sulfur levels, soft chess became increasingly competitive as its population density increased, and

virtually eliminated stork's bill.

Evans (1961) assessed the relative effects of different densities of cheatgrass on growth and survival of crested wheatgrass (Agropyron desertorum (Fisch) Schult) during germination, emergence, and growth of seedlings in a greenhouse experiment. This study showed that competitive effects increased markedly with increasing density of cheatgrass. Risser (1969) also stated that competition was evident in dense stands shortly after germination but operated more slowly and more progressively in populations of lower densities.

CHAPTER III

DISTRIBUTION AND ENVIRONMENTAL RELATIONSHIPS OF SOURGRASS IN HAWAII

Field surveys were conducted to obtain more information about the nature of the sourgrass weed problems and the conditions under which they exist. The distribution of sourgrass and its relationships to topography, climate and edaphic factors were studied, examined, and investigated.

An understanding of these relationships may help to better define the present and potential impact of this weed on agriculture, and to develop effective means of controlling this pest.

MATERIALS AND METHODS

Surveys were conducted in the major areas of sourgrass infestation on Hawaii, Kauai, Maui, Molokai, and Oahu. The annual median rainfall data were obtained from Taliaferro (1959) and soil series data of each infested area were obtained from Soil Survey of State of Hawaii (Anon. 1973). Shade was estimated by visual observation. Soil samples were collected from the main rhizosphere of sourgrass, 0-15 cm, with a Hoffer soil tube. Fifteen cores were taken at each site and composited for analyses.

Soil pH was determined with a Beckman pH meter, using a saturated soil paste. Soil phosphorus was extracted with 0.02N sulfuric acid containing 3 grams of ammonium sulfate per liter (Modified Troug Method) and was determined colorimetrically as phosphomolybdenum blue on a Technicon Autoanalyzer. Exchangeable potassium, calcium, and magnesium were extracted from air-dry soil samples with 1N NH_4Ac. (pH 7.0) and were determined by flame photometer or atomic-absorption spectrophotometer.

Sourgrass tissue samples were also taken for plant analysis from the major infested areas on Oahu, Maui and Hawaii. Mature leaves just below the growing tip on main branches and stems were taken at pre-bloom stage. Samples were dried at 60 C in a forced-draft oven and were ground in a Wiley mill using a #20 mesh sieve. Mineral elements were determined by x-ray flourescence spectrography.

RESULTS

The distribution of sourgrass on Oahu, Maui, Hawaii, Molokai, and Kauai is shown in Figures 1, 2, 3, 4, and 5 and in Table 1. Sourgrass was generally more abundant below 420 meters elevation except at Palehua and Lualualei on Oahu, and Kaupo on Maui where dense sourgrass was found at elevations up to 540 meters. Sourgrass communities generally occur on the hillsides or on gentle slopes at the foot of the hills. It was especially prevalent in the dry zones, 120 to 540 mm of annual rainfall such as on the leeward side of Oahu and East Maui, and at Kahakuloa, Maui. Sourgrass occurred on a variety of soils but soil texture was most commonly silty clay to silty clay loam with shallow top soil. A few sourgrass communities were also found on stony or rocky land. The pH values of the soil ranged from 4.8 to 7.5. Soil analysis data showed a great variation in nutrient levels at the different locations (Table 1). Mineral contents of sourgrass at different locations are presented in Table 2. Average phosphorus and potassium contents of sourgrass were adequate compared to nutrient criteria for coastal bermudagrass (Cynodon dactylon (L.) Pers.), pangolagrass (Digitaria decumbens Stent.), johnsongrass (Sorghum halepense (L.) Pers.), and sudangrass (Sorghum sudanense (Piper) Staph) (Martin and Matocha, 1973).

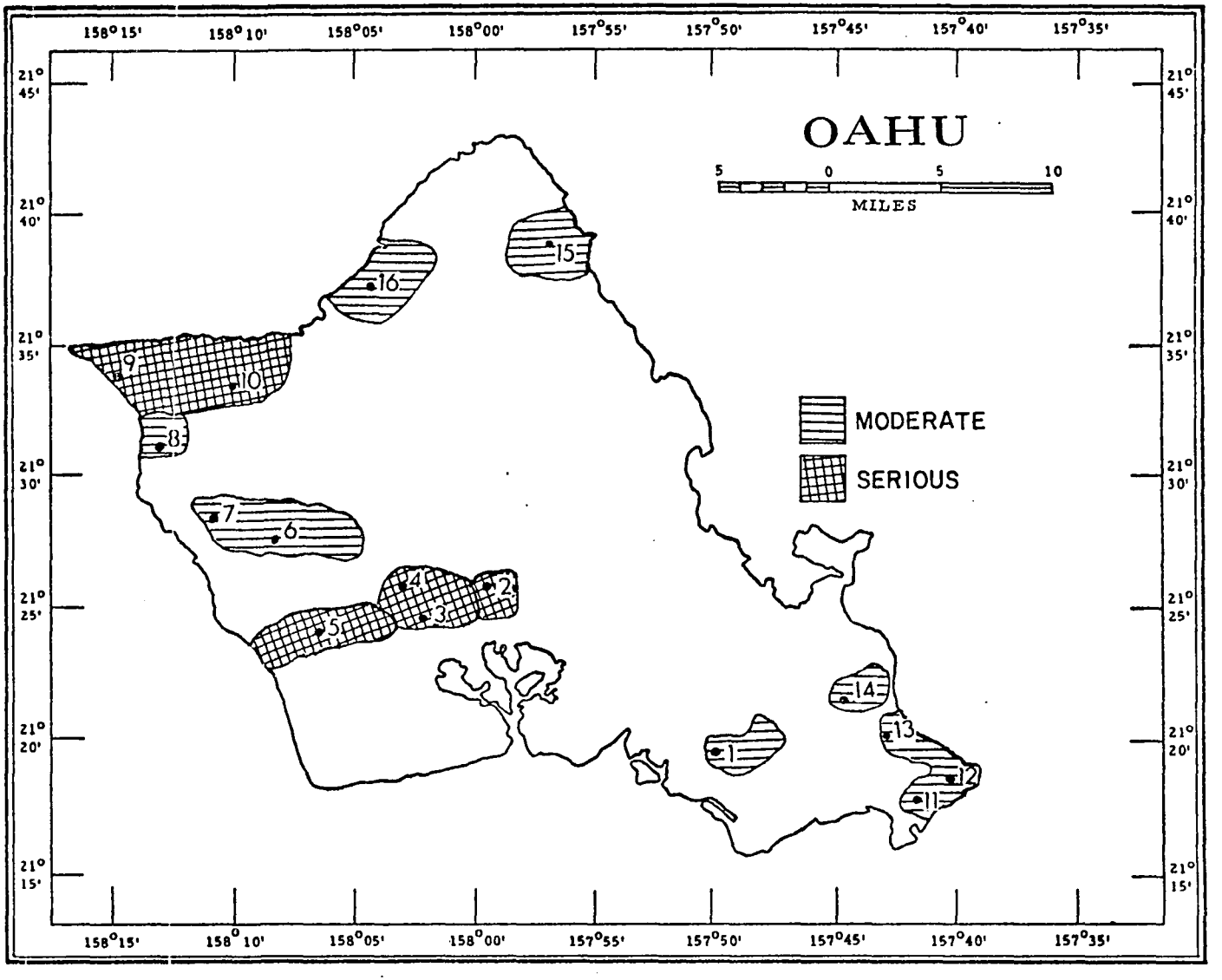


Figure 1. Distribution of sourgrass on Oahu. Figures refer to the site number.

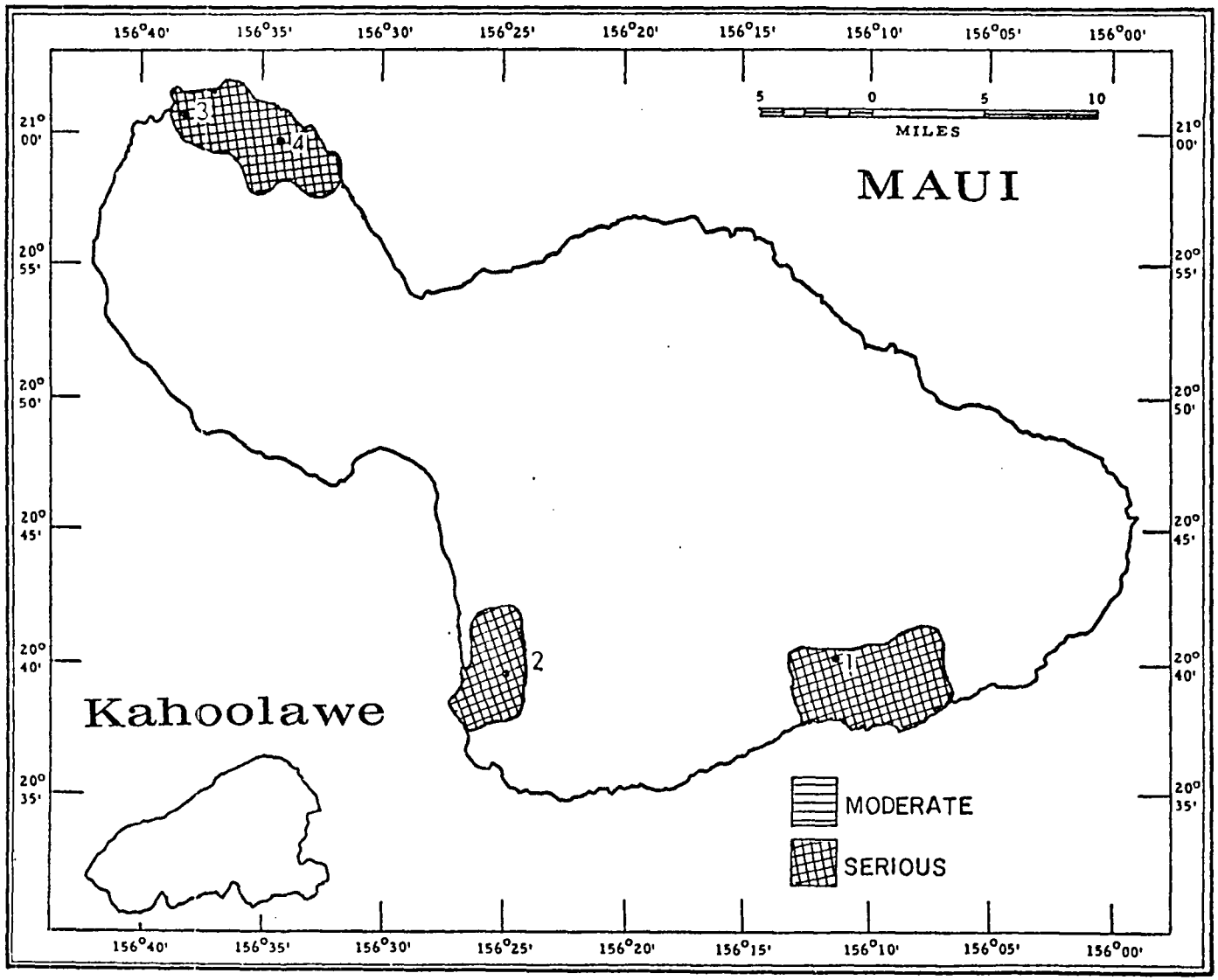


Figure 2. Distribution of sourgrass on Maui. Figures refer to the site number.

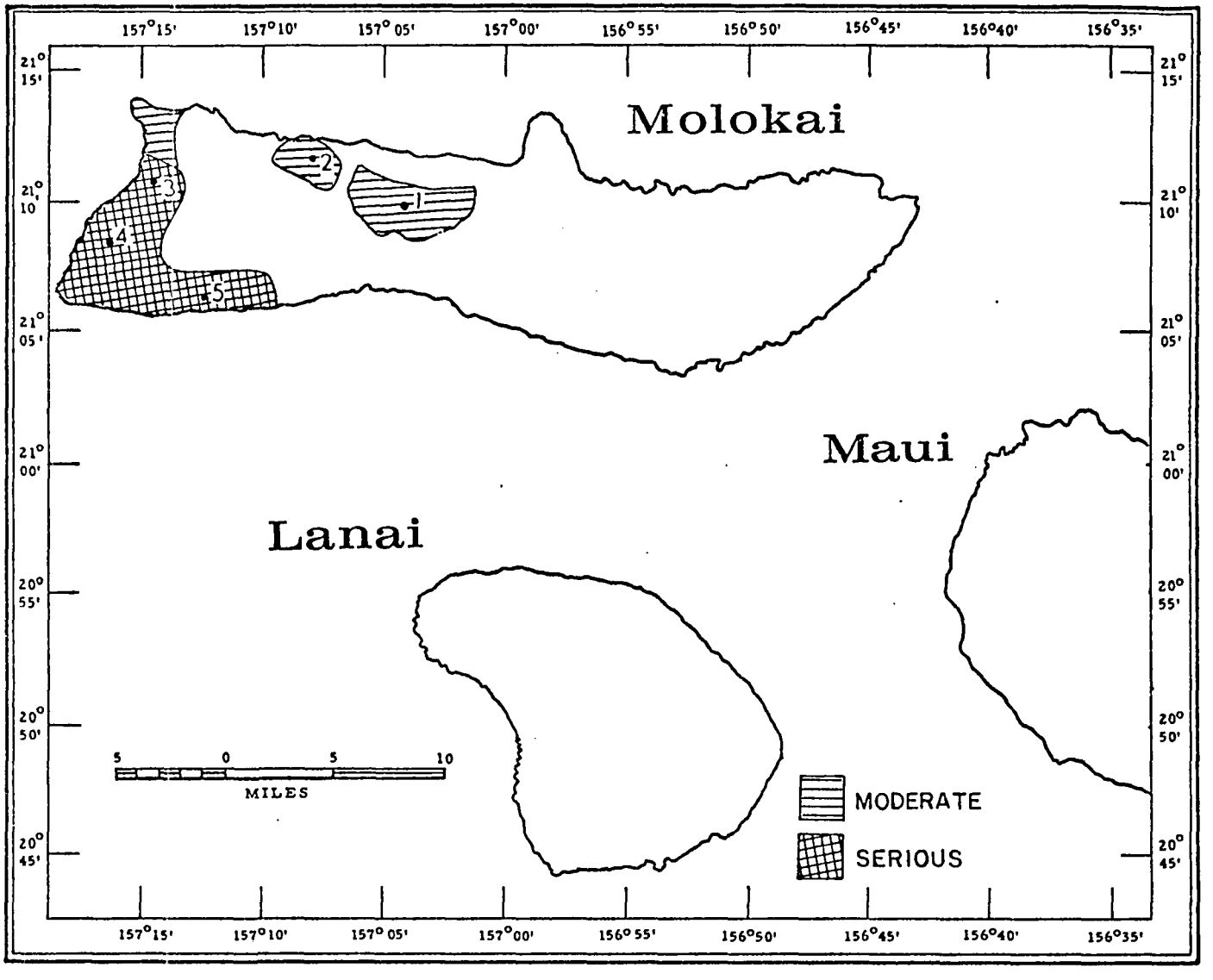


Figure 3. Distribution of sourgrass on Molokai. Figures refer to the site number.

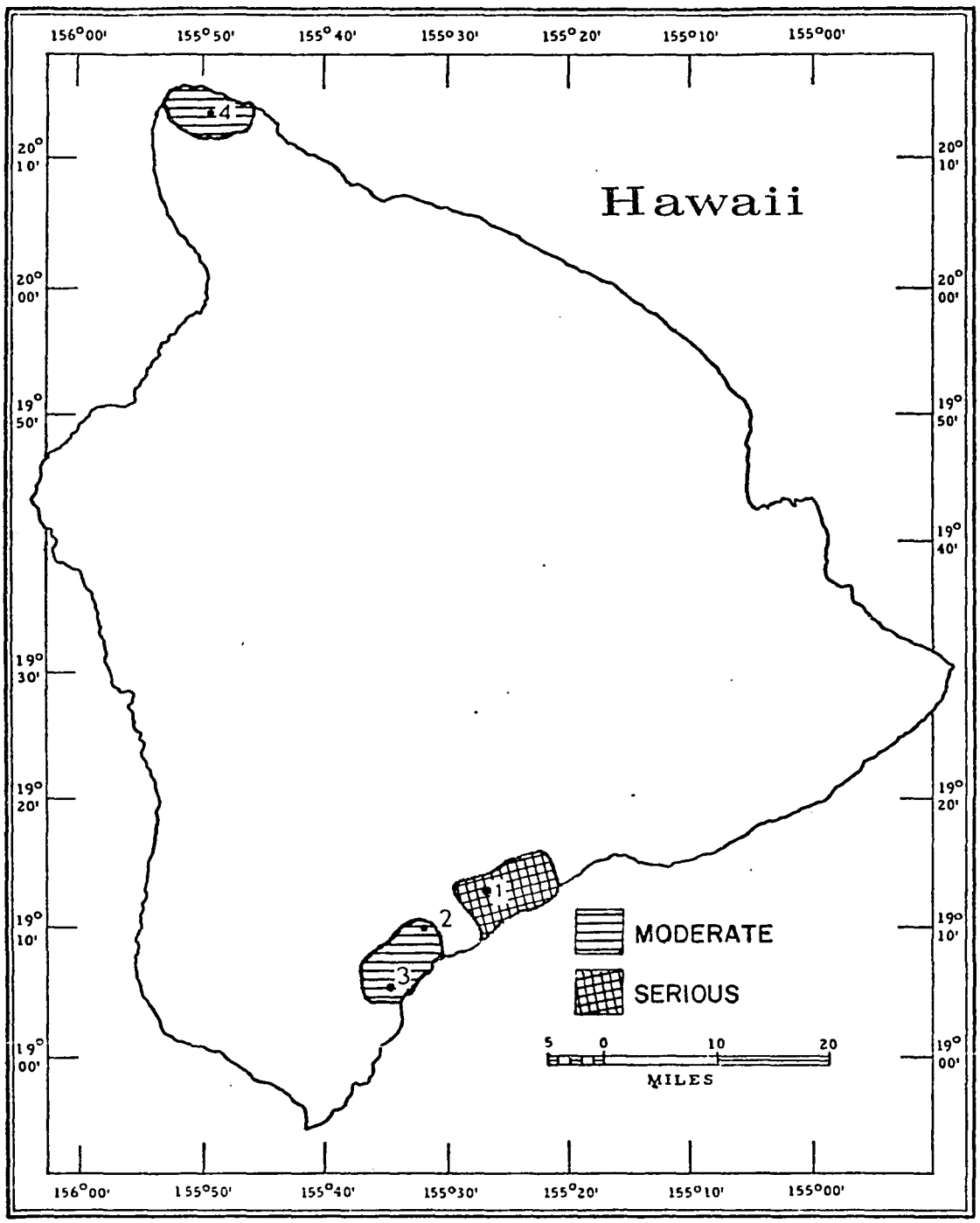


Figure 4. Distribution of sourgrass on Hawaii. Figures refer to the site number.

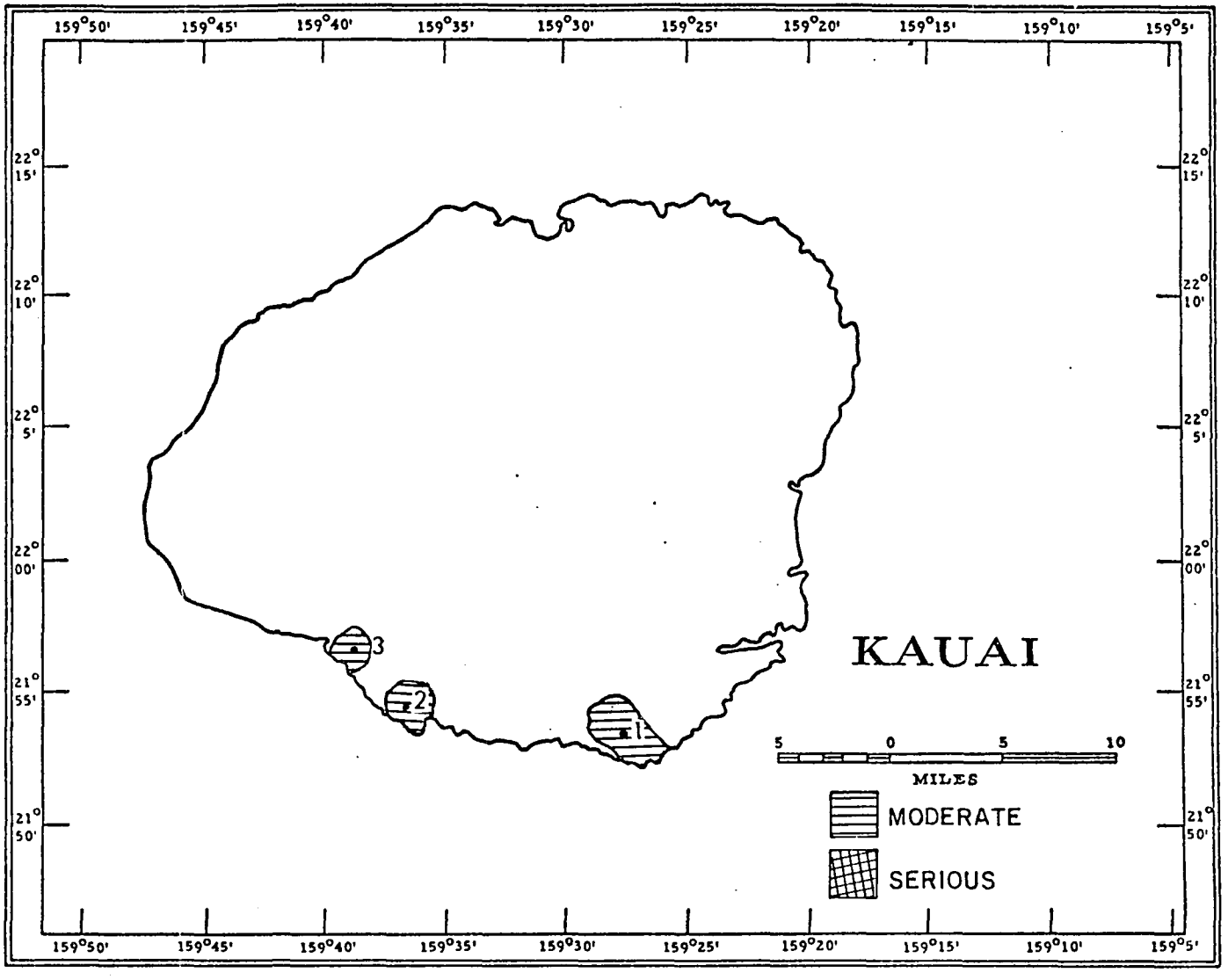
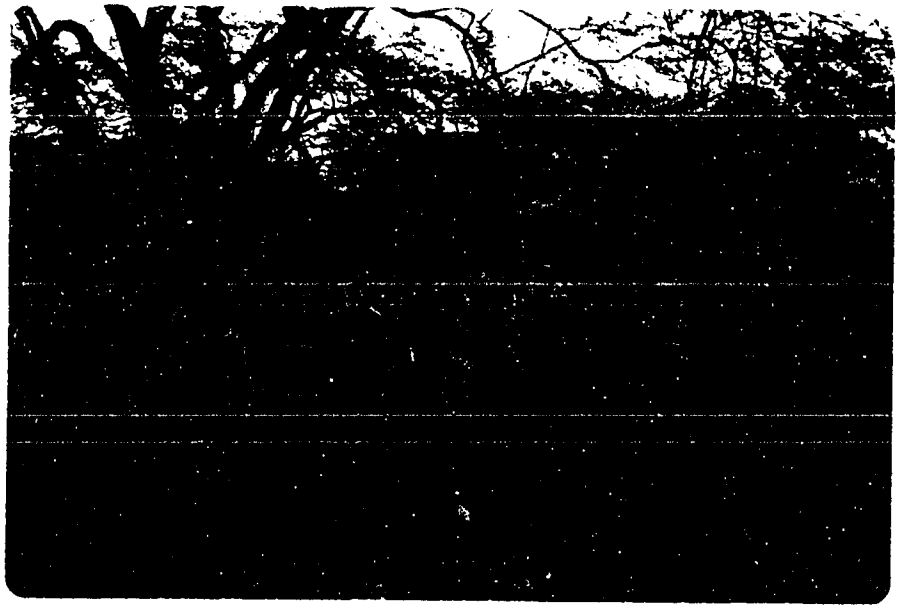


Figure 5. Distribution of sourgrass on Kauai. Figures refer to the site number.

