MODELING THE SPROUTING OF *CYPERUS ROTUNDUS* L. TUBERS IN RESPONSE TO SOIL TEMPERATURES UNDER SOIL SOLARIZATION

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DEDICATION

This dissertation is dedicated to the memory of my late wife,

HIDA MOREI MILES

1952 - 1986

without whose support and encouragement this project would never have been initiated, and in whose memory it was completed.

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ABSTRACT

Experiments were conducted to characterize and predict the sprouting of tubers of purple nutsedge (*Cyperus rotundus* L.) in response to temperature. Tubers were collected from the University of Hawaii Waimanalo Experiment Station and allowed to sprout in 9 cm petri dishes on 2 layers of moistened filter paper in incubators.

In experiments to determine methodology it was demonstrated that tubers often initiate growth, but shoots do not continue to elongate. Tubers were therefore counted as sprouted when at least one shoot exceeded 1.0 cm in length. Daily counting of sprouted tubers depressed final cumulative sprouting by 1 to 15 percentage points. Tubers from water-stressed plants sprouted faster and had higher final sprouting than tubers from well watered plants. Experiments using constant and diurnally alternating temperatures showed that sprouting rate and final cumulative sprouting are increased by temperature alternation.

To develop a sprouting model, tubers were exposed to all combinations of constant and alternating temperatures from 20 to 45 C in 5 degree increments. Cumulative sprouting of the tubers over time at each temperature regime was characterized by fitting the Richards function. Response surface regression was used to predict the four parameters of the Richards function for tuber sprouting at any temperature regime. A model was developed utilizing the predicted Richards parameters to predict cumulative tuber sprouting in response to daily minimum and maximum soil temperature.

The model satisfactorily predicted daily and final cumulative tuber sprouting in the field from observed daily minimum and maximum soil temperatures. Predicted final cumulative sprouting for the bare soil treatment was within 8 percent of observed sprouting, and for the solarized treatment within 4 percent.

This study demonstrated the ability of soil solarization to increase final cumulative tuber sprouting and to concentrate tuber sprouting in time. Soil solarization has potential as part of an integrated control program for purple nutsedge in combination with a systemic herbicide such as glyphosate.

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CHAPTER I

INTRODUCTION

Purple nutsedge (*Cyperus rotundus* L.) has been called the world's worst weed (Holm *et al.*, 1977). It is a serious pest in virtually every country and region in the tropics and subtropics. Numerous studies on the biology, effects on crop yields, and control of nutsedge have been done or are underway, yet this weed continues to be a serious problem in all areas where it is found. As Schreiber (1982) has pointed out, modeling is a useful approach to understanding and predicting weed growth. Modeling was the approach taken in this study.

In the past two decades, a new method of weed control, soil solarization, has come into use in some areas. Pioneered in Israel, the technique consists of covering moist soil with clear plastic and allowing the sun to heat the soil. Soil temperatures in excess of 50 C have been reported at a depth of 5 cm (Katan *et al.*, 1976).

Originally developed for control of soilborne plant pathogens, the solarization technique was observed to result in reduced weed populations as well (Grinstein *et al.*, 1979; Katan, 1981; Katan *et al.*, 1976). Further research has shown good control of many annual weeds, but control of herbaceous perennials, including purple nutsedge, has been less promising (Egley, 1983; Horowitz *et al.*, 1983, Jacobsohn *et al.*, 1980). A model for predicting soil temperatures under soil solarization has been developed, based on the characteristics of solar radiation, soil, and plastic (Mahrer, 1979).

This study had two objectives: First, to quantify the sprouting response of purple nutsedge tubers to temperature in the laboratory; and second, to develop a model to predict tuber sprouting in the field from soil temperatures experienced under soil solarization.

At the same time, an attempt was made to identify some causes of the variability in tuber sprouting, and to report on soil temperatures under soil solarization and bare soil conditions in Hawaii.

CHAPTER II

LITERATURE REVIEW

PURPLE NUTSEDGE

As noted in the introduction, purple nutsedge has been called the world's worst weed. As an indication of its importance, Holm *et al.* (1977) noted that they found over 700 entries referring to purple nutsedge from over 90 countries prior to 1977. According to this review, no other weed has drawn so much attention or prompted so many reports. In the 13 years since their report, publications on purple nutsedge have continued to proliferate, making a literature review of the topic a monumental task. Bendixen and Nandihalli (1987) reported that purple nutsedge is a serious or principal weed of several crops on all continents and in Oceania.

Due to its extensive underground system of rhizomes, tubers, and corms, purple nutsedge is prolific and difficult to control. Propagation of purple nutsedge is nearly or entirely by this underground system of rhizomes, tubers, and corms. Nutsedge is considered a poor competitor for light, and fast-growing crops which form a thick canopy early in the growing season can compete well with it. Most vegetable crops, however, do not compete well with nutsedge.

DESCRIPTION OF PURPLE NUTSEDGE

Purple nutsedge (*Cyperus rotundus* L.) is a small herbaceous perennial up to 100 cm tall, but more often less than 50 cm tall (Ambasht, 1964, Wills and Briscoe, 1970). It is a member of the

family Cyperaceae. Purple nutsedge is a C-4 plant, which may contribute to its competitiveness, especially in high temperature, high illumination situations (Bendixen and Nandihalli, 1987; Black *et al.*, 1969; Stoller and Sweet, 1987). The aboveground portion of the plant is a rosette of narrow grasslike leaves with, at maturity, a slender triangular culm bearing a reddish or purplish-brown inflorescence (Holm *et al.*, 1977; Mercado, 1979; Ranade and Burns, 1925; Wills and Briscoe, 1970; Wills, 1987). Flowering may occur within from 2 to 8 weeks after shoot emergence, depending on growing conditions (Hammerton, 1974; Hammerton, 1975b; Hauser, 1962b; Horowitz, 1965; Ranade and Burns, 1925; Wills, 1969). The inflorescence is in the form of an umbel, and in most cases produces few or no viable seeds (Ranade and Burns, 1925; Justice and Whitehead, 1946; Tripathi, 1969c; Andrews, 1946).

Underground is a complex and extensive system of rhizomes, tubers, and corms (also called basal bulbs or tuberous bulbs), with a deep root system (Andrews, 1940a; Ranade and Burns, 1925). Smith and Fick (1937) reported roots as deep as 120 cm, while Andrews (1940a) reported roots as deep as 137 cm, and averaging 116 cm deep. Tuber number usually greatly exceeds shoot number, and the underground portion of the plant normally outweighs the aboveground portion (Ambasht, 1964; Bhardwaj and Verma, 1968; Davis, 1942; Hauser, 1962b; Horowitz, 1965; Rochecouste, 1956; Williams *et al.*, 1977). Ratios of underground to aboveground plant parts have been reported for field and pot studies, for fresh and dry weights, and for tuber and shoot

numbers, and the results are quite consistent. Ambasht (1964), for example, reported a dry weight ratio from the field ranging from 1.3 to 3.3; Rochecouste (1956) reported fresh weight ratios from three locations in the field ranging from 1.6 to 5.0; Davis (1942), reporting on pot studies, found fresh weight ratios from 3.9 to 6.4, with the ratio increasing as soil moisture decreased; and Horowitz (1965) reported a fresh weight ratio of 3 from pots. Hauser (1962b) reported that after 6 weeks or more of growth underground parts always outweighed the aboveground parts. Bhardwaj and Verma (1968) reported tuber numbers 2 to 6 times shoot numbers over a period of more than a year, with the highest ratio occurring at the end of the dry season.

Ranade and Burns (1925) described purple nutsedge as a "geophilous" plant, because very early in its life cycle it begins partitioning a large portion of its energy to underground reproductive organs. Researchers have noted increased partitioning to underground structures, particularly tubers, in response to such stresses as crowding or insufficient moisture and/or nutrients (Davis, 1942; Parker, 1985; Williams *et al.*, 1977). Tuber production is reduced by heavy shade, but is not stopped entirely. Patterson (1982) found some tubers produced even in 85 percent shade; the plants in this study recovered very rapidly when the shade was removed.

The tubers are the principal means of propagation for purple nutsedge (Justice and Whitehead, 1946; Muzik and Cruzado, 1953; Ranade and Burns, 1925; Rochecouste, 1956). Seeds are generally

considered unimportant in propagation of purple nutsedge, as it generally produces very few viable seeds (Andrews, 1946; Justice and Whitehead, 1946; Ranade and Burns, 1925; Smith and Fick, 1937). Tripathi (1969c), however, reported a significant number of viable seeds at Varanasi, India, and recommended that the plants not be allowed to set seed. This difference in seed production may be due to environmental influences or genotypic differences, or both. The resolution of this question awaits further research.

When a bud on a tuber sprouts, it produces a rhizome which may either terminate in another tuber, or produce an aerial shoot. Sprouting of an isolated tuber usually results in the vertical growth of a single rhizome to the soil surface, where it terminates in an aerial shoot (Hauser, 1962a,b); Muzik and Cruzado, 1953; Ranade and Burns, 1925; Sierra, 1973; Smith and Fick, 1937). In some cases, a tuber will produce two or more shoots, but this is the exception. At the base of the shoot is a swelling generally known as a basal bulb, but which may more accurately be termed a corm, although there is some question whether this organ may need some other classification entirely (Holm *et al.*, 1977; Jha and Sen, 1980; Siriwardana, 1986; Wills and Briscoe, 1970). It is often difficult to distinguish between tubers and corms (Hauser, 1962b, Holm *et al.*, 1977), and the best distinguishing feature appears to be the presence or absence of leaves (Siriwardana, 1986). Stoller (1981) has defined the yellow nutsedge basal bulb as consisting of "a region on the rhizome where internode length is diminished and leaves are elongated." This

definition is also applicable to purple nutsedge. The tubers have short internodes, but have only scale leaves. The corm has axillary buds which may produce from one to several rhizomes, each of which is capable of producing more corms and/or tubers, which may produce more rhizomes *ad infinitum*, thus producing an extensive underground system (Hauser, 1962a; Horowitz, 1972b; Wills and Briscoe, 1970). It is common for a single corm to have more than one rhizome arising from it.

Smith and Fick (1937) found that one tuber planted in sterile soil could produce 146 tubers and basal bulbs in 3.5 months in the greenhouse, all connected in an intricate network. Bhardwaj & Verma (1968) similarly reported a single tuber producing 921 shoots and 103 tubers in 4 months. Rao (1968) reported 99 tubers in 90 days. Horowitz (1972b) reported a density of over 1,000 tubers per m^2 where a single tuber had been planted 20 months earlier, and a density of over 3,500 tubers per m^3 in the upper 20 cm of the soil in the same location. Baker (1964) reported an average of 1900 tubers per square meter after 4 months from single tubers planted at 0.46 m spacing, and Hauser (1962a) calculated 5.7 million plants and 6.8 million tubers per hectare in 20 weeks from tubers planted at 0.9 m spacing. Obviously, the reproductive potential is great.

El-Masry and Rehm (1976) pointed out that the corm is the "focal point of vegetative activity and propagation" for the purple nutsedge plant. An isolated tuber normally produces one corm, from which secondary rhizomes arise. The parent tuber may or may not

subsequently produce more rhizomes, but most of the new shoots and tubers arise directly or indirectly from the first corm formed (Ranade and Burns, 1925). Tuber production may be influenced by photoperiod (Bendixen and Nandihalli, 1987; Berger and Day, 1967; Hammerton, 1975b; Stoller and Sweet, 1987; Williams, 1978, 1982; Wills, 1969). Gibberellic acid has also been shown to increase tuber production and flowering (Shiam *et al.*, 1987).

Preventing formation of secondary rhizomes from the corm is one control strategy, since this can prevent increases in the plant population. Kawabata and DeFrank (1990), in ongoing research, have had success in preventing rhizome elongation and new tuber formation using a growth retardant, paclobutrazol.

If a shoot dies or is removed, another bud on the tuber will normally sprout, replacing the lost shoot. Large tubers have been shown to have a greater capacity to produce regrowth (Baker, 1964). The rhizomes are reported to have no axillary buds (Wills and Briscoe, 1970), and to be incapable of giving rise to new growth (Andrews, 1940a). The rhizomes may branch, however, and the author has observed branched rhizomes in the field. Ranade and Burns (1925) also reported this phenomenon. Rhizomes are white and fleshy at first, but soon slough off their outer layers, resulting in a tough black "wiry rhizome" (Ranade and Burns, 1925; Wills and Briscoe, 1970). Appearances notwithstanding, this rhizome stays alive and capable of translocation for at least one growing season (Muzik and Cruzado, 1953; Wills and Briscoe, 1970).

Hammerton (1974) has reported fluctuations in the dry weight of the parent tuber during the growing season, with an overall upward trend. A similar trend was reported by Sierra (1973), indicating that the parent tuber can act as both source and sink depending on conditions and the phenological stage of the plant, and that it probably acts as a net sink over the course of a growing season. In a study on translocation, however, it was found that the parent tuber did not accumulate assimilates, and that it appeared to act as "a coordinating organ through which concentration gradients between the shoot and the meristematic subterranean organs were channeled" (Akobundu *et al.*, 1970). In a study on glyphosate translocation, Zandstra and Nishimoto (1977) also reported that glyphosate appears to move through the parent tuber to newly forming tubers at the rhizome tips. The question of whether the parent tuber can act as a sink, or can accumulate assimilates from the shoot, has major implications for control of nutsedge with systemic herbicides. Since the oldest plants in the above studies were 10 and 6 weeks old, respectively, the question of whether the parent tuber can act as a sink over a growing season in the field is still open, but it is clear that the parent tuber is not likely to act as a major sink unless its buds are active.

Purple nutsedge grows best in a warm humid environment (Rochecouste, 1956), but is able to survive both very dry and very wet situations, and will grow and proliferate in a variety of soil

conditions (El-Masry *et al.*, 1980). Its distribution worldwide is limited by low temperature and/or moisture (Bendixen and Nandihalli, 1987).

Jha and Sen (1980, 1985) found that while purple nutsedge is not a xerophyte, it has several adaptations which enable it to survive extended dry periods. These include a high bound water content, high percent dry matter, low desiccation rate and volume to mass ratio, development of a thick sclerenchymatous layer, and the presence of cortical vascular bundles. Add to these a deep and extensive root system, as mentioned earlier, which can keep tubers alive by tapping moisture deep in the soil when the surface layers have dried out. While purple nutsedge can survive very low soil moisture, its growth is depressed. Davis (1942) found that purple nutsedge growth decreases even at moisture levels well above the wilting point. Both tuber and shoot growth were affected, but the effect was more pronounced on the shoots.

While the intact plant is able to survive dry situations, the tubers are susceptible to desiccation when separated from their root system. Andrews (1940a) showed that tubers separated from their roots die in soil at less than 20 percent moisture, while those attached to their roots survive unless the soil around the roots is less than 8 percent moisture. Baker (1964) found that tubers survived if soil moisture was above 3 percent. Both Andrews and Ronoprawiro found that tubers will be killed by approximately 2 weeks exposure to drying in the sun (Andrews, 1940a, Ronoprawiro, 1971).

Gill *et al.* (1982) reported tubers lost viability within 24 hours when exposed to sun, and hypothesized heat injury plus a threshold moisture loss as the reason for such rapid loss of viability.

Ambasht (1964) found that plants not only survived, but grew well in partially waterlogged soil in pots. This finding is in contrast with most reports, which indicate that purple nutsedge grows poorly if at all in waterlogged situations, but that tubers survive and can grow as soon as conditions improve (Andrews, 1940a; Gill *et al.*, 1982). Ueki (1969) reported that tubers do not sprout in water without oxygen, but that they do survive and are capable of sprouting when returned to aerated conditions. Ueki also reported that tubers will sprout when immersed in aerated water. Palmer and Porter (1959) reported that oxygen stimulates tuber sprouting. These reports may explain the field and pot observations.

Corms usually form within 2 to 8 cm of the soil surface (Holm *et al.*, 1977), although they can form deeper in the soil. Hauser (1962b) has reported corms forming as deep as 20 cm. The stimulus for differentiation of a shoot into a corm has not been positively identified, but light, red light, and growth regulators have been reported to induce corm formation (Chetram and Bendixen, 1974a,b; Loustalot *et al.*, 1954; Standifer *et al.*, 1966). Hauser's finding that corms may form as deep as 20 cm indicates that light is not essential to differentiation, and the author has shown that corms can differentiate in total darkness (unpublished data). Aleixo and Valio (1976) demonstrated that corms can form in darkness at high

temperature (40 C). Stoller (1981) reported that light or alternating temperatures with a difference greater than 10 C stimulated corm differentiation in yellow nutsedge, and this may be true of purple nutsedge as well. The author has observed a similar response to alternating temperatures in purple nutsedge (unpublished data).

IMPORTANCE OF PURPLE NUTSEDGE

Despite its small size, purple nutsedge is a serious competitor with crops, competing mainly for water and nutrients. It is a serious or principal weed in rice, sugarcane, cotton, maize, and vegetables on all continents and in Oceania (Bendixen and Nandihalli, 1987; Holm *et al.*, 1977). As a C-4 plant, it is most competitive in high light intensity, high temperature environments (Tripathi, 1969b; Wills, 1975). It is not shade tolerant (Komai and Ueki, 1982; Magalhaes, 1967; Moosavi-Nia and Dore, 1979b; Patterson, 1982; Pitelli *et al.*, 1983; Shetty *et al.*, 1982; Sierra, 1973), and may be shaded out by tall crops or crops which quickly form a dense canopy. It can cause serious problems in smaller crops such as most vegetables, however, and in the early growth stages of larger crops, especially if they are slow to form a canopy. Although nutsedge may seem to disappear in the shade of some crops, the tubers remain dormant in the soil, and reinfestation occurs rapidly as soon as the shade is removed (Holm *et al.*, 1977). Nutsedge has a deep and extensive root system, and competes well for moisture and nutrients

(Andrews, 1940a; Ranade and Burns, 1925; Rochecouste, 1956; Smith and Fick, 1937). In a study of weed interference with cotton, it was found that nutsedge was more competitive than *Digitaria sanguinalis*, *Abutilon theophrasti*, and *Sida spinosa* (Elmore *et al.*, 1983).

Several researchers have noted apparent allelopathic effects of either living or decaying nutsedge tubers, but it is not clear to what extent this contributes to the plant's competitiveness (Bradow and Connick, 1988; Friedman and Horowitz, 1971; Gastal and Castela, 1982; Komai *et al.*, 1977; Komai and Ueki, 1977, 1980; Lucena and Doll, 1976; Meissner *et al.*, 1982; Mohamed-Saleem and Fawusi, 1983). Conflicting reports may be a result of different effects of different nutsedge chemotypes (Komai *et al.*, 1991).

Horowitz (1965) reported a negative correlation between nutsedge shoot population and growth of young lemon trees. A population of 700 shoots per square meter was reported to decrease the yield of maize by 43 percent when the field was not cultivated until 30 days after planting (Chase and Appleby, 1979a). Kondap *et al.* (1982) found yield losses from 6 to almost 60 percent in different crops from "heavy" infestations of purple nutsedge. Maize and sorghum were the least affected of the crops studied, and they concluded that these crops have potential for production in nutsedge infested fields. Other reports of yield losses or other interference with crop growth include inhibition of germination and seedling root growth of cotton, carrot, and tomato (Bradow and Connick, 1988), reduced emergence of soybean (Gastal and Castela, 1982), decreased

height and weight of sorghum and soybean (Lucena and Doll, 1976), impaired growth and water economy of barley, grain sorghum, cucumber, garden radish, onion, squash, and tomato (Meissner *et al.*, 1982), 41 percent reduction in upland rice yield (Okafor and DeDatta, 1974), reduction in squash yield from 1.88 tons/ha to 112.7 kg/ha (Ponchio *et al.*, 1984), yield losses in lettuce (Siriwardana, 1986), 83 to 85 percent yield loss in sugarcane (Turner, 1985), and losses of 35 to 89 percent in garlic, okra, carrots, green bean, cucumber, cabbage, and tomato (William and Warren, 1975).

Crop management is made more complex by the presence of purple nutsedge. Okafor and DeDatta (1976) found that nitrogen fertilization actually favored purple nutsedge in upland rice, making yield losses worse. They concluded that nutsedge control is more important in high fertility than in low fertility situations in upland rice. Timing of purple nutsedge control is also important. William and Warren (1975) have reported critical competitive periods for several crops, or the times when the crop must be kept weed free for good production. These periods correspond approximately to the first third of the life cycle of most crops.

TUBER POPULATION AND DISTRIBUTION

Populations of purple nutsedge in the field have been reported by several researchers, and range from 150 to over 2,000 shoots and 300 to over 10,000 tubers per square meter (Bhardwaj and Verma, 1968; Chase and Appleby, 1979a; Hammerton, 1974; Muzik and Cruzado, 1953;

Ranade and Burns, 1925; Rochecouste, 1956). Populations are generally higher in cultivated than in uncultivated situations (Rao, 1968). Tuber populations are generally far in excess of shoot populations, and shoot populations may not be a good indicator of the population underground (Smith and Fick, 1937). Rochecouste (1956), for example, reported fresh weight of 4,900 kg of shoots and 24,700 kg of fresh tubers per hectare.

It is possible for tubers to be found fairly deep in the soil, as deep as 45 cm (Andrews, 1940a,b), but most tubers are found in top 30 cm, and in most cases 80 to 90 percent or more are found in the top 15 cm (Ambasht, 1964; Andrews, 1940a,b; Bhardwaj and Verma, 1968; Davis and Hawkins, 1943; Rao, 1968; Rochecouste, 1956; Siriwardana and Nishimoto, 1987; Smith and Fick, 1937; Tripathi, 1969a; Ueki, 1969). Rao (1968) found tubers deeper in an uncultivated than in a cultivated situation. Andrews (1940a,b) found tubers deeper in deep, friable, well-drained river silt than in heavy clay soil.

APICAL DOMINANCE

Apical dominance within tubers and within chains of tubers in the soil plays an important role in the survival of purple nutsedge in the field. Cultivation and contact herbicides fail to control purple nutsedge because, while they may kill individual shoots, the parent tuber is unaffected, and generally responds by producing a new shoot. This can continue until all the buds on a tuber have sprouted.

Apical dominance occurs both within a tuber and in a chain of tubers (Muzik and Cruzado, 1953; Palmer and Porter, 1959; Ranade and Burns, 1925). In a tuber, the apical bud sprouts first, and in most cases inhibits sprouting and/or elongation of the other buds on the tuber. In a chain of tubers, the apical tuber exerts a similar effect on the subapical tubers. The effect is stronger at low levels of atmospheric oxygen, and high oxygen levels tend to decrease apical dominance (Palmer and Porter, 1959). Apical dominance in a tuber can be overcome by exposure to light (Loustalot *et al.*, 1954). In a chain of tubers, apical dominance may be overcome by inversion, or by breaking or killing the connecting rhizomes (Muzik and Cruzado, 1953). Frequently, subapical tubers in a chain do not sprout at all unless the chain is broken (Muzik and Cruzado, 1953). Breaking of chains by cultivation often leads to an apparent increase in the nutsedge population due to the sprouting of large numbers of formerly dormant tubers (Ranade and Burns, 1925; Smith and Fick, 1937; Teo *et al.*, 1973). Muzik and Cruzado (1953) likened the tuber chain to a long slender stem, with the axillary buds concentrated in the tubers. This analogy helps in understanding the phenomenon of apical dominance.

Evidence of apical dominance within the tuber is the increase in sprouting, and in number of shoots on a per tuber basis, when tubers are cut into pieces (Baker, 1964; Sierra, 1973; Smith and Fick, 1937). Interestingly, in tubers cut transversely, sprouting of the apical end increases over that of uncut tubers, indicating some

inhibition of apical buds by basal buds (Sierra, 1973). Tumbleson and Kommedahl (1962) have reported the same phenomenon from yellow nutsedge (*Cyperus esculentus*). A similar increase does not occur in tubers cut longitudinally (Sierra, 1973), demonstrating that the sprouting increase is not simply a response to physical injury to the tubers.

The tendency of subapical tubers to remain dormant, in addition to the ability of tubers to remain dormant during adverse environmental conditions results in a reservoir of propagative material in the soil which can respond rapidly to favorable conditions (Horowitz, 1965). This presents a serious control problem; to quote Berger and Day (1967): "Dormancy poses particular problems in weed control, since dormant organs are hard to eradicate by any agricultural means." Karssen (1982) has noted for seeds that germination *in situ* is the main loss of seeds from a buried population. As long as viable propagules are present in the soil, they are a potential source of reinfestation. Breaking of tuber dormancy should be a major tactic in any purple nutsedge control strategy.

DORMANCY AND SPROUTING OF TUBERS

While apical dominance plays an important role in maintaining a reservoir of unsprouted tubers in the soil, it is not the only factor contributing to this reservoir. Even when separated from the tuber chain, viable tubers may fail to sprout, often for extended periods. Studies by Smith and Mayton (1938, 1942) indicate that tubers can

survive in the soil for as long as two years. Tuber sprouting in the field has been reported more than once as approximately 70 percent (Hammerton, 1974; Siriwardana and Nishimoto, 1987; Standifer and Chin, 1969). Andrews (1940a) reported that 50 percent or less of the tubers in the field had an aerial connection. Many laboratory studies have also reported considerably less than 100 percent sprouting of tubers, though these often fail to distinguish between dormant and dead tubers (Aleixo and Valio, 1976; Cools and Locascio, 1977a; Hammerton, 1975a; Horowitz, 1972b; Loustalot *et al.*, 1954; Palmer and Porter, 1959; Shamsi *et al.*, 1978; Sierra, 1973; Teo and Nishimoto, 1973; Tripathi, 1967; Ueki, 1969; Wills, 1969).

Despite numerous studies on the dormancy of single tubers, the factors controlling tuber bud dormancy are still not well understood. Exposure to light has been reported to decrease sprouting at low temperatures (Aleixo and Valio, 1976), but it has also been reported to increase percent tuber sprouting, and to increase the number of sprouted buds per tuber (Loustalot *et al.*, 1954). The temperature was unfortunately not reported for this experiment, however. Leaching or washing in cold water has been reported to increase sprouting in yellow nutsedge, but not in purple nutsedge. In fact, leaching has been shown to decrease sprouting of immature purple nutsedge tubers and to have no effect on mature tubers (Aleixo and Valio, 1976). Low temperature storage has also resulted in increased sprouting (Shamsi *et al.*, 1978). Lack of oxygen or air has been

shown to inhibit tuber sprouting (Palmer and Porter, 1959; Ueki, 1969), and oxygen/carbon dioxide balance may also play a role (Palmer and Porter, 1959).

Tuber dormancy is generally believed to be the effect of some endogenous substance or substances, but whether it is due to an excess, a deficiency, or an imbalance is not clear. Jangaard *et al.* (1971) extracted several substances from plants and tubers, and hypothesized that salicylic acid was responsible for inhibiting bud sprouting. Berger and Day (1967) extracted salicylic acid from purple nutsedge leaves, but not from tubers, and again hypothesized that this was the cause of inhibition. This could explain apical dominance, but cannot explain dormancy of isolated tubers, since salicylic acid was not found in tubers. Teo *et al.* (1973) overcame bud dormancy by treatment with BA and kinetin, and hypothesized an imbalance of endogenous growth regulators due to a deficiency of cytokinin. They suggested that a balance of promoters and inhibitors regulated tuber dormancy (Teo *et al.*, 1974). Rehm and El-Masry (1976) and El-Masry and Rehm (1977), showed increased bud sprouting in response to several non-cytokinin compounds. Since all of these were auxin antagonists, they suggested that dormancy is due to an imbalance brought on through induction of an inhibitor by auxin. By antagonizing auxin, they suggest, these substances decrease inhibitor production and allow buds to sprout. These two hypotheses may not be as contradictory as they at first appear, since both hypothesize a promoter/inhibitor imbalance as the cause of tuber dormancy.

Other researchers have isolated phenolic compounds which may play a role in tuber dormancy control (Komai and Ueki, 1975, 1977, 1980; Komai *et al.*, 1983). Aleixo and Valio (1976) suggested that gibberellins induce bud growth, and are primarily responsible for breaking of dormancy, but this does not agree with the findings of other researchers, who found no response to added GA (Rehm and El-Masry, 1976; Teo *et al.*, 1973). Resolution of these differences awaits further research.

Another interesting question regarding tuber dormancy was raised by Parker (1985). This is the question of how the apical bud of a tuber in a growing chain remains dormant while the lateral buds sprout and produce rhizomes to extend the chain.

Tubers can remain dormant for extended periods, apparently at least two years in some instances (Smith and Mayton, 1938, 1942; Standifer and Chin, 1969). This ability to remain dormant allows the tubers to survive adverse conditions and many control methods (Standifer and Chin, 1969). Tuber dormancy may be related to soil conditions, as several researchers have noted not only a delay, but also a reduction in shoot emergence with deeper planting of tubers (Horowitz, 1965; Loustalot *et al.*, 1954; Ranade and Burns, 1925).

In most studies of tuber dormancy and sprouting, researchers have not defined the term "germination" of tubers, nor have they given the criteria upon which they base a classification of "germinated." Shamsi *et al.* (1978) defined any tuber which had initiated shoot and/or root growth as sprouted, but other studies have been silent on

this subject. It should be noted that tuber "germination" is actually sprouting of buds, and is physiologically more closely related to bud sprouting of such organs as potato tubers and other underground stems than it is to seed germination. On the other hand, the course of tuber sprouting over time follows a similar curve to seed germination, and can reasonably be represented mathematically in the same way.

Temperature Effects on Tuber Sprouting

Soil temperature is perhaps the major factor affecting tuber sprouting, assuming moisture is adequate. There is some disagreement on the minimum temperature for sprouting, but this may be due to differences in experimental conditions, or in the time of year when the experiments were conducted. It is also possible, however, that the differences are due to genotypic differences in the clones tested. It has been shown that differences in phenolic content of different clones exist (Komai *et al.*, 1978; Komai and Ueki, 1981; Komai *et al.*, 1983). Claver (1977) has shown other phenotypic differences between clones, as have Chavez and Moody (1986), and Kiatsoonthorn *et al.* (1985). It seems likely that ecotypical differences in temperature response could also exist, considering the wide range of temperature conditions in which purple nutsedge survives. Nutsedge tubers are reported not to sprout at temperatures below 10 to 15 C (Orcutt and Holt, 1990; Shamsi *et al.*, 1978; Tripathi, 1967; Ueki, 1969). There is general

agreement that tubers will not sprout or survive for long above 40 to 44 C (Orcutt and Holt, 1990; Shamsi *et al.*, 1978; Tripathi, 1967; Ueki, 1969). The highest total tuber sprouting at constant temperature has been reported at approximately 30 to 35 C by Ueki. This is in general agreement with other reports (Horowitz, 1972b; Shamsi *et al.*, 1978; Tripathi, 1967; Wills, 1969). Tripathi (1967) has reported a greatly increased rate of sprouting at alternating 23/31 C.

Baker (1964) reported that tubers failed to sprout after freezing in the laboratory, but did not give the temperature, or the time of exposure to freezing temperature. Ueki (1969) reported that tubers died in 7 to 10 days at 0 C, and in 2 hours at -5 C. Shamsi *et al.* (1978), on the other hand, reported no reduction in viability of tubers stored wet or dry for two months at 0 C, and reported that rate and total sprouting actually increased for the dry chilled tubers over freshly collected tubers.

Several studies have been done on the sprouting response to temperature, and there is general agreement that the optimum temperature range for sprouting is from 25 or 30 to 35 C (Aleixo and Valio, 1976; Ueki, 1969; Shamsi *et al.*, 1978; Wills, 1969), but Tripathi (1967) reported the highest total sprouting at 40 C, and Horowitz (1972b) reported 95 to 100 percent sprouting over a range from 19 to 39 C. Horowitz also reported that sprouting was highly variable, with a range from 76 to 100 percent at the same temperature for different lots of tubers. While the optimum for

sprouting is probably within the range of 25 to 35 C, a portion of the tubers can sprout over a much wider range. Sprouting has been reported from a minimum of 13 C (Tripathi, 1967) to a maximum of 45 C (Shamsi *et al.*, 1978). Using a modeling approach, Orcutt and Holt (1990) have recently calculated the temperature range for bud sprouting of purple nutsedge tubers to be from 10 to 44 C.

A difficulty with all of the above studies is that they make no reference to tuber viability, and it is therefore not possible to determine whether unsprouted tubers are dormant or dead. In this study, removing soft or otherwise obviously dead tubers and retaining only firm and apparently viable tubers, I have obtained from 85 to 100 percent viable tubers.

A more serious difficulty with most studies on temperature response, however, is that almost all have worked only with constant temperatures. While these studies provide valuable information, they do not give the true picture, since constant temperatures are not encountered in the field. On the contrary, field soils experience a diurnal temperature alternation, with the maximum and minimum depending on plant cover, atmospheric conditions, and soil properties.

It has long been known that alternating temperatures increase the germination of seeds of many plants (Harrington, 1923; Morinaga, 1926). In the single study comparing alternating and constant temperatures for purple nutsedge tubers, Tripathi (1967) found that alternating 23 to 31 C increased the rate of sprouting over all the

constant temperatures studied, and increased total sprouting as well, over all constant temperatures except 40 C. There are a few reports of similar responses for vegetative buds (Blake, 1972; Erez *et al.*, 1979; Lyr et al, 1970; Powell *et al.*, 1988; Stimart and Ascher, 1981). These are not all reports of bud sprouting - some refer to bud differentiation - but they are reports of bud responses to alternating temperatures which are different from their responses to constant temperatures. There are also reports showing no response to alternating temperatures, such as that of Sale in 1979 for sprouting of potato tubers, and Nelson and Lavender (1979) for western hemlock bud growth initiation. Seeds of 17 species of vegetables were shown to have no response to alternating temperatures (Wagenvoort and Bierhuizen, 1977), while weed seeds often do show such a response. Benech Arnold *et al.* (1988) have recently demonstrated very clearly that the response to alternating temperatures can be an effective mechanism for detection of a plant canopy. It may be that this survival mechanism has been selected against (not necessarily intentionally) in the development of many cultivated plants. As Holm *et al.* (1977) have noted, purple nutsedge may seem to disappear in the shade of some crops, but the tubers remain viable in the soil, and reinfestation occurs rapidly as soon as the shade is removed. It may be that response to increased amplitude of alternating temperature when the crop canopy is removed is the key to this phenomenon.

Considering the importance of alternating temperatures, it is somewhat surprising that there are only two reports in the very extensive purple nutsedge literature on the effects of alternating temperatures on bud sprouting. This is perhaps due to the difficulty of obtaining such temperatures in the laboratory. Also, until recently, it has not been possible to manipulate temperatures in the field. With the advent of soil solarization, however, this is now possible. Whatever the reason, I have only found two reports on the effect of alternating temperatures on sprouting, and only one of these compared alternating and constant temperatures.

Teo *et al.* (1973) reported "markedly greater" sprouting at alternating 25 to 33 C than at 17 to 24 C. Unfortunately, they did not compare these alternating temperatures with comparable constant temperatures. It is interesting to note that there was no response to BA at the lower temperature regime, while there was a striking response at the higher temperatures.

Only Tripathi (1967) has compared alternating with constant temperatures, and only at a limited number of combinations. This study used a 7/17 hour alternation with temperatures 23/31, 20/40 and 40/20 C, respectively, and constant 13, 20, 30, 40, and 50 C. The highest rate of sprouting took place at alternating 23/31 C, which also had higher total sprouting than all constant temperatures except constant 40 C. The total at constant 40 C was 83.3 percent, however, and was probably not significantly different than the total of 81.6 percent at 23/31 C. 17 hours at 20 C with 7

hours at 40 C also gave a high rate of sprouting, but a lower total, while the opposite combination gave both a low rate and a low total. Due to the low number of temperature combinations, it is not possible to make any generalizations about these results, beyond stating that increasing constant temperatures resulted in higher total sprouting, and that at least one combination of alternating temperatures can greatly increase the rate of sprouting. Obviously, there is a major need for research to clarify the response of purple nutsedge tubers to a wide range of alternating temperatures.

CONTROL OF PURPLE NUTSEDGE

In 1973, Sierra reported that there was no satisfactory method of control of purple nutsedge. It is true that no single method has been found which will eradicate this weed, but a combination of methods can usually be employed which will enable a farmer to produce a crop. Ranade and Burns (1925) recommended attempting to eradicate purple nutsedge, to be followed by measures to prevent reinfestation, as being more economical than efforts to control the weed. Eradication would be desirable since the weed can so rapidly reinfest a field, but there appears to be little hope of eradication, except in small isolated infestations.

Rehm and El-Masry (1977) recommend that control of nutsedge should focus on two points: first, inducing all dormant buds on tubers to sprout; and second, preventing formation of secondary rhizomes from

the corms. Doll and Piedrahita (1982) similarly recommend that control should concentrate on inducing all tubers to sprout, to be followed by treatment with a systemic postemergence herbicide to kill the parent tubers. Teo and others (Teo *et al.*, 1971, 1973, 1974; Teo and Nishimoto, 1973) took the first approach in their work using BA to induce bud sprouting. Kawabata and DeFrank (1990) are currently investigating the second approach. They have successfully prevented formation of secondary rhizomes and new corms and tubers with the growth retardant paclobutrazol. In further work (Kawabata and DeFrank, 1991) they have demonstrated a synergistic effect with glyphosate on control of parent tubers.

Mechanical and Cultural Control

Due to the extensive underground portion of the nutsedge plant, and to the large reservoir of vigorous underground propagules, control measures aimed at the aerial portion of the plant are usually unsuccessful. Standifer and Chin (1969) noted that a significant portion of the tubers remain dormant for at least a full crop season and concluded that no control program can be effective in a single crop season. Control measures must therefore be aimed at the store of tubers in the soil. Cultural methods have met with only limited success, the most effective being dry season plowing to bring tubers to the soil surface. The tubers are susceptible to desiccation when separated from their root system, and repeated plowing in areas with a prolonged hot dry season can

greatly reduce nutsedge populations. This control method has also been shown to be effective in the southern United States, where no pronounced dry season exists (Smith and Fick, 1937; Smith and Mayton, 1938). However, repeated cultivation resulted in an increase in tuber populations in a humid tropical environment in Puerto Rico (Loustalot *et al.*, 1954). In Sudan, a technique known as "blading", severing the shoot system from its roots at a depth of 24 to 30 cm during the dry season, has been used to control purple nutsedge for years (Andrews, 1940b; Pothecary and Thomas, 1968). Sinha and Thakur (1967) report "good" control of purple nutsedge by cultivation every 1, 2, or 3 weeks for two years during the rainy season in India.

Reductions in tuber population and size have been reported as a result of repeatedly cutting the tops of the plants to starve the tubers (Horowitz, 1972a; Komai and Ueki, 1982; Ranade and Burns, 1925; Sierra, 1973). Frequent clipping decreases or prevents tuber formation. This technique has not been particularly successful in the field, however, and it is very time consuming and labor intensive. In Arizona, eradication of purple nutsedge by hoeing every two weeks took two growing seasons (Davis and Hawkins, 1943).

Mulching has not been an effective control for purple nutsedge, as the plant grows right through most mulches. The sharp tips of the rhizomes readily puncture polyethylene films commonly used as mulches, and only very thick (at least 0.20 mm) films can resist penetration (Henson and Little, 1969; Swarbrick and Dominick,

1975). Ranade and Burns (1925) found several other mulching materials ineffective; even if they were able to suppress nutsedge growth, the tubers survived in the soil for over 2 years and quickly reinfested the field when the mulch was removed. They did report one success; a mulch of grass 5 feet thick left on for one year eradicated purple nutsedge from a field.

Biological Control

Purple nutsedge has been included in a recently published list of weeds where the prospects for control by classical or augmentative approaches by pathogens appear to be good (Evans, 1987). Fungal diseases have been reported on purple nutsedge (Ito *et al.*, 1988), and attempts to infect it with a rust effective on yellow nutsedge have been reported (Callaway *et al.*, 1985, Phatak *et al.*, 1983). To date, however no effective control by pathogens has been reported.