Figure 6. Typical infestation of sourgrass

(A) Sourgrass under Prosopis pallida (Humb. and Bonpl. ex Willd) HBK. in a pasture, Mokuleia, Oahu.

(B) Sourgrass in abandoned pineapple field, Mililani, Oahu.



A

B

Table 1. Distribution of Sourgrass in Hawaii and its Ecological Parameters

Site No.	Location	Altitude	Slope	Median Annual Rainfall	Soil Series	Soil Analysis					Associated Plant Species and Trees	Shade
						pH	P	K	Ca	Mg		
		m	degree	mm			ppm	m.e./100 gm.				%
Island of Oahu												
1	Waahila Ridge	120	20	760	Rock land	6.0	74	1.4	17.0	13.6	Chloris barbata Rhynchelytrum repens Panicum maximum Leucaena latisiliqua	40
2	Panakauahi	120	5	760	Molokai silt clay loam	5.5	40	1.3	5.5	4.7	Rhynchelytrum repens Psidium guajava Leucaena latisiliqua	5
3	Palehua	540	30	500	Various Tropohumults -Dystrandepts	4.8	30	1.8	6.8	5.8	Chloris barbata Panicum maximum Bothriochloa pertusa Prosopis pallida Leucaena latisiliqua	60
4	Palehua	420	10	500	Various Tropohumults -Dystrandepts	5.5	30	1.7	5.1	4.6	Rhynchelytrum repens Lantana camara Accacia farnesiana	50
5	Lualualei	420	20	500	Lualualei stony clay	7.4	114	1.6	30.8	17.0	Rhynchelytrum repens Chloris barbata Bothriochloa pertusa Panicum maximum	50

Table 1. (Continued) Distribution of Sourgrass in Hawaii and its Ecological Parameters

Site No.	Location	Altitude	Slope	Median Annual Rainfall	Soil Series	Soil Analysis					Associated Plant Species and Trees	Shade
						pH	P	K	Ca	Mg		
		m	degree	mm			ppm	m.e./100 gm.				%
6	Waianae	240	5	760	Ewa silt clay loam	4.9	68	2.0	12.4	8.4	Chloris barbata Echinochloa colonum Eleusine indica Panicum maximum Bothriochloa pertusa Brachiaria mutica Prosopis pallida Leucaena latisiliqua	50
7	Mahaka	300	15	500	Lualualei stony clay	5.9	274	3.8	15.9	8.1	Cenchrus ciliaris Prosopis pallida Leucaena latisiliqua	60
8	Makua	120	10	500	Pulehu stony clay loam	6.0	274	2.9	18.2	7.3	Chloris barbata Panicum maximum Prosopis pallida Leucaena latisiliqua	50
9	Kaena Pt.	60	30	500	Rock Land	6.0	174	2.6	19.4	12.4	Chloris barbata Panicum maximum Rhynchelytrum repens Cynodon dactylon Prosopis pallida Leucaena latisiliqua	40

Table 1. (Continued) Distribution of Sourgrass in Hawaii and its Ecological Parameters

Site No.	Location	Altitude	Slope	Median Annual Rainfall	Soil Series	Soil Analysis					Associated Plant Species and Trees	Shade
						pH	P	K	Ca	Mg		
		m	degree	mm			ppm	m.e./100 gm.				%
10	Mokuleia	240	25	760	Ewa stony clay	5.4	156	2.3	10.3	7.2	Panicum maximum Leucaena latisiliqua Prosopis pallida	60
11	Wawamalu	12	5	760	Koko silt loam	6.5	274	3.9	31.9	18.3	Panicum maximum Prosopis pallida	30
12	Makapuu	60	20	760	Rock land	5.9	216	1.5	12.5	13.0	Panicum maximum Prosopis pallida	40
13	Kaupo	60	20	760	Kawaihapai stony clay loam	6.0	274	2.2	17.7	11.1	Prosopis pallida Leucaena latisiliqua	30
14	Waimanalo	18	5	1000	Waialua clay	6.1	156	1.9	18.2	12.3	Chloris barbata Mimosa pudica Leucaena latisiliqua	10
15	Laie	60	10	1000	Lahaina silt clay	7.5	144	0,7	26.2	6.0	Cenchrus ciliaris Leucaena latisiliqua	60
16	Waimea-Haleiwa	60	5	760	Waialua (stony) silt clay	6.1	114	1.7	16.5	6.2	Panicum maximum Brachiaria mutica Echinochloa colonum Paspalum conjugatum Prosopis pallida Leucaena latisiliqua	60

Table 1. (Continued) Distribution of Sourgrass in Hawaii and its Ecological Parameters

Site No.	Location	Altitude	Slope	Median Annual Rainfall	Soil Series	Soil Analysis					Associated Plant Species and Trees	Shade
						pH	P	K	Ca	Mg		
		m	degree	mm			ppm		m.e./100 gm.			%
Island of Maui												
1	Kaupo	360	20	760	Waiakoa extremely stony silty clay loam	6.1	230	1.8	13.0	6.3	Chloris barbata Rhynchelytrum repens Panicum maximum Cenchrus ciliaris Prosopis pallida Leucaena latisiliqua Lantana camara	60
2	Ulupalakua	300	15	500	Makena loam stony complex	7.1	58	2.8	25.5	11.1	Bothriochloa pertusa Rhynchelytrum repens Cenchrus ciliaris Chloris barbata Prosopis pallida Leucaena latisiliqua	50
3	Honokohau	240	40	760	Koele rocky complex	6.1	136	1.4	7.6	12.5	Schinus terebinthifolius Lantana camara Leucaena latisiliqua Psidium guajava	15
4	Kahakuloa	240	50	760	Koele rocky complex	6.2	44	1.9	8.7	11.8	Chloris barbata Leucaena latisiliqua	60

Table 1. (Continued) Distribution of Sourgrass in Hawaii and its Ecological Parameters

Site No.	Location	Altitude	Slope	Median Annual Rainfall	Soil Series	Soil Analysis					Associated Plant Species and Trees	Shade
						pH	P	K	Ca	Mg		
		m	degree	mm			ppm	m.e./100 gm.				%
Island of Molokai												
1	Hoolehua	120	10	500	Molokai silt clay loam	5.3	24	0.9	3.2	2.5	Panicum maximum Leucaena latisiliqua Lantana camara	10
2	Kawahuna	24	20	500	Waikapu silt clay loam	6.4	40	1.2	3.1	4.6	Cenchrus ciliaris Prosopis pallida Lantana camara	60
3	Papohaku	9	5	250	Mala silt clay	6.5	18	1.8	3.5	4.0	Prosopis pallida	50
4	Kaunalu	60	30	250	very stony land	7.3	28	3.3	6.2	7.1	Bothriochloa pertusa Chloris barbata Prosopis pallida	
5	Hakina	6	15	250	Kapuhika extremely stony clay	7.1	284	3.8	22.1	13.4	Chloris barbata Setaria verticillata Prosopis pallida	50
Island of Hawaii												
1	Paauau	105	10	760	Punaluu extremely rocky peat	5.7	40	1.5	3.1	3.0	Panicum maximum Elusine indica Xathium strumarium Prosopis pallida Accacia farnesiana	10

Table 1. (Continued) Distribution of Sourgrass in Hawaii and its Ecological Parameters

Site No.	Location	Altitude	Slope	Median Annual Rainfall	Soil Series	Soil Analysis					Associated Plant Species and Trees	Shade
						pH	P	K	Ca	Mg		
		m	degree	mm			ppm	m.e./100 gm.				%
2	Punaluu	120	10	760	Punaluu extremely rocky peat	7.1	274	2.9	12.1	4.7	Panicum maximum Amaranthus spinosus Cynodon dactylon Lantana camara Leucaena latisiliqua	10
3	Kawa	15	10	760	Punaluu extremely rocky peat	6.7	216	2.3	12.5	8.1	Panicum maximum Amaranthus spinosus Cynodon dactylon Leucaena latisiliqua Lantana camara	50
4	Upolu	54	20	760	Punaluu extremely rocky peat	6.1	120	2.0	13.8	13.5	Panicum maximum Setaria verticillata Leucaena latisiliqua	70
Island of Kauai												
1	Poipu	9	10	1016	Waikomo very rocky silt clay	6.2	120	1.9	20.1	6.6	Leucaena latisiliqua	60
2	Port Allen	12	5	625	Makaweli silt clay loam	6.6	56	2.1	5.2	4.1	Panicum maximum Leucaena latisiliqua Prosopis pallida	50
3	Kekupua	24	30	635	Mahana silt loam	5.5	274	1.3	12.9	9.2	Panicum maximum Leucaena latisiliqua Prosopis pallida	60

Table 2. Mineral content of sourgrass from various locations

Location	Mineral Content									
	P	K	S	Ca	Mg	Si	Mn	Fe	Cu	Zn
	%						ppm			
Oahu										
Waahila	0.30	2.83	0.21	0.39	0.44	1.31	79	44	12	22
Panakauahi	0.26	2.66	0.22	0.45	0.33	1.67	99	112	17	20
Palehua	0.28	2.79	0.20	0.30	0.30	1.39	51	47	15	17
Palehua	0.24	2.32	0.19	0.36	0.24	1.61	128	116	14	13
Lualualei	0.25	3.18	0.21	0.46	0.48	1.72	37	30	12	14
Waianae	0.29	2.64	0.14	0.31	0.31	1.53	23	45	12	8
Makaha	0.28	3.09	0.19	0.34	0.30	1.80	3	46	14	13
Makua	0.39	2.86	0.19	0.49	0.35	1.56	19	55	11	16
Kaena Pt.	0.33	2.45	0.21	0.33	0.41	1.95	5	9	11	11
Mokuleia	0.37	3.63	0.22	0.39	0.31	1.08	28	150	14	22
Wawamalu	0.27	2.45	0.38	0.33	0.34	2.42	14	26	13	8
Makapuu	0.25	2.53	0.31	0.23	0.38	2.28	-*	-*	13	11
Kaupo	0.27	2.95	0.27	0.37	0.30	1.59	26	105	18	25
Waimanalo	0.30	2.29	0.17	0.31	0.30	2.06	21	27	10	6
Laie	0.23	2.13	0.21	0.93	0.71	0.20	13	95	7	45
Waimea	0.41	2.54	0.20	0.37	0.36	1.40	8	44	13	15
Hawaii										
Paauau	0.28	2.8	0.20	0.26	0.42	2.30	45	4	9	2
Punanulu	0.40	3.52	0.23	0.23	0.30	1.17	-*	116	14	17
Kawa	0.37	2.45	0.19	0.26	0.12	2.17	-*	41	10	2
Upolu	0.25	3.21	0.23	0.24	0.39	0.64	33	103	13	18
Maui										
Honokahua	0.26	1.37	0.41	0.25	0.46	2.42	25	-*	8	1
Kahakuloa	0.21	2.03	0.43	0.27	0.40	2.22	11	16	10	5
Ulupalakua	0.26	2.95	0.15	0.35	0.30	1.66	3	163	12	5
Kaupo	0.27	2.90	0.18	0.38	0.29	2.52	12	51	17	3
Average	0.30	2.71	0.23	0.34	0.33	1.79	25.7	63.3	12.5	13.8

* Trace

Soil tests and plant uptake for P, K, Ca, and Mg did not show good correlation.

In most areas surveyed, sourgrass, though found on roadsides, was essentially limited to the shade of Prosopis pallida (Humb. and Bonpl. ex Willd) HBK. or Leucaena latisiliqua (L.) Gillis and Stearn wherever they form a relatively thin stand (up to approximately 60% shade). Lantana camara L., Schinus terebinthifolius Raddi, and Acacia farnesiana (L.) Willd were also associated with sourgrass. In most sourgrass communities more than 90 percent of the volume of vegetation in shaded areas was composed of sourgrass by visual estimate. A few common accessory species were Chloris barbata (L.) Sw., Rhynchelytrum repens (Wild.) C. E. Hubb., Panicum maximum Jacq. and Cenchrus ciliaris L. In open areas Chloris barbata (L.) Sw., Rhynchelytrum repens (Wild.) C. E. Hubb., Bothriochloa pertusa (L.) A. Camus., Cenchrus ciliaris L. and Panicum maximum Jacq. were dominant, and sourgrass tended to occur in scattered clumps.

DISCUSSION

Sourgrass was more abundant on abandoned dry areas and on ranges where native vegetation has been reduced in density and vigor by continued overgrazing or by fire. Distribution of rainfall on major islands of Hawaii is strongly seasonal, particularly in the leeward areas. Winter storms usually provide variable rainfall between October and April but May-to-September period receives little or no rainfall. New seedlings of sourgrass or new shoots from old sourgrass stools appear immediately after the initiation of rainfall in October or November, and growth continues until after the rains cease about April. The main

growth and flowering period of sourgrass closely parallels the availability of soil moisture.

The absence of sourgrass communities at the higher elevations indicates that germination and/or growth may sufficiently depressed by low temperatures that sourgrass is less able to compete with other species growing at these elevations.

Sourgrass was closely associated with shade conditions. It was most prevalent under trees of Prosopis pallida (Humb. and Bonpl. ex Willd) HBK. or Leucaena latisiliqua (L.) Gillis and Stearn. This may be explained by the following factors. Shade reduces evapotranspiration and so maintains more favorable moisture conditions for seedling development and growth of sourgrass. Trees also provide windbreak effects so that young, weak sourgrass seedlings are protected from strong wind. Competition from other grasses and weeds may be reduced under trees due to reduced sunlight and more intensive grazing by cattle. Palatable plants would also be more susceptible to trampling damage in the shade due to their succulent, etiolated morphology.

Apparently sourgrass infestations usually begin in shaded areas where valuable range grasses do not thrive. They then rapidly spread to adjoining areas since sourgrass produces large amounts of viable hairy seeds which are dispersed easily by wind. Sourgrass probably becomes dominant in open areas only if conditions such as overgrazing or fire reduce the competitiveness of the existing species.

Sourgrass also occupy in old or abandoned pineapple fields. Its occurrence appeared to be a function of minimal competition from the old pineapple plants and a high level of tolerance by sourgrass to

residual diuron (3-(3,4-dichlorophenyl-1,1-dimethylurea).

Sourgrass communities were not restricted to a particular soil type and occurred on a wide variety of soils. Soil analysis data also showed a great variation in nutrient levels at the different locations. Therefore, soil conditions do not appear to be a major determining factor in the distribution of sourgrass. This weed may grow on a wide spectrum of soils if other environmental factors are suitable for its growth.

During the survey a few ranchers stated that sourgrass can eventually be replaced by more permanent and valuable perennial grasses if grazing is properly regulated and fires are avoided. Sourgrass can also be partially controlled by heavy grazing in the dry season because cattle will eat the partially dried sourgrass when other forage is not available.[1]

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[1] Cran, G. J. (Mokuleia Ranch, Oahu) Personal communication.

CHAPTER IV

GERMINATION AND EMERGENCE OF SOURGRASS

Dormancy, whether innate, induced, or enforced, in effect prolongs the viability of seeds (Anon., 1968). This characteristic affords protection to the species from adverse conditions by spacing out germination or by germinating only in response to external stimuli presumably associated with favorable conditions for plant growth. Some individuals of this species thereby escape the adverse conditions. In weed species, seed dormancy thus compounds the problem of weed control.

Moisture, temperature, light, and oxygen are common major determining factors for germination of seeds. Depth of planting is also a very important factor for establishment and growth of emerging seedlings.

The objective of this series of experiments was to determine factors affecting germination and emergence of sourgrass. These included effects of temperature and light (Experiment 1), photoperiodicity (Experiment 2), chemical treatment of seeds (Experiment 3), and moisture stress (Experiment 4) on germination and seeding depth on emergence (Experiment 5).

GENERAL MATERIALS AND METHODS

Germination tests were carried out in the growth chamber. The seeds were placed on two thicknesses of filter paper in petri dishes. One hundred seeds per treatment were used with four replications. Distilled water was added as needed to maintain moist conditions. Germination counts were made at 2-day intervals.

A seed was considered to have germinated if its plumule and radicle protruded through the seed coat. Arc sin transformation was used prior to the analysis of variance whenever the data fell beyond the range of 30-70% germination. All comparisons were made on transformed data but means were transformed back to percent for presentation in the tables. Duncan's multiple-range test was used to compare treatment means.

1. THE EFFECT OF TEMPERATURE AND LIGHT ON GERMINATION OF SOURGRASS SEEDS

MATERIALS AND METHODS

Germination was evaluated at 20, 25, and 30 C in constant dark and under 8-hr. light and 16-hr. dark conditions. The effect of alternating temperatures, 15-25, 20-30, and 25-35 C was also evaluated. Under alternating temperature regimes, the growth chamber was programmed for 8 hr. at the high temperature with light and 16 hr. at the low temperature in darkness.

RESULTS

Germination was greater and proceeded at a more rapid rate with artificial light (Table 3). Optimum temperature regimes were 30 C, 20-30 C and 25-35 C. Germination at 25 C progressed at a somewhat slower rate and the final percentage was slightly lower. At 20 C and 15-25 C germination was delayed, the progress of germination was slower, and the final percentage values were lower than at the other conditions mentioned above.

Table 3. The effect of temperature and light on germination of sourgrass seeds

Temperature	Illumination	Cumulative germination days after treatment			
		3	5	7	9
C		%			
20	Light	0	31.0 c	83.3 b	88.0 b
	Dark				13.3 e[2/]
25	Light	6.0 d	69.0 b	84.0 b	89.8 b
	Dark				14.1 e[2/]
30	Light	56.0 b	91.8 a	95.3 a	96.3 a
	Dark				38.0 d[2/]
15-25	Light	0 e	33.5 c	73.8 b	87.8 b
	Dark				3.5 f[2/]
20-30	Light	44.5 c	85.5 a	94.5 a	95.5 a
	Dark				32.3 d[2/]
25-35	Light	59.8 a	90.3 a	92.5 a	92.5 ab
	Dark				72.8 c[2/]

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

[2/] Final germination counts only were made to prevent exposure to light.

light was important for good germination. Germination in complete darkness was poor at most temperatures. Under continuous darkness, fair germination was obtained at 30 C and 20-30 C and good germination at 25-35 C. Germination at 15-25 C, 20 C, and 25 C without light was extremely poor.

Optimum germination of sourgrass was thus obtained under light conditions with alternating temperatures ore relatively high constant temperature. This agrees with reports by Peters et al. (1964) and Toole (1938).

2. THE EFFECT OF PHOTOPERIOD ON GERMINATION OF SOURGRASS SEEDS

MATERIALS AND METHODS

This experiment was conducted in a growth chamber regulated for a constant temperature of 30 C. Germination tests ran for 11 days and were replicated four times (four dishes per run). The photoperiod treatments consisted of constant light, 16 hours light and 8 hours dark, 12 hours light and 12 hours dark, 8 hours light and 16 hours dark, and constant darkness. Dark effects were simulated by wrapping the Petri dishes in aluminum foil. Germination counts were made at the end of 5, 7, 9, and 11 days.

RESULTS

The effect of photoperiod on germination of sourgrass seed is shown in Table 4. Exposure to 8- or 12-hour photoperiods resulted in high germination percentage and more rapid germination than with 0, 16, or 24 hours light. Although light was previously shown to be

necessary for germination, the germination percentage was reduced at 16 hours light, and only 41% germinated under continuous exposure to light. Germination was severely inhibited under constant darkness. The light period for optimum germination of sourgrass seeds was relatively broad, but germination tended to be somewhat better in short photoperiod than in long photoperiods. Results of this study were similar to those obtained by Ishikawa (1953) who found that in most light-favored seeds, the germination percentage increased as photoperiod was lengthened to a certain critical duration (at which the highest rate of germination was obtained); but germination percentage began to drop when the length of the photoperiod exceeded the critical value, and a comparatively lower rate was obtained under continuous exposure to light.

Table 4. Effect of photoperiod on germination of sourgrass seeds

Photoperiod	Cumulative germination days after treatment			
	5	7	9	11
hr	%			
0	3.0 c[1/]	5.4 d	8.2 d	10.7 d
8	69.8 a	84.6 ab	89.2 a	90.1 a
12	74.8 a	86.7 a	90.0 a	92.0 a
16	61.6 ab	77.3 b	82.3 b	84.6 b
24	46.1 b	35.4 c	40.0 c	41.0 c

[1/] Means within a column followed by different letters are significantly different at the 5% levels by Duncan's Multiple Range Test.

3. EFFECT OF CHEMICAL TREATMENT ON GERMINATION OF SOURGRASS SEED

Germination of sourgrass was very poor in complete darkness and at lower temperatures (Table 3). The purpose of this study was to evaluate the ability of gibberellic acid (GA), kinetin, and thiourea to overcome light and temperature limitations to germination in sourgrass.

MATERIALS AND METHODS

The seeds were pre-soaked for 24 hours in aqueous solutions of GA of 62.5, 125, 250, 500, 1,000 and 2,000 ppm; kinetin of 12.5 , 25, 50, 100, and 200 ppm; and thiourea at 250, 500, 1000, 2000, and 4000 ppm; and in distilled water as control. Presoaking was done in darkness at room temperature (26 C). The seeds were then incubated in darkness at 22 C.

RESULTS

The germination of sourgrass in response to chemical treatments are presented in Tables 5, 6, and 7. Germination percentages of the control seeds of the GA treatment differed from those of the kinetin and thiourea treatments because different lots of seed were used. Germination was clearly stimulated by GA treatments at all treatment concentrations in this trial. None of the concentrations reduced germination of sourgrass. Under dark conditions a concentration of 1000 ppm GA was required to obtain maximum germination. GA not only had an effect upon total germination but also increased the rate of germination.

An appreciable increase in rate of germination was also observed after presoaking in 12.5, 25, and 50 ppm solutions of kinetin (Table 6). Pretreatment of sourgrass seeds with 12.5, 25, and 50 ppm for 24 hours, followed by germination in the dark for 13 days, gave 55, 56, and 60% germination, respectively, as compared to a water control of 37%. However there was no benefit for soaking in 100 and 200 ppm concentrations.

Germination of sourgrass seed was increased slightly by presoaking the seeds for 24 hours in a 1000 ppm solution of thiourea (Table 7). However, there was no increase in germination at other concentrations. On the contrary germination was inhibited by 2000 and 4000 ppm thiourea.

Table 5. Effect of gibberellic acid on germination of sourgrass seeds in the dark at 22 C

Conc GA	Cumulative germination days after treatment					
	3	5	7	9	11	13
ppm	%					
0	0 e[1/]	1.0 e	2.5 f	4.9 e	5.7 f	6.7 g
62.5	7.1 d	15.9 d	17.8 e	20.4 d	20.9 e	20.9 f
125	17.2 c	38.5 c	43.0 d	44.7 c	46.6 d	47.5 e
250	17.5 c	39.7 c	50.0 c	52.8 c	53.5 c	54.4 d
500	21.9 b	55.9 b	63.8 b	66.6 b	68.6 b	69.3 c
1000	36.8 a	76.6 a	82.3 a	84.3 a	85.0 a	87.3 a
2000	16.6 c	43.7 c	64.3 b	70.3 c	72.8 b	74.8 b

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

Table 6. Effect of kinetin on germination of sourgrass seeds in the dark at 22 C

Conc Kinetin	Cumulative germination days after treatment					
	3	5	7	9	11	13
ppm	%					
0	4.5 a[1/]	19.3 b	27.0 bc	31.5 bc	33.5 c	37.0 bc
12.5	10.3 a	35.0 a	49.5 a	53.5 a	54.3 a	55.8 a
25	7.3 a	33.5 a	44.5 a	47.0 a	50.0 a	54.8 a
50	6.5 a	33.8 a	49.6 a	54.0 a	56.3 a	60.3 a
100	7.3 a	27.8 b	36.5 b	36.5 b	40.5 b	43.5 b
200	4.3 a	21.0 b	28.0 c	28.0 c	30.8 c	34.0 c

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

Table 7. Effect of thiourea on germination of sourgrass seeds in the dark at 22 C

Conc Thiourea	Cumulative germination days after treatment					
	3	5	7	9	11	13
ppm	%					
0	4.5 b[1/]	19.3 bc	27.0 b	31.5 b	33.5 b	37.0 b
250	4.5 b	22.5 b	29.8 b	33.3 b	34.8 b	38.0 b
500	3.8 b	22.5 b	27.0 b	31.8 b	34.5 b	37.3 b
1000	7.0 a	28.8 a	38.5 a	41.0 a	43.0 a	45.5 a
2000	1.3 c	14.5 cd	22.3 b	25.8 b	29.0 b	34.0 b
4000	0 d	13.0 d	25.0 b	27.8 b	29.5 b	33.8 b

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

4. EFFECTS OF MOISTURE STRESS ON GERMINATION OF SOURGRASS, BUFFELGRASS, AND GUINEAGRASS

The purpose of this study was to determine the effect of moisture stress on seed germination of sourgrass, buffelgrass, and guineagrass under mannitol-induced moisture tensions.

Mannitol has been used frequently as an osmotic substrate in studies concerning seed germination. Powell and Pfeifer (1956) and Younis et al. (1963) have effectively tested drought hardiness by use of mannitol solutions. Thimann (1954) found mannitol suitable for limiting water uptake in a plant without affecting the metabolic action of the plant. Allsopp (1955) also reported that mannitol is physiologically inert.

MATERIALS AND METHODS

Seeds of three grass species were germinated in solutions of different osmotic pressures. The osmotic tensions were obtained by saturating the substrate in the petri dishes with 0, 0.5, 1, 2, 4, 8, 12, and 16 atm D-mannitol ($C_6H_8(OH)_6$) which is nontoxic to seed (Uhivits, 1946). These solutions were prepared for specific moisture tensions according to the formula described by Helmerick and Pfeifer (1954). The control consisted of distilled water, representing 0 atm. Fifteen ml of the appropriate solution was added to each dish.

The experiment was conducted in an incubator regulated for 30 C. Since the osmotic concentration of solutions varies with temperature, all solutions were adjusted to 30 C. Pans of water were placed in the growth chamber to reduce evaporation from the petri dishes. Germination

counts were made on days 3, 5, 7, 9, 11 and 13 for all petri dishes.

RESULTS

The average germination percentage of the three grass species as affected by moisture stress at 0.5, 1, 2, 4, 8, 12 and 16 atm are presented in Tables 8, 9, and 10, and Figure 7.

Average germination percentage decreased as moisture stress was increased. These results are in agreement with the findings of other workers (Doneen and MacGillivray, 1943; Knipe and Herbel, 1960; McGinnies, 1960). Of the species tested, guineagrass was affected most by increases in moisture tension. Germination was significantly reduced by 0.1 atm moisture tension. There was no germination at 2 atm. The germination of buffelgrass was slightly reduced by 1 atm and was severely inhibited at 8 atm. There was no germination at 12 atm. Germination of sourgrass was not significantly reduced until a moisture tension of 4 atm was reached. At 8 atm, germination was greatly depressed and there was no germination above 8 atm. Delays in germination due to moisture stress were not analyzed statistically, but it was obvious that such effects were appreciable. In guineagrass a delay in germination became apparent at 0.1 atm and more of moisture tension. In sourgrass and buffelgrass a delay in germination was noticed at 2 atm and more of moisture tension.

5. THE EFFECT OF SEEDING DEPTH ON EMERGENCE OF SOURGRASS SEEDLINGS

MATERIALS AND METHODS

Makiki clay loam was used. The soil was obtained from a field never known to be infested with sourgrass so the soil was assumed to

Table 8. Effect of mannitol-induced moisture stress on germination on sourgrass seeds

Moisture Stress	Cumulative germination days after treatment					
	3	5	7	9	11	13
atm	%					
0	33.7 a[1/]	61.8 a	78.7 a	84.6 a	86.5 a	88.1 a
0.1	31.2 ab	58.2 a	76.9 a	78.8 b	79.0 b	79.0 b
0.5	28.7 b	53.0 b	66.8 b	71.3 c	72.8 bc	74.3 bc
1.0	28.2 b	53.0 b	65.8 bc	69.5 cd	72.0 cd	72.3 c
2.0	16.9 c	45.5 c	59.7 c	64.3 de	67.5 cd	69.0 c
4.0	5.7 c	34.7 d	52.2 d	62.0 e	64.5 d	67.3 c
8.0	0 d	4.0 e	10.2 e	13.9 f	15.4 e	16.9 d
12.0	0 d	0 f	0 f	0 g	0 f	0 e
16.0	0 d	0 f	0 f	0 g	0 f	0 e

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

Table 9. Effect of mannitol-induced moisture stress on germination of buffelgrass seeds

Moisture Stress	Cumulative germination days after treatment					
	3	5	7	9	11	13
atm	%					
0	2.0 a[1/]	16.8 a	27.0 a	43.5 a	51.8 a	60.0 a
0.1	2.0 a	10.7 ab	17.7 b	28.7 b	36.3 b	40.7 b
0.5	1.7 ab	11.0 ab	17.7 b	23.3 c	26.7 c	31.0 c
1.0	1.0 b	10.3 b	17.7 b	20.3 c	26.3 c	30.3 c
2.0	1.0 b	5.3 c	9.0 c	11.3 d	12.0 d	13.0 d
4.0	0.3 c	2.7 d	5.3 d	8.3 d	10.3 d	10.7 d
8.0	0 d	0 e	0.7 e	0.7 e	1.0 e	1.7 e
12.0	0 d	0 e	0 e	0 e	0 e	0 e
16.0	0 d	0 e	0 e	0 e	0 e	0 e

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

Table 10. Effect of mannitol-induced moisture stress on germination of guineagrass seeds

Moisture Stress	Cumulative germination days after treatment					
	3	5	7	9	11	13
atm	%					
0	0	1.3 a[1/]	4.3 a	9.0 a	13.0 a	14.7 a
0.1	0	1.0 b	2.3 b	2.7 b	5.7 b	7.0 b
0.5	0	0 c	1.0 b	2.3 b	4.7 b	5.0 c
1.0	0	0 c	0.3 c	0.7 c	0.7 c	1.0 d
2.0	0	0 c	0 c	0 d	0 d	0 e
4.0	0	0 c	0 c	0 d	0 d	0 e
8.0	0	0 c	0 c	0 d	0 d	0 e
12.0	0	0 c	0 c	0 d	0 d	0 e
16.0	0	0 c	0 c	0 d	0 d	0 e

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

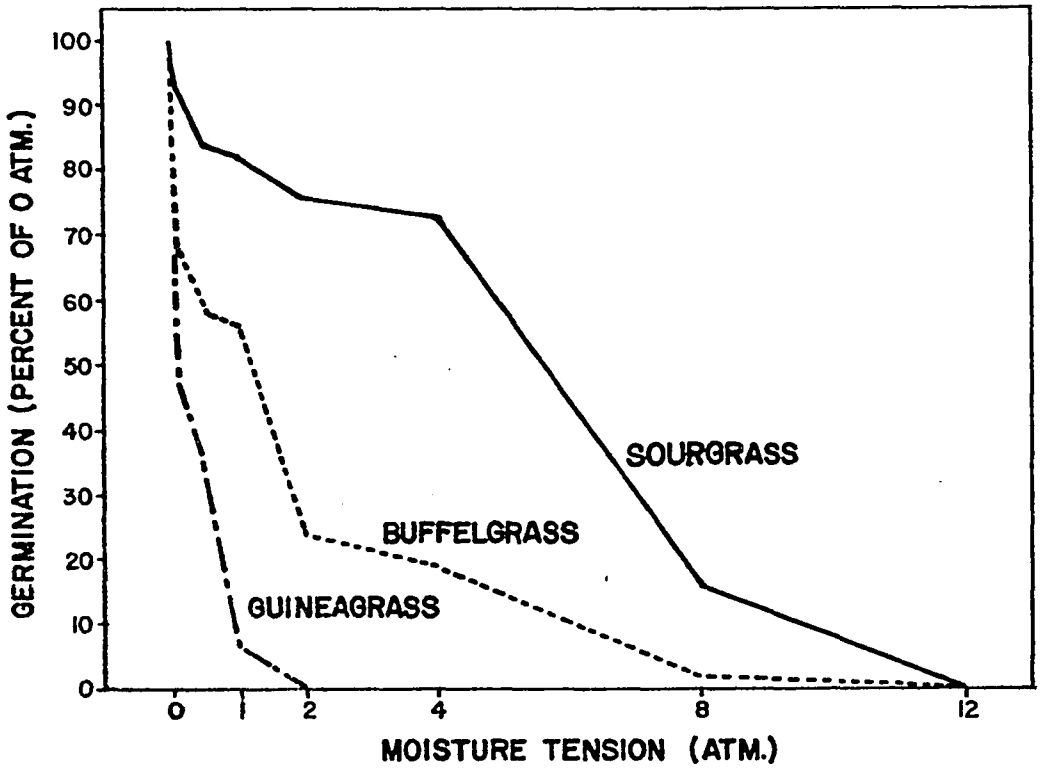


Figure 7. The effect of moisture stress on germination of buffelgrass, guineagrass, and sourgrass seed expressed as percent of 0 atm at 8 days after first seeds germinated

be free of seed of this pest. Pots 15 cm in diameter were partially filled with soil, and one hundred seeds were planted in each pot. The seeds were planted at depths of 0.5, 1.0, 1.5, 2, 3, 4, or 5 cm. The pots were watered as needed. Each treatment was replicated three times. Emerged seedlings were counted at the end of 8, 10, 12, 14 and 18 days and the pots were retained throughout the summer to determine whether or not additional germination would have occurred.

RESULTS

Emergence of sourgrass from different depths are shown in Table 11. The percentage of emerged seedlings was greatest from seeds planted near the surface (0.5, 1 cm) and decreased as the depth of planting increased to 3 cm. Emergence from seeds planted 5 cm deep was very poor. Since freshly harvested sourgrass seeds require light for germination (Table 3), it was expected that their germination percentages would decrease with increased planting depths. The same amount of sourgrass emerged from a depth of 0.5 to 3 cm, but there was a marked decrease in the number of plants which emerged from seeds 4 or 5 cm below the surface.

The rapidity of emergence was also influenced by the depth of planting. At a planting depth of 4 cm or deeper the plants were somewhat slower in emerging than from shallower depths. For instance, emergence time was delayed by 0.3, 0.6, 0.9, 1.5 and 3.6 days to reach 50 percent emergence at 1, 1.5, 2, 3, and 4 cm depths respectively, compared to the 0.5 cm planting. Thus 50% emergence was delayed by approximately 0.6 days per additional cm depth below 0.5 cm.

6. DISCUSSION

The five experiments described in this chapter all indicated that sourgrass seeds were able to germinate under a wide range of environmental conditions.

Sourgrass seeds germinated well in the light at all the temperatures tested, but was best at constant 30 C and alternating 20-30 C and 25-30 C (Table 3). Response of germination to alternating temperatures has

Table 11. Emergence of sourgrass from seeds planted at several depths

Depth of Planting	Cumulative emergence days after planting				
	8	10	12	14	18
cm	%				
0.5	37 a[1/]	67 a	75 a	77 a	80 a
1.0	27 a	68 a	74 ab	76 a	76 a
1.5	18 b	62 ab	72 ab	74 a	77 a
2.0	13 c	56 b	69 c	72 a	76 a
3.0	3 d	46 c	69 c	72 a	76 a
4.0	0 e	15 d	49 d	55 b	57 b
5.0	0 e	0 e	8 e	14 c	15 c

[1/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

widespread occurrence among plants (Harrington, 1923; Morinaga, 1926). Reduced germination at the lower temperatures was probably due to decreased enzyme and metabolic activity with consequent suppression of germination. Germination in complete darkness was poor except at the alternating temperature of 25-35 C which gave good germination. Cohen (1958) studied the effects of temperature fluctuations on dark germination of light-sensitive lettuce seeds, and concluded that a complex macromolecular compound, such as an enzyme precursor, or a membrane which separates reactants exists in the seed and inhibits its germination in darkness. This hypothetical compound is thermo-labile and may be sufficiently modified by the temperature change to initiate germination.

Photoperiods significantly influenced germination of sourgrass, with the best germination occurring at 8 and 12 hour photoperiods (Table 4). Although light was necessary for germination, germination was reduced by 16 and 24-hour photoperiods. The mechanism of inhibitory action of continuous light is still not clear but Briggs and Fork (1969) suggested that prolonged or continuous irradiation leads to cycling between absorption spectra of the two end forms of phytochrome, so that all available phytochrome may be diverted into an inactive side product.

Dark inhibition of germination was overcome to an even greater extent by treatment with GA. Kinetin and thiourea had lesser effects but also stimulated dark germination at some concentrations. Sourgrass is thus similar to a number of other light-requiring plants which will germinate in the dark when treated with GA (Anderson, 1968; Corn, 1959), kinetin (Miller, 1956; Skinner et al., 1958), or thiourea (Ashiru, 1969; Jordan and Jolliffe, 1960; Thompson and Horn, 1944; Tukey and Carlson, 1945). The mechanism is unknown but may be related to modification of

the macromolecular compound hypothesized by Cohen (1958).

An important competitive characteristic of sourgrass is its ability to germinate rapidly under low soil moisture. This could easily give it a competitive advantage over the less-tolerant buffelgrass and guineagrass under semiarid to arid conditions. This characteristic undoubtedly is a contributing factor in the dominance of sourgrass in extensive areas under limited moisture availability.

Although the sourgrass seed is so light that it is easily dispersed by wind, it is capable of emerging from depths up to 4 cm. However, most sourgrass emergence occurs from the 0-3 cm horizon. Optimum germination is thus best at relatively shallow depths, and this is a characteristic shared by numerous weedy grasses (Dawson and Bruns, 1962; Wiese and David, 1967).

It is interesting that sourgrass germinated at depths up to 3-4 cm even though germination under dark conditions in the growth chamber was very poor. Either there was sufficient light penetration through the soil to trigger the phytochrome system and stimulate germination, or the dark inhibition was moderated by other factors. Koller et al. (1964) studied the role of sensitivity to light for seed germination in the soil with light-requiring seeds of Artemisia monosperma Delil and found that germination was promoted by light filtered through a 2-mm thick layer of dry sand, when the source (mixed incandescent and fluorescent) supplied about 1.5% of full sunlight at filter level. However, effective levels should be encountered at greater depths when the source is sunlight and sand is not dry.

Emergence of a particular species is often influenced by a combination of several factors. Wiese and Davis (1967) cited

temperature, depth of planting, soil type, and soil moisture as influencing the emergence of several weed species. It is very likely that emergence of sourgrass occurs as a result of the combined effects of diurnal fluctuations of temperature, moisture, and other factors in addition to light. Difference in soil type and moisture would undoubtedly result in some variation in the degree of emergence from different depths.

Since the seeds of sourgrass mostly emerge from less than 5 cm below the surface, seeds at shallow depths in cultivated areas can be encouraged to germinate and the seedlings destroyed by shallow cultivation or with herbicides. Viable seeds at greater than 5 cm depths would be unable to germinate and produce emerged seedlings. Therefore, it is suggested that deep cultivation is unnecessary for control of sourgrass and that fields be left undisturbed or if cultivation were required that it be confined to the surface of the soil. Wesson and Wareing (1969) reported that germination of weed seeds from soil which had been used for pasture for several years was markedly increased when it had been disturbed by cultivation.

In conclusion, the widespread occurrence of sourgrass in the drier districts can be attributed at least in part to the wide range of conditions under which germination occurs. In the light, germination is excellent under a wide range of temperature regimes and photoperiods. Although germination is inhibited by continuous dark conditions, this is moderated somewhat by alternating temperatures, and GA, kinetin, and thiourea treatments. Sourgrass seeds will germinate and produce seedlings from depths to 4 cm in soil. Sourgrass germination is much more tolerant of moisture stress than the improved forage grasses,

buffelgrass and guineagrass. Finally, no dormancy of sourgrass has been observed; even freshly harvested seeds germinate readily upon contact with moist soil.

CHAPTER V

GROWTH AND DEVELOPMENT OF SOURGRASS, BUFFELGRASS, AND GUINEAGRASS

Plants respond differently to environmental conditions. One of the more important factors is population densities since this may reduce both vegetative growth and flowering of weeds. Photoperiod often has very marked effects on vegetative growth, reproduction, distribution and adaptation of species. The rate and pattern of the growth of plants is also greatly influenced by light intensity since radiation level can effect the photosynthesis rate both directly and by its effect on several other plant and microclimate variables. Nitrogen is also one of the most important elements needed by plants for growth and development since it is used in such large quantities. Application of nitrogen fertilizer usually enhancesboth vegetative and reproductive growth.

This series of experiments were conducted to better characterize the growth of sourgrass, buffelgrass, and guineagrass in relation to specific environmental variables. The effects of plant density were evaluated in Experiment 1; photoperiod in Experiment 2; and shade and nitrogen fertilization in Experiment 3.

1. THE EFFECT OF PLANTING DENSITY ON THE GROWTH AND DEVELOPMENT OF SOURGRASS

MATERIALS AND METHODS

Treatments consisted of six levels of sourgrass densities. The density levels were established by over-seeding sourgrass and then thinning to the required density shortly after emergence. Densities

were 5, 10, 20, 40, 80, and 160 plants per pot (9.5 liters) having a surface area of 452 cm^2.

The height and number of tillers were measured one day prior to harvesting. The plants were cut off at ground level 60 days after planting. Seedling weight and seed yield were determined for the ten inner plants (except at the density of 5 plants per pot where all 5 plants were measured). Dry weight was obtained by oven drying for 24 hours at 70 C.

The data were evaluated by analysis of variance, and exponential regression equations were calculated to describe density effects on various plant characters.

RESULTS

The height, number of tillers, dry weight, and seed yield per plant were greatly decreased as the density was increased from 5 plants to 160 plants per pot. Figures 9 to 13 illustrate the growth responses to the six levels of density. Highly negative curvilinear regressions were found between plant density and plant height (Figure 9), dry weight (Figure 10), number of tillers per plant (Figure 12), shoot-root ratio (Figure 11), and seed yield per panicle (Figure 13). Height of sourgrass at harvest gradually decreased with increasing planting density (Figure 9). The number of tillers per plant decreased greatly as the density varied from 5 plants to 40 plants per pot, and no tillers were produced at densities greater than 40 plants per pot (Figure 12). Seedling dry weight of shoot and root (Figure 10) and seed yield (Figure 13) also decreased drastically as planting density increased. Similar

Figure 8. Effect of plant density on growth and development of sourgrass. From left to right, plant densities are: 5, 10, 20, 40, 80, and 160 plants per pot.

relationships between density and weight of roots and shoots were obtained by De Peralta (1935) with sudangrass (Holcus sorghum sudanensis Hitch.) and by Troughton (1956) with perennial ryegrass (Lolium perenne L.) and timothy (Phleum pratense L.). Donald (1954) also reported that seed production per plant decreased drastically with increasing density. As density increased, the dry weight of sourgrass shoots was reduced proportionately more than was root weight. Shoot-root ratios thus decreased with increasing density (Figure 11).

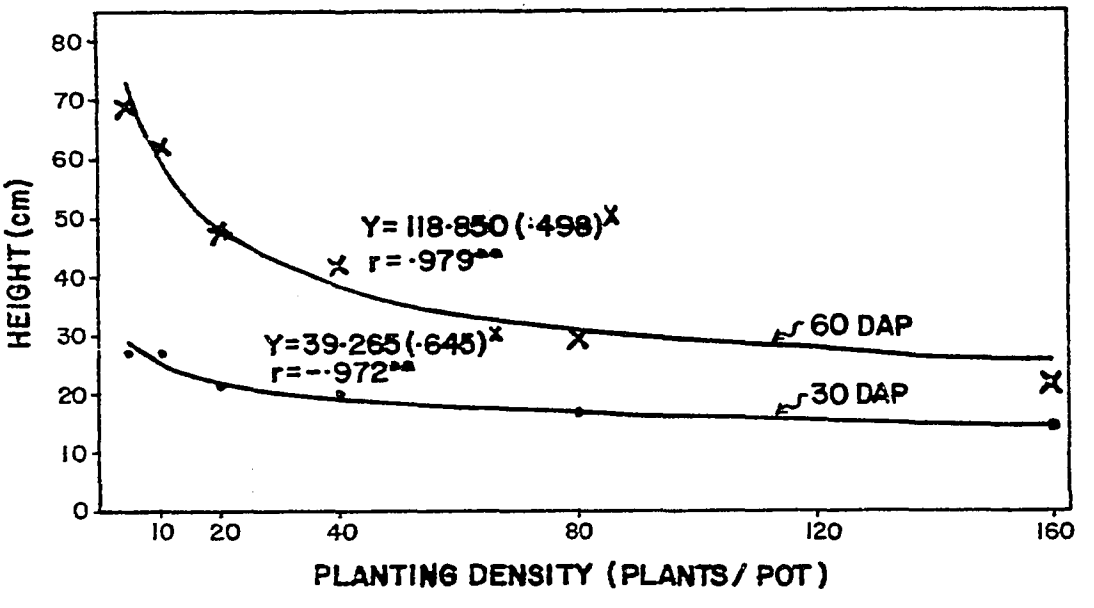


Figure 9. Effect of population density on height of sourgrass 30 and 60 days after planting

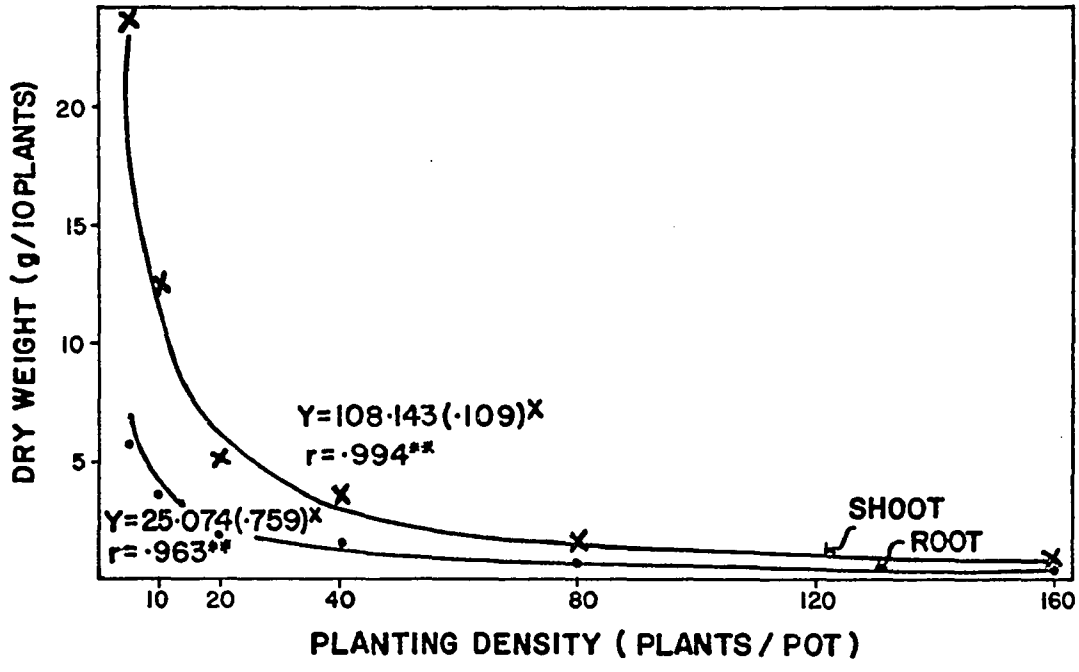


Figure 10. Effect of population density on dry weight of sourgrass 60 days after planting