Biological control with insects has been somewhat more successful, but requires augmentation by insect releases (Frick, 1976; Frick and Chandler, 1978; Frick *et al.*, 1978). Phatak *et al.* (1987) recently published a list of over 100 insects which are known to feed on purple or yellow nutsedge or both. "Classical" biological control of purple nutsedge by insects has not been reported.

Higher animals have also been utilized in purple nutsedge control. Pigs, chickens, and geese have been demonstrated to be capable of clearing limited areas of nutsedge infestation

(Hammerton, 1968; Mayton *et al.*, 1945). These may not be feasible control techniques for large scale commercial farms, but they should be of great interest to small scale subsistence farmers and part-time market gardeners.

Chemical Control

A number of herbicides have been tested for nutsedge control, mostly with limited success (Hammerton, 1975a; Parker *et al.*, 1969). Its tolerance to many herbicides has led to shifts in population in many situations (Romanowski and Nakagawa, 1967), and vegetable growers and researchers in tropical regions are reportedly reluctant to use herbicides because of the potential for increased nutsedge problems (William, 1976). Contact herbicides, such as paraquat, are ineffective since they only kill the aboveground portion of the plant, and do not affect the tubers. (Teo *et al.*, 1973). EPTC and other thiocarbamates can be applied preemergence, and they delay the emergence of the nutsedge plants for a few weeks, allowing a crop to become established, but they apparently do not kill the tubers (Antognini *et al.*, 1959; Rincon and Warren, 1978). The most promising herbicides are those which are translocated. 2,4-D has given partial control of purple nutsedge, particularly following cultivation, but repeated applications are usually necessary (Doll and Piedrahita, 1975; Hammerton, 1974; Zandstra *et al.*, 1974). Rochecouste found the dimethylamine salt of 2,4-D most effective, progressively reducing

shoot density when applied at 3 month intervals. Glyphosate has shown greater success, and varying degrees of control have been reported (Abad and San Juan, 1981; Beltrao *et al.*, 1983; Chase and Appleby, 1979a; Chivinge, 1985; Deuber and Forster, 1977; Doll and Piedrahita, 1975; Magambo and Terry, 1973; Zandstra and Nishimoto, 1975; Zandstra *et al.*, 1974). Glyphosate is perhaps the most effective chemical tool available today for purple nutsedge control.

Glyphosate

Glyphosate is a broad spectrum systemic herbicide which acts as a competitive inhibitor of 5-enolpyruvylshikimic acid, an enzyme of the shikimic acid pathway (Cole, 1985; Jaworski, 1973; Steinrucken and Amrhein, 1980). It is readily translocated in plants through both the symplast and apoplast (Caseley and Coupland, 1985; Baird *et al.*, 1971), and accumulates in areas of highest metabolic activity (Sprankle *et al.*, 1975c). In milkweed (*Asclepias syriaca*) and quackgrass (*Agropyron repens*), glyphosate is more effective on distal than on proximal buds (Claus and Behrens, 1976; Devine *et al.*, 1983; Waldecker and Wyse, 1985). This is in agreement with findings on translocation and control in purple nutsedge (Siriwardana, 1986; Zandstra and Nishimoto, 1977). Glyphosate has no herbicidal activity when applied to mineral soil at normal use rates, being quickly adsorbed by soil minerals, and subsequently metabolized by soil microorganisms

(Baird *et al.*, 1971; Sprankle *et al.*, 1975a,b). Glyphosate is metabolized by some plants, but apparently not by purple nutsedge (Coupland, 1985; Zandstra and Nishimoto, 1977). Activity of glyphosate on plants has been increased by high relative humidity and high soil moisture; even moderate water stress significantly decreases its efficacy (Caseley and Coupland, 1985; Chase and Appleby, 1979b; Jordan, 1977; Klevorn and Wyse, 1984; Moosavi-Nia and Dore, 1979a; Waldecker and Wyse, 1985). Shade grown plants have been demonstrated to be more susceptible to glyphosate (Caseley and Coupland, 1985; Moosavi-Nia and Dore, 1979b). Glyphosate has relatively low toxicity to animals, which combined with its low soil mobility and rapid degradation, makes it an attractive chemical for environmental reasons as well (Atkinson, 1985; Baird *et al.*, 1971; Scherp, 1975).

There is general agreement that more than one application of glyphosate is needed for good control of purple nutsedge (Abad and San Juan, 1981; Chivinge, 1985; Cools and Locascio, 1977b; Deat, 1975; Gomez and Cruz, 1975; Martinez and Pulver, 1975; Standifer, 1980; Swietlick, 1989; Zandstra *et al.*, 1974), although good control has been reported with a single application (Suzuki *et al.*, 1988; Terry, 1985; Zaenudin, 1988; Zandstra and Nishimoto, 1975). This apparent contradiction is due at least in part to differences in definitions of "good" control, and in the objectives of the researchers. Most researchers report reductions in shoot populations from 70 to 90 percent or more,

for periods of from 30 days to several months (Deuber and Forster, 1977; Doll and Piedrahita, 1975; Gossett *et al.*, 1975; Magambo and Terry, 1973). Comparable, or somewhat lower, reductions in viability of recovered tubers have also been reported (Chase and Appleby, 1979a; Chivinge, 1985; Hammerton, 1975a; Toth and Smith, 1979; Zandstra and Nishimoto, 1975). Complete eradication has never been reported, however, and reinfestation is the reason for the recommended repeat applications. There is always a fraction of tubers which survive or escape treatment and are available to reinfest the treated area. Tillage soon after treatment has been reported to improve control (Campeglia, 1983; Chase and Appleby, 1979a), but control has also been reported to last longer if the soil is not disturbed (Gomez and Cruz, 1975; Gossett *et al.*, 1975). The loss of control due to tillage several months after treatment is easily explained by loss of dormancy of tubers which escaped or survived the glyphosate treatment, since tillage disturbs tubers and exposes them to light, higher atmospheric oxygen, and higher temperatures, all of which are known to stimulate sprouting. It may be possible to explain the enhancement of control by tillage following soon after treatment of plants with glyphosate, and this will be addressed later.

Several factors can contribute to or decrease the effectiveness of glyphosate on purple nutsedge. Among the variables to be considered are plant variables such as age (both chronological

and physiological), leaf area, shoot to tuber ratio, leaf area per tuber, number of dormant tubers, and number of parent tubers in a chain. Environmental variables include temperature of air and soil, relative humidity, photoperiod, light intensity, and soil moisture.

Perhaps as a result of the variability of these factors, there is a range of recommendations for good control of purple nutsedge with glyphosate. Recommendations are consistent regarding relative humidity and moisture stress; the former should be high and the latter, low (Chase and Appleby, 1979b; Moosavi-Nia and Dore, 1979a). Regarding plant age, however, the picture is more confusing. Among the recommended best times for spraying are pre-flowering (Beltrao *et al.*, 1983), early flowering or flowering (Campeglia, 1983; Gossett *et al.*, 1975), late flowering (Siriwardana, 1986; Toth and Smith, 1979), 3 weeks old (Suwunnamek and Parker, 1975), and 12 weeks old (Zandstra and Nishimoto, 1975). Two authors have recommended tillage 3 or 4 days after spraying, while at least two others have noted loss of control due to tillage several weeks or months after spraying. An increase in the efficacy of glyphosate control of purple nutsedge has been observed with addition of the monovalent cations NH_4^+, K^+, and Na^+ (Wills and McWhorter, 1985). The same effect is probably responsible for the improved control from added ammonium sulfate (Suwunnamek and Parker, 1975), and perhaps with urea (Purea, 1985). This enhancement may only be noticeable

on younger plants; Suwunnamek and Parker found no effect of ammonium sulfate with plants more than 6 weeks old, and Zaenudin (1988) reported no effect when the mixture was applied to plants approximately 2 months old.

Glyphosate has been shown to move from treated purple nutsedge leaves into tubers (Baird *et al.*, 1971; Zandstra and Nishimoto, 1977). As noted previously, however, repeated applications are usually required for good control. This is probably due mainly to the presence of dormant tubers in the soil, which sprout subsequent to glyphosate treatment. Some parent tubers apparently survive glyphosate treatment as well, however. There is some question as to why this is so, since in several pot studies glyphosate was translocated to and killed all or almost all of the tubers of treated plants (Doll and Piedrahita, 1982; Hammerton, 1975a; Kramarovsky and Salvador, 1976; Zandstra and Nishimoto, 1977). Siriwardana (1986) also had good control of parent tubers in pots, but found less control in the field. He demonstrated that corms and parent tubers are not as susceptible to glyphosate as newly forming tubers under field conditions.

In pots, glyphosate applied at the correct rate and time can give nearly 100 percent kill of tubers with an aerial connection, and systems arising from those tubers. It remains to be determined what factors are responsible for the less complete control in the field reported by Siriwardana (1986). He suggested as possible reasons that the plants in the field had

lower shoot to tuber ratios, less leaf area per plant, and more parent tubers per plant. He also found better control in the field during summer and fall than in spring, and it appears that temperature was the major difference. In summer and fall, at higher temperatures, the plants probably grew faster, and thus had more total leaf area. Additionally, he suggested that a higher rate of assimilate transport at higher temperatures would result in faster translocation of higher amounts of glyphosate.

A third possible reason for better control in summer and fall than in spring suggested by Siriwardana (1986) was more rapid kill of primary sinks (newly developing shoots and tubers), followed by activation of secondary sinks (in corms and parent tubers) which would then accumulate, and be killed by, glyphosate. All of these hypotheses are reasonable, and very likely all three were operating to a greater or lesser degree. The hypotheses which explain better control by the effect of higher temperatures would also help to explain the greater efficacy of glyphosate on purple nutsedge grown in pots. Soil in pots has much less thermal mass than field soil and will likely experience higher temperatures and wider temperature fluctuations.

Another possibility which should be considered, however, is that the fall and summer plants may have been physiologically more advanced than the spring plants. The stage of growth of the nutsedge plant probably has an important effect on control by

glyphosate, although there is some disagreement on what the best stage of growth is. Workers have reported greatest effectiveness of glyphosate at pre-flowering, early flowering, and late flowering, as noted earlier. This needs to be investigated further.

Hammerton (1974) and Sierra (1973) have shown that while the parent tuber initially loses weight as it sprouts and as the new sprout grows, it eventually begins to gain weight again. In other words, it begins by acting as a source for the newly developing shoot, but at some point in its life cycle it becomes a sink for photosynthate produced by the shoot. Presumably, a parent tuber at this phenological stage would accumulate glyphosate from a treated shoot. It seems likely that plants would reach this stage more rapidly at higher temperatures, and this may account as well for better control during summer than spring of parent tubers from plants of the same chronological age (Siriwardana, 1986).

A parent tuber acting as a sink may not necessarily have active buds. In this situation, photosynthate (and glyphosate) could be expected to accumulate in storage tissue, possibly without affecting the (inactive) buds. This glyphosate might not have an immediate effect, but it could explain the distorted growth of new shoots following treatment (Siriwardana, 1986; Cole, 1985). While glyphosate is not metabolized by purple nutsedge to any significant extent (Zandstra and Nishimoto, 1977), it cannot be

expected to remain in the tuber indefinitely. Dissipation of glyphosate could explain the value of thorough tillage a few days following application of glyphosate (Chase and Appleby, 1979a). Tillage stimulates sprouting of tubers (Smith and Fick, 1937; Muzik and Cruzado, 1953). Sprouting will be followed by uptake of carbohydrate from the parent tuber by the developing shoot. If the tuber contains stored glyphosate, it may be taken up as well, and if the level is high enough, may result in death of the sprouting buds. If tillage is delayed too long, the stored glyphosate can dissipate, thus reducing control, but possibly causing distorted growth, as reported by Siriwardana (1986).

Apparently only Siriwardana has identified treated tubers with an aerial connection in the field. Other workers who have recovered tubers from treated fields did not separate parent tubers from those with no aerial connection. Therefore it is not possible to determine whether viable tubers survived the glyphosate treatment, or if they escaped it altogether due to lack of an aerial connection. Thus, only Siriwardana's results can be accepted as truly representative of actual parent tuber response to glyphosate in the field.

Perhaps the most important factor in purple nutsedge control is the presence of dormant tubers in the soil. Siriwardana and Nishimoto (1987) found approximately 30 percent of the natural tuber population in the soil had no aerial connection. From 1,000 tubers planted 2.5 cm deep in soil, Standifer and Chin

(1969) found that 35 percent remained dormant for at least 90 days. Other researchers have reported similar findings (Andrews, 1940a; Hammerton, 1974). Obviously, dormant tubers will not be affected by applied glyphosate since it has essentially no soil activity (Baird *et al.*, 1971; Sprankle *et al.*, 1975a,b). If eradication is the ultimate goal, this problem must be addressed.

There are thus two keys to improving control of purple nutsedge with glyphosate. The first is to induce sprouting of all tubers in the soil. Then all will have an aerial connection, and can potentially be reached by applied glyphosate. The second is to ensure that enough glyphosate reaches the parent tuber to kill all buds on that tuber. Much of what is already known about glyphosate translocation will help to reach this second goal:

Environmental conditions: high relative humidity, high temperature, and adequate soil moisture will all improve the efficacy of applied glyphosate .

Rate of application: It is known that higher rates of application result in higher translocation (Caseley and Coupland, 1985). Increased toxicity to the buds of potato parent tubers at higher rates of glyphosate application has been reported (Smid and Hiller, 1981). Low rates may be adequate to suppress purple nutsedge, but if the goal is death of the parent tuber, higher rates may be justified.

Phenology: Glyphosate should be applied at the optimum stage for translocation to the parent tuber. More study is needed to determine when this stage is reached.

Tubers which survive glyphosate treatment, with the store of dormant tubers in the soil, can subsequently sprout and rapidly reinfest a field, necessitating repeated sprayings. Even a small number of escapes is sufficient to rapidly reinfest a field; 99 percent control of parent tubers at a typical population of 2,000 tubers per square meter would leave 20 tubers per square meter, far more than are needed to reinfest a field in one season (Hauser, 1962a).

As noted above, much is already known about the effects of environment and application rate which can help to ensure that adequate amounts of glyphosate are translocated to the corms and parent tubers. It remains to be discovered what stage of growth of purple nutsedge is best to ensure translocation of glyphosate to those plant parts which are most difficult to control, and of which control is most critical: the parent tubers.

If control of parent tubers can be maximized, then reinfestation in the field will be mainly from previously unsprouted tubers. Teo *et al.* (1973) were able to obtain nearly 100 percent sprouting of tubers by the use of benzyladenine, but the cost was prohibitive. They were hopeful that a less

expensive substance could be found to induce high germination, which would then be followed by herbicide application. While such a chemical has not yet been found, it will be shown in this study that it is possible to increase tuber sprouting in the field to near 100 percent through manipulation of soil temperatures by soil solarization.

This study has concentrated on obtaining complete sprouting of tubers. Ongoing research with the growth retardant paclobutrazol (Kawabata and DeFrank, 1990) has already demonstrated a synergistic effect with glyphosate on purple nutsedge. This strategy, in combination with soil solarization to increase tuber sprouting, may offer real hope of purple nutsedge eradication. By preventing formation of new tubers and corms, paclobutrazol halts propagation of purple nutsedge, and the efficacy of glyphosate on parent tubers is greatly enhanced. This new approach, in combination with treatments to induce 100 percent tuber sprouting, holds great promise for future efforts to control purple nutsedge.

Integrated Control

For effective control of purple nutsedge, Glaze (1987) recommends a combination of several methods, including preplant tillage to increase tuber sprouting and to expose tubers to desiccation and/or chilling, high population of competitive crops, and cultivation during the growing season to prevent tuber formation; all of these

combined with herbicide use as necessary. Keeley (1987) has also recommended the use of cultural practices which give crops an advantage over nutsedge.

Another strategy is to grow a competitive crop with a nutsedge population which has been weakened or reduced by some other method or combination of methods. Several crops have been recommended as being able to compete more or less successfully with nutsedge. Nutsedge was reported to have no effect on yield of cassava in the field (Villamayor, 1983), but this was at relatively low populations of 30 and 60 shoots per square meter. Purple nutsedge reportedly does not compete well with green beans (*Phaseolus vulgaris*) (Gamboa and Vandermeer, 1988), and Siriwardana (1986) reported no yield loss in this crop. William and Warren (1975), however, reported a 41 percent yield reduction in green beans due to a population of approximately 1,600 nutsedge shoots per square meter. The results of Gamboa and Vandermeer are somewhat open to question since the nutsedge plant was restricted to one shoot, thus removing one of its main competitive advantages, prolific and rapid shoot production. This treatment very likely reduces tuber production as well, since it is comparable to clipping of shoots, which has been reported more than once to reduce tuber production (Horowitz, 1965; Komai and Ueki, 1982; Sierra, 1973).

These and other crops can compete against low or moderate populations of purple nutsedge, so if eradication is not possible they present an alternative. Many techniques which reduce the

population or vigor of purple nutsedge temporarily will be helpful in this effort. As mentioned above, cassava, green beans, maize, and sorghum have been shown capable of producing acceptable yields in moderately infested fields. Other crops which reportedly can compete successfully with limited nutsedge populations include sweet potato and cotton (William, 1976), and soybean (Pitelli *et al.*, 1983). These crops do not usually result in decreases in nutsedge tuber populations unless combined with frequent cultivations (William, 1976).

A few cover or forage crops have been reported able to compete effectively with purple nutsedge. These include *Dolichos lablab* (El Saeed, 1967), jackbean (*Canavalia ensiformis*) (Magalhaes, 1967; Magalhaes and Franco, 1962), and kudzu (*Pueraria sp.*) (William, 1976). These are all leguminous forages or cover crops which are characterized by rapid and dense growth. As with commercial crops, however, these crops do not usually result in decreases in viable tuber populations in the soil.

Quimby and Frick (1985) took a novel integrated approach to nutsedge control by coating larvae of the nutsedge stem boring moth, *Bactra verutana* with bentazon or glyphosate. They achieved some control of nutsedge, but unfortunately the larvae also indiscriminately attacked the crop (cotton and turnip), resulting in yield losses.

Another possible integrated approach would be to follow larval release in a few days with glyphosate spray. Damage to, or loss of the shoot apex can reactivate buds on the parent tuber and corms by

releasing them from apical dominance. Since the larvae destroy the apical meristem of the shoot without damaging the leaves, new sinks would be created in the form of newly sprouting buds on the corms and parent tubers, while an absorbing surface would still be available in the undamaged leaves. This should enhance control of parent tubers and corms, reported by Siriwardana (1986) to be the organs most likely to survive glyphosate treatment. The phenomenon of bud sprouting on tubers and corms following attack by *Bactra venosana*, a close relative of *B. verutana*, has been observed by the author at the Waimanalo Experiment Station, where this research was conducted.

Soil solarization offers potential for integrated control of purple nutsedge in combination with glyphosate treatment, as described in this study.

SOIL SOLARIZATION

In 1976, an article was published (Katan *et al.*, 1976) describing a new method of plant pathogen control, which also showed potential for effective control of weeds. Since that landmark paper, interest in this technique, known widely now as "soil solarization", has grown. As of 1986, 10 years after publication of the first article, at least 173 articles, reviews, and abstracts had been published describing efforts at weed and pathogen control by this method (Katan *et al.*, 1987). Soil solarization utilizes the energy of sunlight, trapped under transparent

polyethylene mulch, to raise soil temperatures to levels lethal to many weed propagules (Egley, 1990; Horowitz *et al.*, 1983; Katan, 1981; Rubin and Benjamin, 1983).

Most of the research on soil solarization to date has been for control of soil-borne plant pathogens, but some of these studies have mentioned weed control as well. In addition, there have been several studies dedicated specifically to the control of weeds by solarization. Since this study is a weed control project, most of the literature on pathogen control is not included in this review.

As stated above, soil solarization was originally developed for control of soilborne plant pathogens, but it was observed to reduce weed populations in treated plots as well (Katan *et al.*, 1976). Research is now being done on soil solarization for weed and pathogen control in Israel, where the method was first described, in the United States, Japan, and in several countries in South and Central America and Africa (Katan *et al.*, 1987). Katan *et al.* (1987) report that soil solarization has been investigated in at least 24 countries since 1976. At least two trials have been conducted in the Pacific islands since that report was published (Ragone and Wilson, 1988), as well as this study in Hawaii. Solarization is now used commercially in Israel, Japan and the United States (Katan *et al.*, 1987).

In addition to broad spectrum control of weeds and pathogens, solarization has other benefits. These include improved crop growth, yield increases over and above those accounted for by removal of specific weeds or pathogens, compatibility with other weed control

methods, simplicity, non-toxicity, and a residual effect exceeding one year in duration in some cases (Katan, 1981, Stapleton and DeVay, 1986). Other benefits are the potential for effective weed control in crops where no safe herbicide is available (Horowitz *et al.*, 1983), reduced irrigation requirements (Stapleton and Garza-Lopez, 1988), and possibly reduced fertilizer needs (Chen and Katan, 1980; Stapleton and DeVay, 1986). Soil solarization has been referred to by many other names, including solar heating, solar pasteurization, solar sterilization, and plastic mulching or tarping.

SOIL TEMPERATURES UNDER SOIL SOLARIZATION

The main effect of soil solarization is a marked increase in maximum and mean soil temperature, and in the amplitude of the daily temperature cycle. Rubin and Benjamin (1983) report maximum temperatures 10 to 18 C higher in solarized than in bare soil, and Horowitz *et al.* (1983) similarly report temperatures 12 to 19 C higher. Reports of maximum temperatures under solarization of over 50 C at 5 cm soil depth are common, and average maxima at this depth in summer frequently are reported greater than 45 C (Egley, 1983; Horowitz et al, 1983; Jacobsohn *et al.*, 1980; Katan *et al.*, 1976; Sauerborn *et al.*, 1989; Standifer *et al.*, 1984). The temperature elevation is dampened with increasing soil depth, but temperatures in excess of 40 C have been reported at 15 cm soil depth (Hildebrand, 1985; Jacobsohn *et al.*, 1980; Jahns, 1983; Katan *et al.*, 1976). These temperatures can be lethal to seeds of many weeds if applied

for a long enough period of time (Egley, 1990; Horowitz and Givelberg, 1982; Horowitz and Taylorson, 1983; Powles *et al.*, 1988; Rubin and Benjamin, 1984), but more research is needed into temperatures and times necessary to kill weed propagules in the soil.

The mechanism by which solarization results in such high soil temperatures has been studied in some detail, and a model has been developed to simulate and predict soil temperatures under different sunlight and soil conditions (Mahrer, 1979). According to this publication, the so-called "greenhouse effect", reduction of outgoing longwave radiation, makes only a small contribution to the total increase in temperature, approximately 20 percent. The main cause of the striking temperature increases under clear plastic is the almost complete prevention of heat loss to evaporation.

The high temperatures observed under soil solarization are a result of the transparent plastic mulch allowing energy to be absorbed by the soil, then preventing or slowing its subsequent loss to the environment. Incoming solar radiation can either be reflected or absorbed when it strikes the soil surface. For most soils, more radiation is absorbed than reflected, and moist soils generally absorb more radiation than dry soils (Ekern, 1966). Once solar energy is absorbed by soil, it is partitioned to several sinks. This

partitioning has been summarized by Mahrer (1979). Mahrer's explanation of energy partitioning can be simplified as follows:

NET INCOMING RADIATION - (SOIL STORAGE + EVAPORATION + TRANSFER TO AIR) = 0

This is a gross oversimplification, but for the purposes of explaining how soil solarization causes increases in soil temperature it is adequate. To summarize, incoming energy from solar radiation can go to three sinks: it can be stored in the soil; it can provide energy for evaporation of soil water; or it can be transferred to the air. Some energy is lost from the soil as longwave radiation, but this loss is accounted for in the term "NET INCOMING RADIATION". This loss is small compared to the amount of incoming radiation in the daytime, but it is important in soil cooling at night, when there is no incoming radiation.

Under the polyethylene mulch used in soil solarization, evaporation is near zero, so losses of energy to evaporation are also near zero. Also, since the air underneath the plastic is still, there is little or no transfer of energy to the air. The thermal contact coefficients for stable and unstable air have been reported by Ekern (1965) as 0.10 and 0.00013, respectively. The prevention of evaporation and air movement by the polyethylene mulch results in almost all incoming solar radiation being stored in the soil, with the result that soil temperatures rise to very high levels, as has

been reported. Mahrer (1979) concluded that the major factor in this temperature increase in moist soil was the prevention of evaporation. Regarding penetration of this effect into the soil, Ekern (1966) reported that the presence of a vapor barrier mulch "markedly increases apparent thermal conductivity", resulting in more rapid penetration of heat into the deeper soil layers.

In comparisons of black with transparent polyethylene mulches, it has been reported that soil temperatures under transparent mulch are consistently higher (Horowitz *et al.*, 1983; Standifer *et al.*, 1984). This can be explained by the fact that solar radiation heats the black polyethylene, which then re-radiates the energy to the soil, while transparent mulch transmits the solar energy to the soil, where it is absorbed directly. As a result, temperatures are higher under transparent mulch, and the amplitude of temperature fluctuation is greater. Transparent mulch has also been demonstrated to be more effective than black in controlling weeds (Horowitz *et al.*, 1983; Standifer *et al.*, 1984).

SOLARIZATION METHODS

Soil solarization is a very simple technique, requiring only the preparation of a smooth soil surface and wetting the soil to field capacity. Transparent polyethylene film is then spread and the edges sealed by covering with soil. The soil may also be moistened after applying the mulch, by drip irrigation (installed before the mulch is laid). Adequate moisture is essential to the method, because

moisture increases the susceptibility of organisms to heat (Baker, 1962; Taylorson and Hendricks, 1977). There are many reports of no damage to dry seeds at temperatures lethal to imbibed seeds (Jennings and de Jesus, 1964; Uhlinger, 1970; Vora and Patel, 1975). Moisture is also important because soil moisture may increase the transfer of heat to greater soil depths. Jahns (1983) reported higher temperatures at 30 cm soil depth in moist than in dry solarized soil. The thickness of the plastic film affects the maximum temperature attained to a small degree, 0.03 mm thick plastic having been shown to raise temperatures 1 to 2 degrees C higher than 0.1 mm thick plastic at 5 and 10 cm soil depth (Horowitz *et al.*, 1983). It is important to keep the plastic film as close as possible to the soil surface, providing less air for soil moisture to evaporate into. This is accomplished by good soil preparation and by care in the laying of the plastic mulch.

MECHANISM OF GERMINATION STIMULATION

Supra-Optimal Temperatures

It was once believed that cardinal temperatures - minimum, optimum, and maximum - could be found for the germination of all seeds. It is now clear that, for total germination at least, an optimum range is a more accurate term, and that over this range the rate of germination will vary (Bewley and Black, 1982; Edwards, 1932; Harrington, 1963; Heydecker, 1977; Mayer and Polyakoff-

Mayber, 1963). Additionally, any lot of seeds apparently has a distribution of temperature responses throughout its temperature range, with some seeds germinating better in the lower part of the range and others germinating better in the upper part of the range. This lack of a clear optimum makes defining the term supra-optimal rather difficult. For the purposes of this discussion, a supra-optimal temperature is one at which the seeds in question, when continuously exposed, will not germinate, and which will eventually lead to injury and death of the seeds. This corresponds to a heat stress, as defined by Levitt (Levitt, 1980).

Levitt defines a biological stress as "any environmental factor capable of inducing a potentially injurious strain on living organisms." A strain, according to Levitt, is any physical or chemical change induced by a stress, and may be elastic (reversible) or plastic (irreversible). In contrast to plastic strains in nonliving substances, a plastic strain in a living organism, while in itself irreversible, may be reparable. Thus, once the stress is removed, the organism may be able to repair the damage done and resume its normal functions. This accounts for the importance of time in any consideration of the effects of stress on biological systems; when continuously applied stress results in a strain too great for repair, or when no opportunity is allowed for repair, then the organism (such as an embryo in a seed, or an apical meristem in a bud) is killed (Levitt, 1980). It has been shown that recovery is possible with seed (Berjak and Villiers,

1972a; Heydecker, 1977). A logarithmic relationship between temperature and time of exposure to cause death has been demonstrated with microorganisms (Pullman *et al.*, 1981).

Responses to Supra-Optimal Temperatures

There are two responses of seeds to heat stress; enhanced germination/breaking of dormancy, or inhibition of germination, usually due to injury, and often leading to death. (With some seed, e.g., lettuce, there is a high temperature "thermodormancy" which prevents germination at temperatures not harmful to the seed (Roberts and Ellis, 1982)). Two factors are responsible for separating these responses, and these are interrelated. Time has already been mentioned as a factor, and the other is moisture content of the organism. Several studies reporting enhanced germination of seeds following high temperature treatments have also reported damage and/or death to the same seeds following longer exposures (Horowitz and Taylorson, 1983; Jennings and de Jesus, 1964; Khan *et al.*, 1973; Onwueme, 1975a; Rincker, 1954; Staker, 1925; Stewart, 1926). It is also well known that imbibed seeds are much more susceptible to heat damage than dry seeds, so that temperatures lethal to imbibed seed may be harmless to, or even stimulate the subsequent germination of, dry seed (Baker, 1970; Belehradek, 1935; Heydecker, 1977; Jennings and de Jesus, 1964; Leach, 1956; Mayer and Polyakoff-Mayber, 1963; Siegel, 1950; Tapke, 1924; Taylorson and Hendricks, 1977; Waggoner, 1917).

Enhanced germination

Enhanced germination has resulted from elevating temperatures as a pretreatment of dry or imbibed seed, and during incubation of imbibed seed. In the case of dry seed, enhancement of germination by heat pretreatment is often due to increased permeability of the seed coat. This has been shown for alfalfa and several other leguminous species (Quinlivan, 1961; Quinlivan, 1966; Rincker, 1954; Staker, 1925). A similar response has been reported for *Abutilon theophrasti*, a member of the family Malvaceae, which has some members resistant to soil solarization (Horowitz and Taylorson, 1984). In other cases, the cause for enhanced germination has not been elucidated, although increased imbibition has been noted (Jennings and de Jesus, 1964; Khan *et al.*, 1973; Onwueme, 1975a,b; Stewart, 1926; Uhlinger, 1970). Heat pretreatment of dry seed has been demonstrated to enhance not only germination, but subsequent yield of the crop as well (Khan *et al.*, 1973; Kydrev and Kolev, 1962; Onwueme and Atakoumi, 1975).

In the case of imbibed seeds, it has long been known that alternating temperatures during incubation increase the germination of many types of seeds, even when the higher temperature in the alternation is inhibitory to germination when applied continuously (Bewley and Black, 1982; Cohen, 1958; Harrington, 1923; Hendricks and Taylorson, 1976; Morinaga, 1926;

Taylorson and Hendricks, 1972a; Toole *et al.*, 1955; Totterdell and Roberts, 1980). Not only have alternating temperatures stimulated germination of non-dormant seeds of several species, they have also been shown to break dormancy. In some cases alternating temperatures or even single temperature shifts have substituted for or enhanced the light-induced breaking of dormancy mediated by phytochrome, indicating that temperature and light may break dormancy by the same mechanism (Bewley and Black, 1982; Taylorson, 1969; Taylorson and Hendricks, 1972a; Toole *et al.*, 1955; Toole, 1973). Several hypotheses have been advanced to explain this effect: high temperature brings about a change in the balance of reactants which then promotes germination at lower temperatures; or a sequence of reactions taking place, some at high temperature and some at low temperature break dormancy (Cohen, 1958); or a germination inhibitor intermediate between two reversible reactions prevents germination (Koller, 1972). Work by Cohen in 1958, however, indicated that the site of action of the temperature change is an organized structure, either an enzyme or a membrane (Cohen, 1958). Correlation was found in his studies between breaking of dormancy and the magnitude of the temperature change, rather than the rate or duration of the change. Koller in 1972 suggested another possibility; that two or more diurnal cycles of processes within the seed are out of phase during dormancy, and that a temperature shift may act to synchronize the processes, thereby breaking dormancy (Koller,

1972). There is little evidence by which to evaluate this hypothesis, but there is mounting interest and a considerable body of research which is giving support to the hypothesis that membranes are the site of action (Bewley and Black, 1982; Hendricks and Taylorson, 1976, 1978, 1979; Taylorson and Hendricks, 1977, 1979; Wood and Paleg, 1974; Wood *et al.*, 1974). Much work also implicates membrane changes as the major factor leading to deterioration and loss of viability of seeds, both at normal and at supra-optimal temperatures (Berjak and Villiers, 1972a,b,c,d; Bewley and Black, 1982; Roberts and Ellis, 1982; Siegel, 1953; Simon, 1974). In related work, Hendricks and Taylorson have implicated membranes both in heat injury and in dormancy-breaking by phytochrome (Hendricks and Taylorson, 1976; Taylorson and Hendricks, 1972b).

Injury and death

Imbibed lettuce seed can survive, dormant, at 30 C for 2 to 3 years or more (Roberts and Ellis, 1982). Temperatures not much higher than this, however, have been shown to be detrimental to many seeds, including those of lettuce.

Among the reported symptoms of heat injury to seeds or seedlings are:

1) Decreased germination percentage and/or rate (Berjak and Villiers, 1972a,d; Heydecker, 1977; Jennings and de Jesus, 1964; Staker, 1925; Tapke, 1924);

2) Delayed or decreased emergence (Laude *et al.*, 1952; Onwueme and Adegoroye, 1975; Sprague, 1943);

3) Decreased elongation (Allan *et al.*, 1962; Burleigh *et al.*, 1964; Onwueme, 1974; Onwueme and Laude, 1972);

4) Accelerated senescence (Berjak and Villiers, 1972b;);

5) Changes in enzyme activity (Kydrev and Kolev, 1962; Onwueme *et al.*, 1971);

6) Decreased chlorophyll content (Onwueme and Lawanson, 1975);

7) Membrane disruption (Berjak and Villiers, 1972b,c; Bewley and Black, 1982; Roberts and Ellis, 1982);

8) Leakage of endogenous substances (Berry and Raison, 1981; Hendricks and Taylorson, 1976, 1979; Siegel, 1953; Siegel and Carrol, 1975); and

9) Death (Baker, 1970; Berjak and Villiers, 1972a,d; Jennings and de Jesus, 1964; Khan *et al.*, 1973; Laude *et al.*, 1952; Leach, 1956; Rincker, 1954; Siegel, 1950; Siegel and Carrol, 1975; Staker, 1925; Tapke, 1924).

The moisture content of seeds is a very important factor in heat injury. Several studies have shown that imbibed seeds are much more susceptible to heat injury, and that injury increases with moisture content of partially dried seeds (Baker, 1970; Belehradek, 1935; Heydecker, 1977; Jennings and de Jesus, 1964; Leach, 1956; Mayer and Polyakoff-Mayber, 1963; Siegel, 1950;

Tapke, 1924; Taylorson and Hendricks, 1977; Waggoner, 1917). As the temperature increases, the time to injury or death of the seeds decreases exponentially (Levitt, 1980). In general, temperatures of 40 to 60 C can result in death in a few hours or days (Berjak and Villiers, 1972a; Harrington, 1963; Levitt, 1980), while temperatures greater than 60 C usually kill imbibed seed in less than 30 minutes (Baker, 1970;). Much higher temperatures and/or longer times of exposure are required to kill dry seeds.

To summarize the effects of heat on weed propagules, it seems fairly certain that damage to cellular membranes is the cause of heat injury in most cases. Interestingly, temporary membrane disruption is also implicated in the breaking of physiological dormancy in seeds. Complete or partial loss of membrane integrity, as well as differential sensitivity of organelle and cell membranes, accounts well for the progressive increase in metabolic disruption, followed by leakage of cell contents and eventual death. It should be noted, however, that in some cases denaturation of a single enzyme not associated with a membrane, or the reversal of relative reaction rates due to differing activation energies might result in injury as well.

There is still considerable room for investigation into the mechanism of heat injury, as well as of germination enhancement by temperature shifts and alternations. Of particular importance is

the role of cellular membranes in these processes, and the respective roles played by membrane proteins and lipids.

SOIL SOLARIZATION FOR WEED CONTROL

Solarization has been found to be quite effective against many annual weeds, but has shown less promise against perennial weeds. In 1986, Stapleton and DeVay (1986) published a list of 32 weed species which had been found to be susceptible to solarization, and another 7 species which were resistant or tolerant. Some of those listed as susceptible have been reported tolerant by other authors, however. These include *Oxalis pes-caprae* (Powles *et al.*, 1988), *Sorghum halepense*, and *Cynodon dactylon* (Rubin and Benjamin, 1984). Other weeds which have subsequently been reported to survive solarization are leguminous weeds with hard seed coats (Powles *et al.*, 1988; Sauerborn *et al.*, 1989). In general, weeds with hard seeds, mostly legumes and one or two species in the family Malvaceae (Horowitz and Taylorson, 1984; Rubin and Benjamin, 1983), and perennial weeds with perennating vegetative structures located deep in the soil are less likely to be controlled. In the case of the herbaceous perennial weeds, this is apparently due to the location of these structures to deep enough in the soil to escape the lethal temperatures reached in shallower soil layers (Rubin and Benjamin, 1984; Standifer *et al.*, 1984). Some large seeds whose seedlings can emerge from greater soil depths apparently also escape solarization by this mechanism (Rubin and Benjamin, 1983).

Standifer *et al.* (1984) have suggested that deep tillage following solarization can result in loss of control of small-seeded weeds as well, by bringing seeds up from deeper in the soil where they escaped lethal temperatures to shallow depths, from which they are capable of emerging.

The length of time the plastic mulch remains in place is another important variable; the level of weed control increases with length of exposure to soil solarization up to 4 weeks, with less improvement in control after 4 weeks (Horowitz *et al.*, 1983). For resistant weeds, however, control can be significantly improved by longer solarization (Rubin and Benjamin, 1983). A recent report (Stevens *et al.*, 1990) demonstrated good control of purple nutsedge, formerly considered tolerant to solarization, by solarization for 98 days (14 weeks)

The mechanism by which solarization controls weeds has not been fully elucidated. A suggested hierarchy of mechanisms has been summarized by Rubin and Benjamin (1984) as follows:

1. Direct thermal killing of propagules;
2. Thermal breaking of dormancy, followed by thermal kill of seedlings;
3. Thermally induced changes in the soil atmosphere involved in dormancy release, followed by thermal kill of seedlings;
4. Direct interaction of high temperature and release of toxic volatiles from decomposing organic matter; and

5. Indirect effects, such as microbial attack of weakened propagules.

Further study is needed on all of these potential mechanisms to determine whether and to what extent they are responsible for the effectiveness of soil solarization. Such knowledge may also make it possible to enhance the effectiveness of soil solarization. For example, use of added organic matter for decomposition under solarization has been demonstrated to enhance the control of cabbage yellows (Villapudua and Munnecke, 1986). This study has concentrated on the second mechanism, thermal release from dormancy or induction of sprouting, to be followed in this case by herbicide application.

Solarization is very attractive as a weed control method for several reasons; it is simple and non-hazardous, and controls not only weeds, but soil pathogens as well. Other benefits include increased crop yields and profits (Baharanyi *et al.*, 1988), possibly less fertilizer use (Stapleton and DeVay, 1986), long-term effects, and water conservation (Stapleton and Garza-Lopez, 1988). Work by several researchers, however, indicates that solarization is less effective against some weeds than against others, and control is frequently less than complete. Particular problems have been encountered with control of perennial weeds, perhaps due to location of propagules deeper in the soil.

Some of these resistant weeds may actually have their populations increased by solarization due to increased germination as a result of higher temperatures and greater amplitude of temperature fluctuation.

Several reports have indicated increased emergence of weeds that were not controlled, due to heat tolerance, too short a solarization period, or insufficiently high temperatures (Ashley, 1990; Egley, 1983; Horowitz *et al.*, 1983; Rubin and Benjamin, 1984; Sauerborn *et al.*, 1989).