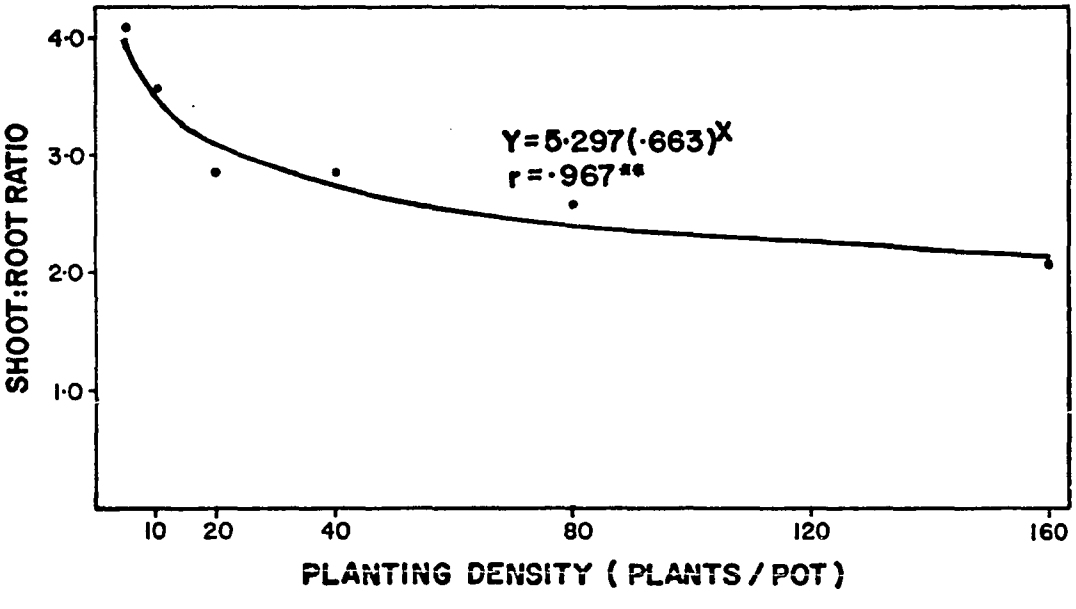


Figure 11. Effect of population density on shoot-root ratio of sourgrass of 60 days after planting

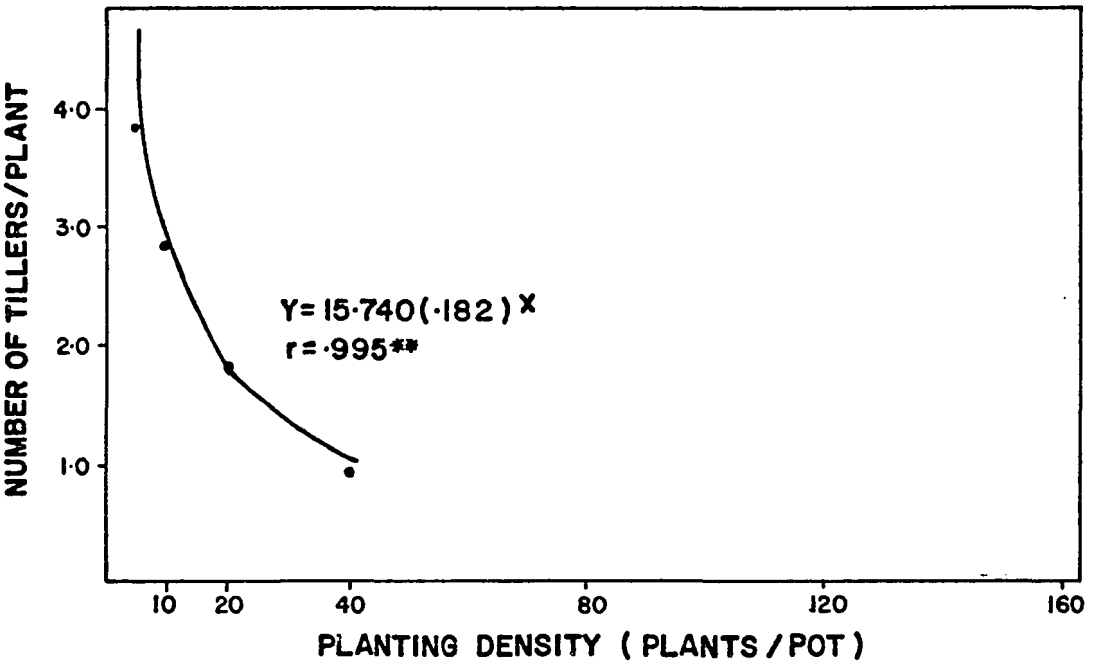


Figure 12. Effect of population density on tillering in sourgrass 60 days after planting

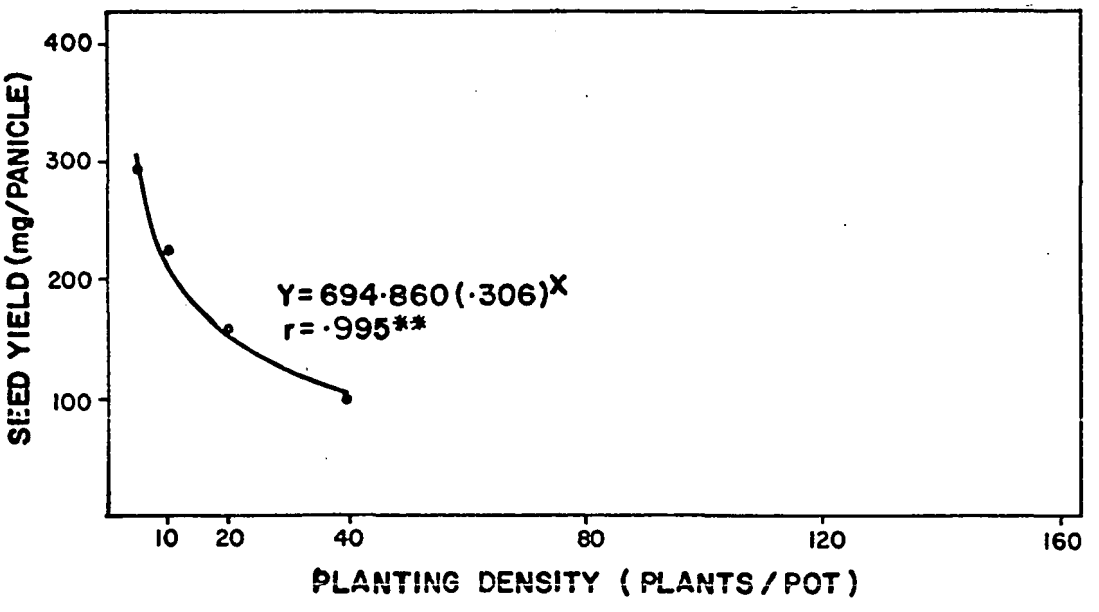


Figure 13. Effect of population density on seed yield of sourgrass 60 days after planting

2. THE EFFECT OF PHOTOPERIOD ON GROWTH AND FLOWERING OF SOURGRASS

MATERIALS AND METHODS

Plants were exposed to photoperiods of 9, 11, 13, and 15 hours. The 9 and 11 hour photoperiods were obtained by covering the plants with wood frame cages covered with black 6 mil polyethylene. The 13 and 15 hour photoperiods were obtained by supplemental lighting. Supplementary illumination was provided by three 20-watt fluorescent lamps and two 40-watt incandescent lamps. However, artificial lights were used for all photoperiods in the early seedling stage.

Two-week old sourgrass seedlings were transplanted in 25 cm plastic pots filled with soil. The pots were immediately placed in appropriate photoperiodic chambers. The plants were clipped 7 days after transplanting. The plants were watered with tap water or nutrient solution throughout the experiment. Plant development was noted along with measurements of plant height, number of tillers, dry weight, and time required for first flowering.

RESULTS

As shown in Table 12 and Figure 14, sourgrass flowered under 11-, 13- and 15-hour photoperiods but failed to flower under 9-hour photoperiod. The plants grown in the longer photoperiods flowered earlier than those grown in the shorter photoperiod. Although the plants under 11 hour photoperiod flowered, there was some delay in the appearance of heads. The longer time required with short photoperiod is most likely the result of slow floral development rather than a response to photoperiod. Growth at the 9-hour photoperiod was poor and

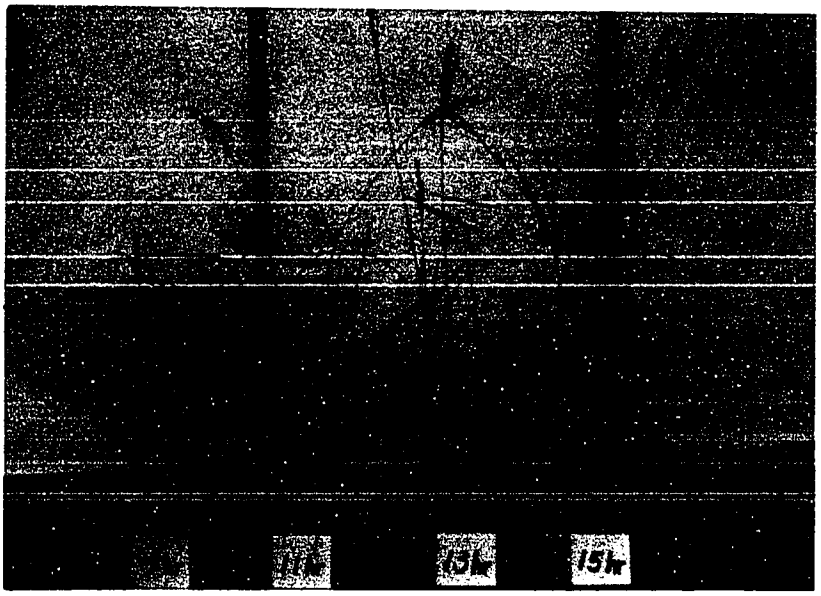


Figure 14. Effect of photoperiod on growth and development of sourgrass 10 weeks after planting

no flowering heads appeared. Sourgrass flowering appeared not to be sensitive to photoperiod. Sourgrass may be classed as day-neutral in flowering behavior.

Plant height and dry weight of sourgrass increased as photoperiod increased. Plants grown under 9- and 11-hour photoperiods showed growth inhibition of shoots as compared with the 13- and 15-hour photoperiods, probably because of insufficient light energy rather than as a photoperiodic response. The number of tillers per plant was not significantly different in all the tested photoperiods.

Table 12. Effects of photoperiod on growth and development of sourgrass 120 days after planting

Photoperiod	Plant Ht.	Dry Wt.	Tillers per plant	Days to Head
hour	cm	g/plant		
9	73 a[2/]	2.3 a	11.0 a	-[1/]
11	80 a	2.5 a	10.5 a	105 b
13	99 b	3.1 b	10.8 a	84 a
15	108 b	3.9 c	11.0 a	80 a

[1/] Failed to flower

[2/] Means within a column followed by different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

3. EFFECTS OF SHADE AND NITROGEN ON GROWTH OF SOURGRASS, BUFFELGRASS AND GUINEAGRASS

MATERIALS AND METHODS

The plants which were grown for the competition studies (Chapter VI) were allowed to regrow for this experiment. After pure stands of three grass species were harvested, each pot was thinned to 5 plants. Shade treatments were applied with polypropylene shade cloth that reduced light 30 and 60%. Each shade treatment was studied at two levels of nitrogen, i.e., 0 and 60 kg of N per hectare based on soil volume. Ammonium phosphate was the source of nitrogen and was applied in three split applications. All plots were watered with a sprinkler type irrigation system. The maximum height and number of tillers per plant were measured. All plants were harvested twice to a stubble height of 5 cm at two months intervals. Immediately after the second harvest, the soil was washed from the roots. Tops and roots were dried in a forced draft oven at 70 C for 24 hours.

RESULTS

The results are the means of three replications each consisting of five plants. Representative plants and roots in the different treatments are shown in Figures 15 and 16 respectively.

Seedling height

Shade increased plant height in comparison to no shade (Figure 17) especially when N fertilizer was applied. The heights of the three species increased as the shade increased from 0 to 60%. The greatest

Figure 15. Effect of shade and nitrogen on the growth and development of (A) sourgrass, (B) buffelgrass, and (C) guineagrass

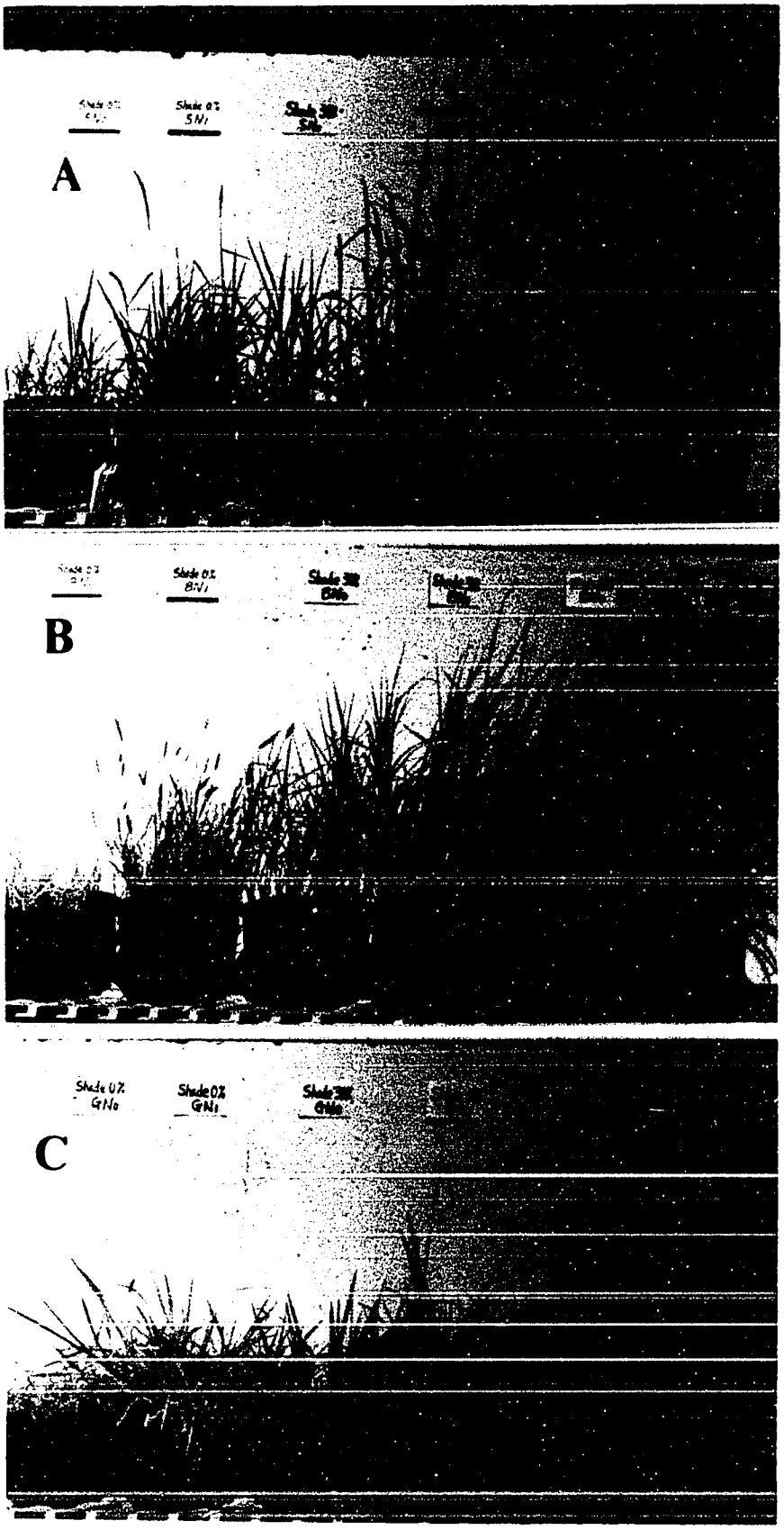

A
B
C

Figure 16. Effect of shade on root growth of sourgrass (top), buffelgrass (middle), and guineagrass (bottom).

From left to right: shade 0, 30 and 60%

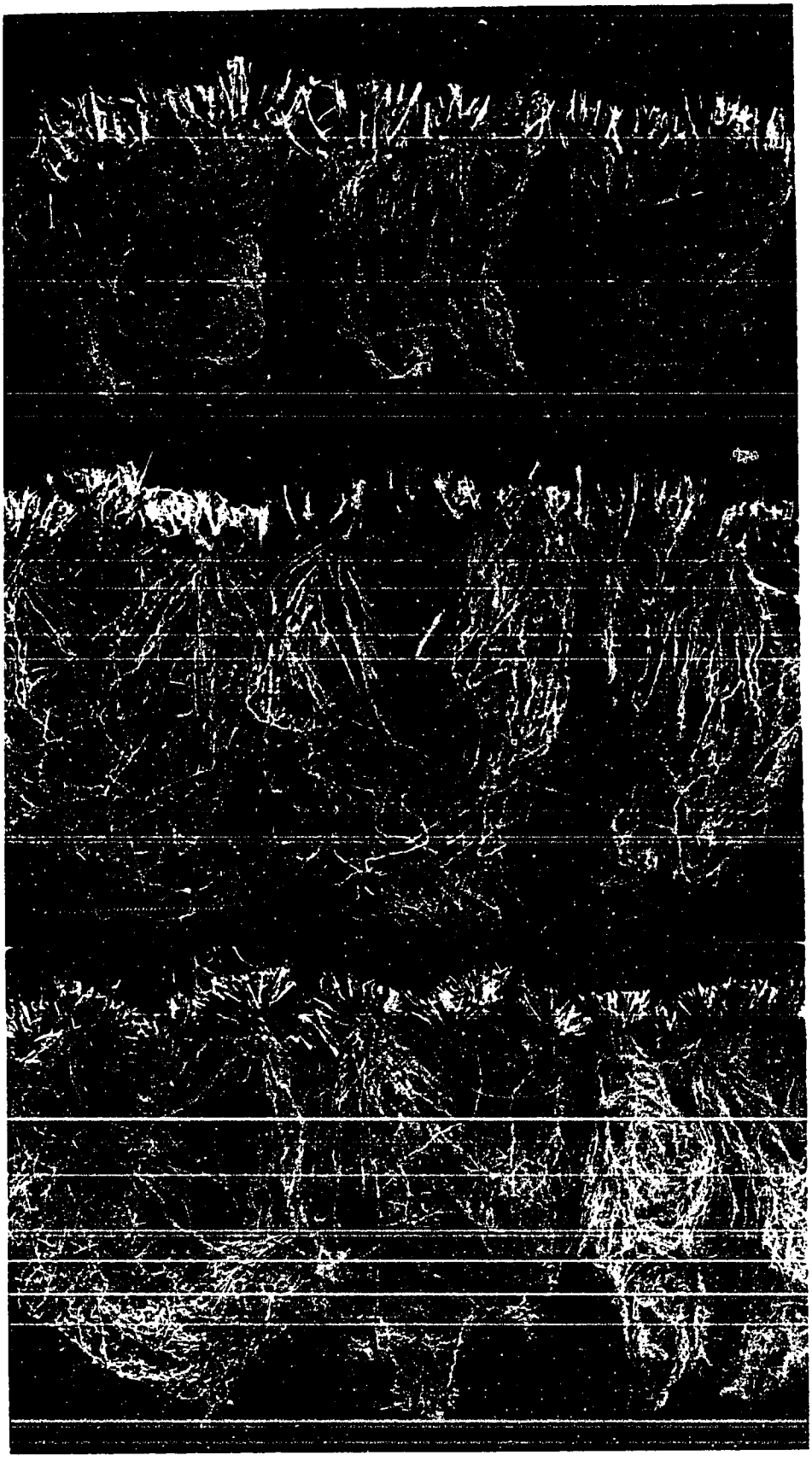
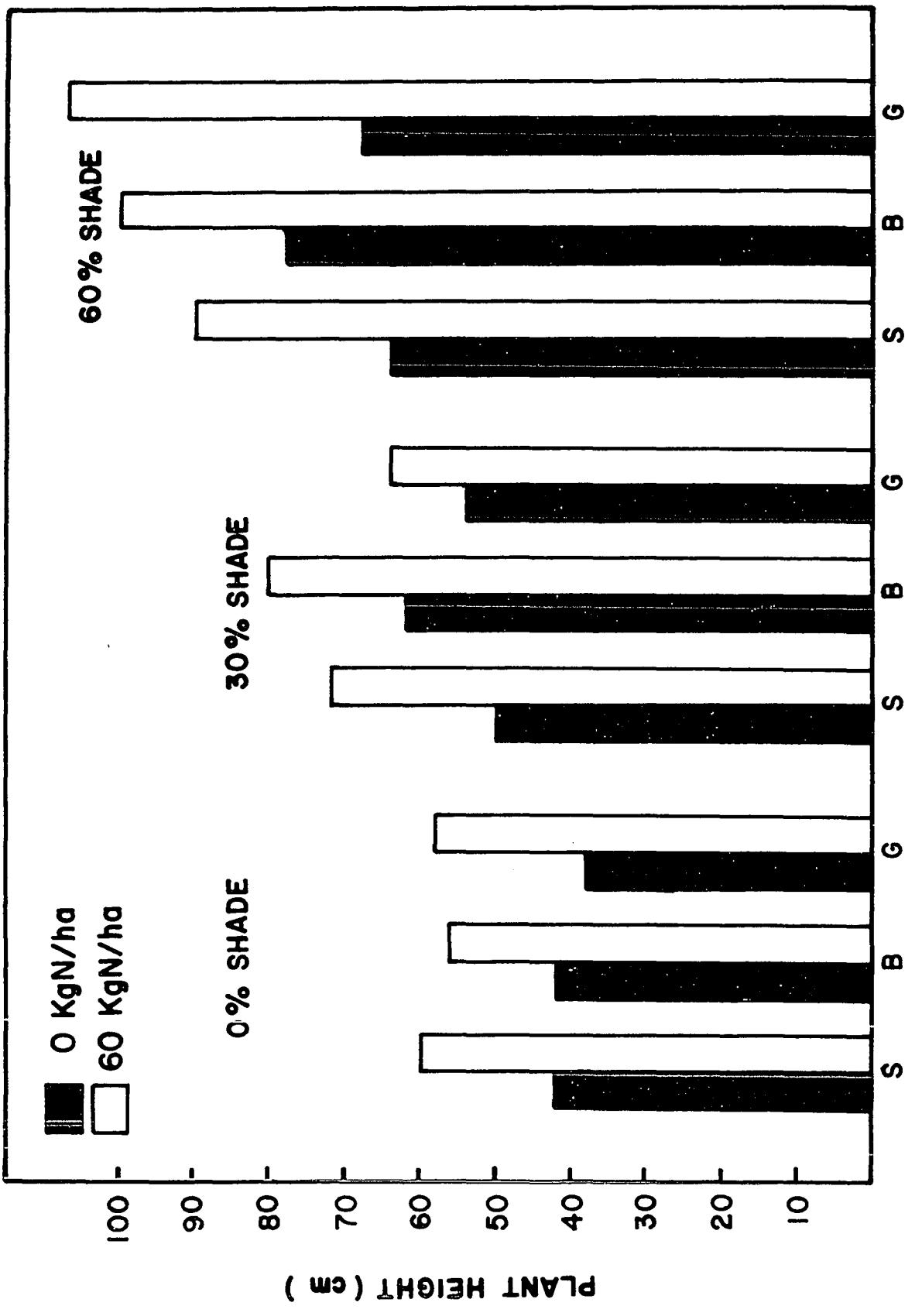


Figure 17. Effect of shade and nitrogen on the height of sourgrass (S), buffelgrass (B) and guineagrass (G)


PLANT HEIGHT (cm)
100
90
80
70
60
50
40
30
20
10
0 KgN/ha
60 KgN/ha
0% SHADE
30% SHADE
60% SHADE
S
B
G
S
B
G
S
B
G

height was attained under 60% shade for the three grass species. More significant increase in height was observed on buffelgrass and guinea-grass under shade conditions than sourgrass. With increasing shade stems became thinner and less rigid. The plants grown under 60% shade were slightly elongated and spindly, whereas the unshaded plants were short and assumed rosette type of growth.

Nitrogen significantly increased the plant height for all grass species. Buffelgrass and guineagrass showed a greater response to nitrogen under all shade conditions than sourgrass.

Dry weight of shoots and roots

Dry weight of buffelgrass and guineagrass tops were generally greater than those of sourgrass. Dry weight of shoots showed an increase with increasing shade for all species (Figure 18). However, dry weights of buffelgrass and guineagrass were more markedly increased by shade than sourgrass. The nitrogen fertilized plants produced higher total dry weight of plants but buffelgrass and guineagrass showed greater response to nitrogen fertilization than sourgrass.

Buffelgrass and guineagrass were observed to have much deeper root systems than sourgrass (Figure 16). Dry weights of root of buffelgrass and guineagrass were also generally greater than that of sourgrass (Figure 19). Increasing shade caused a decrease in dry weight of the roots for all grass species, but nitrogen application increased the root yields of all three species.

Number of tillers per plant

In general, buffelgrass and guineagrass produced more tillers per plant than sourgrass. Number of tillers per plant was reduced by shade

Figure 18. Effect of shade and nitrogen on the dry weight of shoots of sourgrass (S), buffelgrass (B), and guineagrass (G)

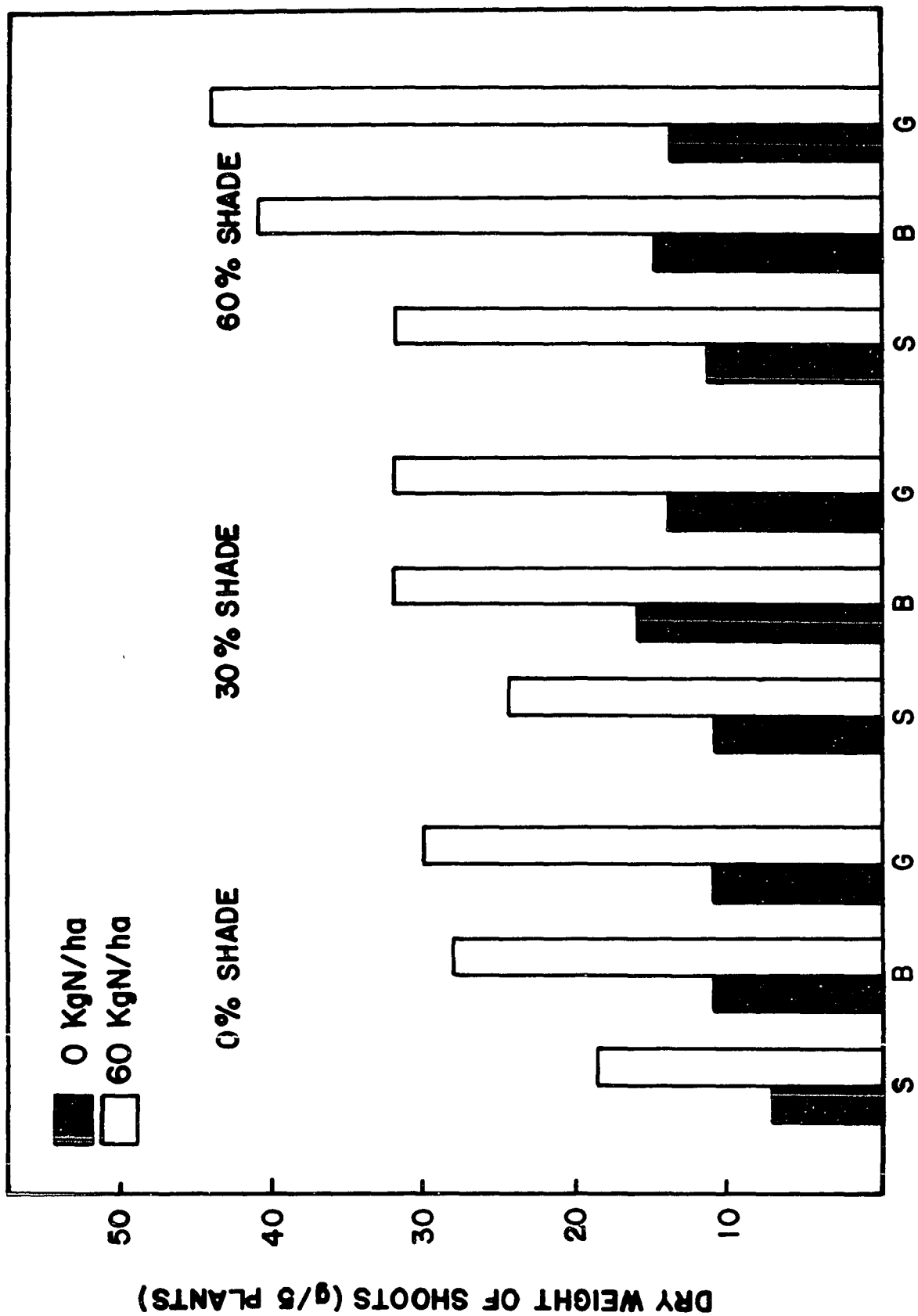

DRY WEIGHT OF SHOOTS (g/5 PLANTS)
50
40
30
20
10
0 KgN/ha
60 KgN/ha
0% SHADE
30% SHADE
60% SHADE
S
B
G
S
B
G
S
B
G

Figure 19. Effect of shade and nitrogen on dry weight of roots of sourgrass (S), buffelgrass (B), and guineagrass (G)

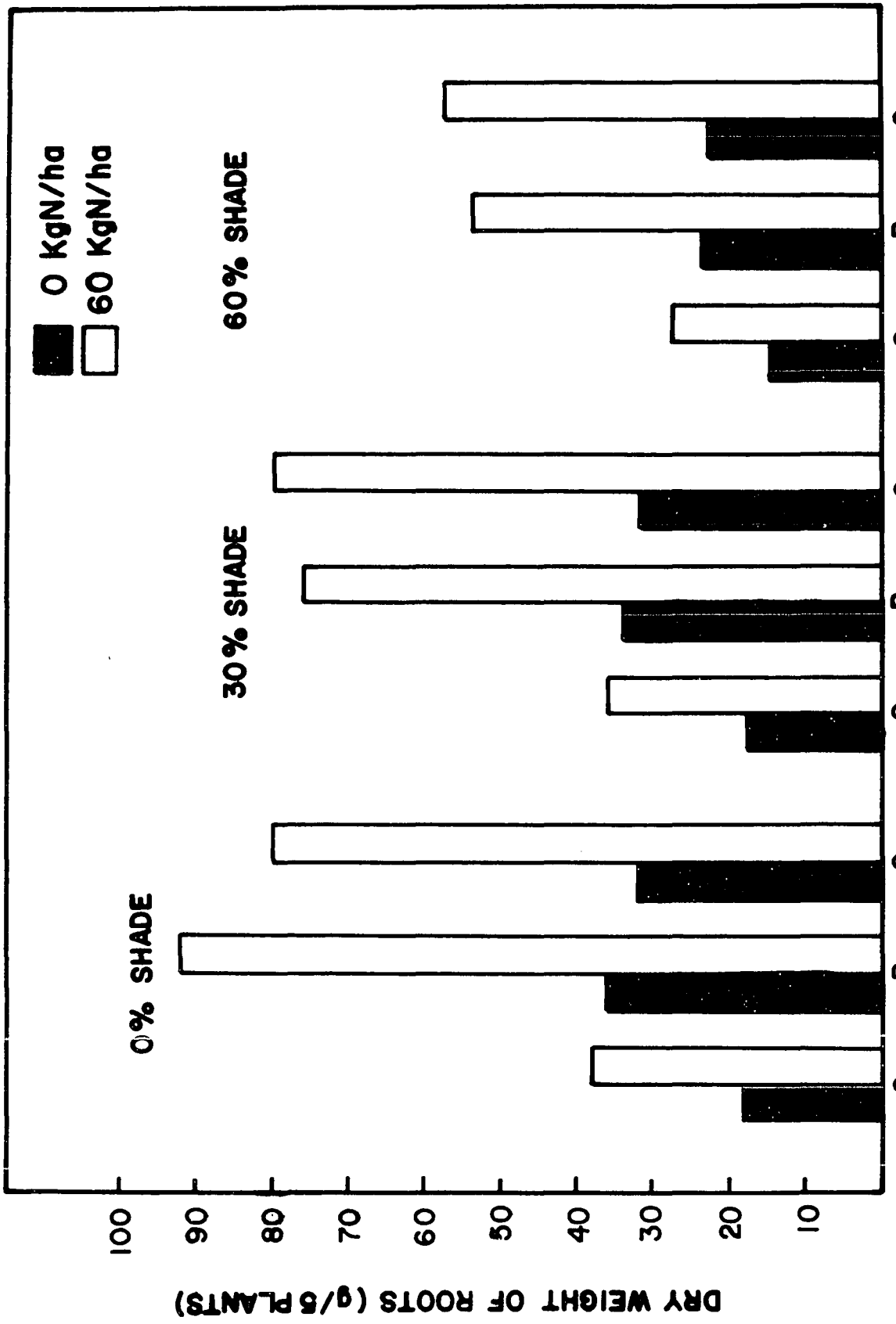
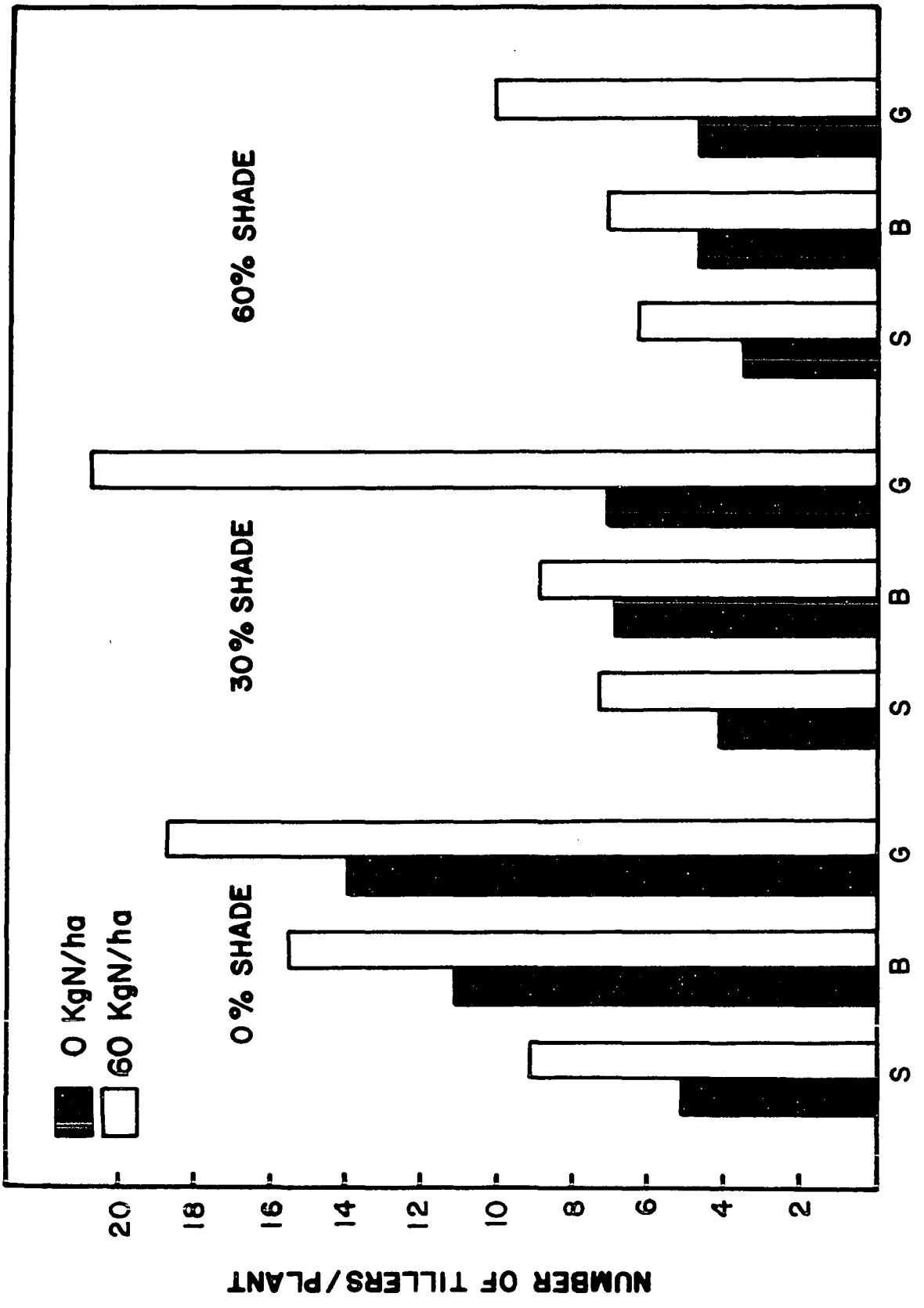

DRY WEIGHT OF ROOTS (g/5 PLANTS)
100
90
80
70
60
50
40
30
20
10
0% SHADE
30% SHADE
60% SHADE
S
B
G
0 KgN/ha
60 KgN/ha

Figure 20. Effect of shade and nitrogen on tillering in sourgrass (S), buffelgrass (B), and guineagrass (G)


NUMBER OF TILLERS/PLANT
20
18
16
14
12
10
8
6
4
2
0 KgN/ha
60 KgN/ha
0% SHADE
30% SHADE
60% SHADE
S
B
G
S
B
G
S
B
G

except for fertilized guineagrass at 30% shade. However, nitrogen significantly increased tiller numbers at all shade levels (Figure 20). Buffelgrass and guineagrass showed greater responses to nitrogen than did sourgrass.

Chemical composition

The percentages of N, P and K in sourgrass was higher than in buffelgrass and guineagrass in all treatments (Table 13). No difference in N, P and K contents of buffelgrass and guineagrass was shown. The percentages of Ca and Mg were similar for sourgrass and guineagrass but greater than in buffelgrass.

N, K, and S levels were not affected by shade but P, Ca, and Mg contents for all three grass species were increased. N and K levels were significantly increased by nitrogen fertilization, while P, Ca, and Mg contents were generally decreased.

4. DISCUSSION

Stand density studies of sourgrass showed that there were highly negative curvilinear relationships of all measured plant characters with planting density (Figures 9-13). Growth suppression first became operative at the highest densities and then developed at the lower densities as the plants developed. With increasing density, competition became more intense until growth was completely arrested.

Dry weights of shoots and roots per plant decreased drastically as planting density increased. No tillers or flowers were produced at densities greater than 40 plants per pot. However, height was less affected than the other plant characters. Therefore, it appears that

Table 13. Effects of shade and N fertilization on the chemical composition of sourgrass, buffelgrass, and guineagrass

Treatment		Mineral Content					
Shade	Nitrogen	N	P	K	Ca	Mg	S
%	kg/ha	%					
		Sourgrass					
0	0	8.39	0.75	1.73	0.62	0.51	0.15
30	0	9.54	0.51	1.97	0.53	0.40	0.14
60	0	8.66	0.61	2.16	0.51	0.42	0.15
0	60	9.63	0.34	2.26	0.49	0.36	0.09
30	60	10.78	0.54	2.16	0.50	0.42	0.13
60	60	11.49	0.30	2.39	0.53	0.36	0.10
		Buffelgrass					
0	0	5.48	0.57	1.69	0.42	0.22	0.13
30	0	5.12	0.44	1.62	0.31	0.18	0.14
60	0	5.65	0.37	2.00	0.27	0.19	0.16
0	60	7.42	0.35	2.38	0.33	0.21	0.11
30	60	7.42	0.29	2.12	0.27	0.20	0.13
60	60	7.60	0.27	2.25	0.27	0.20	0.12
		Guineagrass					
0	0	6.45	0.78	0.64	0.96	0.61	0.12
30	0	4.77	0.42	0.69	0.71	0.45	0.07
60	0	4.77	0.44	1.01	0.60	0.39	0.16
0	60	6.18	0.23	0.91	0.79	0.35	0.08
30	60	7.24	0.20	1.14	0.75	0.34	0.10
60	60	6.45	0.17	1.09	0.52	0.26	0.07

sourgrass under the stress of severe intra-specific competition will grow to nearly its normal height but will produce fewer tillers, fewer panicles, and therefore less dry weight per plant. It was observed that dense stands of sourgrass seedlings may emerge in the field since sourgrass seeds are easily dispersed by wind. However, only a few seedlings eventually became established-probably because of the competition among seedlings for water, light, and space. Visual observations of seedling mortality indicated that mortality increased markedly at densities greater than 80 plants per pot. Intra-specific competition is thus a major factor controlling seedling development and survival of sourgrass.

The photoperiodic experiment showed that sourgrass flowered under 11 to 15 hour photoperiod (Table 12 and Figure 14). Its failure to flower under a 9 hour photoperiod was probably due to slower floral development in response to insufficient light energy rather than a photoperiodic response. Flower initiation in sourgrass was thus apparently insensitive to photoperiod, and this species may be classed as day-neutral in flowering behavior. Accordingly, this grass is adapted to a wide range of photoperiodic conditions. This fact that grass occur naturally over a wide range of latitude from the southern United States to Argentina is further evidence of its photoperiod insensitivity.

Shading to reduce light intensity dramatically increased the growth of all three grasses tested. Sourgrass, buffelgrass, and guineagrass all increased in height as shade was increased from 0 to 60% (Figure 17). The height responses are in agreement with the results of numerous other workers (e.g. Allen, 1975; McGinnies, 1966; Pritchett et al., 1951).

Treshow (1970) states that high light intensity inhibit cell elongation and limits growth of most plants. Knake (1972) also reported that height differences were due primarily to differences in length of internodes rather than to number of internodes in giant foxtail (Setaria faberii Herrm.).

The positive dry matter responses to shade were unexpected (Figure 18) and are contrary to most reports. For example, Bosch et al. (1970) reported seedling yields of Panicum maximum Jacq. grown in light shade were only slightly more than one-third the yields of seedlings grown in full sunlight both in fertile and infertile soil. A number of other workers have also reported negative effects of shade on various grasses (e.g. Watkins, 1940; Benedict, 1941; Pritchett et al., 1951).

A positive response from shade was obtained by Daccarett (1968) who grew Panicum maximum Jacq. in the shade of the trees Erythrina poeppiana, Pithecolobium saman, Gliricidia sepium, and Cordia alliodora. Also, herbage yields of crested wheatgrass were increased substantially by season-long shading with saran cloth in the range of 6-60% shade (McGinnies, 1966). Allen (1975) also reported that soybeans grew larger and gave about same or somewhat higher dry matter yield under shade cloth wind screen. Seedlings of Agropyron intermedium (Host) Beauv. and Bromus inermis Leyss. made better growth under saran shade cloth providing 6% shade than when under 20, 30, or 40% shade or with no shade (McDonough, 1969).

Allen (1975) studied the microclimate of shade cloth and reported that the shade cloth decreased water stress and water use, increased the amount and improved the distribution of diffusive irradiance, and increased the diffusive to direct-beam irradiance ratio. The increase

in diffuse radiation under shade cloth had the effect of increasing the rate of photosynthesis in leaves not receiving direct beam radiation. Shade cloth was moderatively effective in trapping released CO_2 and the uptake of CO_2 was also enhanced in the shade because the stomatal diffusive resistance of the shade-grown leaves was relatively low in comparison with the resistance of the unshaded leaves. However, shading had little effect on air temperatures and minimum soil temperatures, but substantially reduced maximum soil temperatures (Allen, 1975). Other microclimate effects of shade cloth include reduction in wind velocity (McGinnies, 1966) which would be expected to also reduce stomatal closure with subsequent enhancement of dry matter accumulation (Whitehead, 1957).

Treshow (1970) stated that high light intensity not only promoted rapid transpiration but degraded the chlorophyll molecules by photo-oxidation and probably inhibited chlorophyll synthesis. Intense light intensity would thus impair photosynthesis due to its effects on chlorophyll concentration.

The saran shade cloth used in the present experiment obviously provided a more favorable environment for the three grasses tested than was present in full sunlight, probably due to the effects on evapotranspiration, CO_2 diffusion rate, and chlorophyll concentration. It also appears that all three of the grasses tested are relatively shade-tolerant. Chen et al. (1970) reported that sourgrass, buffelgrass, and guineagrass had low CO_2 compensation concentrations (<10 ppm) and are highly efficient in CO_2 assimilation even at low levels of radiation. These grasses were thus able to make significant growth at low light

intensities under which the dry weight of plants of plants with high compensation concentration would grow very poorly.

Dry weight of roots and number of tillers per plant were decreased with increasing shade (Figures 19 and 20). This is in agreement with the results obtained by others (Watkins, 1940; Tiedmann et al., 1971; Knake, 1972). The shaded plants were more succulent but lacked vigor. As the level of shade increased, flowering lagged behind that of the no-shade control plants. However, nitrogen application stimulated flowering of all three species. Buffelgrass and guinea-grass failed to flower without nitrogen application.

Fertilization with nitrogen increased height, dry weight of tops and roots, and number of tillers per plant for all species regardless of shade conditions.

CHAPTER VI

EFFECTS OF COMPETITION ON THE GROWTH AND DEVELOPMENT OF SOURGRASS, BUFFELGRASS, AND GUINEAGRASS

The role of plant competition in pasture management is very important because the control of weeds in pastures by cultural methods is more economically feasible than by the use of herbicides. One of the most useful cultural methods is the introduction of more vigorous forage species which can compete effectively with the weed species.

The experiment described in this chapter was conducted to study competition among sourgrass, buffelgrass, and guineagrass under different levels of shade and nitrogen fertilization. This information should provide a better basis for devising management methods for replacing sourgrass with buffelgrass or guineagrass under field conditions.

MATERIALS AND METHODS

Sourgrass, buffelgrass, and guineagrass were planted in monospecific, bispecific, or trispecific combinations in pots 30 cm diameter and 23 cm deep. Stands were thinned to 69 plants per pot to achieve a uniform number of plants. Treatments were 0, 30, or 60% shade, and 0 and 60 kg/ha of nitrogen (0 and 2.84 g N/pot). Shade was provided by polypropylene shade cloth stretched over the top and sides of wooden frames (1.1 m x 1.8 m x 1.5 m) (Figure 21). Plants were watered by hand during the seedling stage and irrigated twice a day with a sprinkler system at later stages. The experiment was laid out in a split plot design with shading as the main-plot and nitrogen fertilization and grass combinations as the sub-plots.