The phenomenon of increased emergence of weeds can be taken advantage of, however. Longer solarization is one option, since seedlings are less heat tolerant than dormant seeds (Rubin and Benjamin, 1983; Standifer *et al.*, 1984). Longer solarization has also been shown to be more effective on herbaceous perennials (Rubin and Benjamin, 1983; Stevens *et al.*, 1990). Another option is to use solarization as part of a modified stale seedbed technique. This was recently recommended by Ashley (1990). Weed propagules can be induced to germinate or sprout by solarization, and thereby be made susceptible to thermal effects or to subsequent herbicide treatment.

A short solarization of 1 to 2 weeks may concentrate weed seed germination, and the resulting seedlings can be killed with a post-emergence herbicide once the polyethylene mulch has been removed. In cold climates, a late fall solarization could be used to induce germination and seedlings would then be killed by freezing temperatures in winter. The modified stale seedbed approach has been the approach taken in this study; solarization induces high and concentrated sprouting of purple nutsedge tubers. The mulch can be removed following sprouting, and the plants sprayed with glyphosate.

The combination of near 100 percent sprouting and good control of tubers with a systemic herbicide will leave very few viable tubers in the soil.

SOIL SOLARIZATION FOR PURPLE NUTSEDGE CONTROL

It is fairly well established that nutsedge tubers cannot survive temperatures above 45 C for extended periods of time, but that tubers can and do survive and grow at 40 C (Aleixo and Valio, 1976; Orcutt and Holt, 1990; Tripathi, 1967; Ueki, 1969). Soil temperatures greater than 45 C are consistently attained in Hawaii for one or more hours per day under soil solarization, but only to a depth of 5 to 10 cm.

It is not known to what extent, if at all, the tubers are able to recover from heat injury during the portion of the 24-hour temperature cycle when temperatures are below those causing injury. Horowitz *et al.* (1983) have indicated that a daily exposure of seeds to high temperatures of 45 to 55 C resulted in a cumulative inhibition of germination similar to that caused by continuous exposure to these temperatures. From the fact that soil solarization is lethal to many organisms, the conclusion can be reached that heat injury is cumulative, but this phenomenon needs to be quantified before it can be predicted.

Since a fairly large portion of the tuber population is found below the depth where known lethal temperatures occur, solarization alone is not likely to provide complete control of nutsedge, although it

may significantly reduce the viable tuber population (Rubin and Benjamin, 1983; Stevens *et al.*, 1990). There are several reports that soil solarization does not adequately control purple nutsedge (Egley, 1983; Horowitz *et al.*, 1983; Ragone and Wilson, 1988; Rubin and Benjamin, 1983). It may be possible, however, to combine solarization with the use of glyphosate to provide good control. Daily minimum and maximum soil temperatures at 15 cm depth under soil solarization range from 23 to 26 C and 35 to 40 C, respectively, at Waimanalo, Hawaii. Such high maximum temperatures and wide diurnal temperature alternations are known to increase both the rate and total sprouting of purple nutsedge tubers (Shamsi *et al.*, 1978; Tripathi, 1967; Ueki, 1969). Increases in nutsedge shoot populations in the field have been reported following soil solarization (Egley, 1983). These increases are probably due to this phenomenon. After sprouting has been induced by solarization, the plastic can be removed, and the plants arising from the sprouted tubers can be killed with glyphosate, greatly reducing the population of viable tubers remaining in the soil. These temperatures, furthermore, can be obtained in Hawaii in the winter, making it possible to control nutsedge without interfering with the production of summer crops. Decreases in the weed seed reservoir in the soil are primarily due to germination (Karssen, 1982); the same can be made true for nutsedge tubers. If tubers can be induced to sprout by elevated temperatures, and if the subsequent plants can be controlled by herbicides, economic control may be attainable.

MODELING TUBER SPROUTING

Modeling is a useful approach to the analysis of plant responses to environment. In the past two decades, with the advent of powerful computers and powerful statistics and simulation programs, modeling has gained in popularity. In the field of weed science, the past two decades have seen many researchers taking the modeling approach to predict weed emergence, growth, and interference with crop growth.

HEAT SUMS

A common approach to modeling plant responses to temperature is the use of heat sum models. Growing Degree Days (GDD) are a familiar example of this type of model. Heat sum models are based on additive effects of temperature over time, and are usually derived from the response to constant temperatures. For a very simple example, in a heat unit model, A hours at temperature B gives A X B heat units. The models are usually modified by other factors. With heat sum models, a base temperature is determined, and from this the effect of time at any temperature above the base temperature can be predicted.

The base temperature may be found by linear regression of rate on a range of constant temperatures. Bierhuizen (1973) gave the following general heat sum model for seed germination:

$$S = (T - T_{min}) \text{ X } t$$

Where S is the heat sum in degree days to reach 50 percent germination, T is the soil temperature, T_{min} is the base temperature (temperatures are in degrees Celsius), and t is the time in days to reach 50 percent germination at temperature T.

Heat sum models for germination have defined the rate of germination in $days^{-1}$ as the reciprocal of the time to 50 percent germination, or $1/T_{50}$, also known as the reciprocal median response time (Scott *et al.*, 1984). T_{50} has a curvilinear relationship with temperature, while its inverse has a linear relationship over a limited temperature range (Bierhuizen, 1973). The base temperature is commonly estimated by plotting temperature on the Y axis and $1/T_{50}$ on the X axis, the base temperature is the Y-intercept of the regression, and is referred to by several authors as the low temperature threshold for development, or low TTD (Nussbaum *et al.*, 1985; Orcutt and Holt, 1990; Sanborn *et al.*, 1982; Wiese and Binning, 1987. This approach to estimating the low TTD has been criticized for its exclusion of treatments which do not attain 50 percent germination (Scott *et al.*, 1984). This exclusion amounts to a decision to ignore valuable information on the response to treatments, and may lead to incorrect estimates.

With this approach, the sum of the responses to equal times at two temperatures should be equal to the effect of the total time at the mean of the two temperatures. That is, 12 hours at 20 C followed 12 hours at 30 C should result in the same response as 24 hours at 25 C. Heat sum models have been used to predict seed germination. Bierhuizen and Wagenvoort (1974) showed that this relationship holds for 31 species of vegetable seeds. Heat sums have also been used successfully to predict sprouting of potato tubers (Sale, 1979). Recently Orcutt and Holt (1990) reported on an attempt to determine the low TTD for purple nutsedge and two other weeds.

If an organism responds to alternating temperature, however, the model described above becomes unrealistic (Stimart and Ascher, 1981; Wagenvoort and Bierhuizen, 1977; Wagenvoort and Van Opstal, 1979). Many examples of enhanced germination of seeds in response to alternating temperatures can be found in the literature (Benech Arnold *et al.*, 1988; Brown, 1987; Garcia-Huidobro *et al.*, 1982b; Harrington, 1923; Hendricks and Taylorson,1976; Morinaga, 1926; Pollock, 1972; Totterdell and Roberts, 1980; Wagenvoort and Van Opstal, 1979).

It is more difficult to find examples of such responses in vegetative buds, though there are some (Blake, 1972; Erez *et al.*, 1979; Stimart and Ascher, 1981). This may be an effect of environment, however, since most studies of bud responses to temperature have been studies of aerial buds, whereas tubers are found in soil. Air temperatures are subject to wider fluctuation

than soil temperatures, and temperature fluctuation may therefore not be a useful indicator of changes in the aerial environment. A recent study by Benech Arnold *et al.* (1990a) separated dormancy breaking in seeds of johnsongrass (*Sorghum halepense*) from temperature response for germination.

Using the sprouting rate to predict the time to total sprouting (or to any given level of sprouting) assumes a linear course of sprouting over time (constant rate). This is an important weakness of linear heat sum models, which are valid only over the range of temperatures for which the response is linear (Scott *et al.*, 1984). While it is common for a portion of a germination or sprouting curve to be approximately linear, the entire curve is almost always sigmoid and asymptotic at the maximum. The rate of germination changes with time, first increasing, becoming maximum at the point of inflection of the germination curve, then decreasing. Using an average rate distorts this response by assuming a constant rate and linearizing the sprouting curve. Landsberg (1977) has pointed out that linear relations "seldom occur in nature, ... and extrapolated values of the independent variable frequently produce absurd answers."

Another important weakness of heat sum models relative to this study is that they give only a limited information about a process, since they only give the time to a selected event (e.g., 50 percent germination), and give little or no information about progress toward that event.

The heat sum approach as described above is not appropriate for purple nutsedge because it assumes no effect of alternating temperatures, while this study shows that purple nutsedge responds to alternating temperatures with higher sprouting than at constant temperatures. It would be possible to improve the heat sum model, and it is very likely that a model could be constructed to accommodate a response to alternating temperatures, but it would still have the weakness of the inability to describe the entire course of the process. In the specific case of predicting cumulative sprouting of purple nutsedge tubers in response to temperature, another approach is therefore indicated.

CURVE FITTING

Another approach to modeling germination has been fitting of sigmoid curves. The purpose of fitting mathematical functions is to be able to describe the entire course of germination, and not only to predict the time to a given level of germination. Causton *et al.* (1978) make the point that with a fitted function, "A series of estimates ... may be calculated at as many times as desired, and these estimates are less disturbed by biological variability." It is useful for the functions to have biological meaning, but this is not essential. The value of curve fitting, as Hunt (1979) stated, is that "if attempts to assess reality of growth result in a time series of observations scattered randomly about that reality, then a simple

mathematical function fitted to those observations may be expected to regain much of the clarity with which reality is perceived by the experimenter."

There are many mathematical functions which can be fitted to biological data. Landsberg (1977) reviewed many of these, and there are several which can be used to describe germination. Several researchers have fitted curves to seed germination data.

Obviously, seed germination and tuber sprouting are different processes, but they follow a similar pattern over time, take place in the same environment, and have the same purpose: propagation. Purple nutsedge tubers play the same role as seeds: to survive unfavorable periods and produce plants during favorable periods, and to increase the population of the plant. Tubers play an additional role of food storage, but in the case of purple nutsedge they function mainly as propagative structures. It is thus not inappropriate to expect similar responses to environmental stimuli from tubers and seeds.

Cumulative tuber sprouting follows a sigmoid curve in relation to time, of the same general shape as seed germination curves. Another important characteristic of seed germination and tuber sprouting curves is that they are asymptotic at the maximum. This makes polynomial functions inappropriate for the purpose of describing tuber sprouting (Brown and Mayer, 1988b; Hunt, 1982). However, several exponential sigmoid functions are potentially useful for this purpose.

Four sigmoid functions, the logistic, Gompertz, Richards, and Weibull, were tested for their ability to fit the data generated by these experiments. All four of these functions have been used to describe seed germination, and all four are exponential functions. The logistic and Gompertz functions are fairly widely used in biological studies, and both have been used to describe the course of seed germination (Hsu *et al.*, 1984; Schimpf *et al.*, 1977; Tipton, 1984; Torres and Frutos, 1989). The Richards function was first described by Richards in 1959, and it has been used for plant growth studies (Causton *et al.*, 1978) and to describe growth of sea urchins and fish (Ebert, 1980), among others. It has also been evaluated and found useful for characterizing seed germination (Lehle and Putnam, 1982; Moore and Joliffe, 1987). Interestingly, the logistic, Gompertz, and Richards functions are very closely related, the logistic and Gompertz being special cases of the Richards (Brown and Mayer, 1988b; Causton et al, 1978; Richards, 1959). The Weibull function is less widely used in biology (Moore and Joliffe, 1987), but has recently been recommended for description of seed germination (Brown, 1987; Brown and Mayer, 1988b; Moore and Joliffe, 1987).

Both the logistic and Gompertz functions have a defined shape: the logistic function is symmetrical about its point of inflection, whereas in the Gompertz function the inflection point occurs at approximately one third of maximum. The symmetrical shape of the logistic function is its major weakness in describing germination and sprouting since they generally have a "tail" of a few late

germinating seeds, or in this study, tubers. Since the shape of the Gompertz function is naturally skewed, it is better suited to description of germination. Its lack of flexibility is a weakness, however, which it shares with the logistic function.

Nonlinear Regression

Polynomial models can be fitted to data by commonly used methods of linear regression. The term "linear regression" refers not to the shape of the relationship, which may or may not be a straight line, but to the relationship between the variances of the components of the model. In linear models the regression coefficients have a linear relationship to each other. That is, the observations are expressed as sum of terms, such as the familiar $y = a + bx$ for a straight line, or $y = a + bx + cx^2$ for a quadratic equation. In nonlinear models, the coefficients do not have this relationship. In the exponential model used in this study, the error component is not additive; it is multiplicative. It is therefore referred to as a nonlinear model, and cannot be fitted by the usual methods of linear regression.

Nonlinear models are much more difficult to fit than linear models. To quote from Allen and Cady (1982): "... we begin with crude estimates of the parameters and then approximate the nonlinear model by a linear model. Estimates of the parameters of the approximating linear model are found by standard techniques. These estimates are used to improve our initial estimates and the process is repeated.

However, since the initial estimates of the parameters may be far from the final estimates, a sizable number of approximations may be required. Fortunately, computer programs are available for computations."

In the case of the Richards function, used in this study, good starting values are needed if good fits are to be obtained (Causton *et al.*, 1978). The process of estimating starting values was made simpler in this study since the asymptote was known to be approximately equal to total cumulative sprouting. In a few cases, poor fits were obtained on the first attempt, but adjustment of starting values resulted in good fits.

The value of soil solarization for weed control by killing heat-sensitive weeds in the surface layers of the soil has been demonstrated in subtropical and warm temperate regions. What has become apparent in the course of this research, however, is the potential of soil solarization to contribute to the control of heat tolerant weeds, not necessarily by killing weed propagules, but by stimulating germination and/or sprouting. It has been noted that the main loss of soil weed seed reserves is due to germination, and not to loss of viability *in situ* (Karssen, 1982). Numerous possibilities exist to take advantage of and to assist this natural phenomenon. One option can be through breaking dormancy by raising soil temperatures and the amplitude of temperature fluctuations, and following solarization-induced germination with mechanical or chemical control methods.

Before weed control by killing or stimulating germination of weed propagules can become generally recommended or practiced, information on the temperatures and times of exposure required for the desired effect must be obtained by experimentation for specific important weeds in various regions. Since both heat injury and germination stimulation appear to be cumulative (although not additive), there is good potential for the development of a modeling approach to this problem. This has been the major focus of this project.

CHAPTER III

METHODOLOGY

INTRODUCTION

A number of factors can affect tuber sprouting. Some of these occur during or subsequent to tuber collection, while others can exert their effect during the growth of the purple nutsedge plant prior to tuber collection. The act of collecting tubers exposes them to light and higher atmospheric oxygen, breaks tuber chains, and exposes tubers to air temperatures which are higher than the temperature of the soil from which they were removed. All of these may stimulate sprouting (Loustalot *et al.*, 1954; Muzik and Cruzado, 1953; Palmer and Porter, 1959; Shamsi et al, 1978; Sierra, 1973; Teo *et al.*, 1973; Tripathi, 1967; Ueki, 1969).

Early in this study, it was observed that at the less favorable temperature regimes, buds often initiated growth, then failed to elongate and finally senesced at a length of less than one to a few millimeters. Clarification of this phenomenon was necessary.

Daily counting and removal of sprouted tubers exposes them to light and to disturbances in atmosphere. Aleixo and Valio (1976) reported that even a short (5-minute) exposure to light inhibited purple nutsedge rhizome elongation. Other authors have reported that exposure to light stimulates sprouting of purple nutsedge tubers (Loustalot *et al.*, 1954; Muzik and Cruzado, 1953; Shamsi *et al.*, 1978). It is

necessary to ascertain whether the approximately 5 minute exposure to light during daily counting causes shoots to stop growing after initiating growth, as had been observed.

Low rainfall during the summer at Waimanalo sometimes caused senescence of the aboveground portions of purple nutsedge plants due to water stress. It was necessary to determine whether water stress on purple nutsedge plants would affect subsequent sprouting of tubers from those plants.

Several experiments were conducted to determine the effect of tuber growing conditions, and collection and counting methods on tuber sprouting, in order to identify an appropriate methodology for characterizing tuber sprouting. These experiments were conducted in four series: the first to determine the appropriate criteria for counting a tuber as sprouted; the second to evaluate the effect of daily counting of sprouted tubers; the third to evaluate the effects of water stress; and the fourth to determine the effect of cold storage on tuber sprouting (due to the difficulty of collecting the large numbers of tubers needed for this study, it was hoped that tubers could be collected in advance and stored). These experiments were conducted in incubators in the laboratory using tubers collected from natural populations in the field.

MATERIALS AND METHODS

For all four series of experiments, much of the methodology was the same. Those materials and methods which were common to all experiments are described first. Methodology unique to an experiment is described for that experiment separately.

COMMON MATERIALS AND METHODS

Incubators

Five incubators were used for maintaining the temperatures needed for these experiments. Three were convection type bacteriological incubators capable of maintaining temperatures above ambient temperature. Two of these were of 0.09 m^3 capacity, and the third had a capacity of 0.5 m^3. All three were capable of maintaining constant temperatures within 0.5 C of the desired temperature. The other two incubators were forced convection incubators capable of maintaining constant temperatures or any desired combination of diurnally alternating temperatures from -10 to 50 C with a precision of plus or minus 0.5 C in the range of 20 to 40 C, and plus or minus 0.8 C at 50 C. These had a capacity of 1.5 m^3 each.

Tubers

Tubers for these experiments were all collected from the University of Hawaii Waimanalo Experiment Station on the island of O'ahu, from two adjacent fields with high populations of purple

nutsedge. The Waimanalo Experiment Station is located on the windward side of the island, at an elevation of 20 m. The soil on the station is a typic haplustoll with a pH of 6.

O'ahu is located between 21 and 22 degrees north latitude, just inside the northern limit of the tropical belt. Air temperatures at the station average from 22 to 26 C during the year. Rainfall averages 1320 mm per year, and is heaviest from December to March (Jong *et al.*, 1982). From 1975 to 1979, Jong *et al.* (1982) recorded solar radiation at Waimanalo. They reported monthly means ranging from a low of approximately 250 to 300 cal cm^{-2} day^{-1} in the winter to a high of slightly less than 500 cal cm^{-2} day^{-1} in the summer.

1986, when most of the experiments described in Chapters III and IV were conducted, was a relatively dry year, with only 875 mm of rainfall. During the period from March to August, 1990, when the rest of the experiments were conducted, only 121 mm of rain fell, approximately 24 mm per month. The plots used for tuber collection in 1986 were overhead irrigated twice each week, with 15 to 20 mm of water at each irrigation. Tuber collection plots were not irrigated in 1990.

In most experiments, tubers were from plots maintained for the purpose of tuber collection, and the growing conditions and age of the plants were known. Only mature brown or black tubers were used. No selection was made on the basis of size, but any tubers with physical damage, or which were soft, rotten, or otherwise clearly not viable were not used.

Tubers were collected in the morning, and collection took from one to four hours or more depending on the number needed. They were rinsed free of soil in the field, then brought to the laboratory. Tubers were rinsed quickly (in less than 5 minutes), and were not allowed to soak in water since leaching or washing may affect tuber sprouting (Aleixo and Valio, 1976; Teo *et al.*, 1973).

The effects of tuber collection were minimized by collecting as quickly as possible, by keeping collected tubers moist and in shade, and by transporting them to the laboratory, where the temperatures were not favorable for sprouting, as quickly as possible.

Tuber Viability

Percentage sprouting was calculated based on the number of viable tubers in each replication. The number of viable tubers in each dish was obtained by TTC (triphenyl tetrazolium chloride) test on unsprouted tubers at the end of each experiment. TTC turns pink when reduced by the enzyme dehydrogenase, indicating that respiration is taking place. It is a common test of seed viability (Salisbury and Ross, 1978). This test was used by Zandstra (1976) to assess the viability of purple nutsedge tubers from plants treated with glyphosate. The TTC test was not always easy to evaluate, however, so it was generally preceded by subjecting unsprouted tubers to temperatures known to stimulate sprouting for

one to two weeks. Tubers which initiated growth were counted as viable, and the TTC test was then used on those tubers which still failed to initiate growth.

When testing for viability with TTC, tubers were split longitudinally and one half of each tuber was soaked in 0.1% TTC at 30 C until a color response was observed in known viable tubers included as a check on the test (one to three hours). Pink coloration of the vascular system was considered an indication of tuber viability. Total viability was the sum of all sprouted tubers and those testing positive by TTC. Tuber viability generally ranged from 85 to 100 percent in these experiments.

Tuber Sprouting

Tubers were trimmed of roots and rhizomes in the laboratory to enable them to fit into the petri dishes. Except as otherwise noted, tubers were sprouted on two layers of filter paper moistened with deionized water, in 9 cm petri dishes. There were five replications of 20 tubers each, except where otherwise noted, which were stacked and enclosed in 0.028 mm (1.1 mil) polyethylene bags, one bag per treatment, to preserve moisture. Replications were numbered from top to bottom, to make it possible to detect and remove any variation in response due to position in the stack. These were not true replications since they were all in the same bag in the same incubator. They did, however, provide an estimate of experimental error.

In some cases, tubers were placed into the incubators on the evening of the day they were collected, but in most experiments they were kept in the petri dishes on the lab bench overnight at approximately 22 C, and treatments were begun the following morning.

Tubers were counted as sprouted after at least one shoot reached 1.0 centimeter in length. Sprouted tubers were counted and removed daily. In some longer experiments, counts were reduced to once every two or three days after sprouting had leveled off near maximum.

Since the number of viable tubers varied from one replication to another, percentage sprouting was calculated based on the number of viable tubers in each replication. With the small number of tubers in each petri dish, it was important to compute percent sprouting based on the number of viable tubers in each, rather than on an overall estimate of tuber viability (Scott *et al.*, 1984).

Analysis

Two variables were used to compare the sprouting responses in these experiments: final cumulative sprouting; and time to 50 percent of final cumulative sprouting (T_{50}). Several authors have derived a germination rate by taking the reciprocal of the time to 50 percent germination (Reciprocal Median Response Time, Scott *et al.*, 1984) and have used this variable for comparisons. This manipulation is useful in heat sum models since it linearizes the

response to temperature (Bierhuizen, 1973), but for comparison of treatments this was not necessary. Since rate is derived from time, it was decided to use time, rather than a derived variable.

Using the two variables total sprouting and T_{50} it was possible to separate the effects of the various treatments. Using only total sprouting is inadequate because at most combinations of alternating temperatures all or nearly all tubers sprouted, but not always in the same period of time. Nor was T_{50} alone adequate, since some treatments reached different totals in the same amount of time. In general, single-value measures or indices of germination cannot adequately represent germination, and at least two measures are needed (Brown and Mayer, 1988a; Scott *et al.*, 1984).

EXPERIMENTS

Initiation of Growth vs. Tuber Sprouting

To quantify the difference between growth initiation and elongation, two experiments were conducted in which both initiation of growth and sprouting were counted. A tuber was considered to have initiated growth if at least one bud had produced a visible shoot at least 1 mm in length, and as sprouted if at least one shoot was at least 1 cm in length. Temperatures in these experiments were alternating 22.5/27.5 C and ambient laboratory temperature of alternating 22/24 C, the temperature at which the difference between growth initiation and elongation was first

observed. There were 5 replications of 50 tubers each in 15 cm petri dishes. The number of tubers which had initiated growth and the number sprouted were counted daily, with sprouted tubers being removed. The experiment continued for 21 days, by which time both growth initiation and sprouting had leveled off. The experiment was repeated with tubers collected from the same location five days after tuber collection for the first experiment.

Effect of Counting Method

Two experiments were conducted to test for the combined effect of the disturbance and daily exposure of tubers to light caused by the daily counting of sprouted tubers. In the first experiment, tubers were sprouted under four temperature regimes; constant 24 C, and alternations of 18, 20, and 22 C with 24 C. The tubers were allowed to sprout for 5 weeks in total darkness, or were counted daily. The effects of daily exposure to light and daily counting were therefore confounded in this experiment. Final cumulative percent sprouting at the end of the experiment was the variable compared.

In a similar experiment, six temperature regimes were used; constant 20 C, and alternating 20/25, 20/30, 20/35, 20/40, and 20/45 C. The experiment lasted for two weeks, and final cumulative percent sprouting was compared.

Effect of Water Stress

To determine whether water stress on purple nutsedge plants would affect subsequent sprouting of tubers from those plants, an experiment was designed to compare sprouting of tubers from stressed and unstressed plants. Irrigation was withheld from half of a plot heavily infested with purple nutsedge for a period of one month prior to tuber collection. During this 4 week period there were only 42.9 mm of rainfall, and after one month almost all plants in the half of the plot without irrigation had senesced completely, while those in the irrigated half of the plot were green and vigorous. Tubers were collected from both halves of the plot and subjected to constant 30 and 40 C, and alternating 30/40 C with 12 hours at each temperature. Sprouted tubers were counted and removed daily for 54 days, then every three days until the experiment was terminated, 71 days after it began.

In July and August, 1986, an experiment was conducted to evaluate the effects of plant age and water stress on tuber sprouting. Tubers were collected on July 23, 1986 from two adjacent plots. One plot was last rotovated on January 29, 1986, and the other on March 29, 1986, so the plants were 6 and 4 months old, respectively. One half of each plot was irrigated until the day of collection, while the other half had irrigation withheld 6 weeks prior to collection. There were only 57.4 mm of rainfall during these 6 weeks; less than 10 mm per week. The highest daily rainfall during this period was just 6.6 mm. Thus, in half of each

plot the plants were green and vigorously growing, while in the other half the plants were all senesced. Tubers were collected from all four areas and subjected to the following temperatures: ambient laboratory temperature of 22 to 24 C; constant 40 C; and alternating 30/40 C. A fourth set of tubers was incubated in a greenhouse at temperatures of approximately 23 to 39 C. This experiment continued for 70 days.

The experiment was repeated with tubers collected on July 25, 1986, two days after collection for the first experiment, and continued for 72 days.

Effect of Cold Storage

Three experiments were conducted to evaluate the effect of short term storage at temperatures between 0 and 10 C on subsequent tuber sprouting.

Tubers were collected for the first experiment on January 31, 1986 and stored moist in a 0.05 mm (2 mil) thick polyethylene bag at 6 C for 10 days. Fresh tubers were collected from the same location on February 7, 1986 and kept moist on the lab bench for three days at 21 to 23 C. All tubers were placed in petri dishes as previously described on February 10, 1986. The temperature treatments applied were constant 25 and 30 C.

A similar experiment was conducted in March, 1986, with temperatures of constant 25, 30, and 35 C. Tubers were collected on February 21, 1986 and placed in cold storage at 6 C. Tubers

were collected from the same location on March 2, 1986, and treatments began on March 3. This experiment was repeated with tubers collected from the same location on March 7 and 16, with treatments beginning on March 17. Counts in all three experiments continued for 28 days.

RESULTS AND DISCUSSION

INITIATION OF GROWTH VS. TUBER SPROUTING

The results of the two experiments were combined, and the percent of tubers which had initiated growth and the percent which had sprouted were compared. There was an interaction between temperature and treatment effects, so comparisons were made separately for the different temperatures. At both temperature regimes the difference between the number of tubers initiating growth and those sprouting was significant at the 1 percent level. These results are presented in Table 1 and in Figure 1.

At both temperature regimes a large number of tubers had buds which initiated growth, but then did not elongate. These buds eventually senesced. The percent of tubers which initiated growth but whose shoots did not elongate was also determined. The difference was particularly pronounced at the lower temperature regime, where 87.5 percent of the tubers which initiated growth failed to produce a shoot 1 cm long in 21 days. At the higher temperature regime, 13.2 percent failed to elongate after initiating growth. Not

surprisingly, this difference between temperature regimes is significant at the 1 percent level. These results are presented in Table 2 and in Figure 2.

These experiments showed that under certain conditions tuber buds may initiate growth without continuing to grow, with this phenomenon being most pronounced at lower temperature and smaller amplitude of temperature alternation. Without further experimentation it is not possible to determine the cause of this phenomenon, but in this study initiation of growth appears to have been at least in part an artifact of the collection process rather than a response to the treatments applied. Whatever the cause, it is clear that initiation of growth is not a good indicator of whether a shoot will continue to elongate and produce a plant. Initiation of growth is useful as an indicator of tuber viability, but gives misleading information on the sprouting response to temperature. For this reason, tubers in all experiments were counted as sprouted only after at least one shoot reached 1.0 centimeter in length.

I have been able to find only one reference to criteria for sprouting in the several published studies on tuber sprouting. In that study any tuber which initiated shoot and/or root growth was counted as sprouted (Shamsi *et al.*, 1978). It is likely that in other studies tubers were counted as sprouted when an emerged shoot was visible. The sprouting percentages reported in this study may therefore appear low when compared to results from other researchers, but they are an accurate description of reality in this study.

EFFECT OF COUNTING METHOD

In the first experiment, the difference in total sprouting between treatments was approximately 15 percent over the range of temperatures tested. There was no interaction between temperature and treatment, so a single slope regression model was fitted to the two counting treatments. The results are shown in Figure 3 and the analysis of variance for regression is presented in Table 3.

In the second experiment, the difference in mean total sprouting ranged from a high of 17.2 percent at constant 20 C to a low of 1.1 percent at alternating 20/35 C. The effect of counting treatment was significant at the 1 percent level, but the differences in total sprouting diminish to the point of unimportance at temperature regimes which result in near 100 percent sprouting, while the difference is greatest and most important at lower temperatures. There was a significant interaction between temperature and treatment so a separate regression model was fitted to each treatment. The results are presented in Table 4 and Figure 4.

These results indicate that the counting method used in these experiments did depress sprouting at lower temperatures, and in temperature regimes which do not promote complete sprouting. As a result, a sprouting model developed from such experiments may under predict sprouting slightly at these temperatures. This was unfortunate, but unavoidable, since sprouting had to be counted daily, and it was not possible to transfer the tubers between

incubators and to count sprouted tubers in complete darkness. Destructive harvesting techniques could not be used because of the very large numbers of tubers which would have been needed, and because of the limited amount of incubator space available. It is not likely, however, to have a great effect on the prediction of responses to soil solarization, since the effect of daily counting is small at the temperatures encountered under solarization. The effect may be more important in predicting tuber sprouting under non-solarized conditions.

It is interesting to note in the first experiment that there is a downward trend of total sprouting in response to increasing minimum temperature. This seems illogical until one realizes that it is actually a positive response to increasing amplitude of temperature alternation from 0 to 3 degrees. This is an illustration of the important effect of temperature alternation on purple nutsedge tuber sprouting, which will be discussed in Chapter IV.

EFFECT OF WATER STRESS

In the first experiment, final cumulative sprouting was 100 percent for tubers from both stressed and unstressed plants at alternating 30/40 C (Figure 5). At constant temperatures, however, sprouting was lower in tubers from unstressed plants. This difference was significant at the 1 percent level, as presented in Table 5. In all three temperature regimes tubers from unstressed plants took longer

to reach 50 percent of final cumulative sprouting (Figure 6), and this difference was significant at the 1 percent level (Table 6).

The results of the second and third experiments were combined, and the results were similar to those of the first experiment. At temperature regimes which promoted complete sprouting there was no difference in final cumulative sprouting, but cumulative sprouting of unstressed plants was lower in constant temperature and low temperature regimes, and sprouting of tubers from unstressed plants was slower in all treatments (Tables 7 and 8, and Figures 7 and 8).

In all three experiments comparing water stressed and unstressed plants, final cumulative sprouting of tubers from unstressed plants was significantly lower at ambient laboratory temperature and at constant temperatures. At alternating 30/40 C and in the greenhouse, 100 percent of the tubers from both stressed and unstressed plants sprouted, so no differences could be detected. In all temperature regimes, however, tubers from stressed plants sprouted faster, and all differences were significant at least at the 5 percent level.

These results demonstrate that water stress can result in a significant increase in both the rate and level of tuber sprouting, especially at temperatures which are less conducive to sprouting. It is possible that water stress should be treated as a continuous rather than as a discrete variable (stressed vs. unstressed), since there can be varying degrees or intensities of stress. Two obvious

factors contributing to degree of stress are the length of time the plant is under water deficit, and the magnitude of the deficit. These experiments did not attempt to fully elucidate the effects of water stress, and further work is needed to clarify the relationship between water stress and subsequent tuber sprouting. This phenomenon could also serve as a tool to increase tuber sprouting in the field prior to treatment with herbicides.

It is interesting to note that both stressed and unstressed tubers sprouted faster and more completely at alternating 30/40 C than at either constant temperature. Temperature regimes were treated as discrete variables in the analysis rather than as a continuous temperature variable due to the obviously different response to alternating and constant temperatures. This phenomenon will be investigated further in Chapter IV.

EFFECT OF COLD STORAGE

In the first experiment, fresh tubers sprouted faster and had higher total sprouting than chilled tubers (Figures 9 and 10). In the next two experiments, however, the results were the opposite, with higher and faster sprouting in the chilled tubers (Figures 11 and 12).

In the first experiment there was no interaction between storage and temperature effects on final cumulative sprouting so the main effects were compared in the analysis of variance. There was no

effect of temperature on time to 50 percent sprouting so the means for storage treatment were compared using a T test. The results are presented in Tables 9 and 10, and in Figures 9 and 10.

The last two experiments were combined. There was no interaction between storage and temperature effects on either final cumulative sprouting or time to 50 percent sprouting, so only main effects were compared in the analysis of variance. In all three experiments, differences in sprouting between fresh and chilled tubers were significant at the 1 percent level. The results are presented in Tables 11 and 12 and in Figures 11 and 12.

Shamsi *et al.* (1978) reported increased sprouting of dry-chilled tubers, and decreased sprouting from tubers chilled in water. It may be that the tubers in the first experiment were wetter than those in the second two experiments, since all were stored moist. Another possibility is that 3 days on the laboratory bench prior to initiation of the first experiment somehow stimulated the subsequent sprouting of the "fresh" tubers. This does not seem likely, however, because total sprouting is similar for fresh tubers in all three experiments, and the differences are in the total sprouting of chilled tubers. For the purposes of this study, the important point is that in all three experiments total cumulative sprouting and time to 50 percent sprouting were significantly different for stored and fresh tubers. As a result of these experiments, it became clear that cold storage did affect both the rate and extent of sprouting. All subsequent experiments were therefore conducted using freshly

Table 1. Comparison of percent of tubers with buds initiating growth (break) and percent of tubers with shoots at least 1.0 cm in length (sprout) under two temperature regimes.

Regime[x]	Buds	Mean	Std. Err.	T Value	Prob > T
22/24	Break	84.1	2.1	23.2	< 0.0000
	Sprout	10.1	2.4		
22.5/27.5	Break	98.3	0.8	4.8	0.0001
	Sprout	85.4	2.6		

[x] Minimum and maximum temperature in diurnal temperature alternation (degrees Celsius).

Table 2. Comparison of percent of tubers with buds initiating growth but not continuing to elongate under two temperature regimes.

Regime[x]	Mean	Std. Err.	T Value	Prob > T
22/24	87.5	1.9	30.2	0.0001
22.5/27.5	13.2	1.5		

[x] Minimum and maximum temperature in diurnal temperature alternation (degrees Celsius).

Table 3. Analysis of variance for effect of minimum temperature (MINTEMP) and counting method (TREATMENT) on final cumulative tuber sprouting. Counting treatments are counted once after 36 days in total darkness or counted daily for 36 days. Temperature regimes are constant 24 C and 12-hour diurnal alternations of 18/24, 20/24, and 22/24 C.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	13568.10	6784.05	36.48	0.0001
Error	36	6694.73	185.96		
Corrected Total	38	20262.83			

R-Square	C.V.
0.67	22.60

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MINTEMP	1	11286.26	11286.26	60.69	0.0001
TREATMENT	1	2281.84	2281.84	12.27	0.0012

Table 4. Analysis of variance for effect of maximum temperature (MAXTEMP) and counting method (TREATMENT) on final cumulative tuber sprouting. Counting treatments are counted once after 14 days in total darkness or counted daily for 14 days. Temperature regimes are constant 20 C, and 12-hour diurnal alternations of 20/25, 20/30, 20/35, 20/40, and 20/45 C. One missing value each at 20/35 and 20/40 C.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	49598.25	16532.75	256.75	0.0001
Error	54	3477.19	64.39		
Corrected Total	57	53075.45			

R-Square	C.V.
0.93	10.23

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MAXTEMP	1	28148.48	28148.48	437.14	0.0001
MAXTEMP*MAXTEMP	1	20789.87	20789.87	322.86	0.0001
TREATMENT	1	659.90	659.90	10.25	0.0023

Table 5. Analysis of variance for effect of temperature regime and water stress on final cumulative tuber sprouting at constant temperature.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	5627.69	2813.84	24.82	0.0001
Error	17	1927.35	113.37		
Corrected Total	19	7555.04			

R-Square	C.V.
0.74	13.15

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Temp Regime	1	2956.00	2956.00	26.07	0.0001
Water Status	1	2671.69	2671.69	23.57	0.0001

Table 6. Analysis of variance for effect of temperature regime and water stress on time to 50 percent of final cumulative tuber sprouting at constant and alternating temperature.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	191.83	63.94	7.75	0.0007
Error	26	214.47	8.25		
Corrected Total	29	406.30			

R-Square	C.V.
0.47	33.01

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Temp Regime	2	111.80	55.90	6.78	0.0043
Water Status	1	80.03	80.03	9.70	0.0044

Table 7. Analysis of variance for effect of temperature regime and water stress on final cumulative tuber sprouting at constant temperature. Combined second and third experiments.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	44984.06	22492.03	47.39	0.0001
Error	77	36543.12	474.59		
Corrected Total	79	81527.18			

R-Square	C.V.
0.55	32.06

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Temp Regime	1	32967.84	32967.84	69.47	0.0001
Water Status	1	12016.22	12016.22	25.32	0.0001

Table 8. Analysis of variance for effect of temperature regime and water stress on time to 50 percent of final cumulative tuber sprouting at constant and alternating temperature. Combined second and third experiments.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	1430.60	357.65	26.82	0.0001
Error	155	2066.90	13.33		
Corrected Total	159	3497.50			

R-Square	C.V.
0.41	42.34

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Temp. Regime	3	954.500	318.17	23.86	0.0001
Water Status	1	476.100	476.10	35.70	0.0001

Table 9. Analysis of variance for effect of temperature regime and cold storage on final cumulative tuber sprouting. First experiment.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	6226.26	3113.13	15.93	0.0001
Error	17	3322.90	195.46		
Corrected Total	19	9549.16			

R-Square	C.V.
0.65	27.12

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Temp. Regime	1	5076.08	5076.08	25.97	0.0001
Storage	1	1150.18	1150.18	5.88	0.0267

Table 10. Comparison of time to 50 percent of final cumulative percent sprouting of fresh and stored tubers. First experiment.

Treatment	Mean	Std. Err.	T Value	Prob > T
Stored	9.10	0.53	4.27	0.0005
Fresh	5.70	0.60		

Table 11. Analysis of variance for effect of temperature regime and cold storage on final cumulative tuber sprouting. Combined second and third experiments.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	30438.26	15219.13	76.19	0.0001
Error	57	11385.76	199.75		
Corrected Total	59	41824.02			

R-Square	C.V.
0.73	19.36

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Temp. Regime	1	27837.17	27837.17	139.36	0.0001
Storage	1	2601.09	2601.09	13.02	0.0006

Table 12. Analysis of variance for effect of temperature regime and cold storage on time to 50 percent of final cumulative tuber sprouting. Combined second and third experiments.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	132.29	66.15	10.46	0.0001
Error	57	360.44	6.32		
Corrected Total	59	492.73			

R-Square	C.V.
0.27	33.83

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Storage	1	77.07	77.07	12.19	0.0009
Temp. Regime	1	55.23	55.23	8.73	0.0045

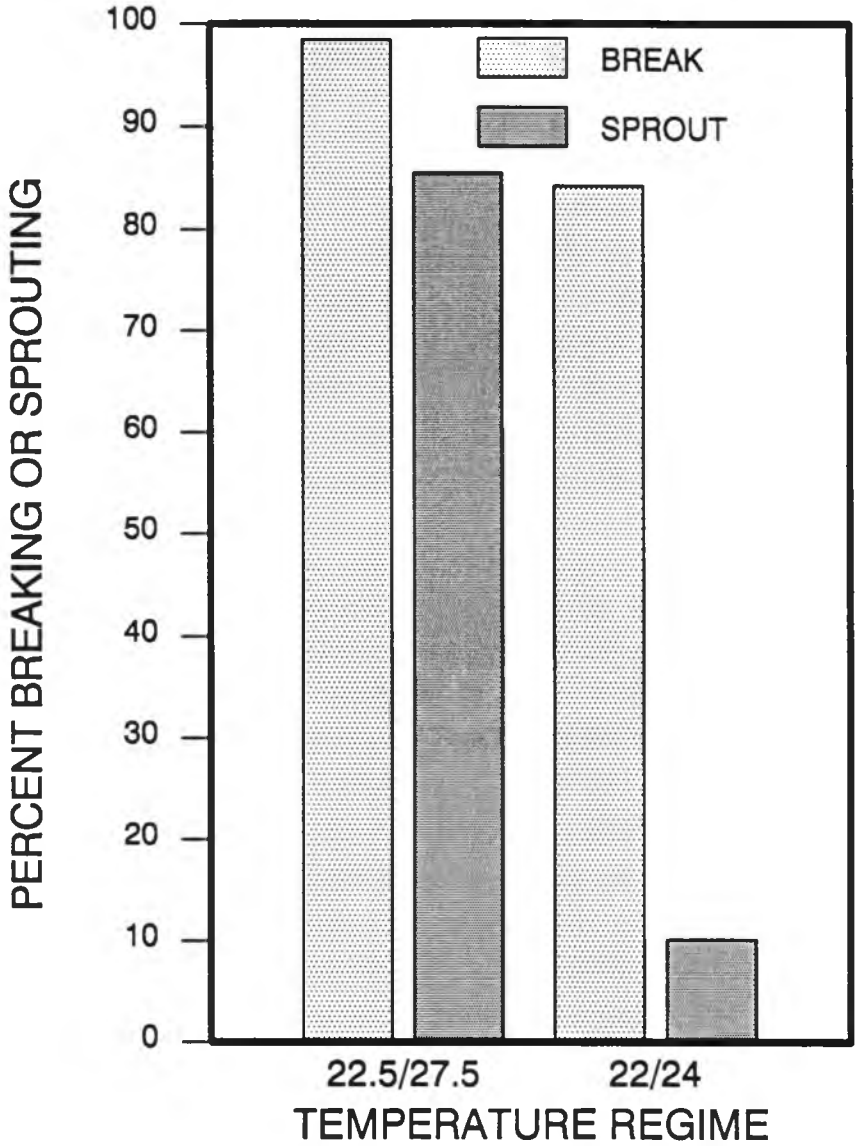

Figure 1. Comparison of percent of tubers with buds initiating growth (break) and percent of tubers with shoots at least 1.0 cm in length (sprout) under two temperature regimes.

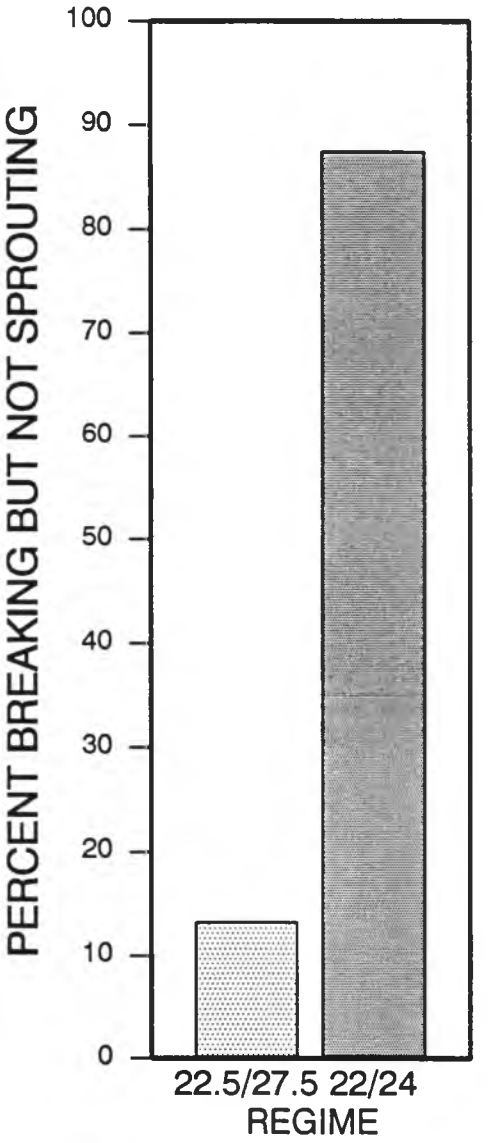

Figure 2. Comparison of percent of tubers with buds initiating growth but not continuing to elongate under two temperature regimes.

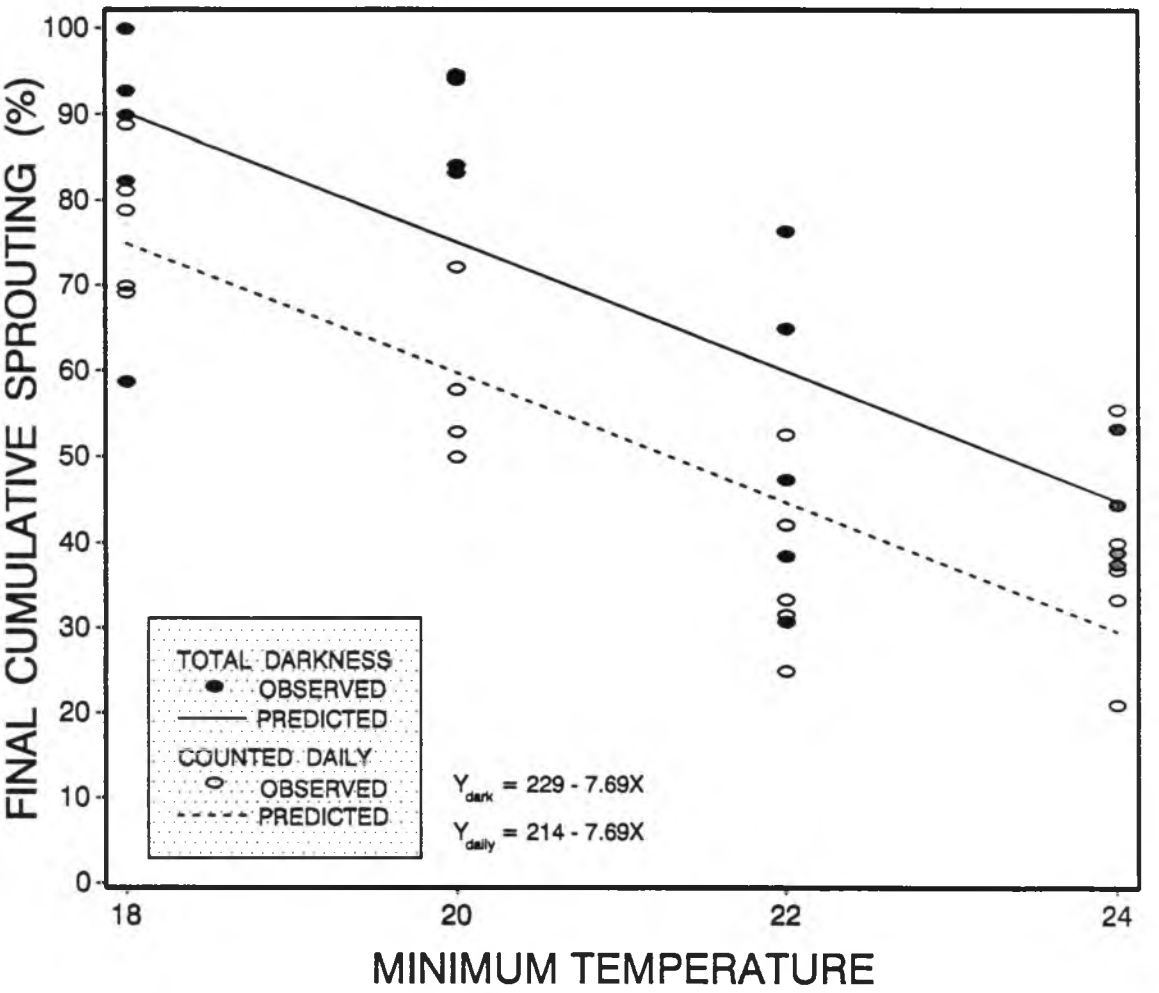

Figure 3. Effect of counting method on final cumulative tuber sprouting. Observed (dots) and predicted (solid line) values for tubers in total darkness for 36 days and observed (circles) and predicted (dashed line) values for tubers counted daily for 36 days. Where 2 or more observations have the same value only one observation can be seen.

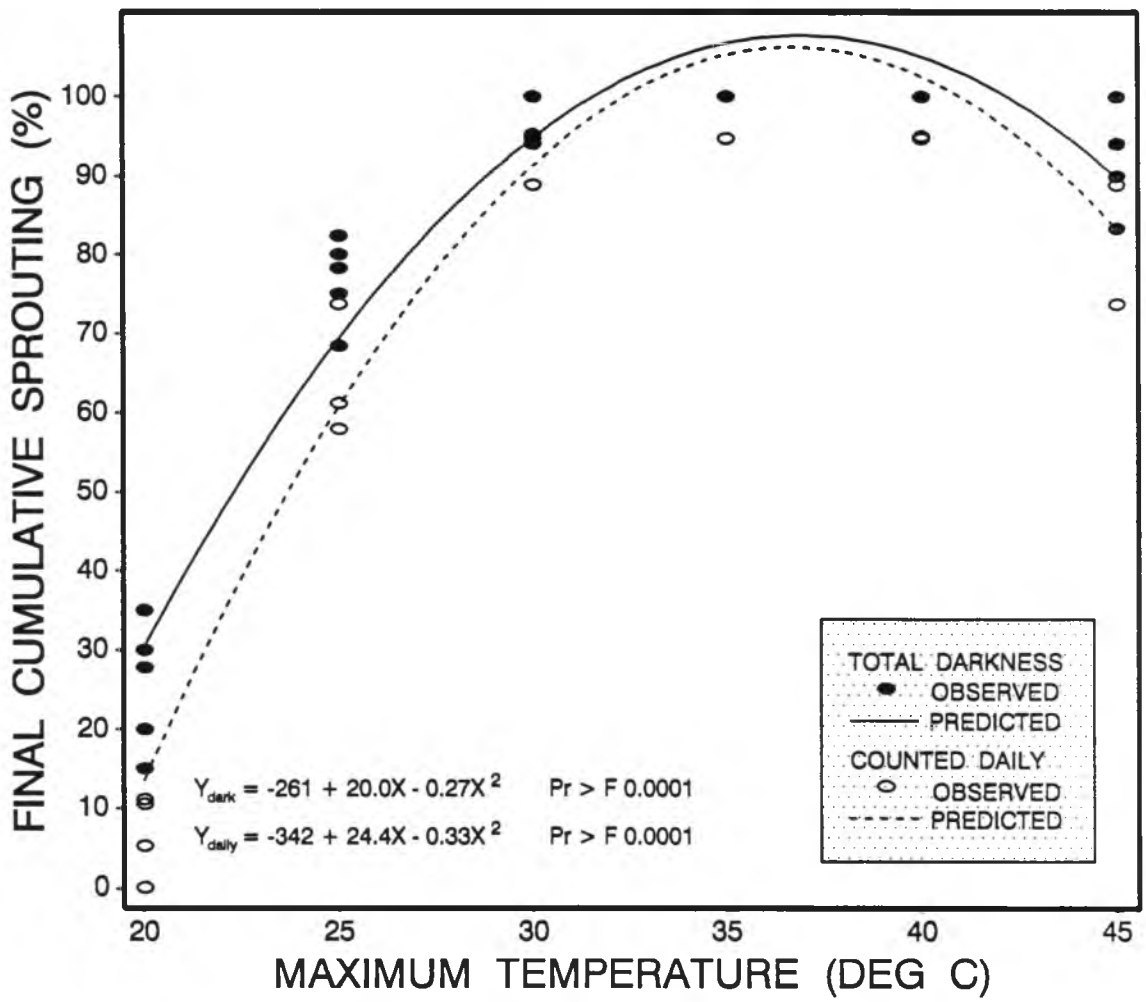

Figure 4. Effect of counting method on final cumulative tuber sprouting. Observed (dots) and predicted (solid line) for tubers in total darkness for 14 days and observed (circles) and predicted (dashed line) values for tubers counted daily for 14 days. Where 2 or more observations have the same value only one observation can be seen.

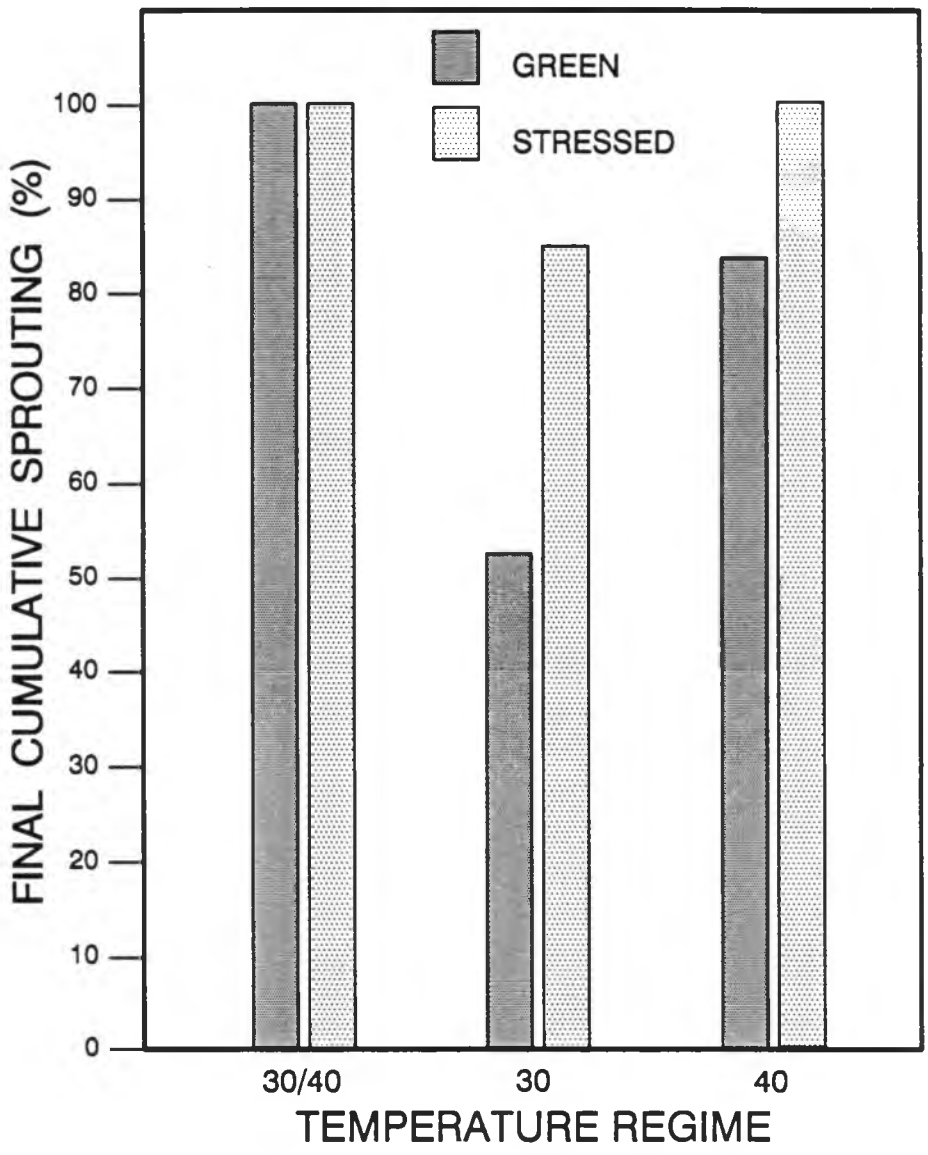

Figure 5. Effect of temperature regime and water stress on final cumulative tuber sprouting at constant and alternating temperature. First experiment.

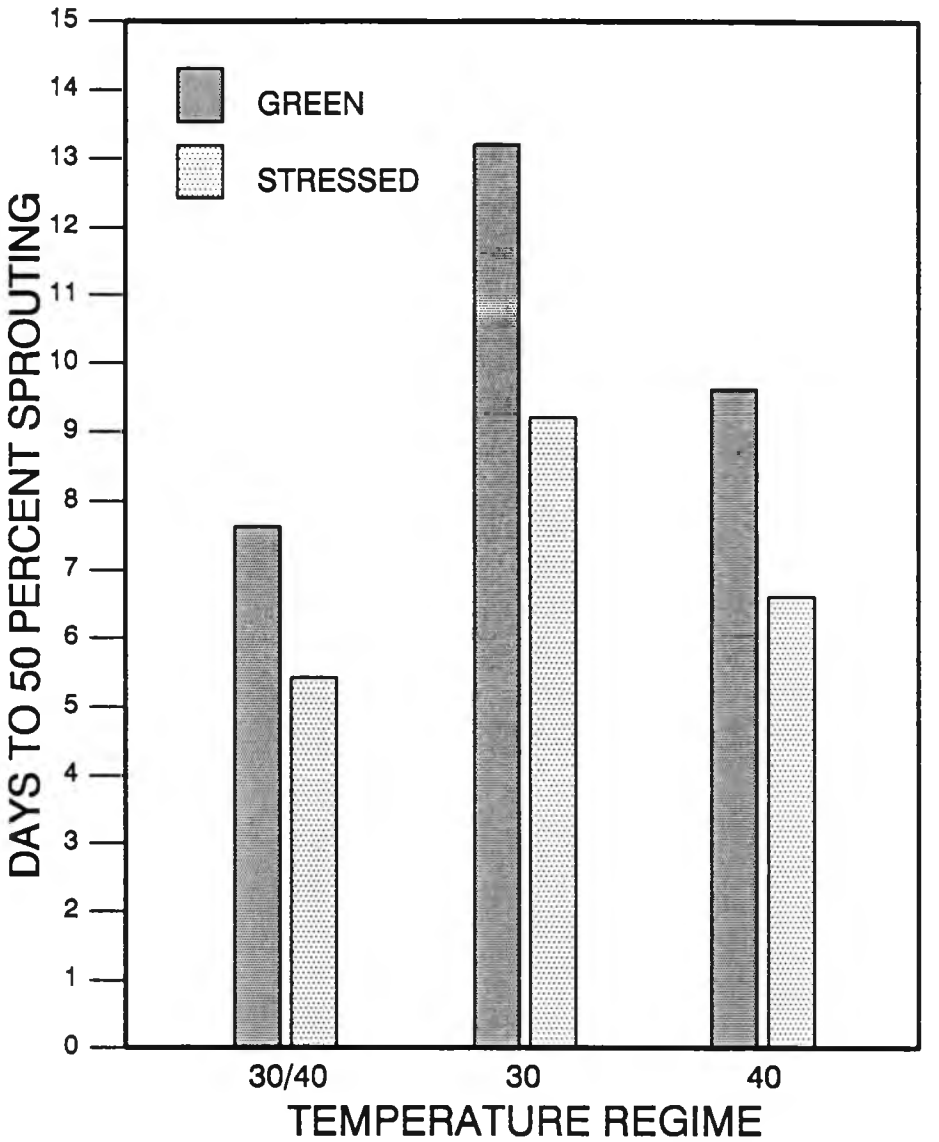

Figure 6. Effect of temperature regime and water stress on time in days to 50 percent of final cumulative tuber sprouting at constant and alternating temperature. First experiment.

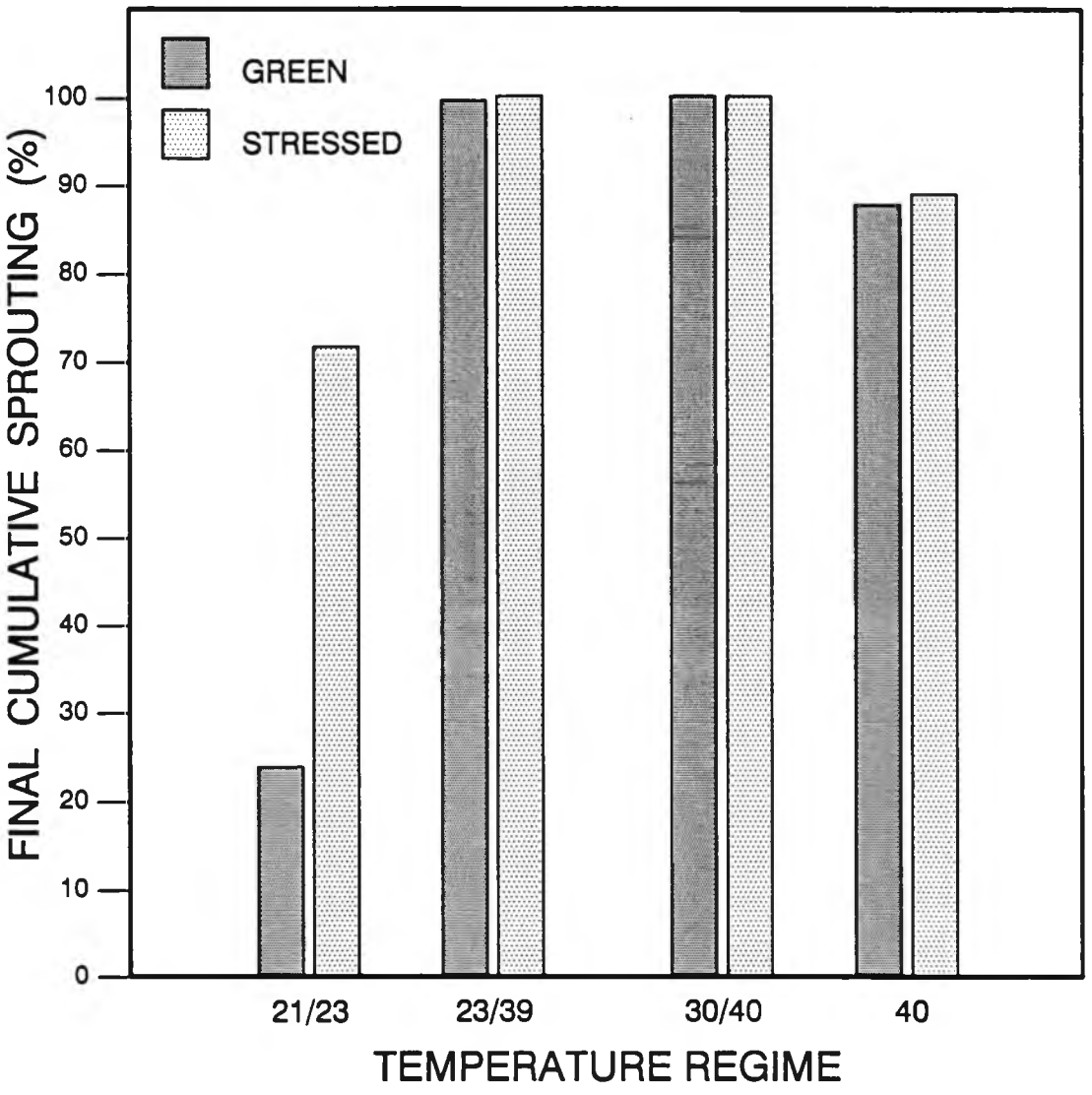

Figure 7. Effect of temperature regime and water stress on final cumulative tuber sprouting at constant and alternating temperature. Combined second and third experiments.

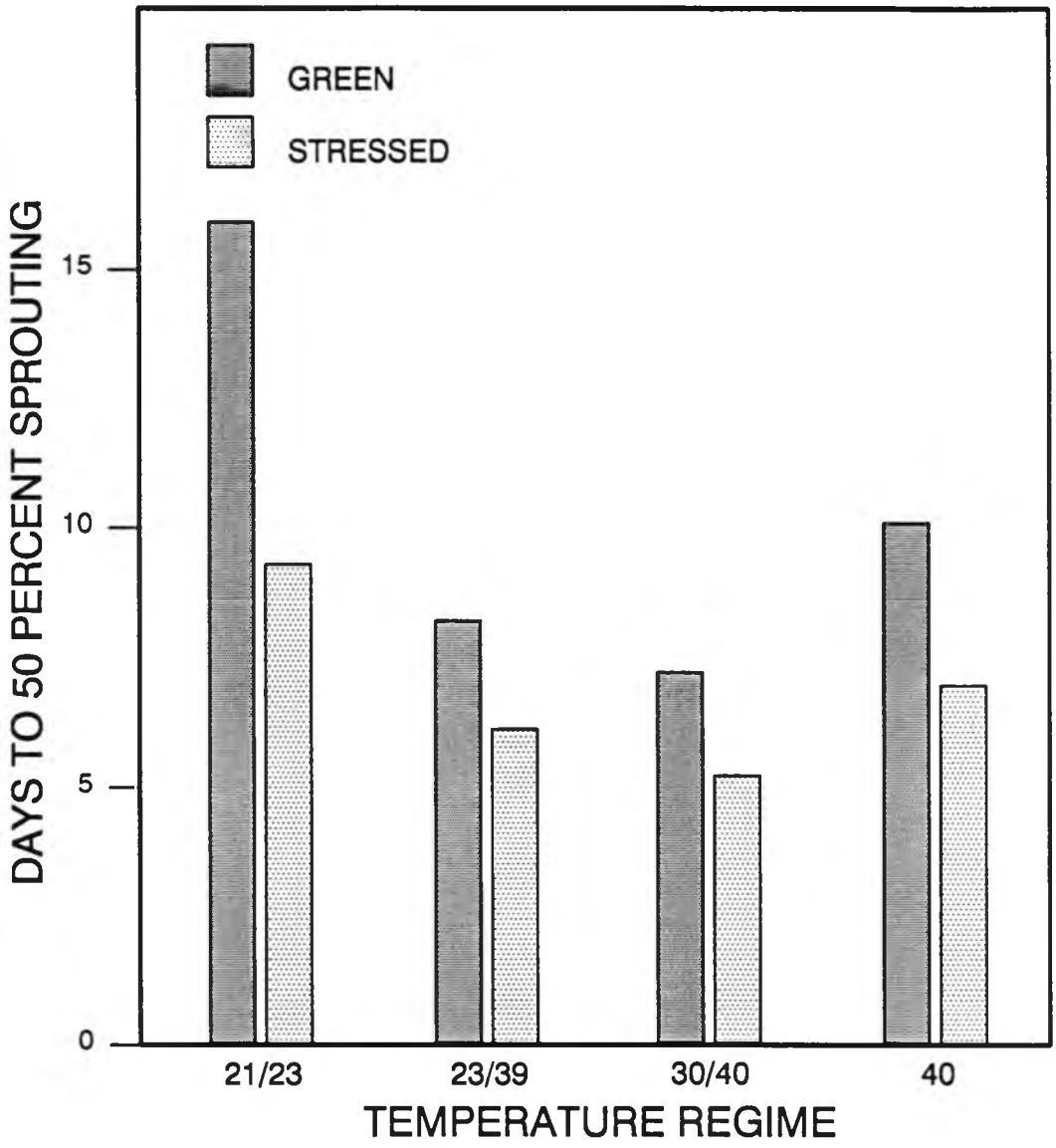

Figure 8. Effect of temperature regime and water stress on time in days to 50 percent of final cumulative tuber sprouting at constant and alternating temperature. Combined second and third experiments.

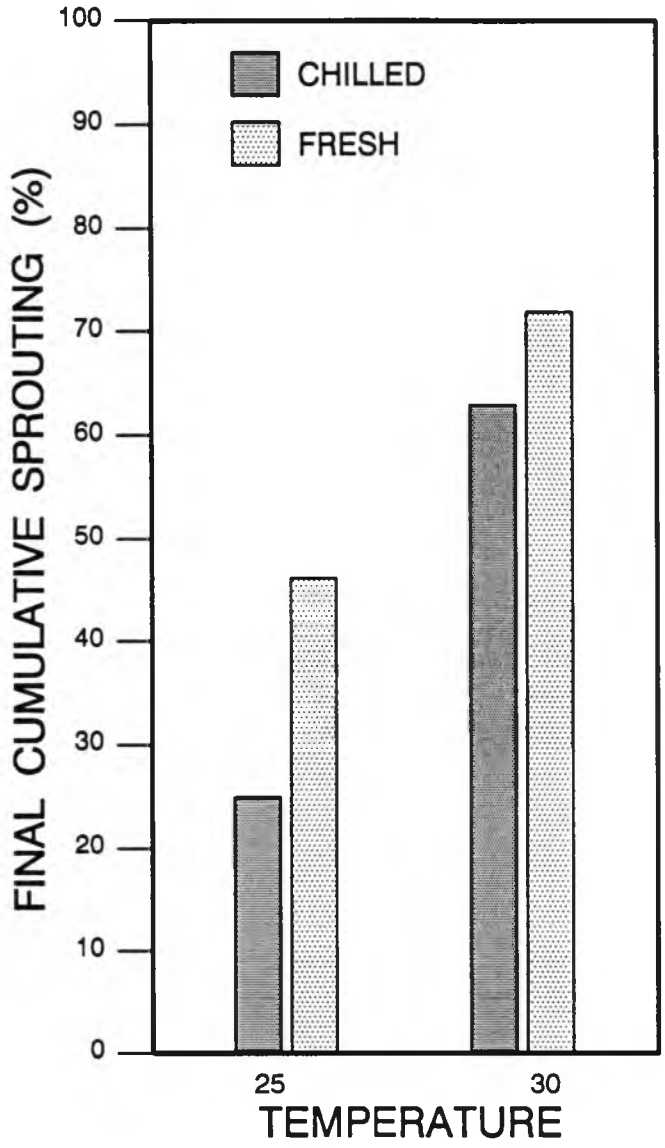

Figure 9. Effect of temperature regime and cold storage on final cumulative tuber sprouting. First experiment.

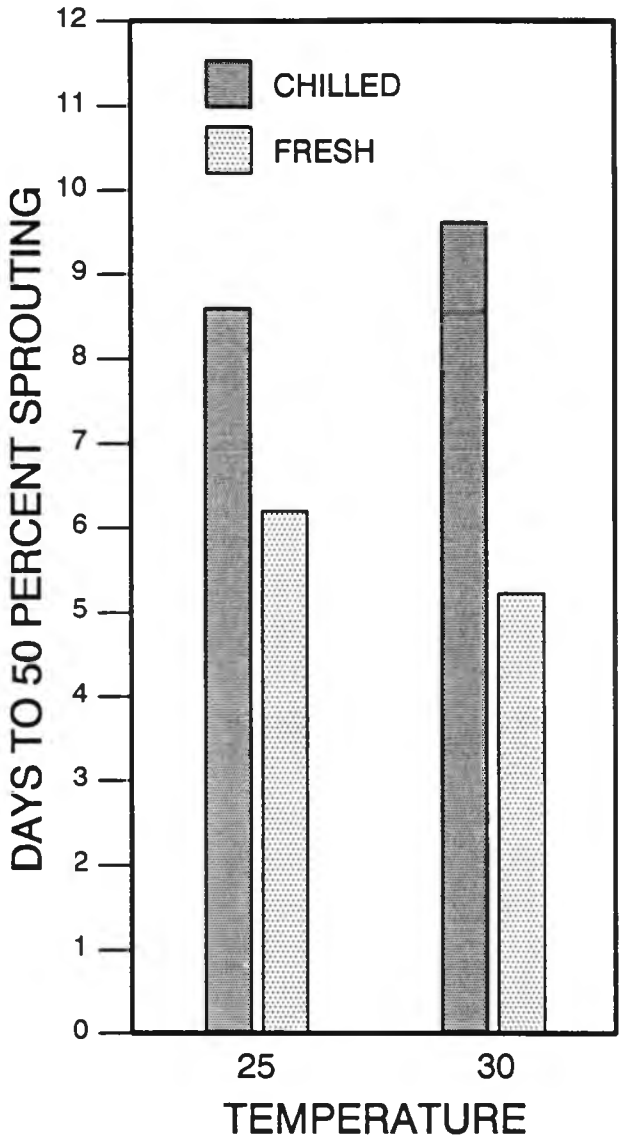

Figure 10. Effect of temperature regime and cold storage on time to 50 percent of final cumulative tuber sprouting. First experiment.

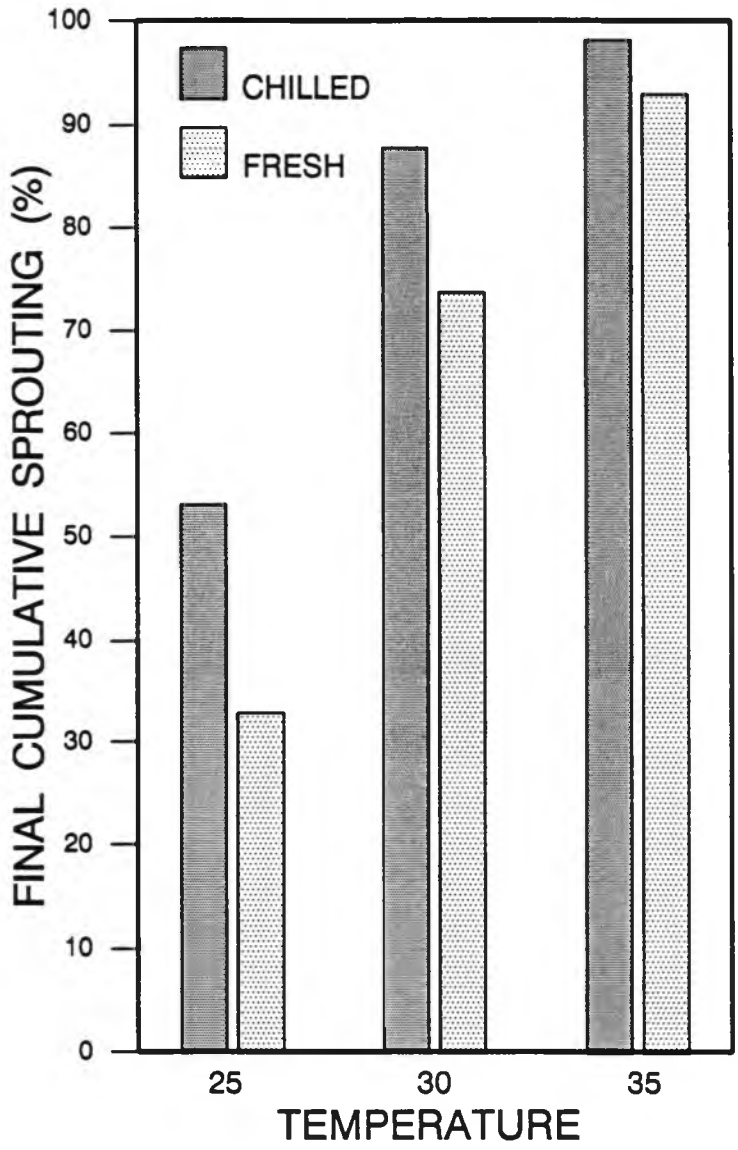

Figure 11. Effect of temperature regime and cold storage on final cumulative tuber sprouting. Combined second and third experiments.

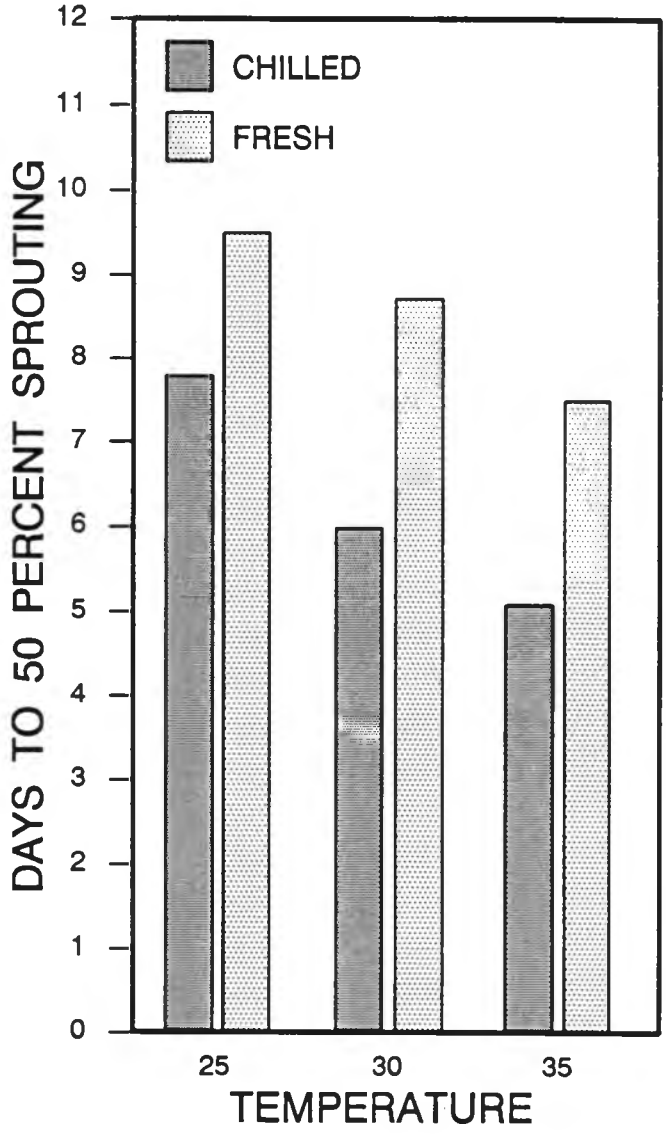

Figure 12. Effect of temperature regime and cold storage on time to 50 percent of final cumulative tuber sprouting. Combined second and third experiments.

CHAPTER IV

TEMPERATURE FACTORS AFFECTING TUBER SPROUTING

INTRODUCTION

The original intent of this study was to develop a heat sum model to predict tuber sprouting over time. Heat sums have been used to predict seed germination in several studies, and it was hoped that a heat sum model could be used for purple nutsedge tuber sprouting. Recently, this approach was used to determine a low TTD (temperature threshold for development) for purple nutsedge (Orcutt and Holt, 1990). Since the type of heat sum model contemplated assumes a linear response to temperature (Bierhuizen, 1973), and is based on responses to constant temperatures, it was necessary to determine at the outset whether the tubers responded differently to constant and alternating temperatures.

Wagenvoort and Bierhuizen (1977) found no response to alternating temperatures in seeds of 17 vegetables, but several authors working with weed seeds have found a response to alternating temperatures, reporting increases in either total germination, rate of germination, or both (Benech Arnold *et al.*, 1988, 1990a, 1990b; Brown, 1987; Cohen, 1958; Evans *et al.*, 1982; Garcia-Huidobro *et al.*, 1982b; Harrington, 1923; Hendricks and Taylorson, 1976; Morinaga, 1926; Pollock, 1972; Totterdell and Roberts, 1980; Wagenvoort and Van Opstal, 1979). A similar response has been reported for purple nutsedge tubers (Tripathi, 1967).

Temperature fluctuation is the natural situation in the field. The amplitude of the fluctuation decreases with increasing soil depth, but even at 30 cm under solarization a range of greater than 1 C between the daily minimum and maximum temperatures can be observed. This diurnal temperature cycle follows a path similar to a sine wave.

This study attempted to simulate the natural diurnal soil temperature alternation using incubators in the laboratory, but the temperature shift in the incubators was much more rapid than the natural alternation in the field. This resulted in the time at minimum and maximum temperatures being considerably longer than in the field. It was important to determine whether the length of time at the maximum temperature would affect sprouting.

Two series of experiments were conducted to characterize the sprouting response of tubers to constant and alternating temperatures. These experiments focused on the effect of alternating temperatures, and the length of time spent at maximum temperature in a diurnal temperature alternation.

MATERIALS AND METHODS

Materials and methods used in these experiments (incubators, tuber collection, tuber viability, sprouting methods, and analysis) were the same as for the experiments described in Chapter III, except as otherwise noted for specific experiments.