Figure 21. Shade cloth and frames used to stimulate shade

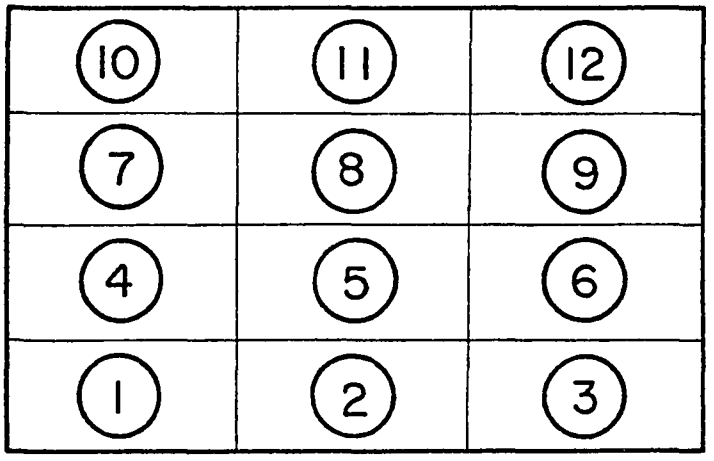
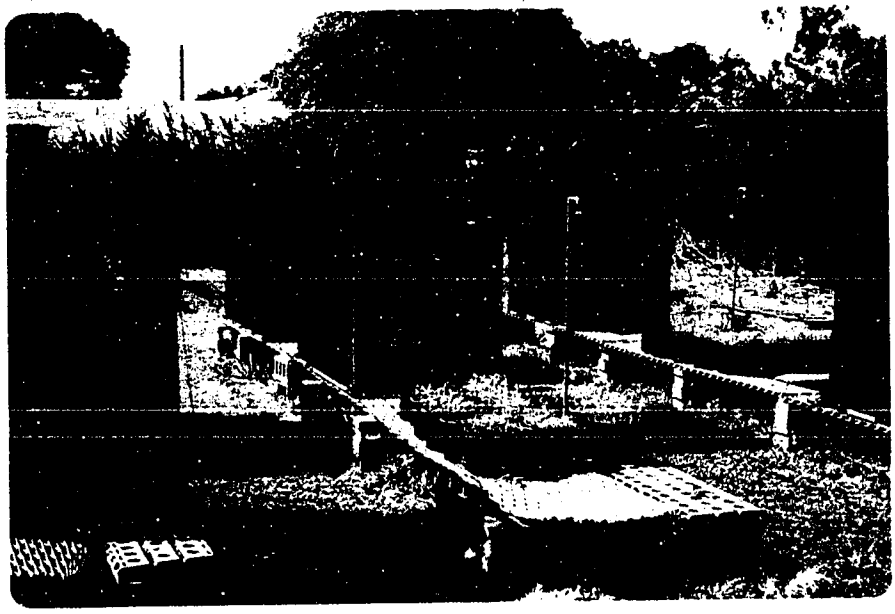
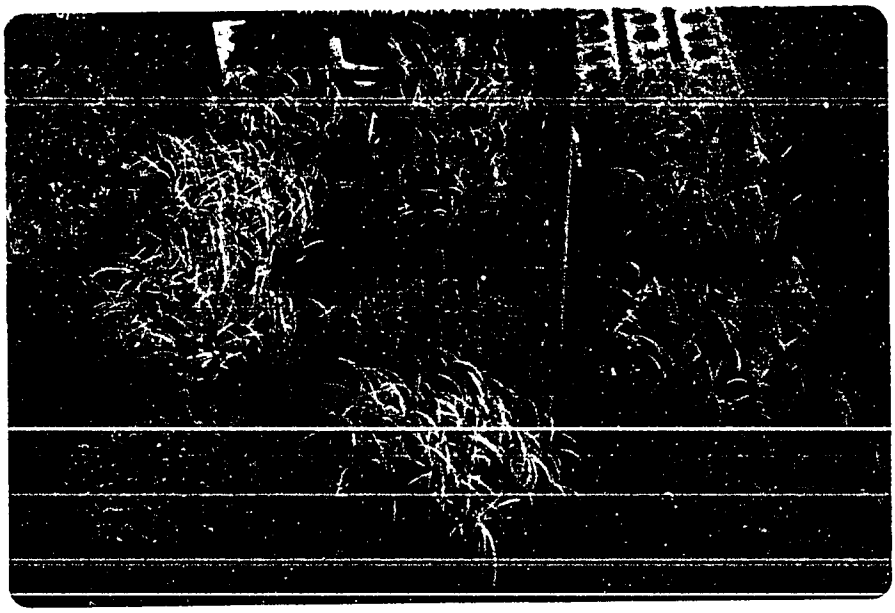


Figure 22. Effect of competition on the growth of sourgrass, buffelgrass, and guineagrass grown in full sunlight, 14 days after planting.
Diagram identifies pot layout; pot 1 and 5 sourgrass, pot 7 and 12 buffelgrass, pot 6 and 10 guineagrass, pot 2 and 11 sourgrass x buffelgrass, pot 3 and 8 sourgrass x guineagrass, pot 4 and 9 sourgrass x buffelgrass x guineagrass.





The plant tops were harvested two months after planting, regrown for two months, and harvested again. Height of plants, number of tillers per plant, number of plants per pot, and dry weight of shoots were measured.

RESULTS

Plant height

The height of the three grass species increased as the shade and nitrogen levels increased in all treatments (Figures 23 and 24). At the time of harvest the plants which were both shaded and fertilized with nitrogen attained the greatest height.

When sourgrass was planted with buffelgrass, guineagrass or both species, the sourgrass did not grow well regardless of shade and nitrogen level. Heights of sourgrass seedlings were very much shorter when competing with other grass species than when grown alone. The growth of sourgrass seedlings was thus severely suppressed by association with buffelgrass, guineagrass, or both species. Growth inhibition of sourgrass associated with the grass species became more severe as shade and nitrogen level increased.

Buffelgrass and guineagrass excelled in competing for nutrients and light because of their more rapid early growth. Buffelgrass and guineagrass seedlings grew taller when competing with sourgrass than when were grown alone.

Dry weight

The dry weights of sourgrass were slightly decreased whereas those of buffelgrass and guineagrass were increased as shade level increased (Figures 25 and 26).

Figure 23. Effect of shade and nitrogen on height (first cutting) of sourgrass (S), buffelgrass (B), and guineagrass (G) grown in monospecific, bispecific, and trispecific combinations.

A : 0% shade
B : 30% shade
C : 60% shade

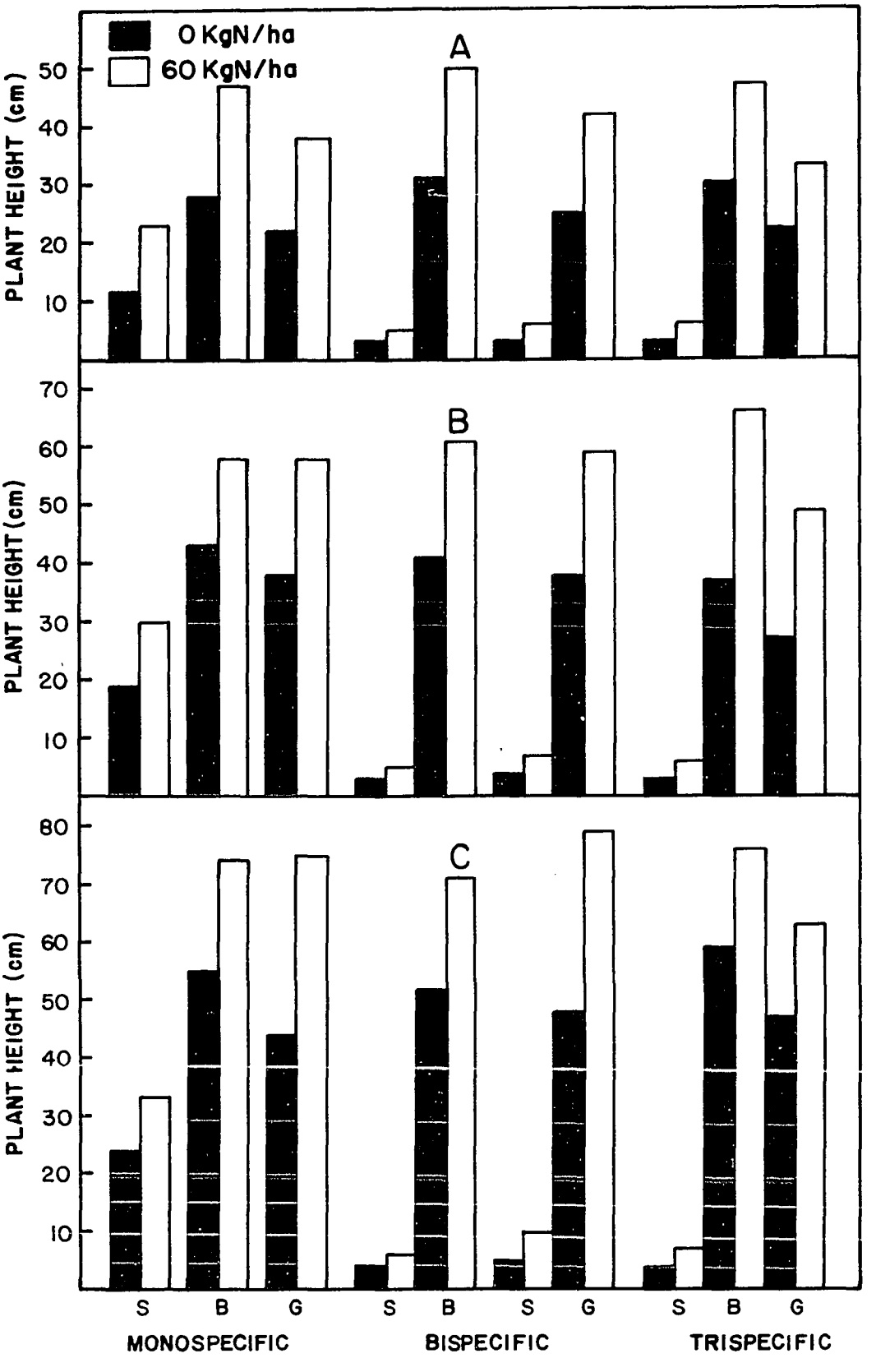

0 KgN/ha
60 KgN/ha
A
B
C
PLANT HEIGHT (cm)
10
20
30
40
50
60
70
80
S
B
G
MONOSPECIFIC
BISPECIFIC
TRISPECIFIC

Figure 24. Effect of shade and nitrogen on height (second cutting) of sourgrass (S), buffelgrass (B), guineagrass (G) grown in monospecific, bispecific, and trispecific combinations.

A : 0% shade
B : 30% shade
C : 60% shade

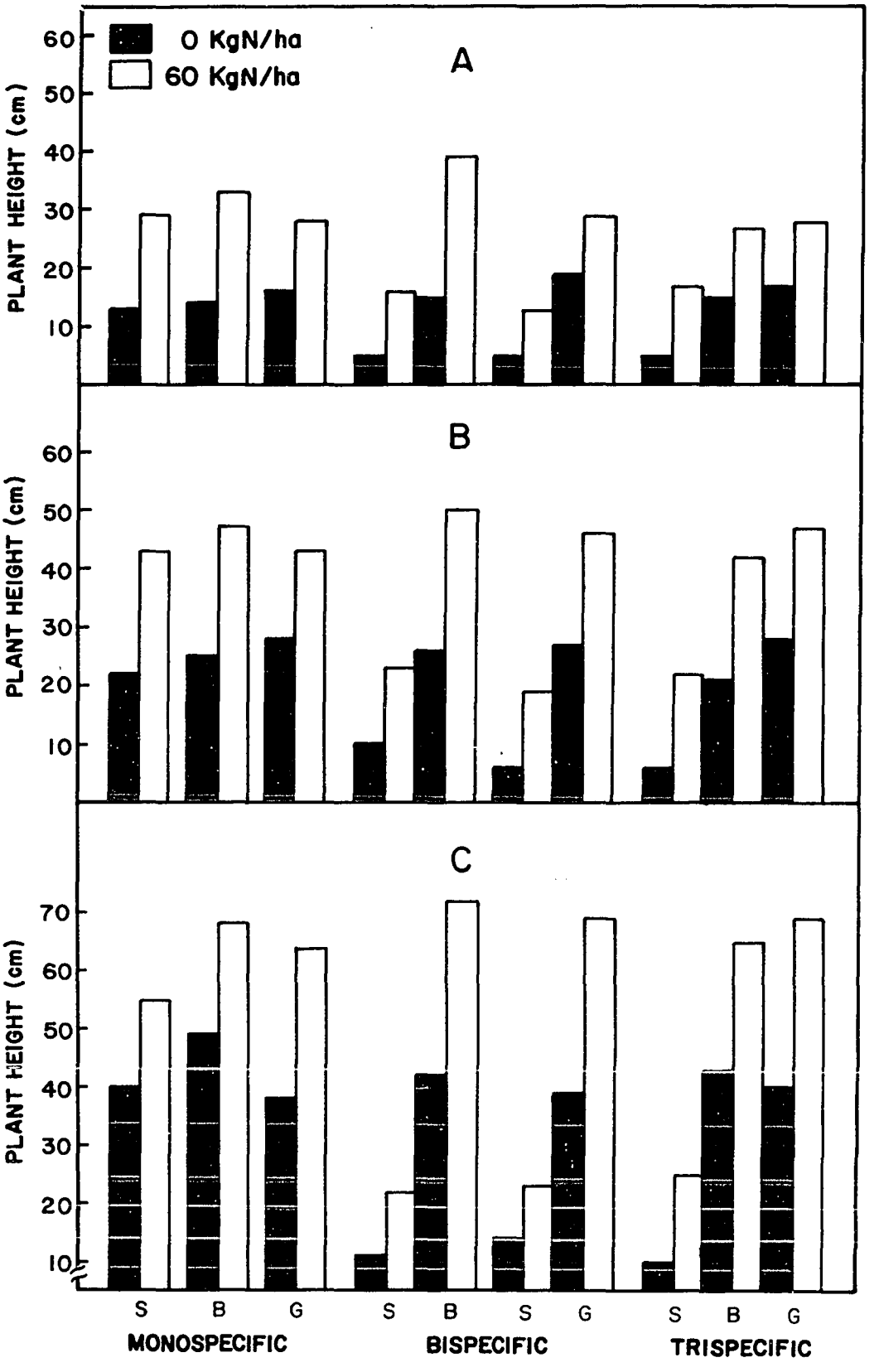

0 KgN/ha
60 KgN/ha
A
B
C
PLANT HEIGHT (cm)
10
20
30
40
50
60
70
S
B
G
MONOSPECIFIC
BISPECIFIC
TRISPECIFIC

Figure 25. Effect of shade and nitrogen on dry weight of shoots (first cutting) of sourgrass (S), buffelgrass (B), and guineagrass (G) grown in monospecific, bispecific, and trispecific combinations.

A : 0% shade
B : 30% shade
C : 60% shade

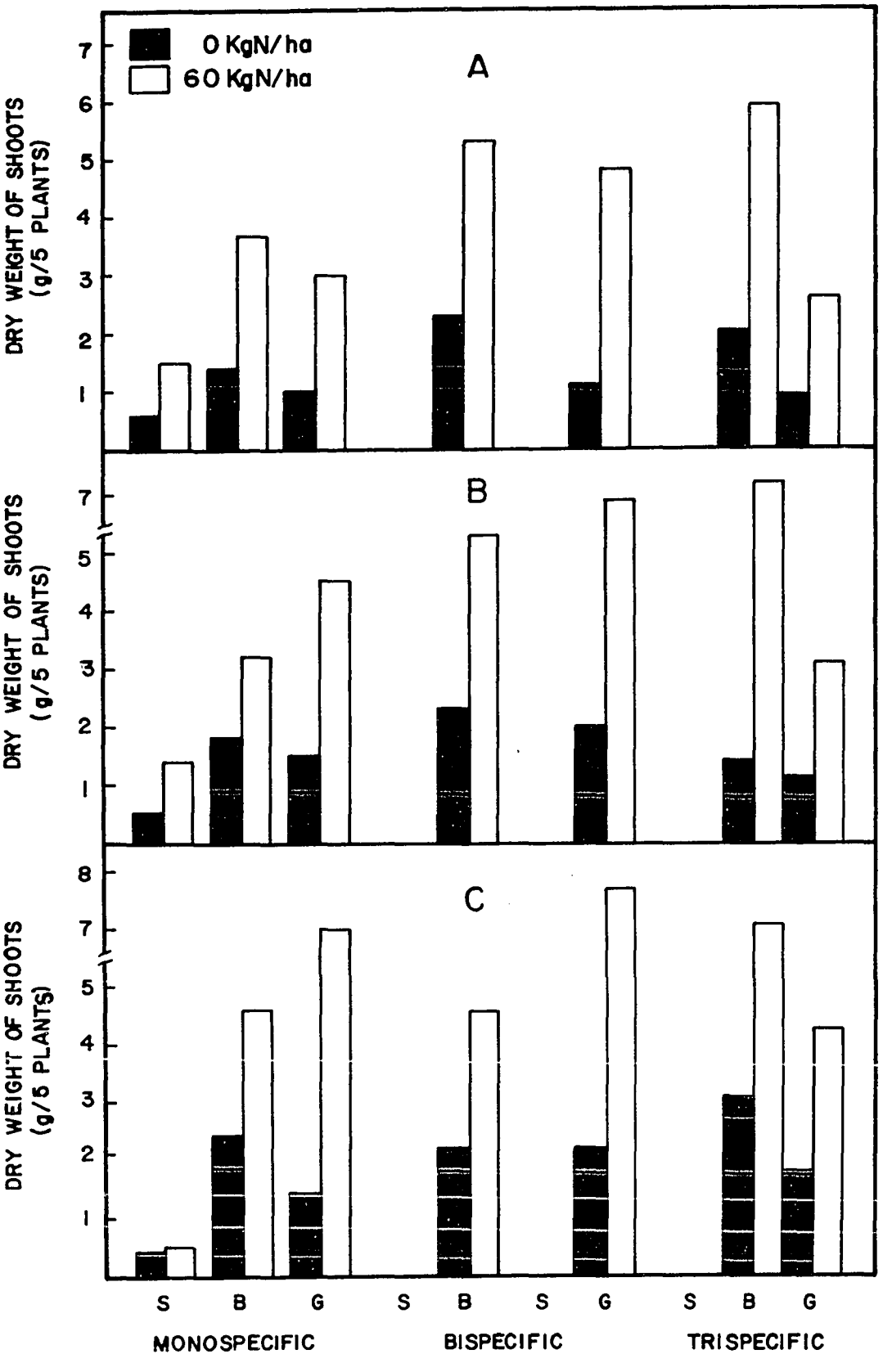
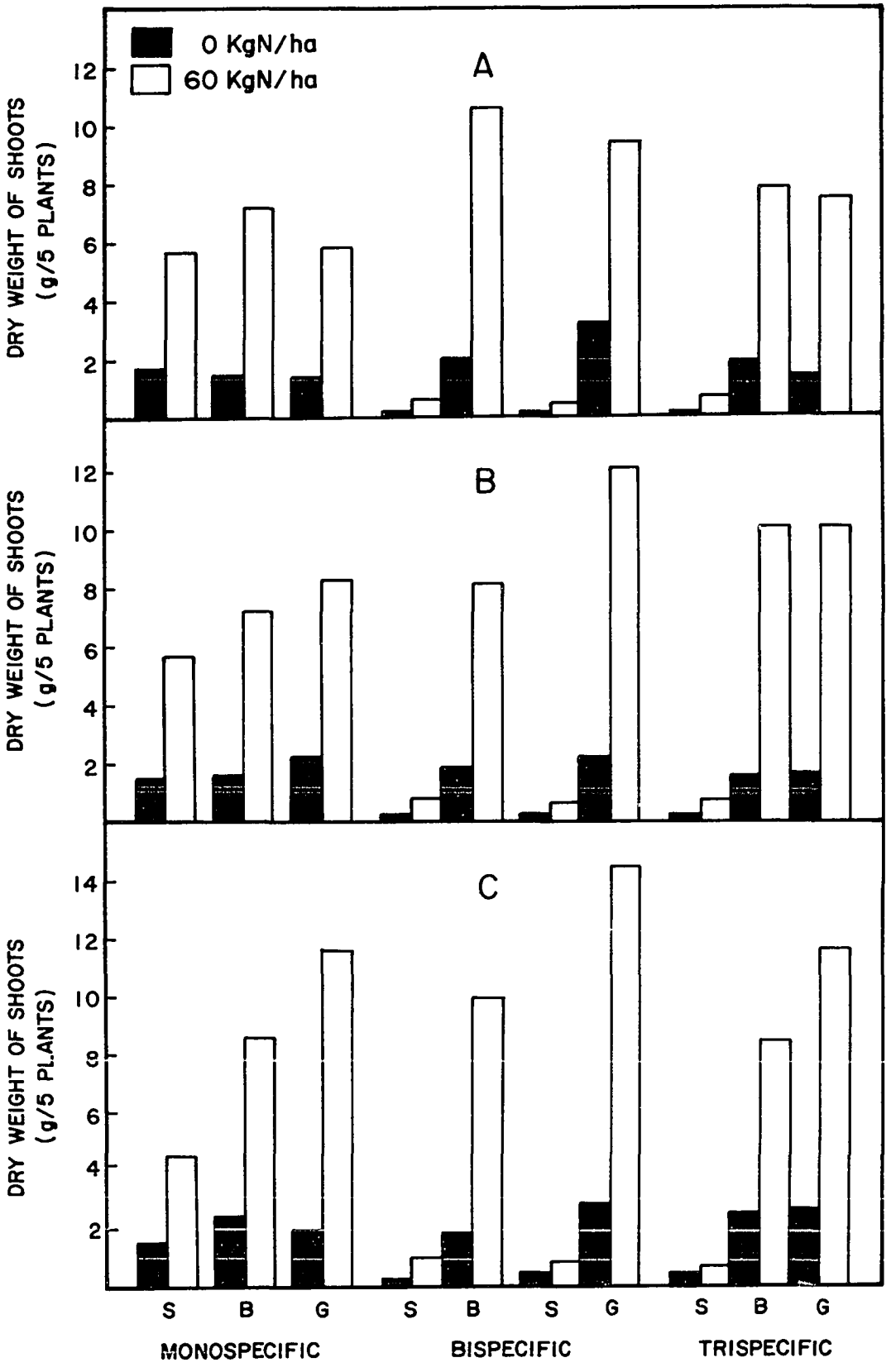

0 KgN/ha
60 KgN/ha
A
B
C
DRY WEIGHT OF SHOOTS (g/5 PLANTS)
S
B
G
MONOSPECIFIC
BISPECIFIC
TRISPECIFIC

Figure 26. Effect of shade and nitrogen on dry weight of shoots (second cutting) of sourgrass (S), buffelgrass (B), and guineagrass (G) grown in monospecific, bispecific, and trispecific combinations.

A : 0% shade
B : 30% shade
C : 60% shade


0 KgN/ha
60 KgN/ha
A
B
C
DRY WEIGHT OF SHOOTS (g/5 PLANTS)
S
B
G
MONOSPECIFIC
BISPECIFIC
TRISPECIFIC

Dry weight of sourgrass was only slightly increased by nitrogen application. In contrast, dry weight of buffelgrass and guineagrass were increased markedly by nitrogen application.

Where sourgrass was planted with buffelgrass, guineagrass, or both species, yields of sourgrass seedlings were negligible regardless of shade and nitrogen level in both cuttings. This may have been the result of the more rapid germination and early growth of buffelgrass and guineagrass. Buffelgrass and guineagrass shaded out the slower growing sourgrass by their greater development of leaf surface. The early growth of sourgrass appeared to be suppressed by the associated grass species. On the other hand, the dry weights of buffelgrass or guineagrass were not greatly affected when grown in any combination of mixture.

Number of tillers per plant

Number of tillers of sourgrass was markedly decreased as shading increased, whereas tiller numbers of buffelgrass and guineagrass were only slightly decreased (Figures 27 and 28). Number of tillers of all three species were increased by nitrogen application. However, tillering of buffelgrass and guineagrass showed greater responses to nitrogen fertilization than did sourgrass. When sourgrass was planted with buffelgrass, guineagrass, or both species, sourgrass did not tiller at all regardless of shade and nitrogen level. When buffelgrass or guineagrass was planted with sourgrass, the number of tillers in these forage grasses generally increased compared with the pure stand culture. Intraspecific competition among dense buffelgrass or guineagrass plants in pure stand was thus more intense than competition between these grasses and sourgrass.

Figure 27. Effect of shade and nitrogen on number of tillers per plant (first cutting) of sourgrass (S), buffelgrass (B), and guineagrass (G) grown in monospecific, bispecific, and trispecific combinations.