ALTERNATING TEMPERATURE

An experiment was designed to compare sprouting at three constant temperatures and one set of alternating temperatures. The temperatures were selected so that the constant temperatures were at the mean and the extremes of the diurnal temperature alternation. The experiment used constant temperatures of 25, 30, and 35 C, and a diurnal alternation of 25 to 35 C (referred to as 25/35 C) with 12 hours at each temperature. Under these conditions, if there is no effect of alternation of temperatures, sprouting at the alternating temperature regime should be equal to sprouting at the constant temperature equal to its mean. Sprouted tubers were counted and removed daily for 28 days.

This experiment was repeated with tubers collected from the same location two weeks after the start of the first experiment.

EFFECT OF TIME AT MAXIMUM TEMPERATURE

Two experiments were conducted to determine the effect of different durations at maximum temperature. Tubers were exposed to a diurnal alternation of 20/35 C, spending 0 (constant 20 C), 0.5, 1, 6, 12, 18, 23, 23.5, and 24 (constant 35 C) hours at 35 C. Each stack of dishes was double-wrapped in aluminum foil to exclude all light, and enclosed in a 0.028 mm (1.1 mil) polyethylene bag to conserve moisture. The first experiment lasted for two weeks, and total sprouting was counted at the end of the experiment. This experiment was repeated three weeks later.

RESULTS AND DISCUSSION

RESPONSE TO ALTERNATING TEMPERATURES

The results of the two experiments were combined and the sprouting rates as the reciprocal of time to 50 percent cumulative sprouting were computed. A linear regression model was fit to the rates at constant temperature, as described by Bierhuizen (1973), and a straight line response was found. This response was significant at the 1 percent level (Table 13 and Figure 13). The response to alternating temperature, however, did not fit this linear heat sum model. Instead, the sprouting rate at alternating temperatures was higher than the highest rate at constant temperature. This difference was also significant at the one percent level (analysis not shown). Similar results were found for final cumulative sprouting, with an increase as temperature increased, and with sprouting highest at alternating temperatures (Figure 14 and Table 14).

It is interesting to note that only three of ten petri dishes at constant 25 C attained 50 percent cumulative sprouting. These results demonstrate another weakness of this type of heat sum approach, which by basing its estimates on time to 50 percent sprouting contains an implicit assumption that sprouting will eventually reach 100 percent (Hsu *et al.*, 1984). This assumption, in the case of purple nutsedge, is not correct. As it turned out, at many constant temperatures and combinations of low temperatures,

total sprouting did not even attain 50 percent, making it impossible to use these data in this type of model. As Scott *et al.* (1984) have pointed out, exclusion of treatments which do not attain 50 percent sprouting amounts to a decision to ignore valuable information on the response to treatments, and may lead to incorrect estimates.

These results clearly demonstrate that the linear heat sum model as described by Bierhuizen (1973) is not appropriate for purple nutsedge tuber sprouting. They also demonstrate that models developed from constant temperatures without evaluating the response to alternating temperatures may be very misleading. In light of the results of these experiments all subsequent experiments included alternating temperatures, and the heat sum approach was discontinued.

It is worthwhile at this point to take another look at the results of one of the experiments on the effect of counting method described in Chapter III. In the experiment conducted at constant 24 C and alternations of 18, 20, and 22 C with 24 C, it was noted that sprouting decreased as the minimum temperature in the alternation increased, and that this response seems to contradict the conclusion that sprouting increases with increasing temperature. Figure 15 presents these results in a slightly different manner; sprouting is plotted against the difference between maximum and minimum temperature in the temperature alternation. It can be seen that as the difference increases, sprouting increases. As reported in Chapter III, this response is significant at the 1 percent level. This is further illustration of the importance of temperature

alternation in sprouting of purple nutsedge tubers. The analysis of variance for the response to increasing temperature difference can be found in Table 15.

EFFECT OF TIME AT MAXIMUM TEMPERATURE

Not surprisingly, total sprouting was lower at constant than at alternating temperatures. Mean total sprouting at alternating temperatures was 94.6 percent, while at constant temperatures it was 59.9 percent. This difference was statistically significant at the 1 percent level (analysis not shown), so regression analysis of these experiments was done on alternating temperatures only.

The results of these two experiments showed a small curvilinear response to time at maximum, but the differences from 0.5 to 18 hours at 35 C were very small. This response is shown in Figure 16, and the analysis of variance table for the regression is Table 16. There was no response to time at maximum temperature from 1 to 18 hours (model not shown). At 0.5, 23, and 23.5 hours at maximum temperature, sprouting was slightly depressed, more so at the longer times. From these results, it is possible to conclude that the 12 hour diurnal temperature alternation in the incubators is an acceptable simulation of soil temperature fluctuation in the field, as it affects tuber sprouting. It is interesting to note that only 0.5 hour at maximum temperature appeared to provide most of the alternating temperature effect.

These data do not strictly fit the assumptions needed for analysis by regression, since the variances of the data at the extreme time values are clearly larger than those in the middle. The trend, however, is clear. It was not the goal of this study to accurately model the sprouting response to time at maximum temperature so no attempt was made to transform or otherwise manipulate these data.

Table 13. Analysis of variance and regression coefficients for linear regression of sprouting rate (reciprocal median response time) on constant temperature.

Analysis of Variance

Source	DF	Sum of Squares	F Value	Pr > F
Model	1	0.019	40.58	0.0001
Error	21	0.0098		
Corrected Total	22	0.029		

R-Square	C.V.
0.66	20.80

Source	DF	Type I SS	F Value	Pr > F
Temperature	1	0.019	40.58	0.0001

Regression Coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
Intercept	- 0.16	- 3.83	0.0010	0.042
Temperature	0.0084	6.37	0.0001	0.0013

Table 14. Analysis of variance and regression coefficients for regression of final cumulative sprouting on constant temperature.

Analysis of Variance

Source	DF	Sum of Squares	F Value	Pr > F
Model	2	18939.94	58.42	0.0001
Error	27	4377.00		
Corrected Total	29	23316.94		

R-Square	C.V.
0.81	19.17

Source	DF	Type I SS	F Value	Pr > F
Temperature	1	18160.02	112.02	0.0001
Temperature^2	1	779.92	4.81	0.0371

Regression Coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
Intercept	-496.54	-2.84	0.0086	175.09
Temperature	31.99	2.70	0.0118	11.85
Temperature^2	-0.43	-2.19	0.0371	0.197

Table 15. Analysis of variance and regression coefficients for effect of magnitude of temperature difference in diurnal temperature alternation on final cumulative tuber sprouting. Treatments are total darkness for 36 days or daily counting for 36 days.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	13568.10	6784.05	36.48	0.0001
Error	36	6694.73	185.96		
Corrected Total	38	20262.83			

R-Square	C.V.
0.67	22.60

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Difference	1	11286.26	11286.26	60.69	0.0001
Treatment	1	2281.84	2281.84	12.27	0.0012

Regression Coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
Intercept	36.66	8.58	0.0001	4.27
Difference	7.69	6.82	0.0001	1.13

Table 16. Analysis of variance and regression coefficients for regression of final cumulative sprouting on time at 35 C in a diurnal alternation of 20 and 35 C.

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	1885.03	942.51	20.24	0.0001
Error	65	3026.66	46.56		
Corrected Total	67	4911.69			

R-Square	C.V.
0.38	7.21

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Time	1	932.17	932.17	20.02	0.0001
$Time^2$	1	952.86	952.86	20.46	0.0001

Regression Coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
Intercept	95.07	57.22	0.0001	1.66
Time	1.36	3.41	0.0011	0.40
$Time^2$	- 0.074	- 4.52	0.0001	0.016

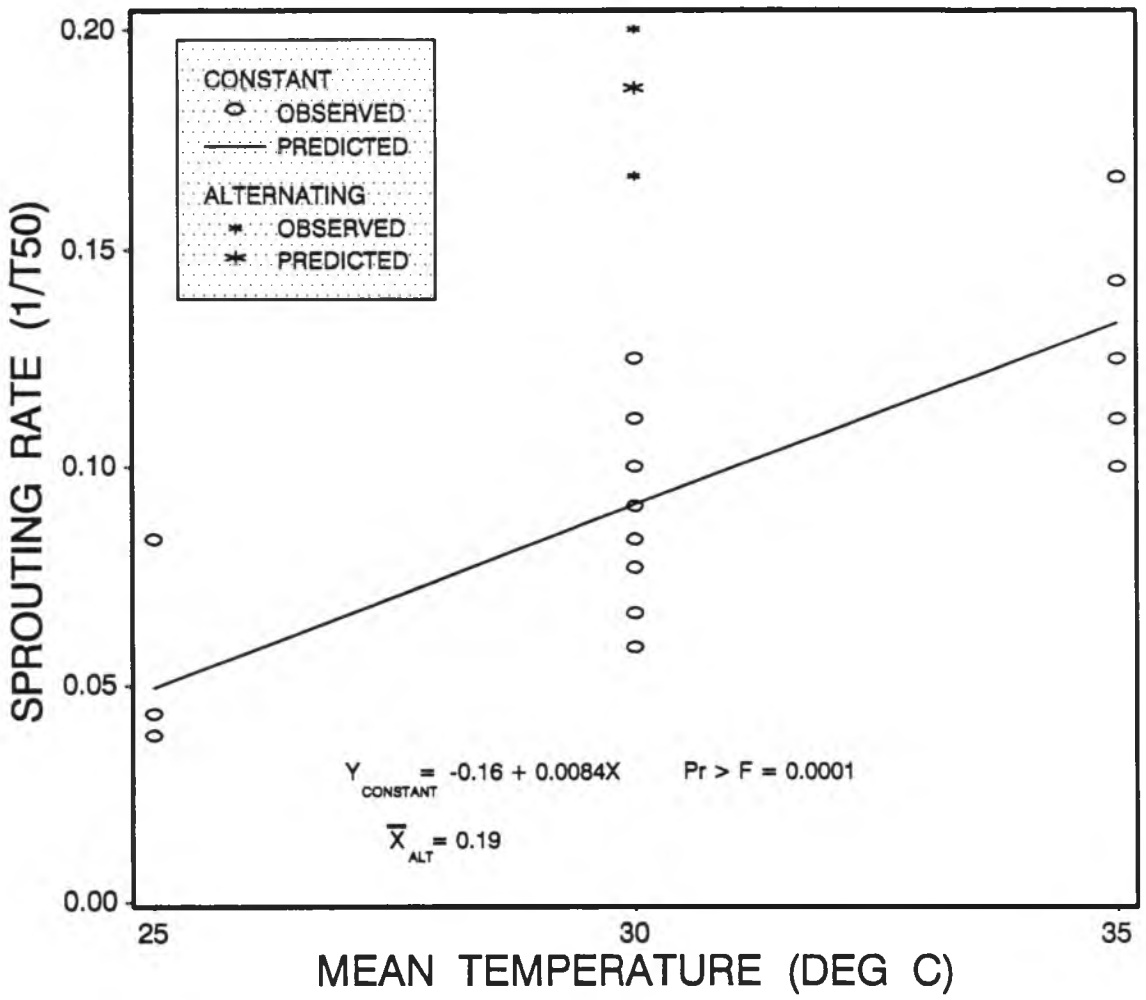

Figure 13. Purple nutsedge tuber sprouting in response to constant and alternating temperature. Observed (circles) and predicted (line) rate of sprouting (as reciprocal of days to 50 percent cumulative sprouting) in response to increasing constant temperature, and observed (small asterisk) and predicted (large asterisk) rate of sprouting in response to alternating 25/35 C. Regression equation for response to constant temperature: Y = -0.16 + 0.0084*X. Where 2 or more observations have the same value only one observation can be seen.

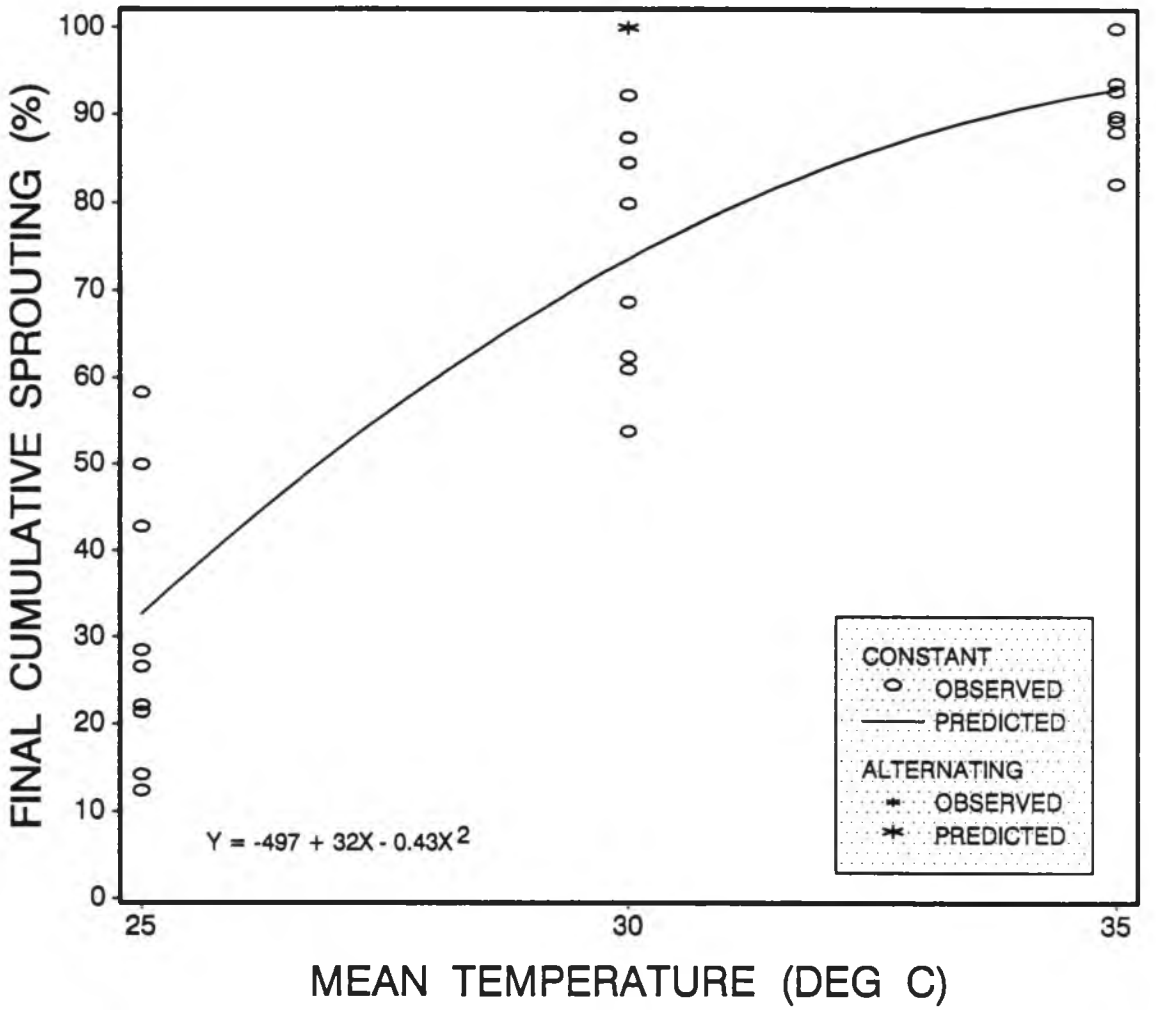

Figure 14. Purple nutsedge tuber sprouting in response to constant and alternating temperature. Observed (circles) and predicted (line) final cumulative sprouting in response to increasing constant temperature, and observed (small asterisk) and predicted (large asterisk) final cumulative sprouting in response to alternating 25/35 C (observed not seen because all replications had 100 percent sprouting). Regression equation for response to constant temperature: $Y = - 496.54 + 31.99*X - 0.43*X^2$. Where 2 or more observations have the same value only one observation can be seen.

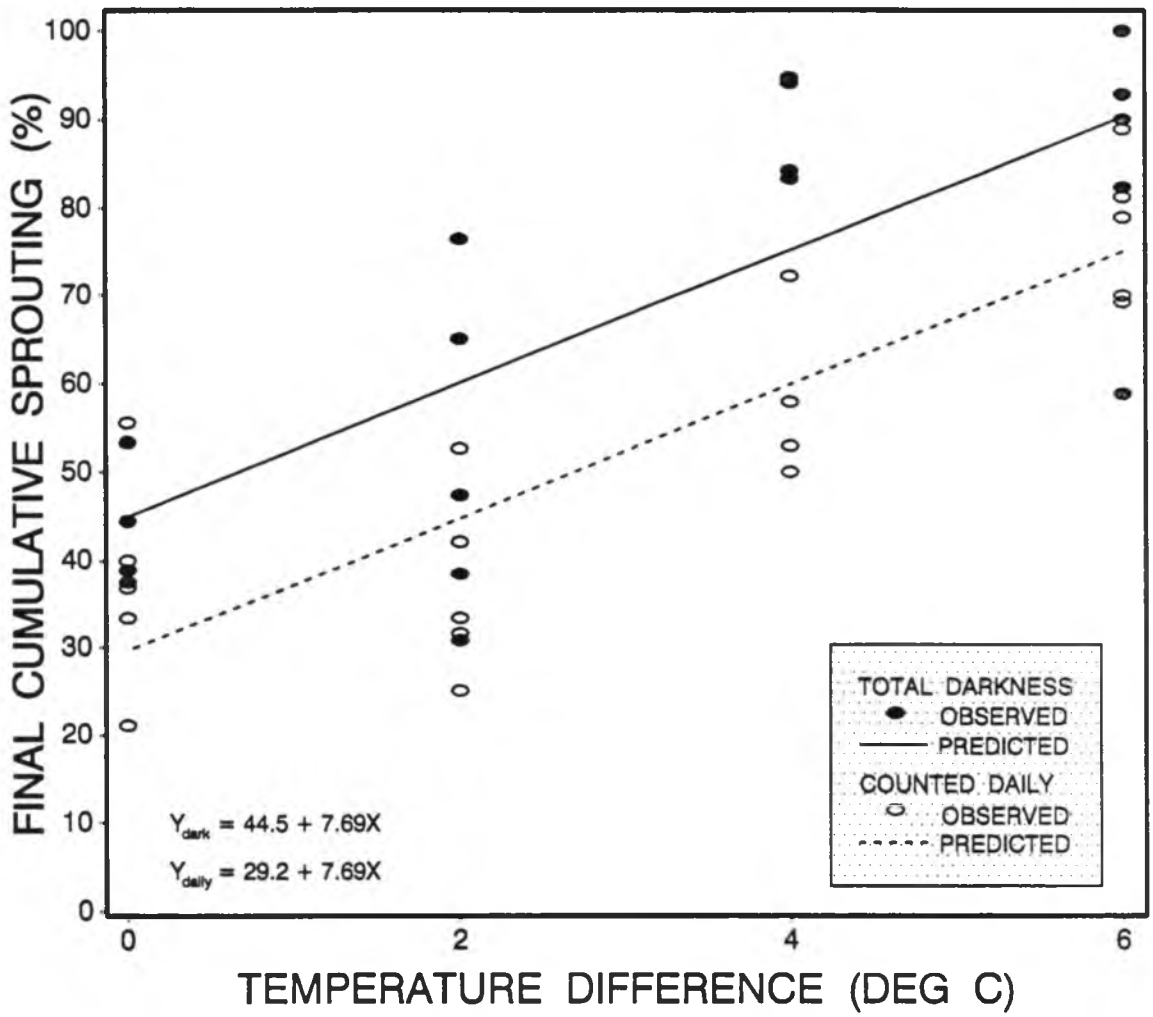

Figure 15. Purple nutsedge tuber sprouting in response to increasing amplitude of temperature alternation. Observed (circles) and predicted (line) final cumulative sprouting. Regression equation for response to difference between maximum and minimum temperature: Y = 36.66 +7.69*X. Where 2 or more observations have the same value only one observation can be seen.

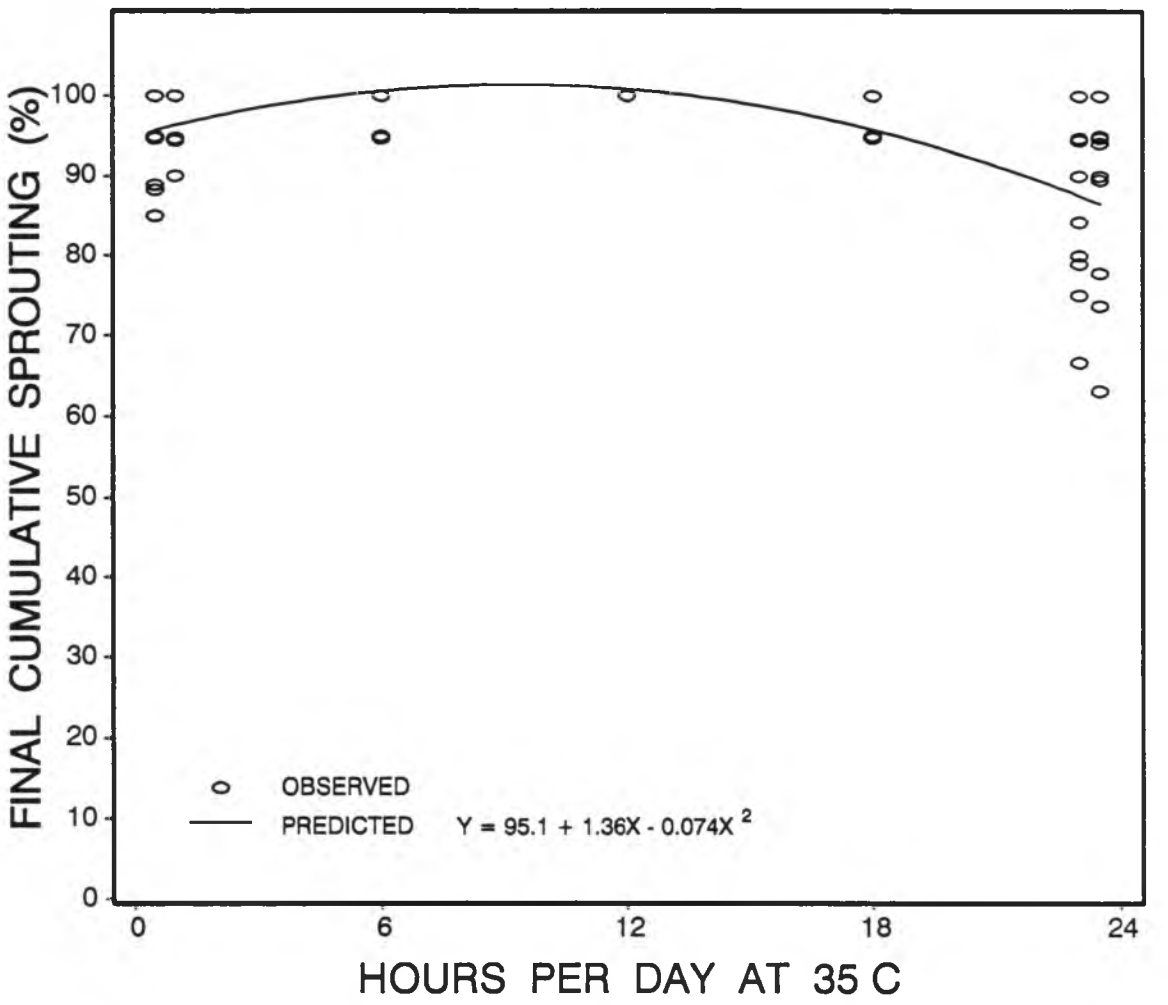

Figure 16. Purple nutsedge tuber sprouting in response to time at 35 C in a diurnal alternation of 20 and 35 C. Observed (circles) and predicted (line) final cumulative sprouting. Regression equation for response to constant temperature: $Y = 95.07 + 1.36*X - 0.74*X^2$. Where 2 or more observations have the same value only one observation can be seen.

CHAPTER V

MODEL DEVELOPMENT

INTRODUCTION

A thorough understanding of the biology of weeds is essential to their effective control. Schreiber noted this fact in a review of weed modeling in 1982. Modeling is a useful approach to understanding and predicting plant responses to environment. A variety of approaches have been taken to modeling weed emergence from seeds or vegetative propagules, and many have included temperature as an important environmental factor influencing germination and emergence (Angus *et al.*, 1981; Benech Arnold *et al.*, 1990a,b; Satorre *et al.*, 1985; Wanjura *et al.*, 1970; Warrington and Kanemasu, 1983).

A commonly used approach to modeling seed germination is the heat sum model (Bierhuizen, 1973; Garcia-Huidobro *et al.*, 1982a). The standard heat sum approach described by Bierhuizen has important weaknesses, however. It is only applicable over the temperature range at which responses are linear (Scott *et al.*, 1984), it is not applicable to seeds which respond differently to alternating than to constant temperatures (Garcia-Huidobro *et al.*, 1982b; Wagenvoort and Bierhuizen, 1977), it overlooks treatments which result in less than 50 percent germination (Hsu *et al.*, 1984; Scott *et al.*, 1984), and it cannot describe the full course of germination over time, being intended to predict the time to a given event, e.g., 50 percent germination.

Curve fitting is a good way to characterize the full course of seed germination, and has been utilized by a number of researchers (Brown, 1987; Brown and Mayer, 1988a,b; Hsu *et al.*, 1984; Lehle and Putnam, 1982; Moore and Joliffe, 1989; Schimpf et al, 1977; Tipton, 1984; Torres and Frutos, 1989). This study has taken the curve fitting approach to characterize and predict purple nutsedge tuber sprouting. Through the use of fitted functions, the entire course of sprouting can be characterized and predicted. By predicting the curve parameters from soil temperature it is possible to accurately and consistently predict tuber sprouting. This is a valuable tool in understanding the dynamics of purple nutsedge populations in the field.

Temperature fluctuation is the natural situation in the field. This study attempted to simulate the natural diurnal soil temperature alternation using incubators in the laboratory. In the incubators, however, the maximum and minimum temperatures were the same every day. If this situation occurred in the field, predicting tuber sprouting could be done simply from the fitted curve. The situation in the field is more complicated, however. In addition to the diurnal temperature fluctuation in the field, there are a different maximum and minimum temperature every day. A model to predict tuber sprouting must therefore be able not only to predict sprouting at any given combination of maximum and minimum temperature; it must also accommodate previous temperature conditions and previous sprouting.

MATERIALS AND METHODS

Once the appropriate methodology had been determined and causes of variability of response had been identified, experiments were conducted to develop the temperature response model. These were conducted in the same five incubators used in previous investigations using tubers collected from similar natural populations in the field. Three field experiments were conducted to evaluate the predictions of the model.

The experiments on the effect of water stress described in Chapter III showed that water stress on purple nutsedge plants affects subsequent tuber sprouting. Since the major area of interest in this study was the humid tropics, it was decided to use tubers from unstressed plants to develop the model. It was felt that this would result in a more "conservative" model with less tendency to over predict sprouting, since sprouting had been demonstrated to be higher in tubers from water stressed plants. The tubers for the first field sprouting experiment in 1986 were therefore collected from unstressed plants in a plot maintained for tuber collection.

This study was interrupted for approximately three years, however, from late 1986 until early 1990. When it was resumed, there was no time to reestablish tuber collection plots, and it was necessary to work with available material. Tubers were collected in 1990 from the same field which had been used in the previous work, but only water stressed plants were available at the beginning of the year, so these were used to develop the sprouting model and for the 1990 field experiments. Only 121 mm of rain fell during the 5-month period when

the model development experiments were being conducted, less than 25 mm per month. The nutsedge plants produced no new growth during the entire period. It was observed that the soil grew progressively drier as time passed; many tubers collected for the last experiment were wrinkled due to water loss.

LABORATORY SPROUTING EXPERIMENTS

Attempts to develop a model based on three experiments covering different portions of the soil temperature range left gaps in the data needed to predict sprouting at the full range of temperatures encountered in the field (data not shown). These gaps made it difficult to combine the results into a single model. It was therefore decided to evaluate tuber sprouting over the full range of temperatures at which tubers had been observed to sprout. The capability to simultaneously evaluate a wide range of temperature regimes was essential to the development of the model to predict the sprouting response to temperature.

Two experiments were conducted over a wide range of temperatures to provide sprouting data for development of the model. Temperatures used in these experiments ranged from 20 to 45 C in 5 degree increments. All constant temperatures and all combinations of alternating temperatures were utilized, providing a total of 21 temperature regimes.

Since these experiments required 6 constant temperatures, and only 5 incubators were available, a laboratory oven was used to provide the temperature of 45 C. This oven was monitored with a thermistor

and micrologger recording instantaneous chamber temperature every five minutes for several weeks, and was found to be capable of maintaining the desired temperature of 45 C with a precision of plus or minus 0.5 C or less, comparable to the incubators (data not shown).

The incubators used were as already described, and unless otherwise noted materials and methods were as described in Chapter III. Alternating temperatures were obtained by transferring tubers between incubators at 7 am and 7 pm. Transfers took three to four minutes to complete, and were always done within five minutes of the designated time.

The tubers for the first experiment were collected on July 31, 1990, and the treatments began on August 1. The experiment was continued for two weeks. The experiment was repeated exactly, except that the length of the experiment was increased to three weeks to improve the estimates of total sprouting. Tubers for the second experiment were collected on August 28, 1990, and treatments began on August 29.

ANALYSIS

There were five steps in the analysis: selection of a mathematical function to characterize cumulative sprouting; fitting the selected function to the sprouting data; response surface regression to predict the parameters of the selected function from maximum and minimum temperature; and developing and validating a model to predict tuber sprouting in the field using the predicted parameters.

Function Selection

Four sigmoid functions, the logistic, Gompertz, Richards, and Weibull, were tested for their ability to fit the data generated by these experiments. All four of these functions have been used to describe seed germination. The range of temperatures utilized in this study resulted in a wide range of curve shapes. The four functions described were fitted to 20 curves with widely differing shapes, and the fits were evaluated. The main criterion for evaluation was the ability of the function to minimize the sum of squares for error (SSE), that is, the ability to explain the maximum amount of the variability in the response. The curves were also evaluated visually. A third criterion was flexibility; the ability to respond to and adequately fit a variety of curve shapes.

Curve Fitting

The form of the Richards function used to fit the data was reparameterized by Causton *et al.* (1978). Reparameterization is simply the rearrangement of the parameters to facilitate fitting by computer (Brown and Mayer, 1988; Causton, D. R., personal communication). The equation is written as follows:

$$W = A(1+e^{B-KT})^{-1/N}$$

where W is the cumulative percent sprouting at any time, T. The four parameters A, B, K, and N determine the shape of the curve.

None of the parameters have a direct biological meaning, but parameter A is the asymptote and is equivalent to final cumulative sprouting. B determines the placement of the curve along the time axis, and K, in combination with N, can be used to determine the rate of sprouting (Richards, 1959). N has also been referred to as the shape factor; it determines the shape of the curve (Causton *et al.*, 1978).

Curve fitting was done using the NLIN procedure in the Statistical Analysis System (SAS). The method used was DUD (Doesn't Use Derivatives). A range of starting values was provided for each parameter, and the program then minimized the sum of squares for error by a series of least-squares iterations. The task of selecting starting values was simplified because the value of the asymptote was known (final cumulative sprouting). For each temperature regime, the Richards function was fitted to the 5 replications collectively, then evaluated visually by comparisons with mean cumulative sprouting.

Nonlinear regression cannot be evaluated as easily as linear regression. An additional difficulty with these sprouting experiments is that repeated measurements (daily counts) on the same population were not independent from each other. This makes it difficult to test the model for lack of fit, since the measurements should be independent. The magnitude of the sum of squares for error (SSE) was useful for comparing models, but it was less useful for evaluating the fit of a function to a given

sprouting curve. Minimizing the SSE gives more weight to the middle of the curve, where the variability is greatest, and can result in poor fits to the upper and lower portions of the curve. I was most interested in fitting the upper portion well. Therefore, visual evaluation of fits was used to supplement use of minimal SSE. If adjustment of the starting values gave a closer fit to the upper portion of the curve without increasing the SSE then this combination of low SSE and good visual fit was selected.

The results of the two experiments were combined and the four parameters from each fit were used in the next step of model development.

Prediction of Richards Parameters

Response surface regression analysis was performed for each parameter using minimum and maximum temperatures as independent variables. The X-variables tested for inclusion in the regression model for each parameter were linear and quadratic effects of minimum and maximum temperature, and the interaction between minimum and maximum temperature. The selection method used was sequential fitting. In sequential fitting, the sum of squares for each independent variable "is the additional sum of squares that can be associated with the variability in the response variable remaining after fitting the previous variables." (Allen and Cady, 1982). In selecting terms to include in the regression models, a P value of 0.25 was used as the criterion for rejection of a term.

This is considerably higher than the standard of 0.05 commonly used for hypothesis testing, but a less rigorous standard is needed in selection of terms for regression models to avoid ignoring important effects and interactions, and to improve prediction. This is in accordance with the recommendations of Freund *et al.* (1986) of the SAS Institute for testing parameters for inclusion in models; they indicate that using P 0.05 as the criterion for inclusion "tends to lead to models that do not have enough terms."

Significant regression allows prediction of the parameter for any combination of minimum and maximum temperature within the range of the temperatures applied, and not only for the temperatures used in the experiments. Regression is recommended for statistical treatment of continuous variables (Evans *et al.*, 1982; Nelson, 1989). The predicted parameters were used to generate curves at the temperature regimes of the experiment from which they were predicted. These curves were visually compared with actual sprouting and fitted Richards curves for those temperature regimes.

Model Development and Evaluation

A SAS program was written which used the daily minimum and maximum temperatures recorded in the tuber sprouting field experiments as the basis for predicting cumulative sprouting. The model uses the maximum and minimum temperature for each day to add a sprouting increment for that day. The curve generated by the model should match tuber sprouting in the field.

The model cannot be based on temperature alone, however. It must also take into account prior sprouting; the cumulative sprouting up to the day in question. This is how the model works: On a given day, the minimum and maximum soil temperatures are used to predict the four parameters. From these parameters, a sprouting curve is generated, and the cumulative sprouting to date is located on the curve (on the first day, cumulative sprouting is equal to zero). Then a day's increment from that point on the curve is added. On the next day the process is repeated, with a new sprouting curve being generated based on this day's temperatures. This continues until sprouting reaches a maximum. The flow of the model is illustrated diagrammatically in Figure 17.

This generation of a new sprouting curve every day is the most important part of the model; if soil temperatures were the same every day, as they are in the incubators, a single fitted curve would be able to predict sprouting at any time. In the field, however, maximum and minimum temperature change every day, and the tubers respond to this change. It was therefore necessary to generate a new curve every day, to locate previous sprouting on that curve, and then to add a day's increment. This is the key to successfully predicting tuber sprouting.

The final step in evaluating the model is to compare the predicted sprouting with actual tuber sprouting in the field. If the predicted sprouting curve lay within the range of the observed

values, and if the predicted total sprouting was within the 95 percent confidence limits of the mean observed total sprouting, the prediction was considered to be good.

FIELD SPROUTING EXPERIMENTS

Three experiments were conducted to follow the course of tuber sprouting in the field to test the model developed in the laboratory. These experiments were all conducted at the University of Hawaii Waimanalo Experiment Station in portions of the same fields from which tubers were collected for the laboratory experiments. The experiments were conducted at different times of the year: in September-October, 1986 (end of summer); March-April, 1990 (end of winter); and June-July, 1990 (early summer).

In all three experiments, the experimental plot was fumigated with methyl bromide at 488 kg/ha before the start of the experiment to prevent any interference with the growth of the plants or shading of the soil by weeds. Treatments were solarized and control. The solarized plots were covered with 0.028 mm (1.1 mil) transparent polyethylene, while the control plots were left bare. Plots were 2 meters square. The size of the plots was selected to prevent any border effect in the solarized plots. Mahrer and Katan (1981) have shown a border effect approximately 0.5 meter wide where temperatures are slightly lower than in the middle of solarized plots due to heat loss to the surrounding environment. In these experiments no tubers were less than 0.5 m from the edge of a plot. The experimental plot

was overhead irrigated every 4 days with 15 to 20 mm of water to maintain adequate moisture for sprouting and growth, and to keep the moisture level in the control plots near that in the solarized plots, which lost very little moisture due to the polyethylene cover.

Tubers were collected, washed, and trimmed in the same way as for the incubator experiments. There were 5 replications of 10 tubers each in a completely randomized design. Percentage sprouting was based on the number of viable tubers in each replication, and tuber viability was determined as described in Chapter III. Tubers for the first experiment were collected from green plants, while those for the other two experiments were collected from plants which had senesced due to water stress. These tubers were collected from the same location as those for the model development experiments.

Tubers were enclosed in bags of nylon mesh to facilitate recovery, and were buried 15 cm deep. This is the lower depth limit of over 90 percent of the tuber population at Waimanalo (Siriwardana and Nishimoto, 1987). The effects of soil solarization on soil temperatures are dampened with increasing depth in the soil, so the tuber sprouting response can be expected to be greater at depths of less than 15 cm.

Tubers were recovered at designated times from separate plots for each time of tuber recovery. In the first experiment, tubers were recovered at 2, 4, 6, 8, 10, 12, 16, 21, 25, and 30 days. In the second experiment, recovery times were 3, 6, 9, 12, 15, and 21 days, and in the third experiment the recovery times were 7, 14, 21, 28, and 35 days.

Global solar radiation and soil temperatures were monitored as described below. Soil temperatures were recorded at the depth at which the tubers were buried, and at two other depths.

ENVIRONMENTAL MONITORING

Soil temperatures were continuously monitored during several months each year from 1984 to 1986, and again during the field experiments in 1990. Total incoming global solar radiation was recorded simultaneously. Monitoring was done at the University of Hawaii Waimanalo Experiment Station, where the tubers were grown and where the field experiments to test the model were conducted. The Waimanalo Experiment Station is described in Chapter III.

Solar radiation and soil temperatures were also monitored at the Hawaiian Sugar Planters' Association Kunia Substation at Kunia, in central O'ahu, from July through September 1985, for comparison with the data from Waimanalo. At this location the soil is a typic torrox, and the elevation is 87 meters. It was hoped that solar radiation would be higher at this location.

From 1983 through June, 1985 a Campbell Scientific CR-21 micrologger was used to record environmental data. Campbell Scientific CS-102 thermistor probes were used to sense soil temperatures, and a Li-Cor model LI-200S silicon pyranometer was used to sense solar radiation. Beginning in July, 1985, an Omnidata Easy Logger replaced the CR-21, and Omnidata TP10 thermistors were used to sense soil temperature. The CS-102 thermistors were also used, and the same Li-Cor pyranometer was used throughout.

Soil Temperature

From 1984 through June, 1985 soil temperature data were collected from soil depths of 1, 5, and 15 cm. In July, 1985 I began collecting data from 5, 10, and 15 cm. Data were also taken from 30 cm soil depth in June and July 1990. Depths of 5 and 15 cm were common to all soil temperature monitoring except March - April, 1990, when temperatures were monitored only at 15 cm. Since most tubers at Waimanalo are in the upper 15 cm (Siriwardana and Nishimoto, 1987), this region was concentrated on in the acquisition of temperature data. The temperature monitoring plots were 2 meters square, and the thermistors were buried in the middle of the plot. By burying thermistors 1 meter from the edge of the plot any border effect on temperature was avoided.

In all soil temperature monitoring, solarized and bare soil plots were maintained side by side. The solarized plot was covered with 0.028 mm (1.1 mil) transparent polyethylene, while the control plot was kept bare. In cooler months, the plots were fumigated to prevent weed growth under the plastic, but in warmer months weed growth was not a problem in the solarized plots. Control plots were kept bare by fumigation, postemergence application of glyphosate, and/or hand weeding. Moisture was maintained in control plots by twice-weekly overhead irrigation applying 15 to 20 mm of water at each irrigation; solarized plots

lost very little moisture since the plastic prevented evaporation. For each field experiment, soil temperatures were monitored in plots identical to those used for tuber sprouting, adjacent to the experiment.

Soil temperatures were scanned every 10 minutes and an hourly mean was recorded for each depth in each treatment. In some cases daily absolute maximum and minimum soil temperature were also recorded. Since soil temperature changes very slowly, the difference between the highest or lowest hourly mean and the daily absolute maximum or minimum was less than one degree Celsius, except at the 1 cm depth, where it was as high as 3 degrees.

Solar Radiation

Solar radiation was scanned every 10 minutes and was summed every hour. A daily sum of incoming radiation was also recorded.

The polyethylene tended to deteriorate and lose its transparency after 8 to 10 weeks, so the cover was replaced every 4 to 6 weeks, before its light transmission was affected. The replacement took only 5 to 10 minutes and no effect on soil temperature was observed.

RESULTS AND DISCUSSION

MODEL SELECTION

The logistic and Weibull functions both gave poor fits. Both had very high sums of squares for error (SSE) compared to the other two

functions, with the Weibull being the worst. The poor fit of the Weibull function was a surprise since it has recently been recommended as very useful for description of seed germination, and is reportedly very easy to fit (Brown, 1987; Brown and Mayer, 1988b). Several adjustments were made in the starting values for this function, but to no avail. The poor fit of the logistic function was less surprising, since it has a rigid symmetrical shape, and tuber sprouting, like seed germination, is not symmetrically distributed (Brown and Mayer, 1988b; Schimpf *et al.*, 1977). As a result of these poor fits, both the logistic and Weibull functions were rejected.

Both the Gompertz and Richards functions fit the data well. There was no consistent difference in the magnitude of the SSE for the two functions, with sometimes one being larger and sometimes the other. In all cases, the differences were small, and they were not significant statistically. The fits were also very good visually. The selection between the two models was therefore made on the basis of flexibility.

Like the logistic function, the Gompertz function has a rigid shape, although it is not symmetrical. By adding a fourth parameter, the Richards function allows flexibility in the shape of the fitted curve. As this fourth parameter approaches zero, the Richards function approaches the Gompertz function in shape. In most of the treatments, N was quite small, but it was not close to zero, indicating that the Gompertz was not the appropriate function to use. Also, the variability of this parameter from one treatment to another

indicated that flexibility in shape was an important factor in predicting sprouting of purple nutsedge tubers. The Richards function was therefore chosen for use in this study.

FITTING THE RICHARDS FUNCTION

Most sprouting curves fit well on the first attempt, but several required a second attempt, and a few required a third. In the first experiment, sprouting at constant 20 C only slightly exceeded 8 percent, and it was not possible to get a good fit for this data set. It was therefore not used in further analysis. Also, in both experiments there was no sprouting at constant 45 C, so no curves could be fit, and no parameters could be predicted. As a result, 19 curves were fitted for the first experiment, and 20 for the second. For each fitted curve, 4 parameters (A, B, K, and N, described earlier) were estimated by the NLIN procedure.

PREDICTION OF RICHARDS PARAMETERS

By combining the two experiments a total of 39 estimates of each parameter were obtained, two for each temperature regime except constant 20 C. An estimate of zero was used for parameter A (final cumulative sprouting) for constant 45 C to allow prediction of total sprouting at temperatures between 40 and 45 C. The 39 estimates of each parameter were then used as observations in regression models to predict the value of each parameter in response to minimum and maximum temperature.

Parameter A

Parameter A is the asymptote of the curve, and estimates final cumulative sprouting. Figure 18 shows the mean observed final cumulative sprouting for the two experiments, and Figure 19 shows the distribution of parameter A as the means of the values for the two experiments. The shape of the distribution of A shows a curvilinear response to high and low temperatures, with a plateau at the middle of the distribution. A quadratic function fits the curves well, but is not able to accommodate the plateau in the middle. The solution to this difficulty was to divide the data set in two and to fit separate regressions to the two halves. One half of the data set consisted of those temperature regimes with minimum temperatures less than 35 C. The other half contained those regimes with minimum temperatures greater than or equal to 35 C. The sum of squares for error (SSE) for a quadratic response surface fit to the entire data set was 5,709 (analysis of regression not shown), while the total SSE for two models fit to the two halves of the data set was 2,116 (analysis of variance for regression in Tables 17 and 18). The total SSE of the two models is less than half that of the single model. This shows that the two models do a much better job of explaining the variability in response. The decision on where to divide the model was based on the best fit, determined by the lowest SSE. The response surfaces in Figures 20 and 21 show this graphically. The very close overlap of the two

models in Figure 21 (the division is at minimum temperature 35 C), and the close approximation of the actual distribution of parameter A show that this two-part model fits the data very well. With this model, the value of parameter A can be predicted for any combination of minimum and maximum temperature from 20 to 45 C. A few values predicted by the model are in excess of 100 percent, which is of course impossible. In practice, a statement is placed in the sprouting prediction model limiting predicted sprouting to a maximum of 100 percent.

Both models included the same parameters, since they were being fitted to different portions of the same data. If a parameter was significant in one model it was included in both, even if its P value was higher than 0.25 in one of the models. The analysis of variance tables for the regression are Tables 17 and 18. The regression equations for the two models are as follows (MINTEMP and MAXTEMP are minimum and maximum temperature, respectively):

If the minimum temperature is less than or equal to 35 C,

$$A = -120.67 + 13.15*MAXTEMP - 0.20*MAXTEMP^2 - 2.00*MINTEMP - 0.033*MINTEMP^2 + 0.093*MAXTEMP*MINTEMP;$$

and if the minimum temperature is greater than 35 C,

$$A = -537.30 + 14.75*MAXTEMP - 0.19*MAXTEMP^2 + 23.84*MINTEMP - 0.41*MINTEMP^2 + 0.012*MAXTEMP*MINTEMP.$$

Parameter B

As can be seen in Figure 22, the distribution of parameter B is less smooth than that of A, but it was easier to fit since its shape was simpler. Parameter B was fit with a single model with only straight line effects of minimum and maximum temperatures. The response surface from this model is shown in Figure 23, and the analysis of variance table for the regression is Table 19.

Parameter B illustrates Hunt's (1979) statement that mathematical models can help to clarify relationships. The trend of parameter B is difficult to discern in the plot of the data, but becomes quite clear in the plot of the response surface. This model is not significant at the 5 percent level, but the P value of 0.16 for the model and P values of 0.14 and 0.23 for maximum and minimum temperatures are less than the criterion of 0.25 used in this study. These values indicate that there is a response to both maximum and minimum temperatures. The small number of observations (2 per temperature regime) and the irregular distribution contribute to the high P values.

The regression equation for parameter B is:

B = -3.05 + 0.029*MAXTEMP - 0.020*MINTEMP.

Parameter K

The distribution of parameter K is similar to that of A, but without the steep drop above 40 C (at least in part because no model could be fit at 45 C). A single model with a quadratic effect of maximum temperature fit these data well. The distribution of K is shown in Figure 24, and the response surface from the regression is shown in Figure 25. The analysis of variance table for the regression is Table 20. The regression equation for parameter K is:

$$K = -3.37 + 0.16*MAXTEMP - 0.0021*MAXTEMP^2 + 0.092*MINTEMP - 0.0017*MINTEMP**2.$$

Parameter N

Parameter N was also fit with a single model with quadratic effect of maximum temperature and straight-line effect of minimum temperature. The distribution of parameter N is shown in Figure 26, the regression model is shown in Figure 27, and the analysis of variance table for the regression in Table 21. The regression equation for parameter N is:

$$N = -0.023 + 0.0015*MAXTEMP - 0.000023*MAXTEMP^2 + 0.00022*MINTEMP.$$

MODEL DEVELOPMENT AND EVALUATION

To evaluate the predictions of the Richards parameters, the predicted values were used to generate curves which were then compared visually to the data and curves from which they were generated. All of the predicted curves were within the range of the data. These results gave me confidence that tuber sprouting could be predicted from maximum and minimum temperatures in incubators, and justified the next step; predicting tuber sprouting in the field from maximum and minimum soil temperatures.

Tuber sprouting was predicted for the three field sprouting experiments based on the soil temperatures observed during those experiments. The only inputs for prediction were the daily maximum and minimum hourly mean temperatures observed in the field. The predicted sprouting for each experiment is shown with the actual sprouting data in Figures 28 to 33. In each experiment, the predicted sprouting is shown, with the raw data and means, and with the curve from a Richards function fitted to the observed data. The figures also show daily maximum soil temperature during each experiment. Observed and predicted tuber sprouting for the 3 experiments are also presented in Table 22. Mean soil temperatures and solar radiation during the three experiments are presented in Table 23.

Experiment 1

This experiment was done at the end of summer, 1986, from September 8 to October 8. At this time of the year, soil temperatures are just beginning their decline from summer highs. In this experiment, an equipment malfunction resulted in the loss of all soil temperature data in the control plot. In the solarized plot, soil temperatures were lost after 16 days. The model is not able to predict sprouting without soil temperatures, so for this experiment prediction is possible only for the solarized treatment, and only for the first 16 days. The observed and predicted sprouting for this experiment are presented in Figures 28 and 29. In the solarized treatment, the initial sprouting closely follows actual sprouting, but then sprouting increases too rapidly. Except for the observation at four days, however, all predicted values fall within the range of observed values. Predicted total sprouting is very close to the observed total; predicted total sprouting at 16 days is 93.6 percent while mean observed total sprouting is 97.1 percent. The 95 percent confidence limit of this mean is ±7.9 percent, and the predicted value falls within this limit.

Experiment 2

This experiment was done in the spring of 1990, beginning on March 7 and continuing through April 11. This is at the time when soil temperatures at Waimanalo have begun to warm up from winter

lows. Figures 30 and 31 show observed and predicted sprouting for this experiment. In the control treatment in this experiment, the predicted sprouting is initiated too soon, but the rate (as indicated by slope) and total are very close to the observed values, and once again, all but one predicted value (9 days) are within the observed values. In the solarized treatment sprouting starts too soon and goes too fast, but the final predicted total is only 0.2 percent less than the observed mean. The predicted values are generally within the range of the observed values. Mean observed total sprouting in the control treatment was 74.2 percent, with a 95 percent confidence limit of ±18.9, while predicted total sprouting is 69.8 percent. For the solarized treatment, mean observed total sprouting was 96.7 percent with a 95 percent confidence limit of ±9.3. Predicted total sprouting for the solarized treatment was 96.5 percent. In both treatments, however, predicted sprouting was higher than observed during most of the time period of the experiment.

Experiment 3

This experiment was done at the beginning of summer, 1990, from June 19 through July 24. Soil temperatures are near their highest at Waimanalo at this time. This experiment was conducted nearest to the time when the tubers were collected for the two experiments used to develop the sprouting prediction model. Tubers for those experiments were collected in July and August, 1990, from the same

location as those used for this field experiment, while the tubers for this experiment were collected on June 18. It is therefore of interest that the predicted sprouting from the model gave the best estimation of field sprouting for this experiment. In the control, observed total sprouting had a mean of 97.1 percent, with a 95 percent confidence limit of ±7.9. Predicted total sprouting was 89.3 percent, with the predictions consistently 6 to 8 percent lower than the observed throughout the course of the experiment. In the solarized treatment, both observed and predicted final sprouting were 100 percent, with no greater than 1 percent difference at any point. These results are presented graphically in Figures 32 and 33.

As can be seen, the predictions are generally good. The model tends to under predict total sprouting in the control treatments, but predicts total sprouting in the solarized treatments very well. For two of the experiments, the model predicts too high a rate of sprouting, but for the third experiment the fit is almost perfect. In all three experiments, most of the values predicted by the model fit within the range of the observed data, even when they are not close to the means.

In Table 23, it can be seen that solar radiation and soil temperatures were higher during the third experiment. It is not surprising that tuber sprouting was faster and more complete in this experiment. It is interesting to note that soil temperatures were

higher in March-April, 1990 than in September, 1986. As can be seen from Tables 24 to 26, solar radiation and soil temperatures were higher in September of 1984 and 1985 than in September, 1986, and that 1986 appears to have been cooler overall than 1984 and 1985.

In Table 27 environmental data from Waimanalo and Kunia are compared. It had been hoped that solar radiation would be higher at Kunia, and that differences in soil temperature could be observed. The results, however, show very little difference. It is not possible to draw any conclusions from this small amount of data.

There are two possible reasons for the better predictions in Experiment 3. First, as already mentioned, the time of collection of tubers for the modeling experiments and for the field experiment was close, so the tubers were possibly in a similar physiological state. Another possible explanation is that there were higher temperatures in Experiment 3. It appears that predictions are better at higher temperatures, and that the model may overestimate sprouting rate at lower temperatures while possibly underestimating total sprouting. In all three experiments, however, predicted total sprouting is within the 95 percent confidence limits for observed total sprouting, and predicted sprouting is generally within observed values over the course of the experiment.

As noted in the discussion of the effect of water stress in Chapter III, the effect of such stress may be continuous, with its effect increasing or decreasing with degree and duration of stress. The tubers used in the 1990 experiments did appear to sprout faster and

more completely with each successive experiment, but it is not possible to state whether this increase was due to increased stress, to longer duration of the stress, to seasonality (change from spring through summer), or to some other factor or factors. Since water stress has been shown to increase tuber sprouting, however, it is possible that the model will slightly overestimate sprouting for tubers from nonstressed plants. Since the effect of water stress on total sprouting was most noticeable at lower temperatures, any overprediction should be most noticeable in the controls. The effect of stress on rate, however, should appear in both solarized and control treatments.

Table 17. Analysis of variance and regression coefficients for regression to predict Richards parameter A for temperature regimes with minimum temperature less than or equal to 35 C.

Analysis of variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	5304.04	1060.81	16.18	0.0001
Error	29	1900.96	65.55		
Corrected Total	34	7205.00			

R-Square	C.V.
0.74	8.82

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MAXTEMP	1	2544.74	2544.74	38.82	0.0001
$MAXTEMP^2$	1	2510.84	2510.84	38.30	0.0001
MINTEMP	1	43.84	43.84	0.67	0.4202
$MINTEMP^2$	1	0.14	0.14	0.00	0.9631
MAXTEMPxMINTEMP	1	204.47	204.47	3.12	0.0879

Regression coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT	-120.67	-2.38	0.0242	50.72
MAXTEMP	13.15	6.73	0.0001	1.95
$MAXTEMP^2$	-0.20	-6.20	0.0001	0.033
MINTEMP	-2.00	-0.63	0.5348	3.18
$MINTEMP^2$	-0.033	-0.56	0.5801	0.060
MAXTEMPxMINTEMP	0.093	1.77	0.0879	0.053

Table 18. Analysis of variance and regression coefficients for regression to predict Richards parameter A for temperature regimes with minimum temperature greater than 35 C.

Analysis of variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	17248.43	3449.69	27.70	0.0001
Error	24	2988.60	124.53		
Corrected Total	29	20237.03			

R-Square	C.V.
0.85	13.05

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MAXTEMP	1	158.97	158.97	1.28	0.2697
$MAXTEMP^2$	1	4344.08	4344.08	34.89	0.0001
MINTEMP	1	6757.43	6757.43	54.27	0.0001
$MINTEMP^2$	1	5986.60	5986.60	48.08	0.0001
MAXTEMPxMINTEMP	1	1.348	1.348	0.01	0.9180

Regression coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT	-537.30	-6.14	0.0001	87.48
MAXTEMP	14.75	3.48	0.0019	4.23
$MAXTEMP^2$	-0.1928	-2.64	0.0144	0.07305
MINTEMP	23.84	5.45	0.0001	4.378
$MINTEMP^2$	-0.4051	-5.55	0.0001	0.07305
MAXTEMPxMINTEMP	0.01241	0.10	0.9180	0.1193

Table 19. Analysis of variance and regression coefficients for regression to predict Richards parameter B.

Analysis of variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	1.409	0.7045	1.91	0.1634
Error	36	13.307	0.3696		
Corrected Total	38	14.716			

R-Square	C.V.
0.096	23.88

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MAXTEMP	1	0.8489	0.8489	2.30	0.1384
MINTEMP	1	0.5601	0.5601	1.52	0.2263

Regression coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT	-3.05085	-5.43	0.0001	0.5620
MAXTEMP	0.02888	1.89	0.0668	0.0153
MINTEMP	-0.02001	-1.23	0.2263	0.0163

Table 20. Analysis of variance and regression coefficients for regression to predict Richards parameter K.

Analysis of variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr >
Model	4	0.8815	0.2204	8.34	0.0001
Error	34	0.8983	0.0264		
Corrected Total	38	1.7798			

R-Square	C.V.
0.50	22.46

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MAXTEMP	1	0.1512	0.1512	5.72	0.0224
$MAXTEMP^2$	1	0.5165	0.5165	19.55	0.0001
MINTEMP	1	0.0478	0.0478	1.81	0.1877
$MINTEMP^2$	1	0.1660	0.1660	6.28	0.0171

Regression coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT	-3.37312	-4.47	0.0001	0.7552
MAXTEMP	0.16072	4.22	0.0002	0.0381
$MAXTEMP^2$	-0.00213	-3.95	0.0004	0.0005
MINTEMP	0.09157	2.34	0.0252	0.0391
$MINTEMP^2$	-0.00168	-2.51	0.0171	0.000668

Table 21. Analysis of variance and regression coefficients for regression to predict Richards parameter N.

Analysis of variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	0.0001282	0.0000427	2.86	0.0507
Error	35	0.0005226	0.0000149		
Corrected Total	38	0.0006508			

R-Square	C.V.
0.20	52.64

Source	DF	Type I SS	Mean Square	F Value	Pr > F
MAXTEMP	1	0.0000003	0.0000003	0.02	0.8852
$MAXTEMP^2$	1	0.0000629	0.0000629	4.21	0.0477
MINTEMP	1	0.0000650	0.0000650	4.35	0.0443

Regression coefficients

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT	-.02275	-1.52	0.1379	0.01498
MAXTEMP	0.001526	1.72	0.0947	0.0008885
$MAXTEMP^2$	-.00002288	-1.82	0.0775	0.00001258
MINTEMP	0.00021676	2.09	0.0443	0.0001039

Table 22. Mean observed final cumulative percent sprouting of tubers in the field and 95 percent confidence limit, with final cumulative percent sprouting predicted by the model from minimum and maximum soil temperatures.

Experiment	Treatment	Mean Observed Sprouting (Percent)	95 Percent Confidence Limit	Predicted Sprouting (Percent)
First	Control	70.5	±24.5	[x]
	Solarized	97.1	±7.9	93.6[y]
Second	Control	74.2	±18.9	69.8
	Solarized	96.7	±9.3	96.5
Third	Control	97.1	±7.9	89.3
	Solarized	100.0	±0.0	100.0

[x] No predicted value due to lack of temperature data.

[y] Predicted value at 16 days because equipment malfunction caused loss of temperature data after 16 days.

Table 23. Mean daily minimum and maximum soil temperatures and temperature range at 15 cm depth with mean daily solar radiation during the three field experiments.

Experiment	Month	Treatment	Minimum[x] Temp.	Maximum[x] Temp.	Temp.[x] Range	Solar[y] Radiation
First (1986)	Sept.	Control[z]				397.4
		Solarized	25.3	29.8	4.5	
Second (1990)	March	Control	21.7	23.2	1.5	361.8
		Solarized	26.1	29.9	3.8	
	April	Control	22.9	24.5	1.6	372.9
		Solarized	28.5	32.3	3.8	
Third (1990)	June	Control	25.7	27.7	2.0	408.2
		Solarized	29.9	33.0	3.1	
	July	Control	26.7	29.1	2.4	503.4
		Solarized	34.1	38.3	4.2	

[x] Temperatures in degrees Celsius.

[y] Total global solar radiation in cal cm^{-2} day^{-1}.

[z] No temperatures were recorded for this treatment due to equipment malfunction.

Table 24. Monthly means and maxima of total daily global solar radiation and maximum soil temperatures at two soil depths at Waimanalo in 1984.

	Solar Radiation[w]		Maximum Soil Temperature[x]			
Month	Mean	Maximum	Depth[y]	Treatment	Mean	Maximum
March	430.5	469.8	5	Control	29.7	30.3
				Solarized	36.5	38.6
			15	Control	25.9	26.2
				Solarized	31.2	32.6
April	416.5	548.3	5	Control	29.9	33.8
				Solarized	38.7	43.0
			15	Control	26.2	29.6
				Solarized	33.5	35.8
May	514.7	589.8	5	Control	33.4	37.7
				Solarized	44.3	48.4
			15	Control	28.3	30.6
				Solarized	37.2	39.8
June	485.7	582.1	5	Control	32.8	36.3
				Solarized	43.9	48.3
			15	Control	29.2	30.5
				Solarized	35.1	37.2
July	519.5	609.6	5	Control	35.1	37.2
				Solarized	47.7	51.1
			15	Control	31.0	32.2
				Solarized	37.8	39.5
August	489.8	580.2	5	Control	35.6	38.1
				Solarized	47.4	51.3
			15	Control	31.3	32.5
				Solarized	37.5	39.6
September	455.9	550.5	5	Control	34.4	37.6
				Solarized	46.7	51.7
			15	Control	30.4	31.9
				Solarized	36.8	39.1

[w] Total global solar radiation in cal cm^{-2} day^{-1}.

[x] Temperature in degrees Celsius.

[y] Soil depth in cm.

Table 25. Monthly means and maxima of total daily global solar radiation and maximum soil temperatures at two soil depths at Waimanalo in 1985.

	Solar Radiation[w]		Maximum Soil Temperature[x]			
Month	Mean	Maximum	Depth[y]	Treatment	Mean	Maximum
July	558.4	681.7	5	Control	33.4	36.2
				Solarized	47.2	51.0
			15	Control	31.2	33.2
				Solarized	39.2	41.7
August	459.1	616.4	5	Control	31.7	35.7
				Solarized	45.0	51.3
			15	Control	30.2	32.0
				Solarized	38.8	41.0
September	428.0	570.2	5	Control	33.6	37.4
				Solarized	43.3	50.2
			15	Control	30.0	31.5
				Solarized	36.8	38.8
October	430.5	683.2	5	Control	33.3	38.1
				Solarized	41.3	45.1
			15	Control	29.6	31.2
				Solarized	35.8	37.0

[w] Total global solar radiation in cal cm^{-2} day^{-1}.

[x] Temperature in degrees Celsius.

[y] Soil depth in cm.

Table 26. Monthly means and maxima of total daily global solar radiation and maximum soil temperatures at two soil depths at Waimanalo in 1986.

	Solar Radiation[w]		Maximum Soil Temperature[xy]			
Month	Mean	Maximum	Depth[z]	Treatment	Mean	Maximum
January	238.8	384.2	5	Control	23.4	27.7
				Solarized	31.0	37.9
			15	Control	24.5	26.1
				Solarized	29.4	32.3
February	302.4	505.2	5	Control	23.6	27.5
				Solarized	29.6	37.3
			15	Control	24.9	27.0
				Solarized	27.8	32.0
March	286.3	494.7	5	Control	25.3	30.8
				Solarized	30.5	38.2
			15	Control	26.6	29.1
				Solarized	29.6	32.8
April	368.9	608.1	5	Control	23.5	28.4
				Solarized	32.8	41.7
			15	Control	26.3	28.8
				Solarized	29.3	33.9
May	470.4	635.7	5	Control	27.2	31.6
				Solarized	38.6	46.3
			15	Control	28.9	31.2
				Solarized	32.9	37.6
June	460.8	621.8	5	Solarized	36.4	43.9
			15	Solarized	31.2	35.7
July	431.8	589.6	5	Solarized	38.8	46.0
			15	Solarized	32.6	35.9
August	423.9	561.9	5	Solarized	38.1	44.1
			15	Solarized	32.4	34.7
September	392.6	513.6	5	Solarized	38.0	45.2
			15	Solarized	30.0	32.7

[w] Total global solar radiation in cal cm^{-2} day^{-1}.
[x] Temperature in degrees Celsius.
[y] No temperatures were recorded in the control treatment from June through September due to equipment malfunction.
[z] Soil depth in cm.

Table 27. Monthly means of total daily solar radiation, and soil temperatures at 15 cm in the solarized treatment at Kunia and Waimanalo. July through September, 1985.

Location	Month	Minimum Temp.[x]	Maximum Temp.[x]	Temp.[x] Range	Solar[y] Radiation
Kunia	July	32.4	37.8	5.4	545.8
	August	33.0	38.3	5.3	512.4
	September	31.7	36.4	4.8	444.5
Waimanalo	July	34.1	39.2	5.2	558.4
	August	34.2	38.8	4.6	486.1[z]
	September	32.4	36.8	4.4	428.0

[x] Soil temperature in degrees Celsius.

[y] Total global solar radiation in cal cm^{-2} day^{-1}.

[z] Data from the first week of August only.

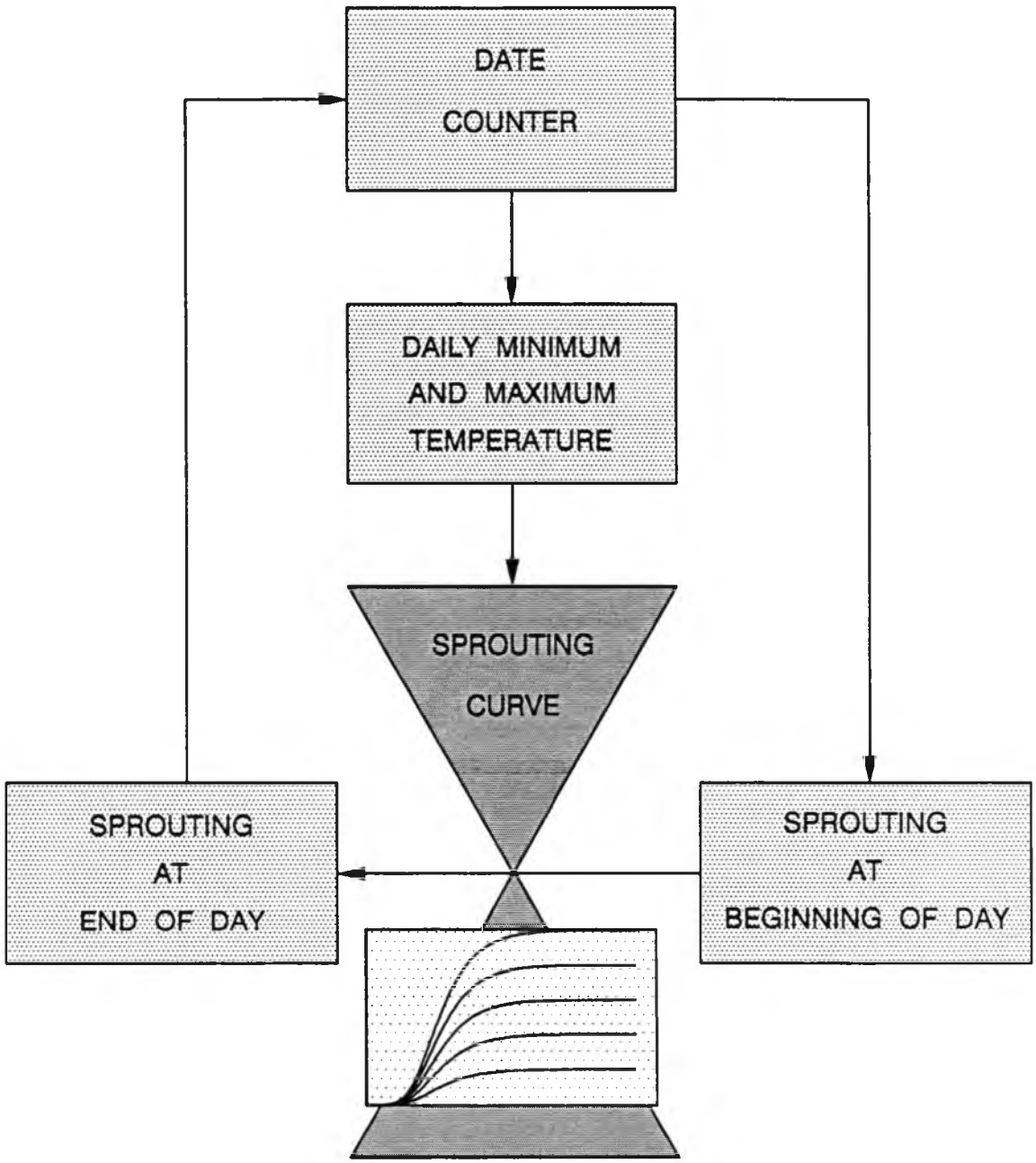

Figure 17. Block diagram of the sprouting model.

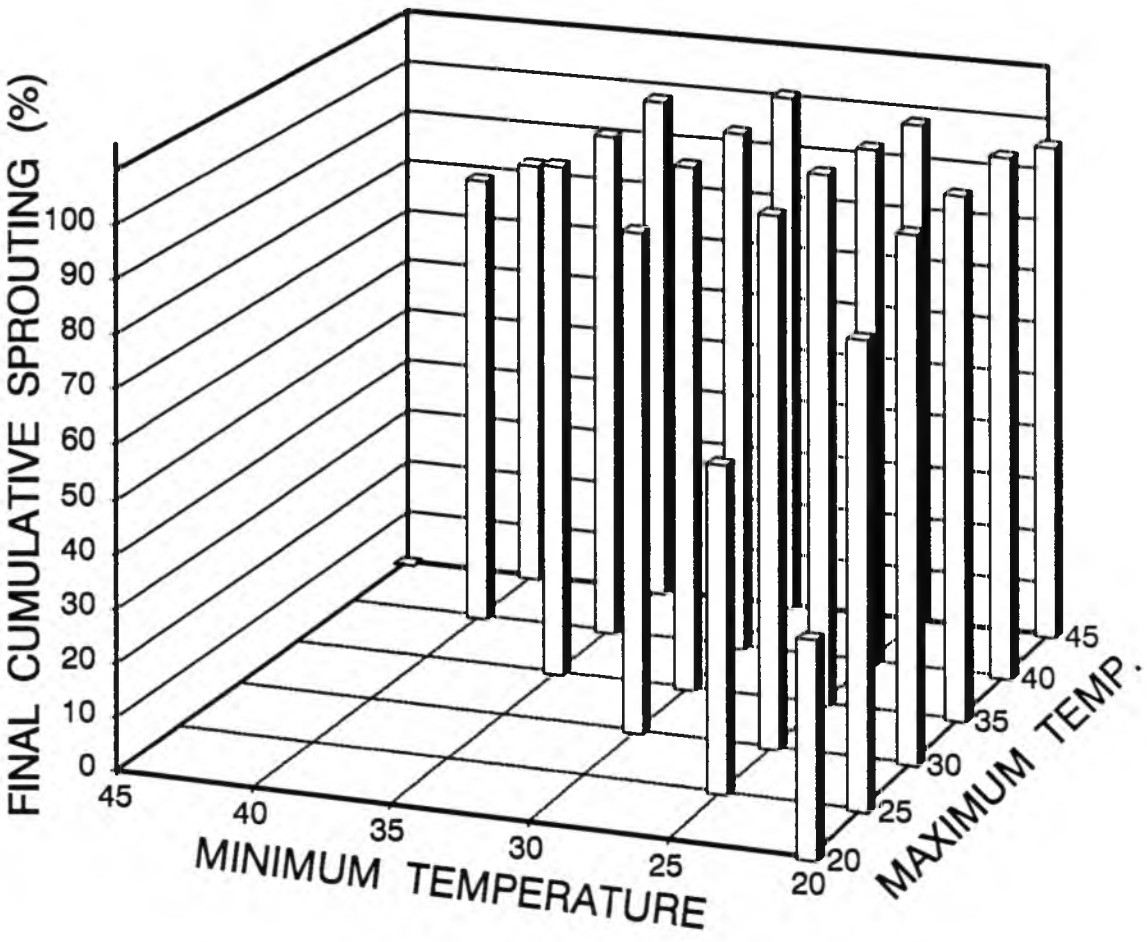

Figure 18. Mean observed final cumulative sprouting from two experiments.

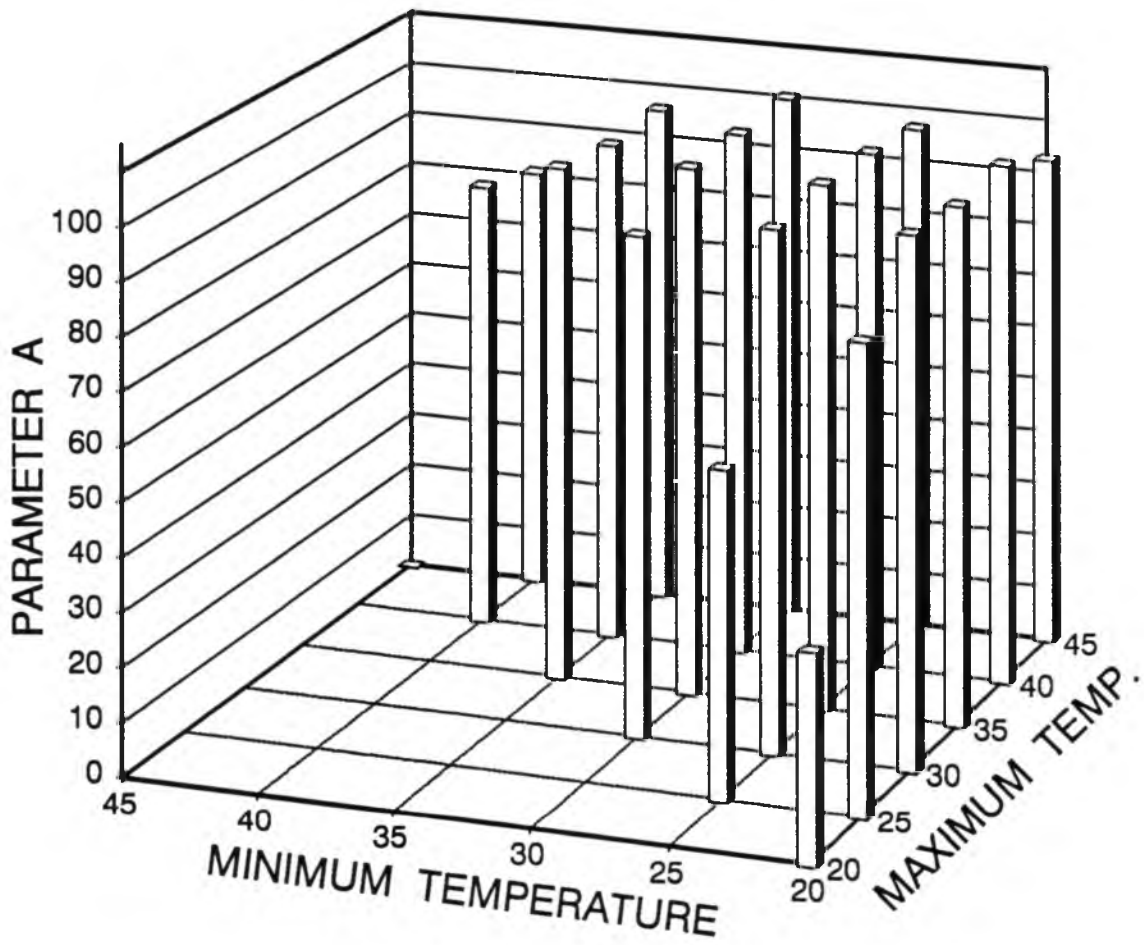

Figure 19. Distribution of Richards parameter A. Means from two experiments.

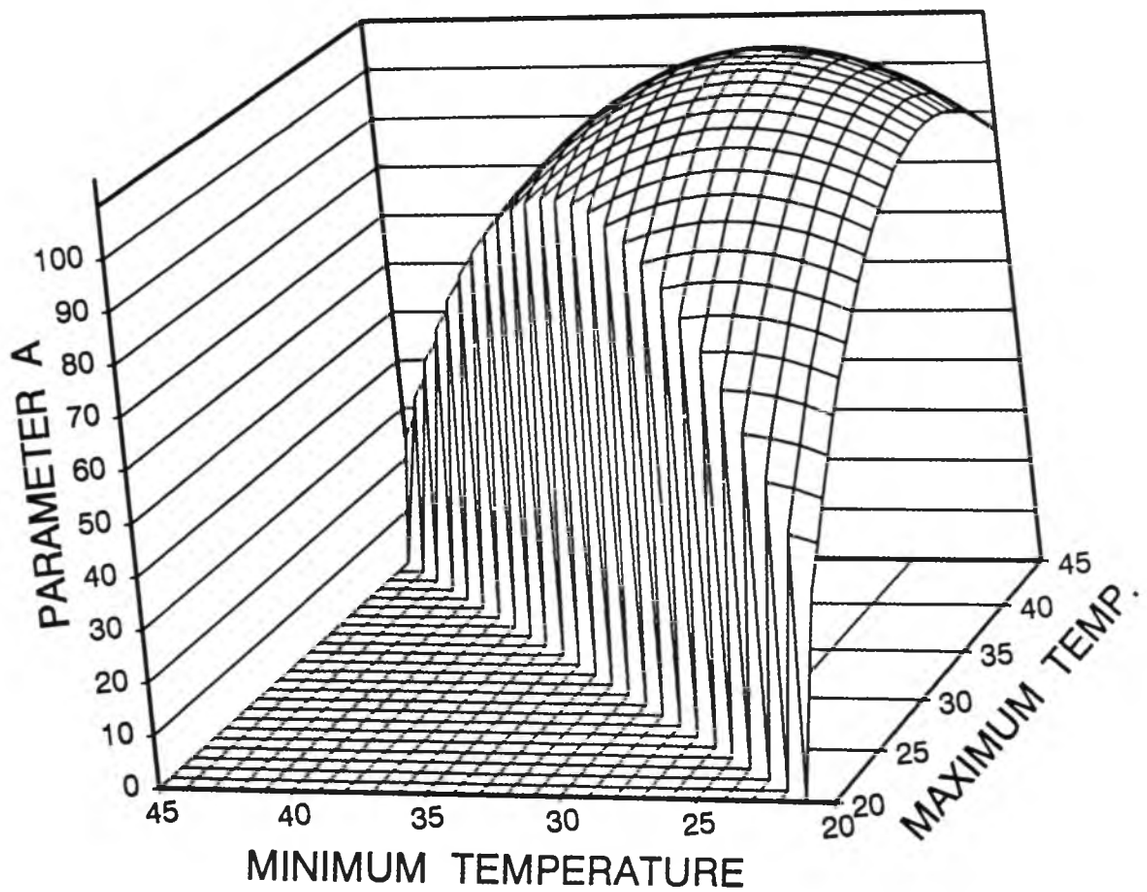

Figure 20. Quadratic response surface for Richards parameter A based on a single regression model. The regression equation is:
A = - 293.5362492 + 13.8061213*MAXTEMP - 0.2104974*MAXTEMP^2 + 10.4557937*MINTEMP - 0.2597861 *MINTEMP^2 + 0.0880272*MAXTEMP*MINTEMP;

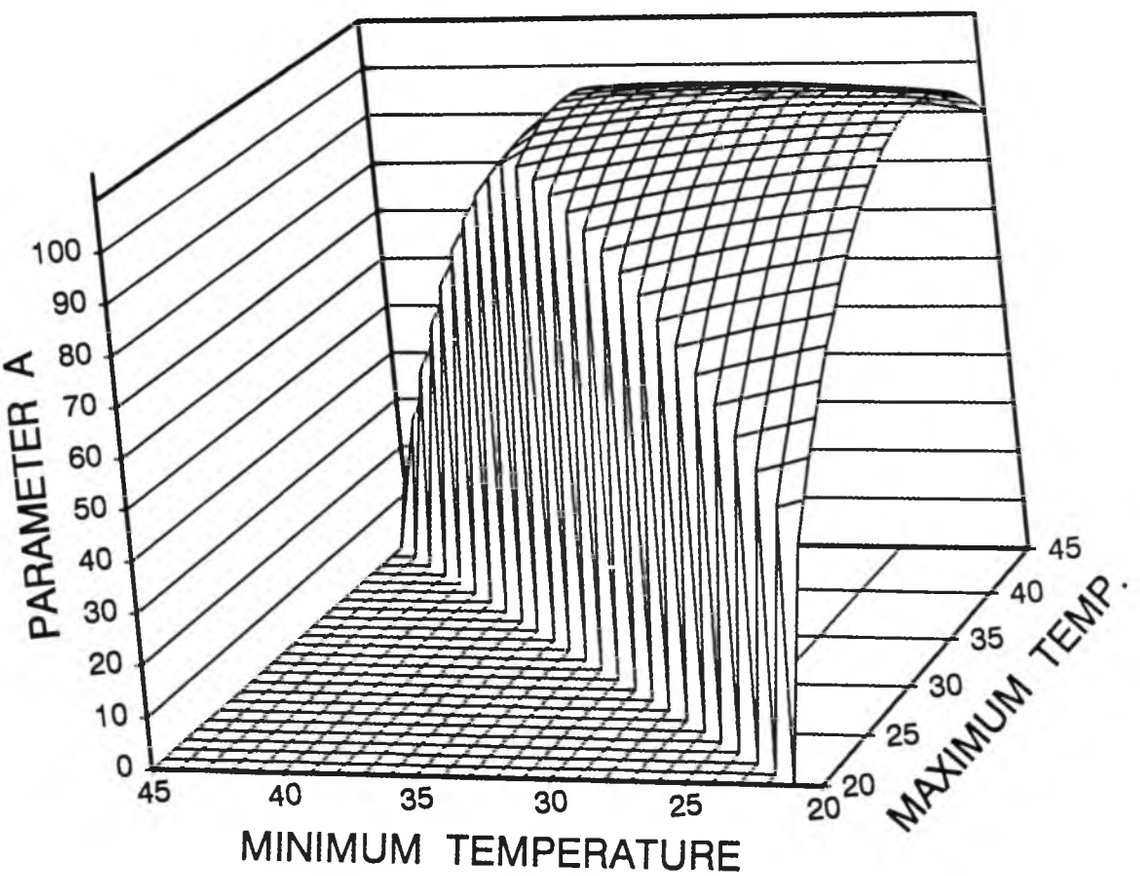

Figure 21. Quadratic response surface for Richards parameter A based on two regression models. If the minimum temperature is less than or equal to 35 C, then A = -120.67 + 13.15*MAXTEMP - 0.20*MAXTEMP^2 - 2.00*MINTEMP - 0.033*MINTEMP^2 + 0.093*MAXTEMP*MINTEMP; and if the minimum temperature is greater than 35 C, A = -537.30 + 14.75*MAXTEMP - 0.19*MAXTEMP^2 + 23.84*MINTEMP - 0.41*MINTEMP^2 + 0.012*MAXTEMP*MINTEMP.