A : 0% shade
B : 30% shade
C : 60% shade

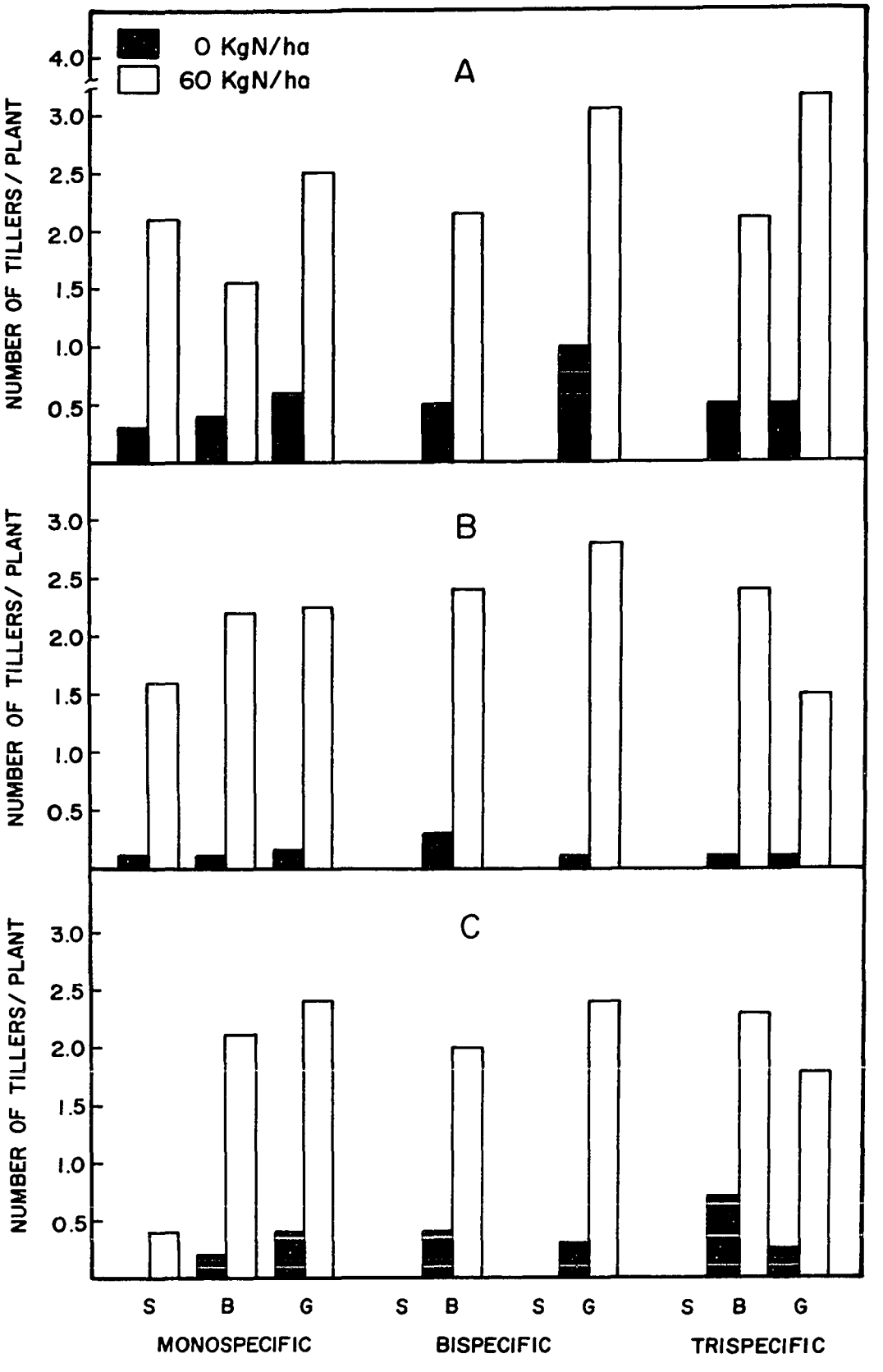
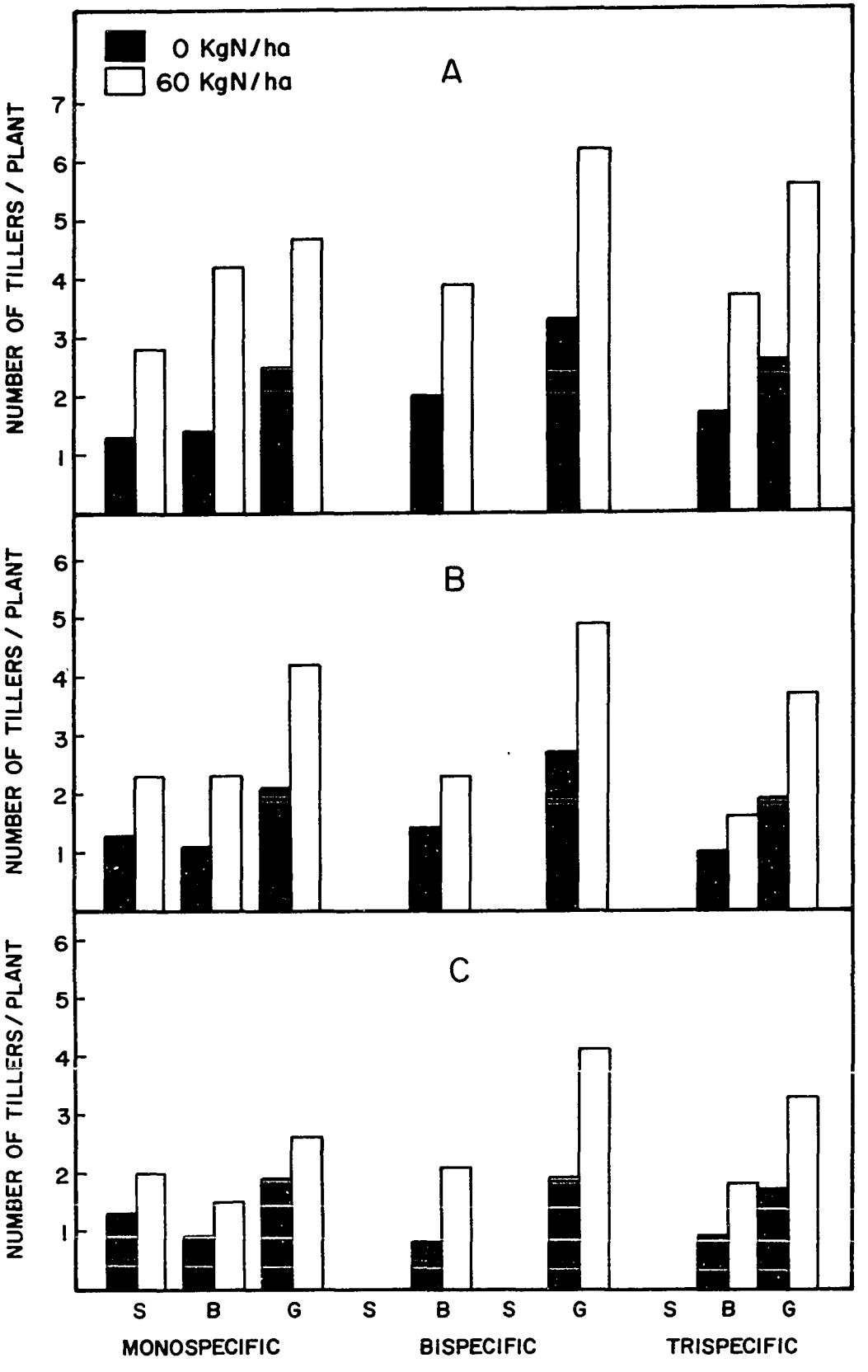

0 KgN/ha
60 KgN/ha
A
B
C
NUMBER OF TILLERS/ PLANT
4.0
3.0
2.5
2.0
1.5
1.0
0.5
S B G S B S G S B G
MONOSPECIFIC
BISPECIFIC
TRISPECIFIC

Figure 28. Effect of shade and nitrogen on number of tillers per plant (second cutting) of sourgrass (S), buffelgrass (B), and guineagrass (G) grown in monospecific, bispecific, and trispecific combinations.

A : 0% shade
B : 30% shade
C : 60% shade


0 KgN/ha
60 KgN/ha
A
B
C
NUMBER OF TILLERS / PLANT
NUMBER OF TILLERS / PLANT
NUMBER OF TILLERS/PLANT
S B G S B S G S B G
MONOSPECIFIC
BISPECIFIC
TRISPECIFIC

Chemical composition

There were no significant differences in tissue concentration of nitrogen, phosphorus and potassium with treatments.

Total nitrogen taken up by unfertilized sourgrass in pure stand was greater than that taken up by unfertilized buffelgrass or guineagrass (Table 13). In contrast, total nitrogen uptake by fertilized sourgrass was less than that taken up by buffelgrass or guineagrass. Total uptake of nitrogen for all three species was higher when nitrogen was applied. When sourgrass was grown with buffelgrass and guineagrass, nitrogen uptake by sourgrass was extremely low compared to the associated species. Buffelgrass and guineagrass have deeper and more extensive root system than sourgrass and thus absorbed nitrogen more efficiently than sourgrass. Consequently, the nitrogen uptake of sourgrass was depressed by association with buffelgrass or guineagrass.

Total phosphorus and potassium taken up by three species were not significantly different with treatments.

DISCUSSION

When sourgrass was planted with buffelgrass, guineagrass, or both species, sourgrass germination, emergence, and shoot growth was very slow during early stages of plant development. The relatively weak seedlings encountered competition from the rapidly growing buffelgrass and guineagrass seedlings as soon as they emerged and were thus severely suppressed. Sourgrass seedlings growing with buffelgrass, guineagrass, or both species were significantly shorter, lighter, and had fewer tillers per plant. The inability of sourgrass to gain a competitive advantage

Table 14. Total uptake of minerals by sourgrass, buffelgrass and guineagrass sown in monospecific, bispecific and trispecific combinations with varying levels of shade and nitrogen fertilization

Shade (%)		0			30			60		
Nitrogen	Grass[1] Combination	N	P	K	N	P	K	N	P	K
kg/ha		g/5 plants								
0	Sourgrass	13.3	1.3	2.7	12.3	1.1	2.9	17.7	1.6	5.8
	Buffelgrass	8.0	0.9	1.8	9.7	0.8	2.7	13.7	1.0	5.3
	Guineagrass	8.1	0.8	1.4	13.8	1.6	1.7	9.1	1.1	2.2
	SB - S	0.8	-[2]	-	1.3	-	-	1.7	-	-
	B	11.4	1.2	3.2	10.8	1.0	3.2	10.2	0.8	3.6
	SG - S	1.0	-	-	1.2	-	-	2.6	-	-
	G	17.0	2.1	2.6	12.8	1.7	2.1	16.4	1.8	3.7
	SBG - S	1.0	-	-	1.0	-	-	2.4	-	-
	B	10.0	0.8	3.1	8.6	0.8	2.6	12.8	1.0	4.9
	G	8.6	1.3	1.4	8.3	1.2	1.6	15.7	1.7	3.5
60	Sourgrass	39.4	2.1	10.7	45.2	2.3	12.7	37.5	1.7	11.8
	Buffelgrass	43.9	1.6	13.8	31.6	1.3	10.3	52.6	2.0	20.3
	Guineagrass	33.6	1.8	5.3	42.6	1.8	8.8	60.6	2.2	18.3
	SB - S	3.0	-	-	5.9	-	-	6.6	-	-
	B	63.2	2.8	18.9	48.6	2.2	16.6	61.0	2.2	23.5
	SG - S	1.9	-	-	3.3	-	-	5.3	-	-
	G	57.1	2.5	10.4	63.7	3.3	15.1	92.8	3.1	23.9
	SBG - S	4.3	-	-	4.8	-	-	5.1	-	-
	B	42.5	1.7	13.9	54.2	2.4	18.5	50.2	1.5	20.1
	G	46.5	1.9	10.9	54.2	2.7	14.3	73.9	2.3	17.3

[1] Abbreviations: S = Sourgrass, B = Buffelgrass, G = Guineagrass
[2] Mineral contents were not determined because of insufficient samples.

over the other grass species during the early seedling stage is perhaps the primary reason for the poor growth of sourgrass in association with buffelgrass and guineagrass (Figure 22). Blaser et al. (1956), Milthorpe (1961), and Rummel (1946) reported that relative earliness of germination and emergence and the size of the plant at emergence and its subsequent growth rate influenced its early competitive ability, so that the plants with the initial competitive advantage became increasingly dorminant during seedling growth. Buffelgrass and guineagrass produced less when growing alone than when growing with sourgrass. This is probably because intra-specific competition for light and nutrients in their pure stands was greater than the competition from bispecific combinations.

The growth of sourgrass in association with buffelgrass, guineagrass, or both species was suppressed by shade and nitrogen treatments because the associated grass species, buffelgrass and guineagrass, were more tolerant to shade and more responsive to nitrogen fertilization than sourgrass. Evans (1960), Lang (1934), McCown and Williams (1968), and Peter and Lowance (1974) reported that fertilization of a crop with nitrogen, phosphorus, potassium, or sulfur enabled it to withstand weed invasion and to outgrow and suppress most of the existing weeds.

The moisture-stress experiment in Chapter IV (see Figure 6) indicated that buffelgrass and guineagrass seeds were more sensitive to moisture tension than sourgrass seeds during germination. Sourgrass seeds would thus be expected to germinate and begin growth under conditions too dry for buffelgrass or guineagrass seeds to germinate. Once established, however, buffelgrass and guineagrass seedlings in the field were more tolerant to growth than sourgrass (personal observation). Buffelgrass

and guineagrass in pots also had deeper and more extensive root systems (Figure 16). These two grasses would thus have a strong competitive advantage in obtaining water and nutrients after establishment. The growth of sourgrass in ungrazed mixtures would therefore be favored under conditions of relatively high moisture tension during establishment followed by adequate moisture. The opposite sequence should favor the more desirable grasses.

It may be concluded that sourgrass can be crowded out by buffelgrass or guineagrass under natural conditions and that this process is enhanced by nitrogen fertilization. Heinrich (1944), Hull and Stewart (1948), Oakes (1968), and Peters and Lowance (1974) similarly concluded that weeds might be reduced or choked out by planting more competitive plants and by applying fertilizers.

CHAPTER VII

SUMMARY AND CONCLUSIONS

Field surveys were conducted on the major islands of Hawaii to determine the distribution of sourgrass and the species associated with it, and to characterize the topography, climate, and edaphic factors of sourgrass-infested areas. Sourgrass was more abundant at lower elevations, below 420 meters, and in dry zones of 120 to 760 mm annual rainfall. Sourgrass communities occurred on hillsides or on gentle basal slopes where Prosopis pallida (Humb. and Bonpl. ex Willd) HBK. or Leucaena latisiliqua (L.) Gillis and Stearn grew. Distribution of sourgrass corresponded to shade conditions. It was also found on abandoned dry areas and in old or abandoned pineapple fields. The species associated with sourgrass were Chloris barbata (L.) Sw., Rhynchelytrum repens (Willd) Hubb., Bothriochloa pertusa (L.) Camus, Panicum maximum Jacq., and Cenchrus ciliaris L. Sourgrass communities were not restricted to a particular soil type. However, sourgrass was mostly found in silt clay to silt clay loam with shallow soil profiles. Soil analysis data also showed a great variation in nutrient levels at the different locations. It is suggested that low rainfall, high temperatures, and shade were the more important factors in the distribution of sourgrass.

A series of experiments were conducted to evaluate effects of temperature and light, photoperiod, chemical treatment, and moisture stress on germination of sourgrass seeds. Germination was greater and proceeded at a more rapid rate under 8-hours illumination daily than in complete darkness. Optimum temperature regimes were constant 30 C and alternating temperatures of 20-30 C and 25-35 C. Germination

of sourgrass seed was best under 8 or 12 hour photoperiods but was reduced under 16 and 24 hour photoperiods although light was previously shown to be necessary for germination. Pre-soaking of sourgrass seeds with GA, kinetin, and thiourea solutions for 24 hours stimulated germination to varying degrees. Germination was clearly stimulated by GA treatment at all concentrations used, especially 1000 ppm. Kinetin at 12.5, 25 and 50 ppm, and thiourea at 1000 ppm was effective in slightly enhancing germination at 22 C in the dark. Germination percentage of sourgrass, buffelgrass, and guineagrass decreased as mannitol-simulated moisture stress was increased. Buffelgrass and guineagrass were sensitive to moisture tension. The capacity of sourgrass to germinate rapidly under low soil moisture could give it a competitive advantage over buffelgrass and guineagrass under semi-arid to arid conditions.

The seeding depth experiment showed that emergence of sourgrass seedlings decreased with increasing planting depths. The 0-3 cm horizon was the zone from which most sourgrass seeds emerged. The maximum depth from which sourgrass seeds emerged and survived was 4 cm. Since viable seeds at greater than 4 cm depths would be unable to germinate and survive it is suggested that fields be left undisturbed or if cultivation was required that it be confined to the surface of the soil.

Stand density studies of sourgrass showed that plant height, number of tillers per plant, and seed yield per plant greatly decreased as the planting density was increased. Highly negative curvilinear regressions were found between planting density and the above growth parameters. Visual observation indicated that seedling mortality increased markedly at higher densities. Thus, intraspecific competition

was a major factor in sourgrass seedling development and survival.

The photoperiod experiment showed that sourgrass flowered under 11, 13, and 15 hour photoperiods. Its failure to flower under 9 hour photoperiod was probably due to slower floral development in response to insufficient light energy rather than to a photoperiodic response. Floral initiation in sourgrass was thus apparently insensitive to photoperiod and this species may be classed as day-neutral in flowering behavior.

In a study of the growth of sourgrass, buffelgrass, and guineagrass under different levels of shade and nitrogen, plant height and dry matter production of shoots of all three species increased with increasing shade. Dry weight of roots and tillers decreased as shade was increased. In addition, flowering was delayed with increasing shade. Nitrogen fertilization increased plant height, dry weights of shoots and roots, and number of tillers per plant for the three grass species regardless of shade conditions.

A pot experiment was conducted to determine the competitive ability of sourgrass, buffelgrass, and guineagrass under different levels of shade and nitrogen regimes, and to devise management methods for replacing sourgrass with buffelgrass and guineagrass through competition. Sourgrass emergence and shoot growth was very slow during early stages of plant development compared to buffelgrass and guineagrass. When sourgrass was grown with buffelgrass, guineagrass, or both it encountered severe competition from the rapidly growing buffelgrass and guineagrass seedlings as soon as they emerged and were severely suppressed. Sourgrass seedlings growing with buffelgrass, guineagrass, or both were significantly shorter and had less dry matter and fewer tillers per

plant. It is evident from these results that sourgrass was not a competitive grass compared to buffelgrass and guineagrass and that sourgrass may be crowded out by buffelgrass and guineagrass with nitrogen fertilization.

It is concluded that sourgrass in pasture can be controlled through competition with buffelgrass and guineagrass under proper management of grazing and fertilization. The knowledge of the biology of sourgrass obtained in these studies should be useful in the development of economical and effective programs for more successful control of this weed. In particular, programs should consider (a) depth of tillage required, (b) moisture requirements for germination and emergence, (c) fertilization, and (d) grazing management.

Appendix Table 1. Analysis of variance for effect of shade and nitrogen on three grass species

Plant height, First cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	30.588
Shade	2	3694.060**
Error (a)	4	19.560
Sub-plot		
Nitrogen	1	5270.782*
Shade x Nitrogen	2	27.171
Grasses	2	348.032**
Shade x Grasses	4	93.900**
Nitrogen x Grasses	2	35.616
Shade x Nitrogen x Grasses	4	39.775
Error (b)	30	15.303
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Plant height, Second cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	85.019
Shade	2	9794.296**
Error (a)	4	40.157
Sub-plot		
Nitrogen	1	7680.296**
Shade x Nitrogen	2	763.630**
Grasses	2	757.241**
Shade x Grasses	4	271.296**
Nitrogen x Grasses	2	17.796
Shade x Nitrogen x Grasses	4	109.630*
Error (b)	30	32.511
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Dry weight of shoots, First cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	0.035
Shade	2	88.046**
Error (a)	4	2.704
Sub-plot		
Nitrogen	1	1980.167**
Shade x Nitrogen	2	61.004**
Grasses	2	74.785**
Shade x Grasses	4	4.105
Nitrogen x Grasses	2	15.591**
Shade x Nitrogen x Grasses	4	8.484**
Error (b)	30	1.721
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Dry weight of shoot, Second cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	14.117
Shade	2	394.509**
Error (a)	4	18.873
Sub-plot		
Nitrogen	1	11860.742**
Shade x Nitrogen	2	209.845**
Grasses	2	252.809**
Shade x Grasses	4	24.668*
Nitrogen x Grasses	2	32.086*
Shade x Nitrogen x Grasses	4	14.152
Error (b)	30	7.333
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Dry weight of roots

Source	Degree of freedom	Mean square
Main plot		
Replication	2	157.987
Shade	2	1865.068**
Error (a)	4	45.735
Sub-plot		
Nitrogen	1	18058.449**
Shade x Nitrogen	2	427.322**
Grasses	2	4210.087**
Shade x Grasses	4	241.939**
Nitrogen x Grasses	2	1251.226**
Shade x Nitrogen x Grasses	4	174.722**
Error (b)	30	24.800
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Number of tillers/plant, First cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	0.963
Shade	2	89.241**
Error (a)	4	2.824
Sub-plot		
Nitrogen	1	85.630**
Shade x Nitrogen	2	1.685
Grasses	2	19.241**
Shade x Grasses	4	10.102**
Nitrogen x Grasses	2	4.241
Shade x Nitrogen x Grasses	4	0.880
Error (b)	30	1.537
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Number of tillers/plant, second cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	0.352
Shade	2	314.741**
Error (a)	4	4.991
Sub-plot		
Nitrogen	1	308.167**
Shade x Nitrogen	2	0.889
Grasses	2	271.185**
Shade x Grasses	4	43.657**
Nitrogen x Grasses	2	6.222
Shade x Nitrogen x Grasses	4	6.694*
Error (b)	30	2.333
Total	53	

* Significant at the 5% level
** Significant at the 1% level

Appendix Table 2. Analysis of variance for competition experiment (shade x nitrogen x grasses)

Plant height, First cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	7.385
Shade	2	5062.549*
Error (a)	4	15.900
Sub-plot		
Nitrogen	1	8561.522**
Shade x Nitrogen	2	59.236*
Grasses	9	7888.773**
Shade x Grasses	18	249.071**
Nitrogen x Grasses	9	296.968**
Shade x Nitrogen x Grasses	18	30.410**
Error (b)	114	12.660
Total	179	

* Significant at the 5% level
** Significant at the 1% level

Plant height, Second cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	89.909
Shade	2	8383.561**
Error (a)	4	16.639
Sub-plot		
Nitrogen	1	14067.976**
Shade x Nitrogen	2	171.092**
Grasses	9	2380.290**
Shade x Grasses	18	211.075**
Nitrogen x Grasses	9	96.444**
Shade x Nitrogen x Grasses	18	24.251**
Error (b)	114	5.537
Total	179	

* Significant at the 5% level
** Significant at the 1% level

Number of Tillers, First cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	1.478
Shade	2	1.072*
Error (a)	4	0.131
Subplot		
Nitrogen	1	73.089
Shade x Nitrogen	2	0.310
Grasses	9	6.933**
Shade x Grasses	18	0.424**
Nitrogen x Grasses	9	3.859**
Shade x Nitrogen x Grasses	18	0.197*
Error (b)	114	
Total	179	

* Significant at the 5% level
** Significant at the 1% level

Number of tillers, Second cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	1.676*
Shade	2	15.241**
Error (a)	4	0.234
Subplot		
Nitrogen	1	57.122**
Shade x Nitrogen	2	3.462**
Grasses	9	33.080**
Shade x Grasses	18	1.236**
Nitrogen x Grasses	9	3.251**
Shade x Nitrogen x Grasses	18	0.389
Error (b)	114	0.246
Total	179	

* Significant at the 5% level
** Significant at the 1% level

Dry weight, First cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	1.013
Shade	2	8.740
Error (a)	4	1.902
Sub-plot		
Nitrogen	1	261.072**
Shade x Nitrogen	2	1.144
Grasses	6	26.131**
Shade x Grasses	12	1.927**
Nitrogen x Grasses	6	8.896**
Shade x Nitrogen x Grasses	12	1.542**
Error (b)	78	0.400
Total		

* Significant at the 5% level
** Significant at the 1% level

Dry weight, Second cutting

Source	Degree of freedom	Mean square
Main plot		
Replication	2	0.370
Shade	2	24.386**
Error (a)	4	1.065
Sub-plot		
Nitrogen	1	1178.931**
Shade x Nitrogen	2	10.260**
Grasses	9	136.022**
Shade x Grasses	18	6.113**
Nitrogen x Grasses	9	65.874**
Shade x Nitrogen x Grasses	18	5.930**
Error (b)	114	0.697
Total	179	

* Significant at the 5% level
** Significant at the 1% level

LITERATURE CITED

Allard, H. A. and M. W. Evans. 1941. Growth and flowering of some tame and wild grasses in response to different photoperiods. J. Agr. Res. 62:193-228.

Allen, L. H. Jr. 1975. Shade-cloth microclimate of soybeans. Agron. J. 67(2):175-181.

Allsopp, A. 1955. Experimental and analytical studies of Pteridophytes. XXVII. Investigations on Marsilea. 5. Cultural conditions and morphogenesis, with special reference to the origin of land and water forms. Ann. Bot. 19:247-264.

Amen, R. D. 1968. A model of seed dormancy. Bot. Rev. 34(1):1-31.

Anderson, A. M. 1947. The effect of atternating temperatures, light intensities and moistening agents of the substratum on the germination of freshly harvested seed of Oregon grown ryegrass. Proc. Assoc. Offic. Seed Analysts N. Amer. 37:152-161.

Anderson, R. N. 1968. Germination and Establishment of Weeds for Experimental Purposes. W. F. Humphrey Press, Geneva, New York.

Anonymous. 1962. Noxious Weeds of Hawaii, Dept. Agr., Hawaii.

_____. 1968. Weed Control. Principles of Plant and Animal Pest Control Volume 2. Nat. Acad. Sci. 267-294.

_____. 1972. Hawaii Conservation Needs Inventory, Soil Conservation Service, U.S. Dept. Agr. 3-16.

_____. 1973. Soil Survey of Island of Oahu, Maui, Molokai, Lanai, Kauai, and Hawaii, State of Hawaii, Soil Conservation Service. U.S. Dept. Agr.

Ashiru, G. A. 1969. Effect of kinetin, thiourea and thiourea dioxide, light and heat on seed germination and seedling growth of Kola (Cola Nitida (Ventenant) Schott and Endlicher). J. Amer. Soc. Hort. Sci. 94:429-432.

Benedict, H. M. 1941. Growth of some range grasses in reduced light intensities at Cheyenne, Wyoming. Bot. Gaz. 102:582-589.

Black, M. and P. F. Wareing. 1955. Growth studies in woody species VII. Photoperiodic control of germination in Betula pubescens Ehrh. Physiol. Plantarum 8:300-310.

Blaser, R. E., T. H. Taylor, W. Griffeth and W. Skrdla. 1956. Seedling competition in establishing forage plants. Agron. J. 48:1-6.

Borthwick, H. A., S. B. Hendricks, M. W. Parker, E. H. Toole, and V. K. Toole. 1952. A reversible reaction controlling seed germination. Proc. Nat. Acad. Sci. 38:662-666.

Bosch, O. J. H. and J. J. P. van Wyk. 1970. Influence of bushveld trees on the productivity of Panicum maximum. Proc. Grassland Soc. S. Afr. 5:69-74. Cited from Herbage Abstracts 41(3):318.

Bradbeer, J. W. 1968. Studies in seed dormancy. IV. The role of endogenous inhibitors and gibberellin in the dormancy and germination of Corylus avellana L. seeds. Planta 78:266-276.

Brian, P. W., H. G. Hemming and D. Lowe. 1962. Relative activity of the gibberellins. Nature 193:946-948.

Briggs, W. M. and D. C. Fork. 1969. Long-lived intermediates in phytoshrome transformation. I. In vitro studies. Plant Physiol. 44:1081-1081.

Britton, N. L. 1918. Flora of Bermuda. Charles Scribner's Sons, New York.

Brown, W. V. 1951. Chromosome numbers of some Texas Grasses. Bull. Torrey Bot. Club. 78(4):292-299.

Cable, D. R. 1971. Growth and development of Arizona cottontop (Trichachne californica (Benth) Chase). Bot. Gaz. 132(2):119-145.

Cardenas, J., C. E. Reyes, and J. D. Doll. 1972. Tropical Weeds. Vol. I:67-68. International Plant Protection Center, Corvallis.

Chen, T. M., R. H. Brown, and C. C. Black. 1970. CO_2 compensation concentration, rate of photosynthesis, and carbonic anhydrase activity of plants. Weed Science 18:399-403.

Chrispells, M. J. and J. E. Varner. 1967. Gibberellic acid enhanced synthesis and release of α-amylase and ribonuclease by isolated barley aleurone layers. Plant Physiol. 42:398-406.

Clements, F. E., J. E. Weaber, and H. C. Hanson. 1929. Plant Competition. Carnegie Institution of Washington. 316-334.

Cohen, D. 1958. The mechanism of germination stimulation by alternating temperatures. Bull. Res. Council Israel Sect. D 6, 111.

Corns, W. G. 1960. Effects of gibberellin treatments on germination of various species of weed seeds. Can. J. Plant Sci. 40:47-51.

Crocker, W. and L. V. Barton. 1953. Physiology of Seeds. Chronica Botanica, Waltham, Mass. 267 p.

Daccarett, M. and J. Blydenstein. 1968. Influence of leguminous and nonleguminous trees on the forage grown under them. Turrialba 18(4):405-408.

Davis, W. E. 1939. An explanation of the advantage of alternating temperatures over constant temperatures in the germination of certain seeds (Abstract). Amer. J. Bot. 26:175.

Dawson, J. H. and V. F. Bruns. 1962. Emergence of barnyardgrass, green foxtail and yellow foxtail seedlings from various soil depths. Weeds 10:136-139.

De Peralta, F. 1935. Some principles of competition as illustrated by Sudan grass, Holcus sorghum sudanensis (Piper.) Hitch. Ecol. Monogr. 5:355-404.

Deschenes, J. M. 1974. Intraspecific competition in experimental population of weeds. Can. J. Bot. 52(6):1415-1421.

Dibbern, J. C. 1947. Vegetative responses of Bromus inermis to certain variations in environment. Bot. Gaz. 109:44-58.

Donald, C. M. 1954. Competition among pasture plants. II. The influence of density and seed production in annual pasture plants. Aust. J. Agric. Res. 5:585-597.

_____. 1963. Competition among crop and pasture plants. Adv. Agron. 15:1-118.

Doneen and MacGillivray. 1943. Germination (emergence) of vegetable seeds as affected by different soil moisture conditions. Plant Physiol. 18:524-529.

Dostal, R. 1950. Morphogenetic experiments with Bryophyllum verticillatum. Acta Acad. Sci. Moravo Siles (Brno) 22:57-98.

Egler, F. E. 1947. Arid southeast Oahu vegetation, Hawaii. Ecol. Monogr. 17:385-435.

Evans, L. T. 1964. Inflorescence initiation in Lolium temulentum L. V. The role of auxins and gibberellins. Aust. J. Biol. Sci. 17:10-23.

Evans, M. W. and H. A. Allard. 1934. Relation of length of day to growth of timothy. J. Agr. Res. 48:571-586.

_____ and J. M. Watkins. 1939. The growth of Kentucky bluegrass and of Canada bluegrass in late spring and in autumn as affected by length of day. J. Amer. Soc. Agron. 31:767-774.

_____ and C. P. Wilsie. 1946. Flowering of bromegrass, Bromus inermis, as influenced by length of day, temperature, and fertility levels. J. Amer. Soc. Agron. 38:923-932.

Evans, R. A. 1960. Differential responses of three species of annual grassland type to plant competitions and mineral nutrition. Ecology 41:305-310.

_____. 1961. Effects of different densities of downy brome on growth and survival of crested wheatgrass in the greenhouse. Weeds 9:216-223.

_____ and J. A. Young. 1972. Competition within the grass community. In the Biology and Utilization of Grasses (Younger, V. B. and C. M. McKell ed.). Academic Press, New York. 230-246.

Evenari, M. 1949. Germination inhibitors. Bot. Rev. 15:153-194.

_____. 1955. Seed Germination. Radiation Biology III (Hollander, A. ed.) McGraw-Hill, New York. 519-549.

_____, G. Neumann, S. Blumenthal-Goldschmidt, A. M. Mayer and A. Poljakoff-Mayber. 1958. The influence of gibberellic acid and kinetin on germination and seedling growth of lettuce. Bull. Res. Council Israel Sect. D6:65-77.

Fender, F. 1960. Aetiological studies on 'Alveld' a disease in lambs caused by grazing Narthecium ossifragum. Proc. VIII. International Grassland Congr. Reading, 664-667.

Fisher, J. E. and W. E. Loomis. 1954. Auxin florigen balance in flowering of soybean. Science 119:71-73.

Gall, H. J. F. 1947. Flowering of smooth bromegrass under certain environmental conditions. Bot. Gaz. 109:59-71.

Gardner, F. P. and W. E. Loomis. 1953. Floral induction and development in orchardgrass. Plant Physiol. 28:201-217.

Garman, H. R. and L. A. Barton. 1946. Response of lettuce seeds to thiourea treatment as affected by variety and age. Contributions from Boyce Thompson Institute 14:229-241.

Garner, W. W. and H. A. Allard. 1920. Effect of length of day on plant growth. J. Agr. Res. 18:553-606.

_____ and _____. 1923. Further studies in photoperiodism; the response of the plant to relative length of day and night. J. Agr. Res. 23:871-920.

Gould, F. W. and T. W. Box. 1965. Grasses of the Texas Coastal Bend. Texas A & M Univ. Press. 58-61.

Hadas, A. 1969. Effects of soil moisture stress on seed germination. Agron. J. 61:325-327.

Hammer, K. C. 1940. Interaction of light and darkness in photoperiodic induction. Bot. Gax. 101:658-687.

_____ and J. Bonner. 1938. Photoperiodism in relation to hormones as factors in floral initiation and development. Bot. Gaz. 100:388-431.

Harrington, G. T. 1923. Use of alternating temperature in the germination of seeds. J. Agr. Res. 23:295-333.

Haselwood, E. L. and G. G. Motter. 1966. Handbook of Hawaiian Weeds. The Hawaiian Sugar Planter's Association. 94-95.

Hashimoto, T. and T. Yamaki. 1959. On the physiological effects of gibberellins A_1, A_2, A_3, and A_4. Bot. Mag., Tokyo. 72:178.

Heinrich, E. F. 1944. Control of weeds. J. Dept. Agr., S. Aust. 47:441-442.

Helmerick, R. H. and R. P. Pffeifer. 1954. Differential varietal responses of winter wheat germination and early growth to controlled limited moisture conditions. Agron. J. 46:560-562.

Hillman, W. S. 1969. Photoperiodism and vernalization. In Physiology of Plant Growth and Development. McGraw-Hill, New York. 559-601.

Hitchcock, A. S. 1950. Manual of the Grasses of the United States. U.S. Dept. Agr. Misc. Publ. 200. 570-573.

Hosaka, E. Y. 1945. Noxious Weeds of Hawaii. Hawaii Board of Commissioners of Agriculture and Forestry.

_____. 1953. Sourgrass in Hawaii. Hawaii Agr. Exp. Sta. Ext. Cir. 336. Univ. of Hawaii. 2 p.

_____ and A. Thistle. 1954. Noxious Plants of the Hawaiian Ranges. Univ. of Hawaii Ext. Bull. 62:32-33.

Hull, A. C. and G. Stewart. 1948. Replacing cheatgrass by reseeding with perennial grass on southern Idaho ranges. J. Amer. Soc. Agron. 40:694-703.

Hunter, J. R. and A. E. Erickson. 1952. Relation of seed germination to soil moisture tension. Agron. J. 44:107-109.

Ikuma, H. and K. V. Thimann. 1963. The action of kinetin on photosensitive lettuce seed as compared with that of gibberellic acid. Plant & Cell Physiol. 4:113-128.

Ishikawa, S. 1954. Light sensitivity against germination. I. Photoperiodism of seeds. Bot. Mag., Tokyo. 67:51-56.

Johnston, I. M. 1943. Plants of Northern Mexico, II. J. Arboretum XXIV. 4:411-412.

Jordan, L. S. and V. A. Jolliffe. 1969. Germination and maturation of Chenopodium humile L. Weed Science 18:382-385.

Junttila, O. 1970. Effect of stratification, gibberellic acid and germination temperature on the germination of Betula nana. Physiol. Plantarum 23:425-433.

Khan, A. A. 1960. Promotion of lettuce seed germination by gibberllin. Plant Physiol. 35:333-339.

_____. 1971. Cytokinins: Permissive role in seed germination. Science 171:853-859.

_____, J. A. Gross, and D. Smith. 1957. Effect of gibberellin on germination of lettuce seeds. Science 125:645-646.

_____ and N. E. Tolbert. 1965. Reversal of inhibitors of seed germination by red light plus kinetin. Physiol. Plantarum 18:41-43.

_____ and E. C. Waters. 1969. On the hormonal control of post-harvest dormancy and germination in barley seeds. Life Sciences 8:729-736.

Kallio, P. and P. Piroinen. 1959. Effect of gibberellin on the termination of dormancy in some seeds. Nature 183:1830-1831.

Knake, E. L. 1972. Effect of shade on giant foxtail. Weed Science 20:588-592.

Knipe, D. and C. H. Herbel. 1960. The effects of limited moisture on germination and initial growth of six grass species. J. Range Managt. 13:297-302.

Koller, D., A. M. Mayer, A. Poljakoff-Mayber, and S. Klein. 1962. Seed germination. Ann. Rev. Plant Physiol. 13:437-464.

_____, M. Sachs, and M. Negbi. 1964. Germination-regulating mechanisms in some desert seeds. VIII. Artemisia monosperma. Plant Cell Physiol. 5:85-100.

Lang, A. 1965a. Effects of some internal and external conditions on seed germination. Encycl. Plant Physiol. 15(2):848-893.

_____. 1965b. Physiology of flower initiation. In Handbuch der Pflanzen physiologie (Ruhland ed.). Springer-verlag, Berlin and New York. 15:1380-1536.

Lang, H. C. 1934. Weed Suppression by Fertilizers and Chemicals. The Birkins, Hook, Surrey. 12-15.

Larson, E. C. 1947. Photoperiodic responses of geographical strains of Andropogon scoparius. Bot. Gaz. 109:132-149.

Lawrence, O. 1960. Effect of water stress on cell wall metabolism of Avena coleoptile tissue. Plant Physiol. 35:443-450.

Leopold, A. C. and K. V. Thimann. 1949. The effect of auxin of flower initiation. Amer. J. Bot. 36:342-347.

Manohar, M. S. and W. Heydecker. 1964. Effects of water potential on germination of pea seeds. Nature 202:22-24.

Martin, W. E. and J. E. Matocha. 1973. Plant analysis as an aid in the fertilization of forage crops. In Soil Testing and Plant Analysis (Walsh, L. M. and J. D. Beaton eds.). 393-426.

McCown, R. L. and W. A. Williams. 1968. Competition for nutrient and light between the annual grassland species Bromus mollis and Erodium botrys. Ecology 49(5):981-990.

McDonough, W. T. 1969. Use of saran shade cloth in greenhouse to improve summer seedling growth of five mountain range grasses and forbs. Res. Note INT-99. U.S.D.A. Forest Serv.

McGinnies, W. J. 1960. Effects of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-162.

_____. 1966. Effects of shade on the survival of crested wheatgrass seedlings. Crop Science 6:482-484.

Miller, C. O. 1956. Similarity of some kinetin and red light effects. Plant Physiol. 31:318-319.

_____. 1958. The relationship of the kinetin and red-light promotions of lettuce seed germination. Plant Physiol. 33:115-117.

Milthorpe, F. L. 1961. The nature and analysis of competition between plants of different species. Symp. Soc. Exptl. Biol. 15:330-355.

Mohlenbrock, R. H. 1972. The Illustrated Flora of Illinois. Grasses Bromus to Paspalum. Southern Illinois Univ. Press. 289-290.

Moore, R. P. 1943. Seedling emergence of small-seeded legumes and grasses. J. Amer. Soc. Agron. 35:370-381.

Morinaga, T. 1926. Effect of alternating temperatures upon the germination of seeds. Amer. J. Bot. 13:141-158.

Murneek, A. E. 1948. History of research in photoperiodism. In Vernalization and Photoperiodism (Murneek, A. E. and R. O. Whyte ed.). Chronica Botanica, Waltham, Mass. 39-58.

Murphy, R. P. and A. C. Arny. 1939. The emergence of grass and legume seedlings planted at different depths in five soil types. J. Amer. Soc. Agron. 31:17-28.

Oakes, A. J. 1968. Replacing hurricane grass in pastures of the dry tropics. Trop. Agr. 45(3):235-241.

Olmsted, C. E. 1943. Growth and development in range grasses. III. Photoperiodic response in the genus Bouteloua. Bot. Gaz. 105:165-181.

Overbeek, J. V. 1966. Plant hormones and regulators. Science 152: 721-731.

Peters, E. J. and S. A. Lowance. 1974. Fertility and management treatments to control broomsedge in pastures. Weed Science 22:201-205.

Peters, R. A. and P. E. Keeley. 1964. The germination and development of small and large crabgrass. Abstracts, Weed Sci. Soc. Amer. 61-62.

Peterson, M. S. and W. E. Loomis. 1949. Effects of photoperiod and temperature on growth and flowering of Kentucky bluegrass. Plant Physiol. 24:31-43.

Powell, L. M. and R. P. Pfeifer. 1956. The effect of controlled limited moisture on seedling growth of Cheyenne winter wheat selections. Agron. J. 48:555-557.

Pritchett and L. B. Nelson. 1951. The effect of light intensity on the growth characteristics of alfalfa and bromegrass. Agron. J. 43: 172-177.

Purvis, O. N. 1934. An analysis of the influence of temperature during germination on subsequent development of certain winter cereals and its relation to the effect of length of day. Ann. Bot. 48:919-955.

Ray, P. M. and W. E. Alexander. 1966. Photoperiodic adaptation to latitude in Xanthium strumarium. Amer. J. Bot. 53:806-816.

Reid, C. S. W. 1973. Limitations to the productivity of the herbage fed ruminant that arise from the diet. In Chemistry and Biochemistry of Herbage (Butler, G. W. and R. W. Bailey ed.). Academic Press, New York. Vol. 3. 215-262.

Ribeiro, O. and A. Machado. 1952. Occurrence of an alkaloid in Trichachne vestita. Engenharfa e quim. 4(2):26. Cited from Chemical Abstracts 46:9264.

Risser, P. G. 1969. Competitive relationships among herbaceous grassland plants. Bot. Rev. 35(3):251-284.

Rudolfs, W. 1921. Effect of salt solutions having definite osmotic concentration values upon absorption by seeds. Soil Science 11:277-293.

Rummell, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. Ecology 27(2):159-167.

Sachs, R. M. 1956. Floral initiation in Cestrum nocturnum L. I. A. long-short day plant. Plant Physiol. 31:185-192.

Schwabe, W. W. 1971. Physiology of vegetative reproduction and flowering. In Plant Physiology VIA (Steward ed.) 233-412.

Sedgley, R. H. 1963. The importance of liquid seed contact during the germination of Medicago tribuloides Desr. Aust. J. Agr. Res. 14:646-653.

Silveus, W. A. 1933. Classification and Description of Grasses. The Clegg Company. 479-480.

Simpson, G. M. and J. M. Naylor. 1962. Dormancy studies in seed of Avena fatua. III. A relationship between maltase, amylases, and gibberellin. Can. J. Bot. 40:1659-1673.

Skinner, G., F. D. Talbert, and W. Shive. 1958. Effect of 6-(substituted) purines and GA on the rate of seed germination. Plant Physiol. 33:190-194.

Small, J. K. 1933. Manual of Southern Flora. Published by author, New York. 49-50.

Stebbins, G. L. and B. Crampton. 1961. A suggested revision of the grass genera of temperate North America. In Recent Advances in Botany. Toronto.

Stebler, F. G. 1881. Uber den Eingluss des Lightes ouf die keimung vierterjahrssckr. Naturforsch. Ges Zurich 26:102-104. Illustrated from Evenari (1955).

Stiles, I. E. 1948. Relation of water to the germination of corn and cotton seeds. Plant Physiol. 20:540-545.

Stoddart, J. L. 1966. Studies on the relationship between gibberellin metabolism and daylength in normal and nonflowering red clover (Trifolium pratense L.). J. Exp. Bot. 17:96-107.

_____ and L. Lang. 1968. The effect of daylength on gibberellin synthesis in leaves of red clover (Trifolium paatense L.). In Biochemistry and Physiology of Plant Growth Substances (Wightman, F. and G. Setterfield, eds.). Runge Press, Ottawa. 1371-1383.

Stowe, B. B. and T. Yamaki. 1957. The history and physiological action of the gibberellins. Ann. Rev. Plant Physiol. 8:181-216.

Tager, J. M. and B. Clarke. 1961. Replacement of an alternation temperature requirement for germination by gibberellic acid. Nature 192:83-84.

Taliaferro, W. J. 1959. Rainfall of the Hawaiian Islands. Hawaii Water Authority. 394 p.

Tateaka, T. 1962. A cytological study of some Mexican grasses. Bull. Torrey Bot. Club. 89(2):77-82.

Thimann, K. V. 1954. The physiology of growth in plant tissues. Amer. Sci. 42:589-606.

Thompson, P. A. 1968. The effect of some promoters and inhibitors on the light controlled germination of strawberry seeds (Fragaria vesca semperflorens Ehr.). Physiol. Plantarum 21:833-841.

_____. 1969. Germination of species of Labiatae in response to gibberellins. Physiol. Plantarum 22:575-586.

Thompson, R. C. and N. L. Horn. 1944. Germination of lettuce seed at high temperature (25 to 35 C) stimulated by thiourea. Proc. Amer. Soc. Hort. Sci. 45:431-439.

Tidemann, A. R., J. O. Klemmedson, and P. R. Ogden. 1971. Response of four perennial southwestern grasses to shade. J. Range Managt. 24:442-447.

Tinckner, M. A. H. 1925. The effect of length of day upon growth and reproduction of some economic plants. Ann. of Bot. 39:721-754.

Toole, E. H., S. B. Hendricks, H. A. Borthwick, and K. Toole. 1956. Physiology and seed germination. Ann. Rev. Plant Physiol. 7:299-324.

Toole, V. K. 1934. Germination requirements of the seed of some introduced and native range grasses. Proc. Assoc. Official Seed Analysts. 30:227-243.

Trelawny, J. G. S. and D. J. Ballantyne. 1963. The effect of gibberellin and temperature on the germination of seed of Bell of Ireland. Can. J. Plant Sci. 43:522-527.

Treshow, M. 1970. Environment and Plant Response. McGraw-Hill, New York. 422 p.

Troughton, A. 1956. Studies on the growth of young grass plants with special reference to the relationship between the root and shoot systems. J. British Grassland Soc. 11:56-65.

Uhivits, R. 1946. Effects of osmotic pressure on water absorption and germination of alfalfa seed. Amer. J. Bot. 33:278-285.

Urban, I. 1964. Symbolae Antillanae Seu Fundamenta Florae Indiae Occidentalis. Reprint A. Asher Co. Amsterdam. 86-87.

van Staden, J. and P. F. Wareing. 1972. The effect of light on endogenous cytokinin levels in seeds of Rumex obtusifolius. Planta 104:126-133.

Watkins, J. M. 1940. The growth habits and chemical composition of bromegrass, Bromus inermis, as affected by different environmental conditions. J. Amer. Soc. Agron. 32:527-538.

Weaver, J. E. 1926. Root Development of Field Crops. McGraw-Hill, New York. 291 p.

Wesson, G. and P. F. Wareing. 1969. The role of light in the germination of naturally occurring populations of buried weed seeds. J. Exp. Bot. 20:402-413.

Whitehead, F. H. 1957. Wind as a factor in plant growth. In Control of the Plant Environment (Hudson, J. P. ed.) Butterworths Scientific Publ., London. 84-95.

Whitney, L. D., E. Y. Hosaka, and J. C. Ripperton. 1939. Grasses of the Hawaiian Ranges. Hawaii Agr. Exp. Sta. Bull. 82:118-120.

Wiese, A. F. and R. G. Davis. 1967. Weed emergence from two soils at various moistures, temperatures, and depths. Weeds 15:118-121.

Williams, M. R., R. F. Barnes, and J. M. Cassady. 1971. Characterization of alkaloids in palatable and unpalatable clones of Phalaris arundinacea L. Crop Science 11:213-217.

Yamada, I. 1954. On the dormancy of weed seeds. I. Effect of thiourea on breaking of dormancy. Hokkaido Nat. Agr. Exp. Res. Bull. 67:58-62.

Yamada, T. and S. Horiuchi. 1961. On the bias of quantitative characters and the change of their distribution in a population, due to interplant competition. Proc. 8th Int. Grassland Congr. Reading, 297-301.

Younis, M. A., F. C. Stickler, and E. L. Scrensen. 1963. Reactions of seven alfalfa varieties under simulated moisture stress in the seedling stage. Agron. J. 55:177-182.