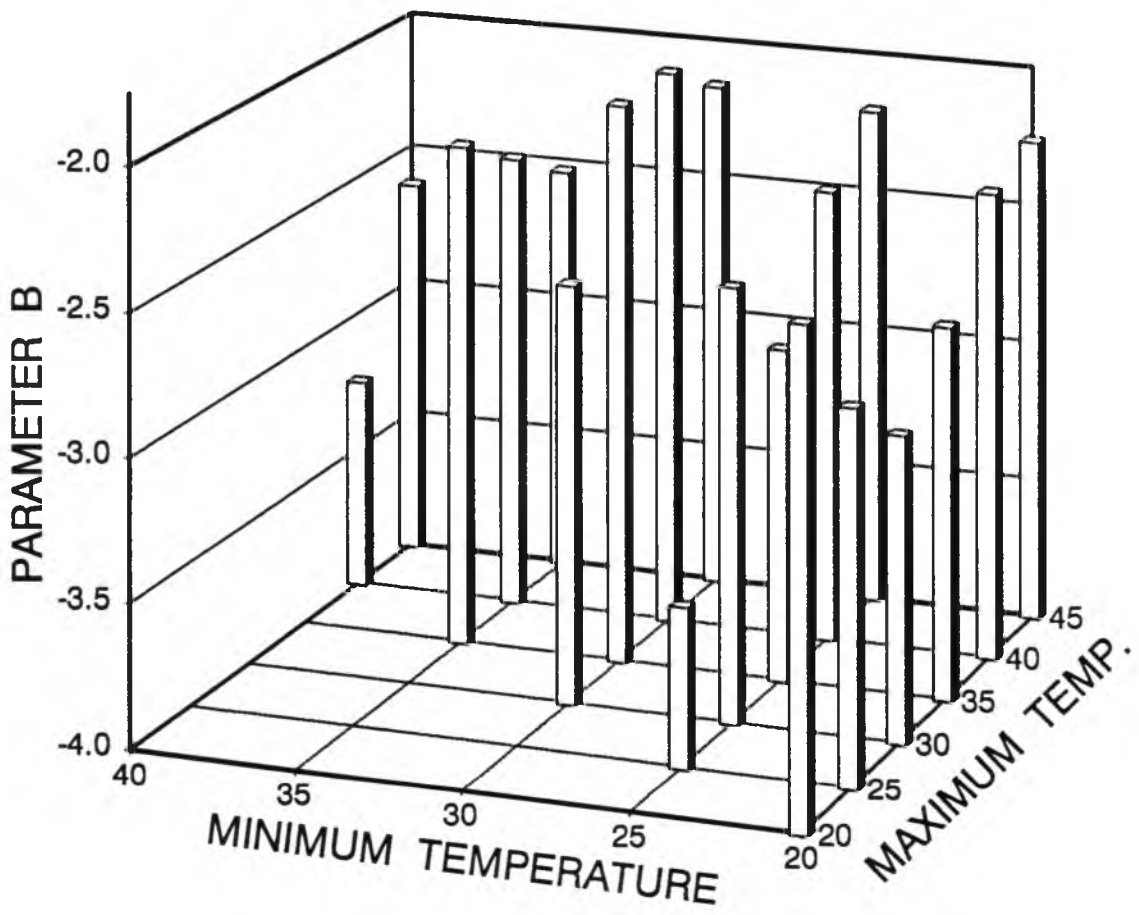

Figure 22. Distribution of Richards parameter B. Means from two experiments.

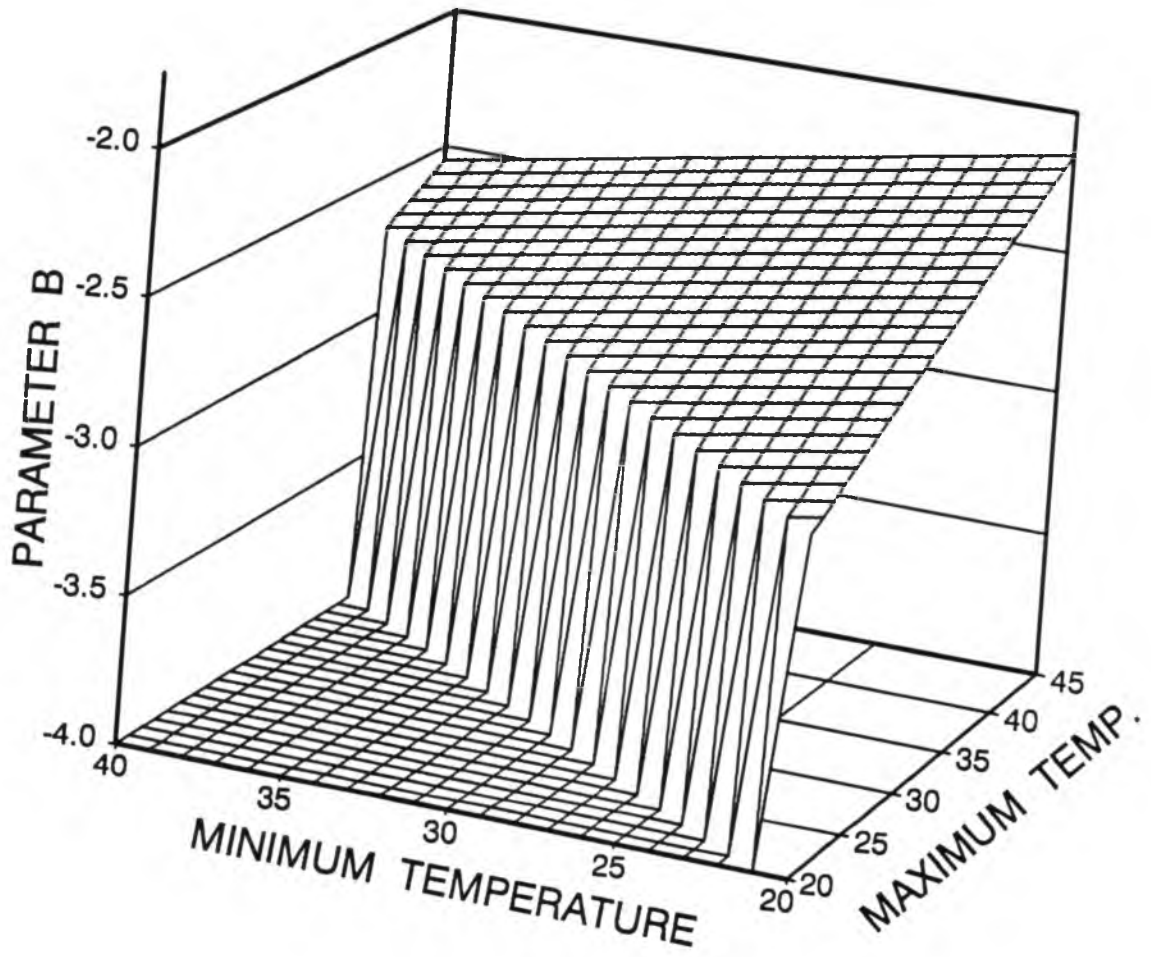

Figure 23. Response surface for Richards parameter B. The regression equation is: B = -3.05 + 0.029*MAXTEMP - 0.020*MINTEMP.

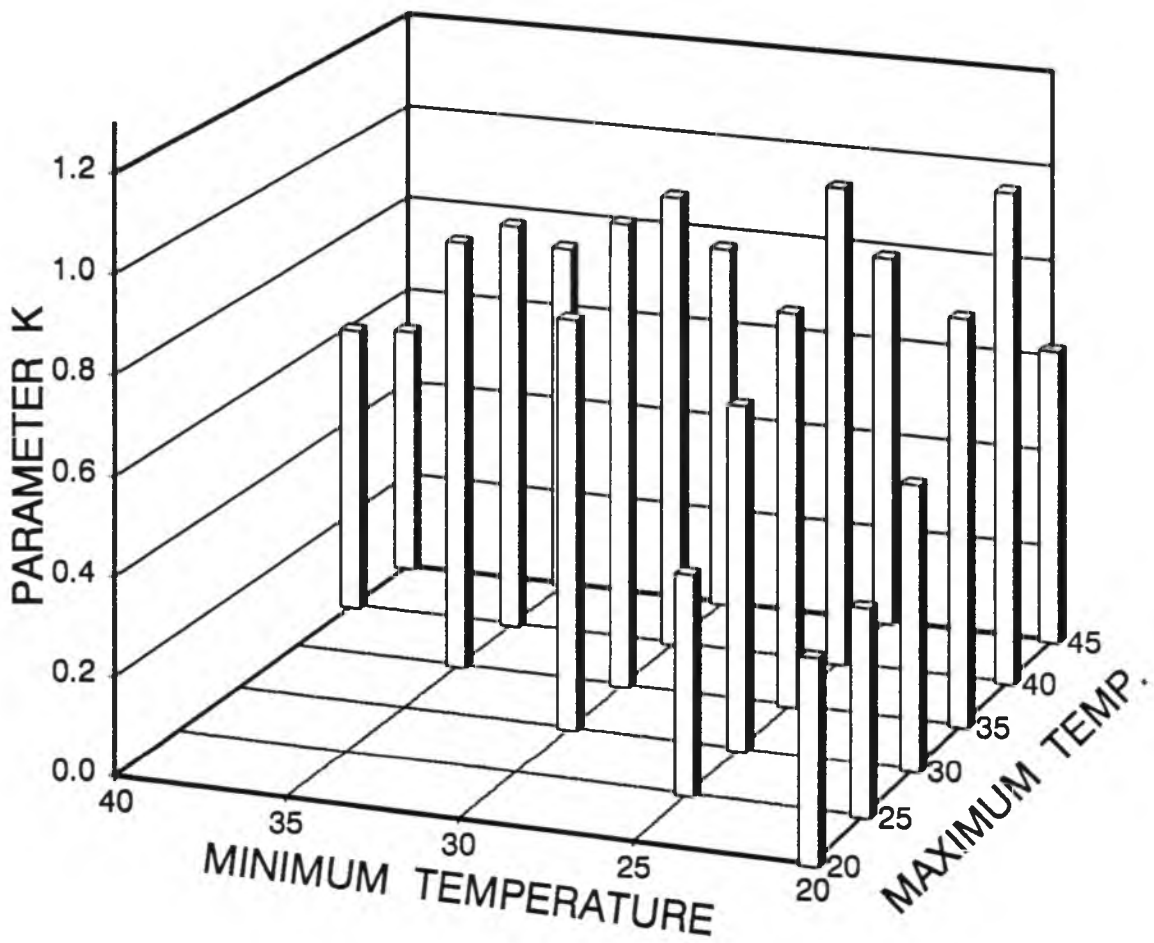

Figure 24. Distribution of Richards parameter K. Means from two experiments.

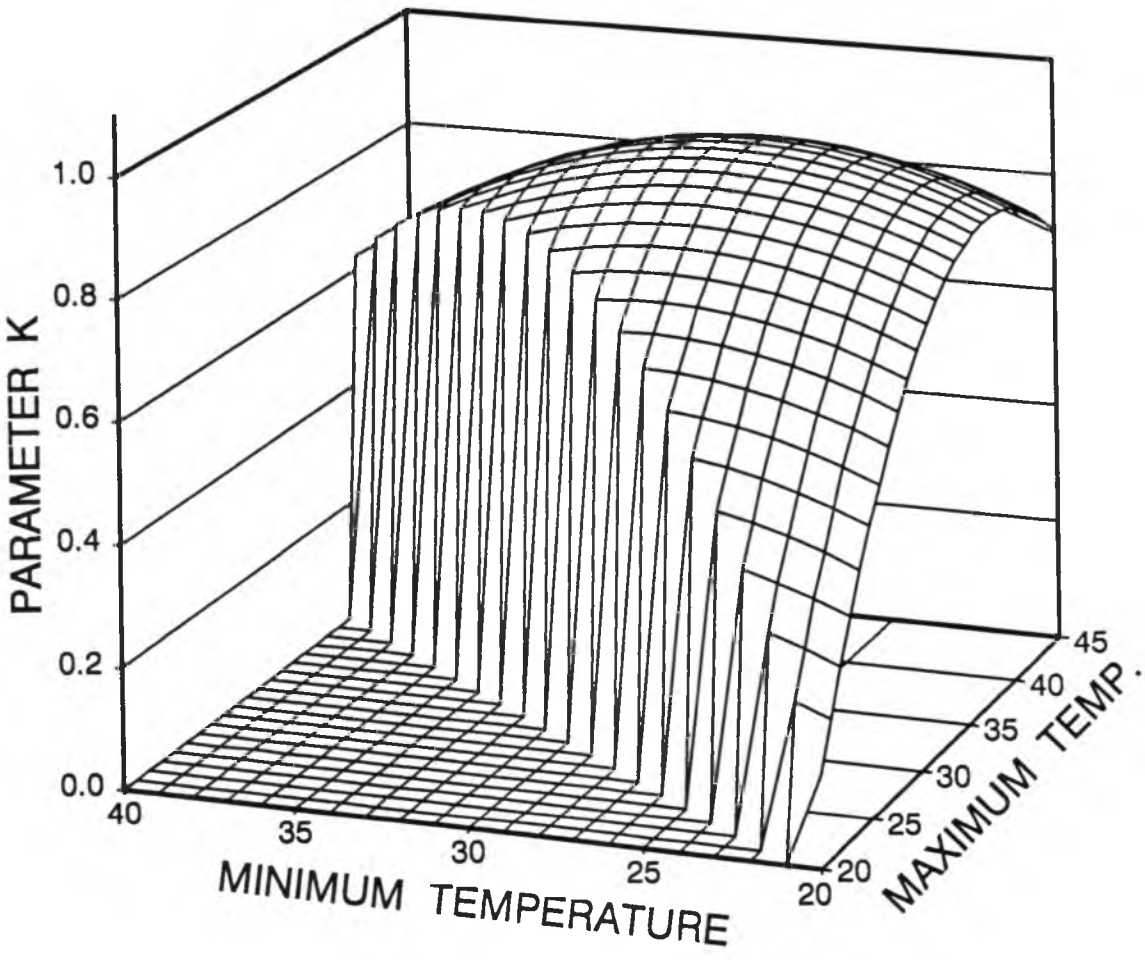

Figure 25. Quadratic response surface for Richards parameter K. The regression equation is: K = -3.37 + 0.16*MAXTEMP - 0.0021*MAXTEMP^2 + 0.092*MINTEMP - 0.0017*MINTEMP**2.

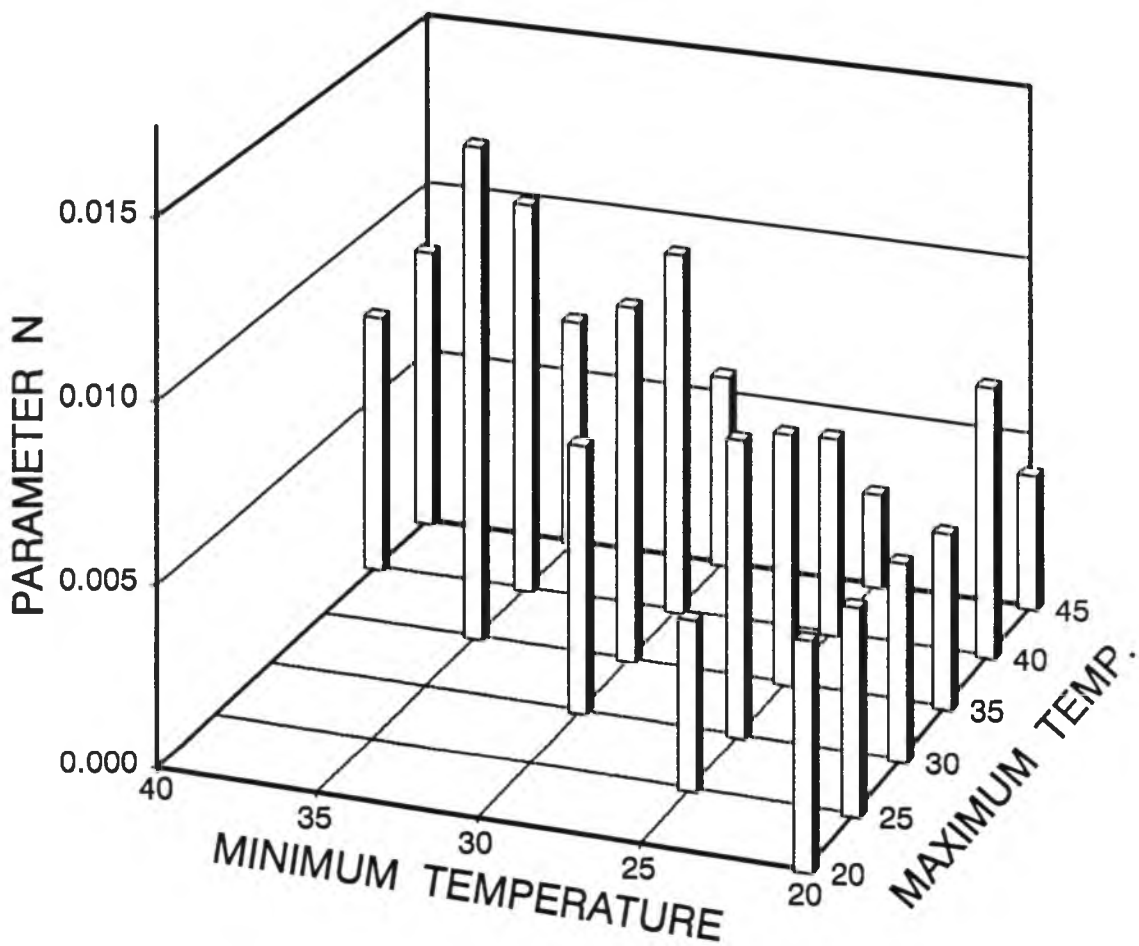

Figure 26. Distribution of Richards parameter N. Means from two experiments.

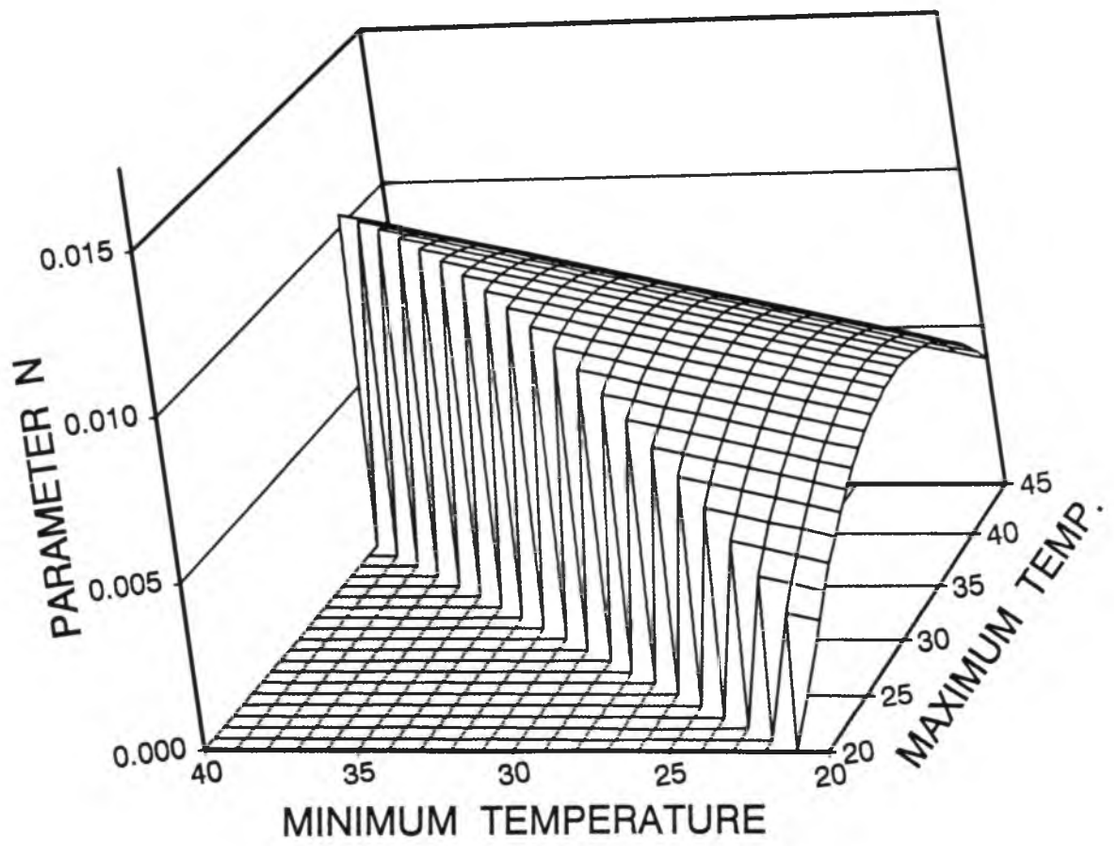

Figure 27. Quadratic response surface for Richards parameter N. The regression equation is: $N = -0.023 + 0.0015*MAXTEMP - 0.000023*MAXTEMP^2 + 0.00022*MINTEMP$.

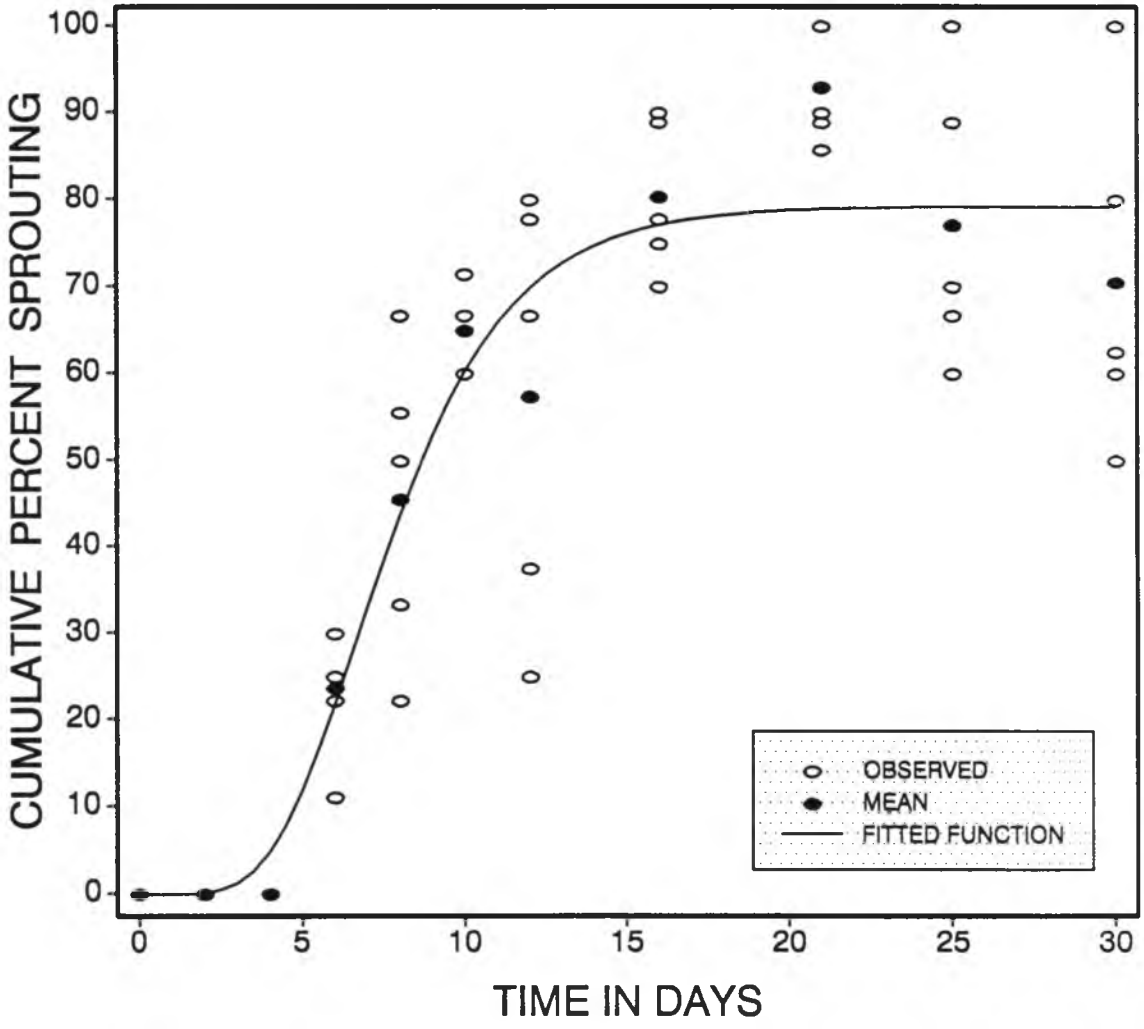

Figure 28. Purple nutsedge tuber sprouting in the field. Experiment 1: September - October, 1986. Observed (circles) and mean (dots) cumulative percent sprouting in the control treatment, with fitted Richards function (solid line). There are no temperatures or predictions due to equipment malfunction (see text for explanation). Where 2 or more observations have the same value only one observation can be seen.

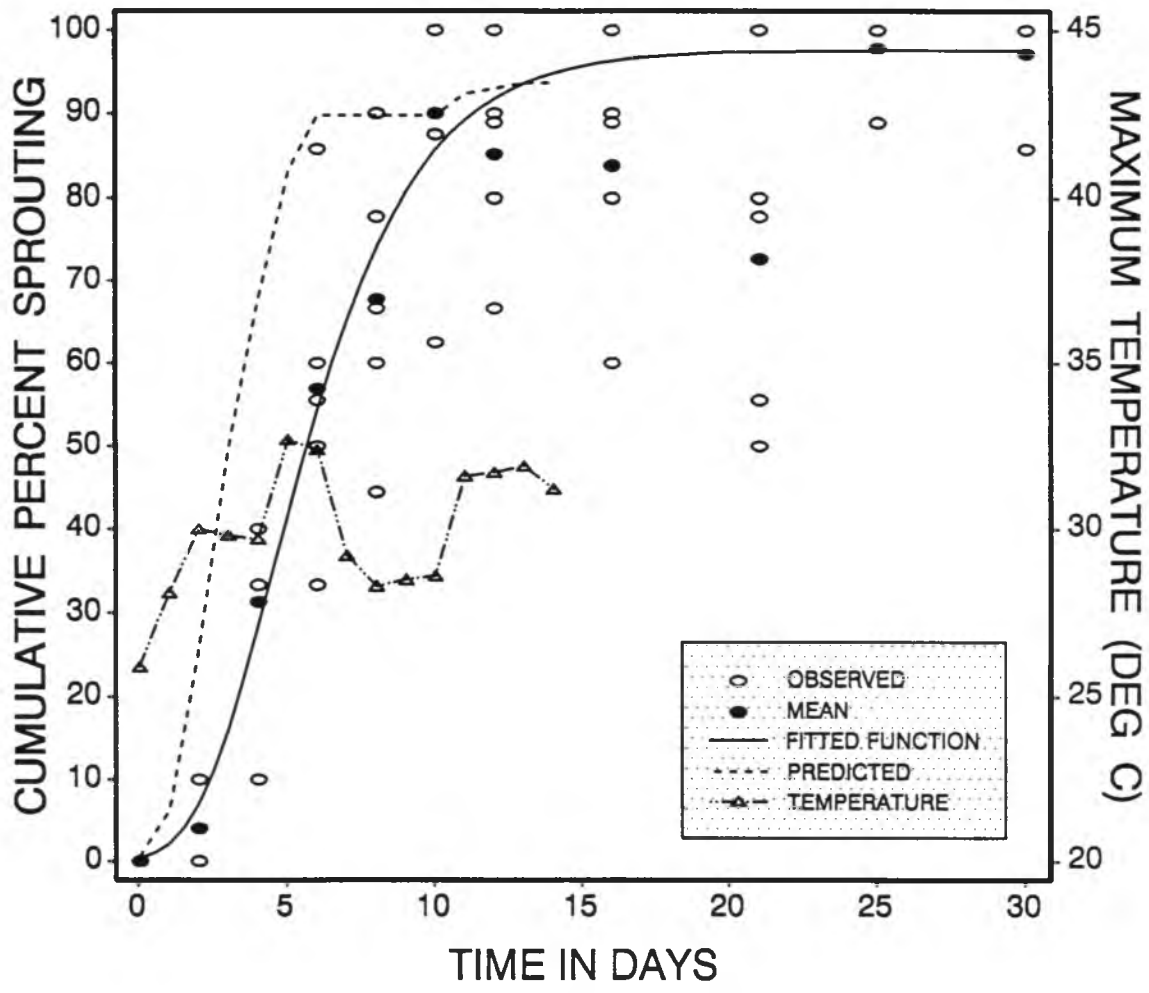

Figure 29. Purple nutsedge tuber sprouting in the field. Experiment 1: September - October, 1986. Observed (circles) and mean (dots) cumulative percent sprouting in the solarized treatment, with fitted Richards function (solid line), daily maximum temperature (triangles) in degrees Celsius, and cumulative sprouting (dashed line) predicted by the model from minimum and maximum soil temperature. Temperatures and predictions end at 16 days due to equipment malfunction (see text for explanation). Where 2 or more observations have the same value only one observation can be seen.

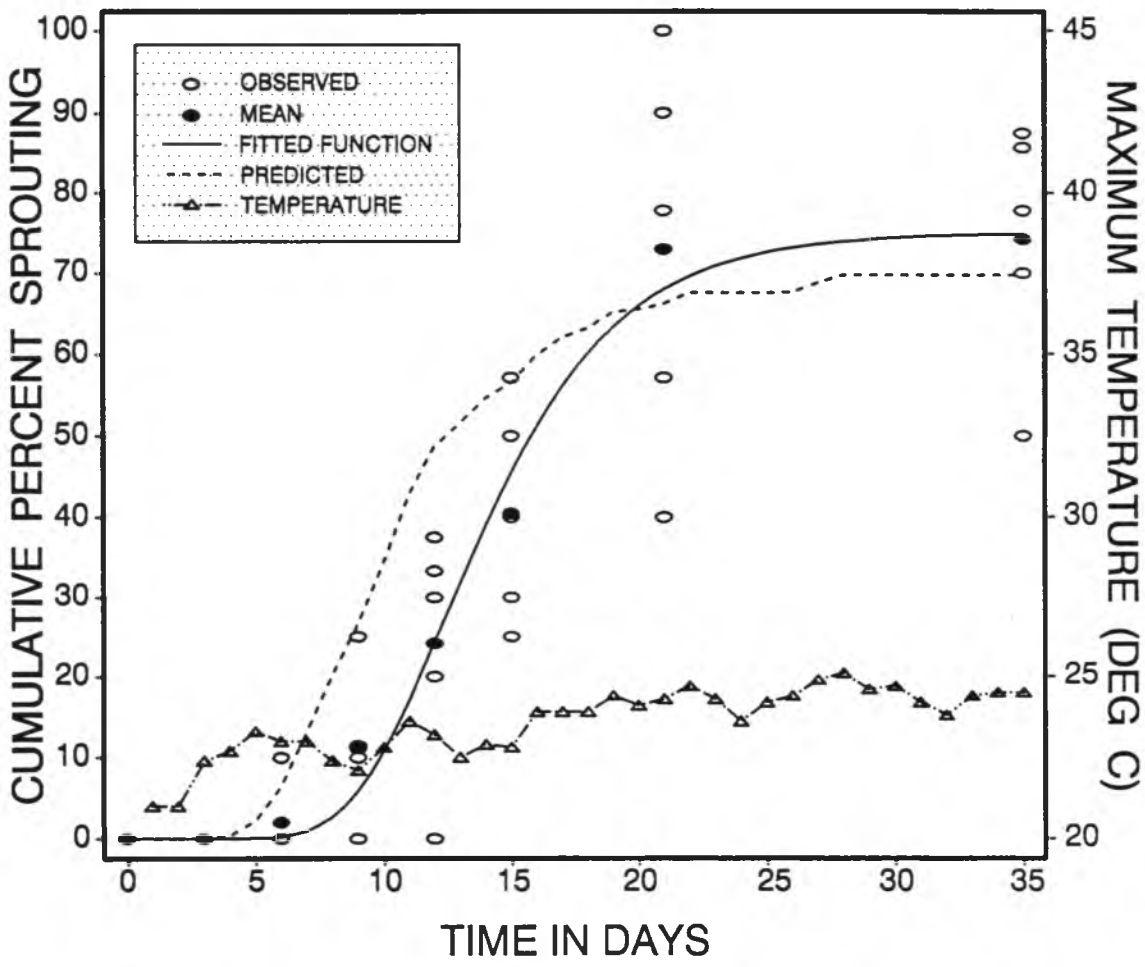

Figure 30. Purple nutsedge tuber sprouting in the field. Experiment 2: March - April, 1990. Observed (circles) and mean (dots) cumulative percent sprouting in the control treatment, with fitted Richards function (solid line), daily maximum temperature (triangles) in degrees Celsius, and cumulative sprouting (dashed line) predicted by the model from minimum and maximum soil temperature. Where 2 or more observations have the same value only one observation can be seen.

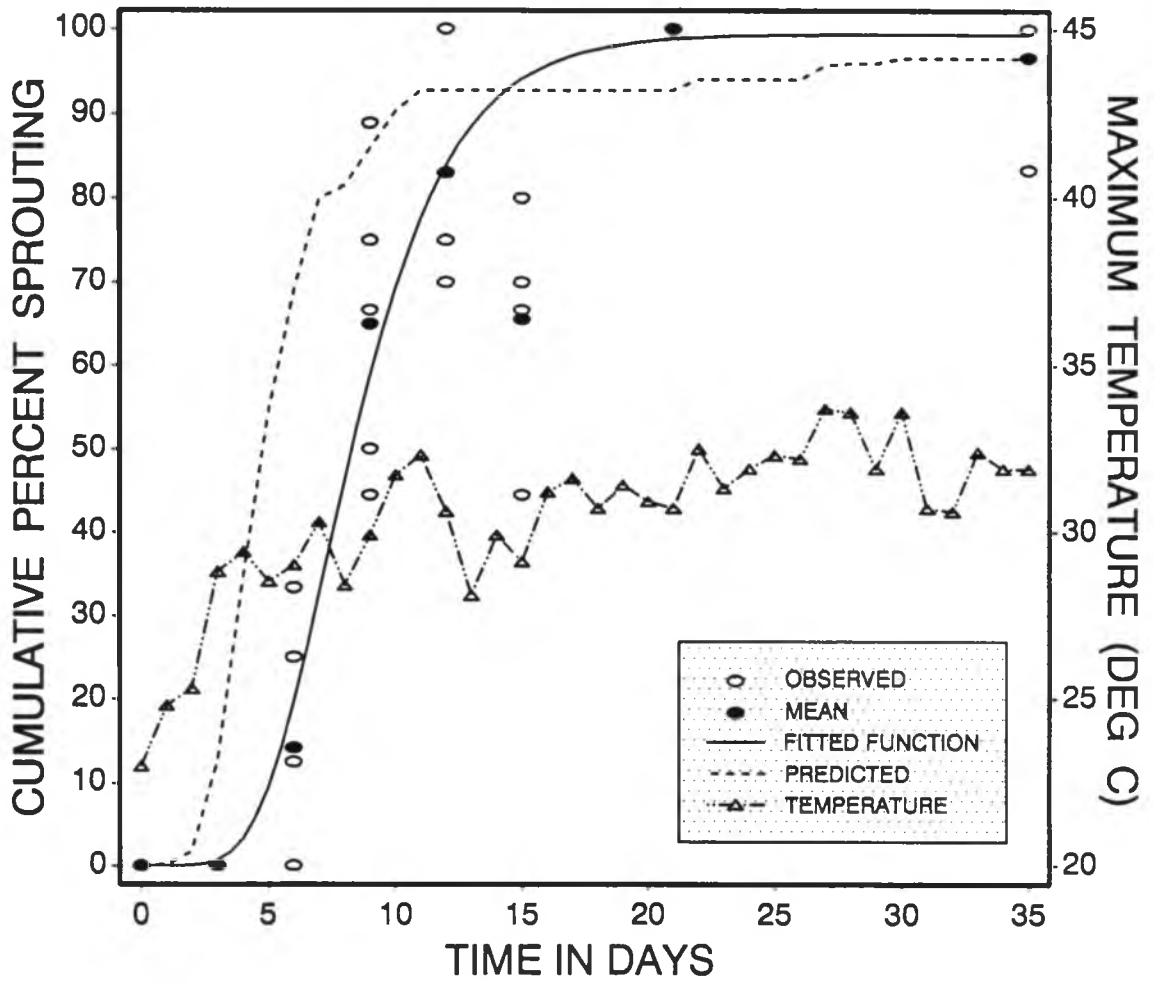

Figure 31. Purple nutsedge tuber sprouting in the field. Experiment 2: March - April, 1990. Observed (circles) and mean (dots) cumulative percent sprouting in the solarized treatment, with fitted Richards function (solid line), daily maximum temperature (triangles) in degrees Celsius, and cumulative sprouting (dashed line) predicted by the model from minimum and maximum soil temperature. Where 2 or more observations have the same value only one observation can be seen.

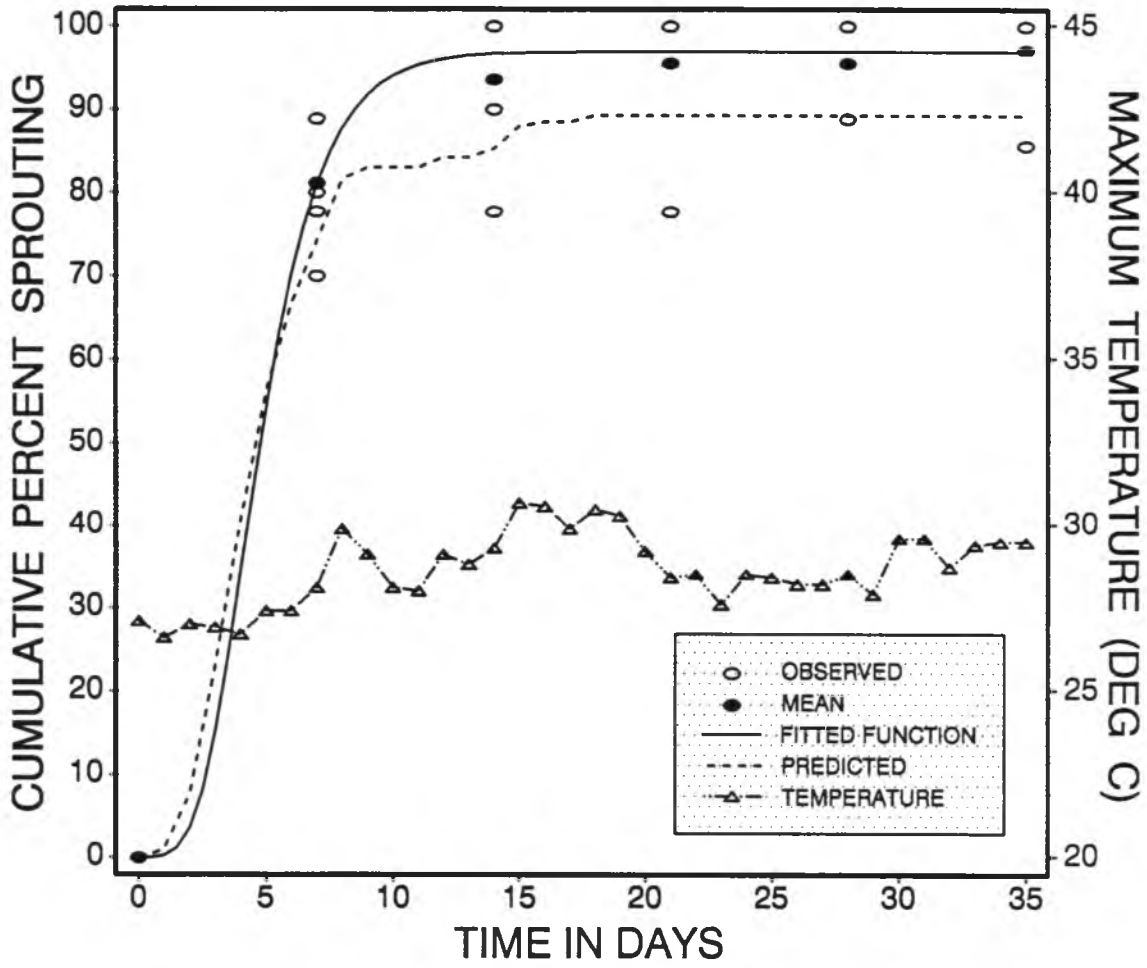

Figure 32. Purple nutsedge tuber sprouting in the field. Experiment 3: June - July, 1990. Observed (circles) and mean (dots) cumulative percent sprouting in the control treatment, with fitted Richards function (solid line), daily maximum temperature (triangles) in degrees Celsius, and cumulative sprouting (dashed line) predicted by the model from minimum and maximum soil temperature. Where 2 or more observations have the same value only one observation can be seen.

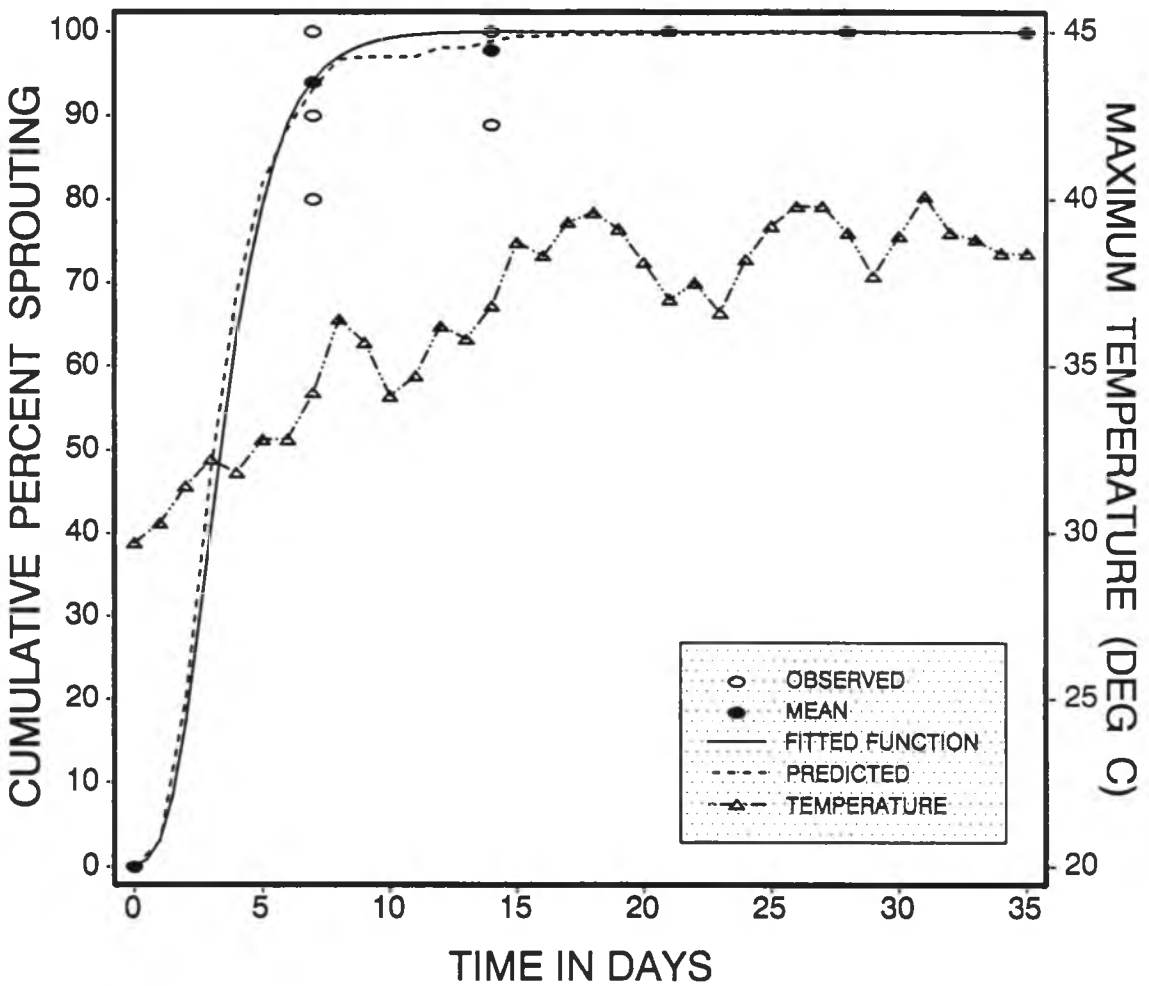

Figure 33. Purple nutsedge tuber sprouting in the field. Experiment 3: June - July, 1990. Observed (circles) and mean (dots) cumulative percent sprouting in the solarized treatment, with fitted Richards function (solid line), daily maximum temperature (triangles) in degrees Celsius, and cumulative sprouting (dashed line) predicted by the model from minimum and maximum soil temperature. Where 2 or more observations have the same value only one observation can be seen.

CHAPTER VI

DISCUSSION AND CONCLUSIONS

Several conclusions can be drawn from this study, and a number of questions have been raised. These are discussed below.

PREDICTING TUBER SPROUTING

It is possible to predict purple nutsedge tuber sprouting if minimum and maximum soil temperatures are known. The accuracy of the prediction with reference to time is variable, with the best predictions coming from a model based on tubers collected near the time that the predictions are to be made. This raises the question of how broadly applicable these results are. Still, in all cases the predictions of total sprouting under solarization are accurate, and the predictions of time to near maximum sprouting are not off by more than a few days. Thus it is possible to reliably predict the percent tuber sprouting under solarization, but the predictions of the time to a given percentage of sprouting are less accurate.

The prediction of total sprouting is less reliable under nonsolarized conditions. There are clearly other factors influencing tuber sprouting, and these may account for variable accuracy in predictions. It seems clear that if the temperature is high enough, and the amplitude of fluctuation wide enough, temperature will override all other factors and induce 100 percent, or near 100 percent sprouting. At temperatures which are less stimulatory, the other factors

apparently play a greater role. This would explain the consistent under-prediction of total sprouting for control treatments in the field while the prediction of total sprouting in the solarized treatments was very accurate.

A possible cause of underprediction of total sprouting in the controls was indicated in the experiments on methodology. In two of those experiments, sprouting was found to be higher in total darkness than in the treatments which were counted and exposed to light every day. It was noted in that section that the reduction in sprouting was most pronounced at lower temperatures, and that this could result in underprediction of sprouting at low temperatures if tubers were undisturbed. This condition is true of tubers buried 15 cm deep and not subjected to solarization. Soil temperatures at this depth under natural conditions are in the range where sprouting was shown to be low.

This model may not be immediately applicable to other regions because of possible ecotypical differences in purple nutsedge. Apparently, at low temperatures sprouting of tubers from warm temperate regions such as the southern United States is higher than that of tubers from Hawaii. For example Orcutt and Holt (1990) reported a minimum temperature of 10 C for sprouting of purple nutsedge tubers, while the tubers used in this study barely sprouted at 20 C. The methodology developed in this study can be used, however, and not only for purple nutsedge. This model can be adapted to any weed propagule which responds to alternating temperatures. Studies on tubers require

incubators with enough space to accommodate the large number of treatments needed to provide the range of temperatures needed to develop a good model. For seeds, however, much less space is required, and the experiments could be done on a thermogradient bar. A complete series of experiments could be completed and a preliminary model developed in a single year. It would be desirable to continue experiments over a period of years to identify any seasonal effects.

VALUE OF THE CURVE FITTING APPROACH

As several researchers have noted, curve fitting is a good way to characterize seed germination. This study has demonstrated the value of this approach for purple nutsedge tuber sprouting. Through the use of fitted functions, the entire course of sprouting can be characterized and predicted. By predicting the curve parameters from soil temperature it is possible to accurately and consistently predict tuber sprouting. This is a valuable tool in understanding the dynamics of purple nutsedge populations in the field.

ALTERNATING TEMPERATURES

This study has demonstrated the importance of the effect of alternating temperature on purple nutsedge tuber sprouting. Had the model been based on constant temperatures alone, the results would have been very misleading. This of course is not true for all plants. Many species of vegetables have shown no response to temperature alternation (Wagenvoort and Bierhuizen, 1977), and the same is true for potato

tubers (Sale, 1979). Response to alternating temperatures is common in weed seeds, however, and it is incumbent on any researcher investigating temperature responses to determine whether such a response exists in the organism under investigation. The extensive literature on temperature and bulb forcing deals with prolonged exposure (days or weeks) to constant temperatures (Rees, 1972). To date, there appears to have been very little work on quantifying responses to temperature fluctuations, and this is a very promising area of research. This is particularly true for researchers who are interested in predicting weed emergence and populations.

Benech Arnold *et al.* (1988) reported on the response of johnsongrass (*Sorghum halepense*) seed to alternating temperature. They demonstrated that this response is a mechanism for detecting gaps in a plant canopy. The presence of a canopy shades the soil, keeping mean soil temperature lower and damping the amplitude of temperature fluctuation. When the canopy is removed, mean soil temperature, and more importantly amplitude of temperature fluctuation, are increased. In response, johnsongrass seeds germinate in large numbers. This is a valuable mechanism for seeds which are buried too deeply in the soil to detect changes in light quantity and/or quality. In at least some species of plants with light-sensitive seeds, e.g., *Rumex* spp., a temperature shift or alternation can substitute for exposure to light in breaking dormancy (Taylorson and Hendricks, 1972a).

Purple nutsedge is known to be shade sensitive, and it often apparently disappears under a dense canopy. Its rapid reappearance when the canopy is removed, however, demonstrates that viable tubers

are present even when no aboveground plants can be observed. This also demonstrates that the tubers have some mechanism for detecting the removal of the canopy. However, most tubers are located too deeply in the soil for light penetration. They therefore need another mechanism for detecting openings in the canopy. In light of the report by Benech Arnold *et al.* (1988), and of the results of this study, it is reasonable to hypothesize that the response of purple nutsedge tubers to alternating temperatures provides such a mechanism, and that tubers can detect and respond to the removal of plant cover through the effect of soil temperature fluctuation on sprouting. It would be useful to look for similar responses in weeds known to colonize cleared land and those not tolerant of shade. It would also be interesting to see whether the same response exists in plants which are more shade tolerant.

It is common in the literature on purple nutsedge to find references to "dormant" tubers. The phenomenon of initiation of growth followed by failure to elongate observed in this study raises some questions regarding the nature of tuber bud dormancy. Are tubers which do not sprout at, for example, constant 20 C truly dormant, or are the conditions just not favorable for sprouting? Does true internal dormancy exist in tubers, or will all tubers sprout if given the proper conditions (i.e., alternating temperatures)? Are some buds dormant and others not? There is considerable room for investigation into these questions.

SOLAR RADIATION AND SOIL TEMPERATURE

The soil temperatures under solarization in this study were not as high as have been reported from California and Israel. Solar radiation levels are probably the major factor in this difference, but soil thermal properties may play a role as well (Ekern, 1967). Jahns (1983) reports total solar radiation in excess of 600 cal/cm^2/day for most days in June and July, 1982, while at Waimanalo the total was usually less than 500. Mean annual solar radiation can be expected to be higher in the tropics than at higher latitudes, but monthly means in the summer may actually be lower. Yoshihara and Ekern (1977) report mean total daily solar radiation for the month of June at Makiki on O'ahu as 503 cal/cm^2/day, while Phoenix, Arizona has a June mean of 732 cal/cm^2/day. Jong *et al*. (1982) reported the June mean at the Waimanalo Experiment Station as less than 500 cal/cm^2/day, a figure in agreement with the data obtained in this study.

For maximum soil heating and thus maximum weed control, high solar radiation is needed. It should be possible to evaluate areas for soil solarization potential from weather data, and the best months of the year could be selected. In the humid tropics, the total daily solar radiation is likely to be less than in summer in temperate regions, but it is possible to solarize for a longer time period, which may help to improve weed control (Rubin and Benjamin, 1983; Stevens et al, 1990).

AREAS FOR FUTURE RESEARCH

This study has indicated some areas where future research would be beneficial for purple nutsedge control, and for weed control in general. Among these are possible seasonal effects on tuber sprouting. Purple nutsedge sprouting is higher at Waimanalo in the summer than in winter, and this may be simply a temperature effect. Research has been done on daylength effects on tuber production and flowering, and it would be interesting and useful to know whether daylength or other seasonal variables have an effect on tuber sprouting.

Another factor affecting plant growth which affects subsequent tuber sprouting is water stress. This study demonstrated that tubers from stressed plants have higher and more rapid sprouting than tubers from unstressed plants.

It is possible that water stress should be treated as a continuous rather than as a discrete variable (stressed vs. unstressed), since there can be varying degrees or intensities of stress. Two obvious factors contributing to degree of stress are the length of time the plant is under water deficit, and the magnitude of the deficit. Research to quantify the response to water stress as a continuous variable would be very beneficial in understanding tuber sprouting. The effect of plant age on tuber sprouting should be evaluated in such a study as well.

Several questions have been raised regarding the characteristics, and even the existence, of tuber dormancy. Research to separate dormancy breaking from induction of sprouting (if this can be done) would help

to answer some of these questions. The question of whether buds lose their viability if they initiate growth but fail to elongate also needs an answer.

SUMMARY

Under natural conditions in the field, a substantial number of tubers do not sprout (Siriwardana and Nishimoto, 1987; Standifer and Chin, 1969). Even if it is possible to kill plants from sprouted tubers, and the tubers from which they arise, the unsprouted tubers are a potential source of reinfestation. A major tactic in any nutsedge control program must therefore be to maximize tuber sprouting.

Once tubers have sprouted, the second part of a control strategy is to maximize control of the plants and tubers. Glyphosate is at present the best available tool for nutsedge control, but it has not provided complete control. Glyphosate has been demonstrated to kill plants and attached tubers in pots, but has been less successful in the field. This may, however, be in part due to low rates of application. In the only study which looked specifically at control of parent tubers in the field, the highest rate used was 2 kg/ha (Siriwardana, 1986), and it may be that a higher rate would be more effective. In all other studies evaluating tuber viability following glyphosate application in the field, it is impossible to determine whether viable tubers were attached to treated plants and survived treatment, or whether they were not sprouted at the time of treatment and thus escaped treatment altogether. Clearly, more information is needed in this area to

determine appropriate timing and rate of application for complete control of parent tubers. It will be essential to identify parent tubers in field studies if such research is to be successful. Recent work by Kawabata and DeFrank (1991) using the growth retardant paclobutrazol to enhance the effectiveness of glyphosate holds great promise for an integrated control program with solarization for more effective purple nutsedge control, and perhaps even eradication, as recommended over 60 years ago (Ranade and Burns, 1925). The few tubers which survive this combined approach can be dug up as they sprout, and good sanitation practices can then prevent reinfestation. Smith and Mayton concluded in 1942 that it is likely that "... any farmer who will plow at regular intervals for two growing seasons to destroy nut grass will complete the eradication of the pest by digging up each tuber as it sprouts the following year." It is to be hoped that the same will be true of the farmer who attempts to eradicate purple nutsedge with solarization and glyphosate.

It is not likely that many farmers will be able to monitor soil temperatures on a daily basis as is needed for this model. Mahrer (1979) has developed a model to predict soil temperature from solar radiation and soil properties. Satorre *et al.* (1985) have developed a model to predict johnsongrass rhizome sprout emergence based on air temperature. Either of these approaches could be used to modify the model developed in this study to make it more accessible to the farmer.

This study established that solarization for as little as one week can result in the rapid sprouting of a high percentage of purple nutsedge tubers in the soil, and solarization for two weeks

consistently results in near 100 percent sprouting. In light of this knowledge, it may be possible simply to recommend a two to three week solarization to induce tuber sprouting without worrying unduly about precision of prediction. Dispersal of sprouting over time is a valuable survival mechanism, making repetition of control measures necessary and increasing the expense of purple nutsedge control. By accelerating and concentrating tuber sprouting into an approximately two week period, solarization will be a valuable tool in an integrated nutsedge control program.

APPENDIX

Table 28. Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from March through October, 1984.

Date	Solar Radiation	Date	Solar Radiation	Date	Solar Radiation
Mar 28	437.1	May 07	553.6	Jul 01	532.2
Mar 29	441.3	May 08	436.3	Jul 02	569.8
Mar 30	374.0	May 09	589.6	Jul 03	484.7
Mar 31	469.8	May 10	570.1	Jul 04	508.6
Apr 01	503.1	May 11	582.0	Jul 05	601.7
Apr 02	420.0	May 12	561.0	Jul 06	576.4
Apr 03	486.8	May 13	564.7	Jul 07	563.9
Apr 04	442.7	May 14	535.1	Jul 08	481.2
Apr 05	441.2	May 15	476.7	Jul 09	545.1
Apr 06	303.2	May 31	552.7	Jul 10	396.0
Apr 07	453.9	Jun 01	552.2	Jul 11	553.3
Apr 08	416.8	Jun 02	530.7	Jul 12	609.9
Apr 09	492.9	Jun 03	556.9	Jul 13	543.3
Apr 10	259.0	Jun 04	548.4	Jul 14	503.1
Apr 11	408.4	Jun 05	490.2	Jul 15	552.5
Apr 12	488.2	Jun 06	494.2	Jul 16	517.0
Apr 13	461.4	Jun 07	365.8	Jul 17	498.6
Apr 14	89.0	Jun 08	348.7	Jul 18	575.7
Apr 15	379.8	Jun 09	538.1	Jul 19	527.0
Apr 16	316.0	Jun 10	513.8	Jul 20	440.2
Apr 17	489.4	Jun 11	450.8	Jul 21	557.8
Apr 18	387.8	Jun 12	527.9	Jul 22	523.0
Apr 19	265.1	Jun 13	398.4	Jul 23	485.5
Apr 20	397.3	Jun 14	574.3	Jul 24	431.4
Apr 21	336.0	Jun 15	398.7	Jul 25	495.9
Apr 22	435.0	Jun 16	385.8	Jul 26	533.7
Apr 23	424.1	Jun 17	563.9	Jul 27	424.2
Apr 24	433.2	Jun 18	582.1	Jul 28	534.1
Apr 25	202.4	Jun 19	511.8	Jul 29	549.5
Apr 26	245.9	Jun 20	395.6	Jul 30	497.7
Apr 27	534.1	Jun 21	257.6	Jul 31	490.8
Apr 28	420.2	Jun 22	572.1	Aug 01	438.5
Apr 29	493.3	Jun 23	437.8	Aug 02	531.0
Apr 30	548.3	Jun 24	525.9	Aug 03	416.7
May 01	321.3	Jun 25	559.9	Aug 04	319.2
May 02	435.6	Jun 26	542.3	Aug 05	509.1
May 03	391.6	Jun 27	554.6	Aug 06	573.4
May 04	535.6	Jun 28	385.7	Aug 07	556.8
May 05	544.5	Jun 29	445.6	Aug 08	580.3
May 06	573.3	Jun 30	544.5	Aug 09	540.8

Table 28 (continued). Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from March through October, 1984.

Date	Solar Radiation	Date	Solar Radiation
Aug 10	393.2	Sep 19	452.6
Aug 11	544.4	Sep 20	483.2
Aug 12	497.7	Sep 21	458.3
Aug 13	520.1	Sep 22	492.0
Aug 14	571.5	Sep 23	344.7
Aug 15	526.3	Sep 24	408.5
Aug 16	514.7	Sep 25	433.0
Aug 17	490.7	Sep 26	399.8
Aug 18	523.8	Sep 27	441.1
Aug 19	568.3	Sep 28	414.9
Aug 20	518.6	Sep 29	424.0
Aug 21	572.6	Sep 30	413.3
Aug 22	450.1	Oct 01	414.7
Aug 23	299.8	Oct 02	436.8
Aug 24	488.8	Oct 03	421.1
Aug 25	426.0	Oct 04	409.1
Aug 26	403.9	Oct 05	431.5
Aug 27	484.3	Oct 06	459.8
Aug 28	487.8	Oct 07	395.1
Aug 29	520.6	Oct 08	354.4
Aug 30	478.7	Oct 09	464.5
Aug 31	469.1	Oct 10	459.9
Sep 01	433.7	Oct 11	342.6
Sep 02	490.8	Oct 12	307.5
Sep 03	427.5	Oct 13	412.5
Sep 04	473.2	Oct 14	330.0
Sep 05	550.6	Oct 15	394.6
Sep 06	509.3	Oct 16	408.9
Sep 07	454.6	Oct 17	412.9
Sep 08	464.5	Oct 18	461.2
Sep 09	471.7	Oct 19	399.6
Sep 10	399.2	Oct 20	288.7
Sep 11	487.5	Oct 21	334.0
Sep 12	533.0	Oct 22	230.3
Sep 13	518.3	Oct 23	290.7
Sep 14	511.5		
Sep 15	400.7		
Sep 16	477.4		
Sep 17	451.4		
Sep 18	458.1		

Table 29. Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from July through December, 1985.

Date	Solar Radiation	Date	Solar Radiation	Date	Solar Radiation
Jul 03	509.3	Aug 27	615.3	Oct 06	362.0
Jul 04	617.2	Aug 28	483.5	Oct 07	.
Jul 05	559.9	Aug 29	611.9	Oct 08	414.3
Jul 06	641.4	Aug 30	425.1	Oct 29	356.8
Jul 07	486.9	Aug 31	451.7	Oct 30	362.3
Jul 08	601.5	Sep 01	487.7	Oct 31	233.2
Jul 09	527.3	Sep 02	440.0	Nov 01	405.0
Jul 10	550.8	Sep 03	510.8	Nov 02	342.1
Jul 11	633.6	Sep 04	549.8	Nov 03	315.5
Jul 12	679.2	Sep 05	506.9	Nov 04	402.2
Jul 13	612.0	Sep 06	571.6	Nov 05	244.1
Jul 14	599.5	Sep 07	457.1	Nov 06	286.7
Jul 15	511.3	Sep 08	287.9	Nov 07	215.7
Jul 16	510.0	Sep 09	319.5	Nov 08	317.6
Jul 17	457.9	Sep 10	357.7	Nov 09	143.0
Jul 18	608.1	Sep 11	451.9	Nov 10	191.1
Jul 19	650.4	Sep 12	547.1	Nov 11	232.9
Jul 20	497.6	Sep 13	534.6	Nov 12	298.6
Jul 21	625.1	Sep 14	504.3	Nov 13	193.0
Jul 22	551.9	Sep 15	455.6	Nov 14	431.2
Jul 23	611.4	Sep 16	411.2	Nov 15	127.1
Jul 24	558.5	Sep 17	358.3	Nov 16	149.2
Jul 25	493.1	Sep 18	459.2	Nov 17	363.9
Jul 26	.	Sep 19	176.6	Nov 18	101.5
Jul 27	623.1	Sep 20	569.1	Nov 19	425.6
Jul 28	585.8	Sep 21	330.1	Nov 20	263.8
Jul 29	672.9	Sep 22	468.0	Nov 21	331.3
Jul 30	333.2	Sep 23	409.3	Nov 22	272.7
Jul 31	461.5	Sep 24	523.5	Nov 23	157.0
Aug 01	468.7	Sep 25	447.0	Nov 24	323.1
Aug 02	556.3	Sep 26	220.2	Nov 25	100.3
Aug 03	434.5	Sep 27	479.7	Nov 26	316.9
Aug 04	535.0	Sep 28	514.2	Nov 27	252.6
Aug 05	502.7	Sep 29	397.8	Nov 28	322.0
Aug 06	337.5	Sep 30	417.4	Nov 29	287.4
Aug 07	553.3	Oct 01	340.6	Nov 30	73.6
Aug 23	560.4	Oct 02	468.1	Dec 01	149.9
Aug 24	582.1	Oct 03	263.4	Dec 02	214.0
Aug 25	236.6	Oct 04	509.6	Dec 03	291.1
Aug 26	378.3	Oct 05	337.9	Dec 04	212.2

Table (continued). Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from July through December, 1985.

Date	Solar Radiation	Date	Solar Radiation	Date	Solar Radiation
Dec 05	270.0	Dec 15	200.1	Dec 25	225.5
Dec 06	294.1	Dec 16	318.0	Dec 26	184.7
Dec 07	304.2	Dec 17	243.0	Dec 27	201.0
Dec 08	332.0	Dec 18	230.3	Dec 28	210.3
Dec 09	367.3	Dec 19	186.0	Dec 29	168.2
Dec 10	122.3	Dec 20	326.8	Dec 30	265.4
Dec 11	252.1	Dec 21	270.4	Dec 31	251.8
Dec 12	259.4	Dec 22	314.9		
Dec 13	325.8	Dec 23	92.6		
Dec 14	275.0	Dec 24	170.0		

Table 30. Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from January through September, 1986.

Date	Solar Radiation	Date	Solar Radiation	Date	Solar Radiation
Jan 01	243.6	Feb 10	153.9	Mar 22	293.1
Jan 02	264.5	Feb 11	66.3	Mar 23	109.3
Jan 03	263.3	Feb 12	449.4	Mar 24	405.9
Jan 04	261.7	Feb 13	334.3	Mar 25	238.4
Jan 05	263.1	Feb 14	312.8	Mar 26	303.9
Jan 06	153.6	Feb 15	271.2	Mar 27	208.8
Jan 07	250.2	Feb 16	476.2	Mar 28	282.7
Jan 08	197.8	Feb 17	227.4	Mar 29	397.5
Jan 09	237.2	Feb 18	436.5	Mar 30	323.9
Jan 10	355.0	Feb 19	289.8	Mar 31	418.3
Jan 11	247.4	Feb 20	149.7	Apr 02	471.1
Jan 12	262.7	Feb 21	344.9	Apr 03	254.4
Jan 13	227.6	Feb 22	132.6	Apr 04	.
Jan 14	338.5	Feb 23	407.7	Apr 05	221.4
Jan 15	214.8	Feb 24	382.9	Apr 06	378.9
Jan 16	263.6	Feb 25	241.3	Apr 07	332.8
Jan 17	207.4	Feb 26	446.9	Apr 08	204.2
Jan 18	193.5	Feb 27	401.3	Apr 09	178.1
Jan 19	297.8	Feb 28	504.8	Apr 10	53.4
Jan 20	197.0	Mar 01	269.9	Apr 11	305.1
Jan 21	314.3	Mar 02	194.8	Apr 12	354.7
Jan 22	288.8	Mar 03	315.2	Apr 13	205.8
Jan 23	151.9	Mar 04	209.9	Apr 14	390.3
Jan 24	106.5	Mar 05	382.5	Apr 15	269.6
Jan 25	155.4	Mar 06	228.7	Apr 16	577.7
Jan 26	151.4	Mar 07	429.6	Apr 17	485.1
Jan 27	302.1	Mar 08	317.4	Apr 18	607.6
Jan 28	233.3	Mar 09	494.0	Apr 19	571.0
Jan 29	230.3	Mar 10	478.9	Apr 20	534.8
Jan 30	383.7	Mar 11	466.2	Apr 21	466.1
Jan 31	170.1	Mar 12	263.8	Apr 22	471.2
Feb 01	167.4	Mar 13	129.8	Apr 23	462.7
Feb 02	232.7	Mar 14	220.5	Apr 24	277.2
Feb 03	370.1	Mar 15	137.1	Apr 25	526.2
Feb 04	209.7	Mar 16	169.7	Apr 26	502.4
Feb 05	387.1	Mar 17	438.9	Apr 27	425.4
Feb 06	263.8	Mar 18	320.2	Apr 28	442.4
Feb 07	312.2	Mar 19	292.8	Apr 29	323.6
Feb 08	271.7	Mar 20	127.6	Apr 30	208.8
Feb 09	208.7	Mar 21	123.0	May 01	532.0

Table 30 (continued). Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from January through September, 1986.

Date	Solar Radiation	Date	Solar Radiation	Date	Solar Radiation
May 02	375.7	Jun 11	579.5	Jul 21	530.8
May 03	415.0	Jun 12	569.6	Jul 22	329.8
May 04	414.8	Jun 13	568.8	Jul 23	282.4
May 05	483.5	Jun 14	368.4	Jul 24	165.7
May 06	434.6	Jun 15	524.3	Jul 25	77.7
May 07	.	Jun 16	.	Jul 26	498.1
May 08	392.7	Jun 17	291.3	Jul 27	445.6
May 09	301.9	Jun 18	.	Jul 28	547.0
May 10	189.2	Jun 19	512.4	Jul 29	510.6
May 11	418.9	Jun 20	515.3	Jul 30	445.3
May 12	593.2	Jun 21	304.4	Jul 31	553.7
May 13	612.8	Jun 22	525.3	Aug 01	453.7
May 14	612.3	Jun 23	473.2	Aug 02	504.2
May 15	519.2	Jun 24	328.6	Aug 03	561.6
May 16	548.6	Jun 25	469.3	Aug 04	473.3
May 17	551.0	Jun 26	621.8	Aug 05	459.5
May 18	466.1	Jun 27	363.7	Aug 06	.
May 19	568.3	Jun 28	329.4	Aug 07	509.4
May 20	483.9	Jun 29	381.2	Aug 08	388.4
May 21	546.0	Jun 30	451.8	Aug 09	281.5
May 22	635.5	Jul 01	513.9	Aug 10	327.2
May 23	624.2	Jul 02	551.8	Aug 11	181.1
May 24	572.0	Jul 03	398.9	Aug 12	399.6
May 25	485.8	Jul 04	398.7	Aug 13	189.3
May 26	371.2	Jul 05	487.8	Aug 14	251.9
May 27	234.4	Jul 06	494.4	Aug 15	239.0
May 28	409.9	Jul 07	386.3	Aug 16	511.3
May 29	434.2	Jul 08	431.9	Aug 17	448.1
May 30	428.0	Jul 09	310.9	Aug 18	334.2
May 31	446.9	Jul 10	464.6	Aug 19	293.5
Jun 01	546.8	Jul 11	500.2	Aug 20	531.8
Jun 02	464.9	Jul 12	517.2	Aug 21	340.4
Jun 03	422.7	Jul 13	312.2	Aug 22	391.5
Jun 04	614.8	Jul 14	378.1	Aug 23	436.5
Jun 05	515.0	Jul 15	412.7	Aug 24	494.7
Jun 06	396.9	Jul 16	438.6	Aug 25	572.5
Jun 07	542.1	Jul 17	377.0	Aug 26	560.4
Jun 08	438.3	Jul 18	530.4	Aug 27	496.1
Jun 09	534.4	Jul 19	497.1	Aug 28	352.0
Jun 10	.	Jul 20	589.2	Aug 29	323.3

Table 30 (continued). Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo from January through September, 1986.

Date	Solar Radiation	Date	Solar Radiation	Date	Solar Radiation
Aug 30	452.9	Sep 09	186.3	Sep 19	359.9
Aug 31	532.9	Sep 10	390.3	Sep 20	438.4
Sep 01	447.3	Sep 11	513.5	Sep 21	436.2
Sep 02	433.8	Sep 12	512.4	Sep 22	461.6
Sep 03	548.2	Sep 13	361.5	Sep 23	394.1
Sep 04	584.2	Sep 14	512.5		
Sep 05	456.0	Sep 15	506.3		
Sep 06	393.9	Sep 16	255.6		
Sep 07	459.2	Sep 17	260.5		
Sep 08	.	Sep 18	297.1		

Table 31. Total daily global solar radiation in cal cm^{-2} day^{-1} at Waimanalo during field experiments in 1990.

Date	Solar Radiation	Date	Solar Radiation
Mar 08	204.9	Jun 18	323.7
Mar 09	178.4	Jun 19	418.0
Mar 10	396.8	Jun 20	285.8
Mar 11	354.1	Jun 21	345.1
Mar 12	334.6	Jun 22	413.4
Mar 13	309.6	Jun 23	360.2
Mar 14	406.6	Jun 24	397.2
Mar 15	156.4	Jun 25	427.9
Mar 16	516.6	Jun 26	523.9
Mar 17	529.9	Jun 27	586.6
Mar 18	484.7	Jun 28	368.7
Mar 19	214.5	Jun 29	354.7
Mar 20	160.5	Jun 30	414.0
Mar 21	450.3	Jul 01	511.1
Mar 22	297.6	Jul 02	500.1
Mar 23	449.8	Jul 03	558.4
Mar 24	417.6	Jul 04	629.2
Mar 25	286.9	Jul 05	455.1
Mar 26	438.0	Jul 06	640.3
Mar 27	366.4	Jul 07	590.1
Mar 28	386.5	Jul 08	489.7
Mar 29	502.6	Jul 09	405.1
Mar 30	397.4	Jul 10	353.0
Mar 31	443.5	Jul 11	507.9
Apr 01	389.4	Jul 12	394.8
Apr 02	396.0	Jul 13	594.9
Apr 03	524.1	Jul 14	540.4
Apr 04	435.6	Jul 15	524.4
Apr 05	303.6	Jul 16	560.3
Apr 06	428.7	Jul 17	490.7
Apr 07	259.4	Jul 18	373.5
Apr 08	317.6	Jul 19	540.6
Apr 09	401.2	Jul 20	619.5
Apr 10	273.1	Jul 21	199.5
		Jul 22	585.1
		Jul 23	510.0

LITERATURE CITED

1. Abad, R. G. and San Juan, N. C. 1981. Effect of different rates of glyphosate followed by paraquat on the weed population in coconut (*Cocos nucifera* L.) nurseries. Philippine Journal of Weed Science 8:5-14.

2. Akobundu, I. O., Bayer, D. E., and Leonard, O. A. 1970. The effects of dichlobenil on assimilate transport in purple nutsedge. Weed Science 18:403-409.

3. Aleixo, M. De F. D., and Valio, I. F. M. 1976. Effect of light, temperature and endogenous growth regulators on the growth of buds of *Cyperus rotundus* L. tubers. Zeitschrift fur Pflanzenphysiologie 80:336-347.

4. Allan, R. E., Vogel, O. A., and Burleigh, J. R. 1962. Length and estimated number of coleoptile parenchyma cells of six wheat selections grown at two temperatures. Crop Science 2:522-524.

5. Allen, D. M. and Cady, F. B. 1982. *Analyzing Experimental Data by Regression*. Wadsworth, Belmont, California.

6. Ambasht, R. S. 1964. Ecology of the underground parts of *Cyperus rotundus* L. Tropical Ecology 5:67-74.

7. Andrews, F. W. 1940a. A study of nutgrass (*Cyperus rotundus* L.) in the cotton soil of the Gezira. I: The maintenance of life in the tuber. Annals of Botany 4:177-193.

8. Andrews, F. W. 1940b. The control of nut grass in the Sudan Gezira. Empire Journal of Experimental Agriculture 8:215-222.

9. Andrews, F. W. 1946. A study of nut grass (*Cyperus rotundus* L.) in the cotton soil of the Gezira. II. The perpetuation of the plant by means of seed. Annals of Botany 10:15-30.

10. Angus, J. F., Cunningham, R. B., Moncur, M. W., and Mackenzie, D. H. 1981. Phasic development in field crops I. Thermal response in the seedling phase. Field Crops Research 3:365-378.

11. Antognini, J., Dye, D. F., Probandt, G. F., and Curtis, R. 1959. Control of quackgrass and nutgrass in horticultural and agronomic crops with Eptam™ (EPTC). Proceedings Northeastern Weed Control Conference 13:50-51.

12. Ashley, R. A. 1990. Solarization as a weed control alternative for Connecticut. Proceedings Northeastern Weed Science Society 44:23.

13. Atkinson, D. 1985. The toxicological properties of glyphosate--a summary. in Grossbard, E. and D. Atkinson, eds. *The Herbicide Glyphosate*. Butterworths, London.

14. Baharanyi, N., Stevens, C., Khan, V., Wilson, M. A., Tang, A. Y., and Siaway, A. 1988. Economic returns of on-farm soil solarization trials for cabbage and collard greens. HortScience 23(5):829.

15. Baird, D. D., Upchurch, R. P., Homesley, W. B., and Franz, J. E. 1971. Introduction of a new broadspectrum postemergence herbicide class with utility for herbaceous perennial control. Proceedings North Central Weed Control Conference 26:64-68.

16. Baker, K. F. 1962. Principles of heat treatment of soil and planting material. The Journal of the Australian Institute of Agricultural Science 28:118-126.

17. Baker, K. F. 1970. Selected killing of soil microorganisms by aerated steam. in Tousson, T. A., Bega, R. V., and Nelson, R. E., eds. *Root Diseases and Soilborne Pathogens*. University of California Press, Berkeley.

18. Baker, R. S. 1964. Reproductive capacity of nutsedge (*Cyperus rotundus* L.) tubers. Abstracts Weed Science Society of America, 63-64.

19. Belehradek, J. 1935. Temperature and Living Matter. Protoplasma-Monographien 8. Borntraeger, Berlin.

20. Beltrao, N. E. De M., De Paula, P. H. F., Alves, J. F., and Tavora, F. J. F. 1983. Effects of glyphosate dosage on purple nutsedge (*Cyperus rotundus* L.) control (in Portuguese). Planta Daninha 6:51-57. [Weed Abstracts 35:258;1986]

21. Bendixen, L. E. and Nandihalli, U. B. 1987. Worldwide distribution of purple and yellow nutsedge (*Cyperus rotundus* and *C. esculentus*). Weed Technology 1:61-65.

22. Benech Arnold, R. L., Ghersa, C. M., Sanchez, R. A., and Garcia Fernandez, A. E. 1988. The role of fluctuating temperatures in the germination and establishment of *Sorghum halepense* (L.) Pers. Regulation of germination under leaf canopies. Functional Ecology 2(3):311-318.

23. Benech Arnold, R. L., Ghersa, C. M., Sanchez, R. A., and Insausti, P. 1990a. Temperature effects on dormancy release and germination rate in *Sorghum halepense* (L.) Pers. seeds: a quantitative analysis. Weed Research 30:81-89.

24. Benech Arnold, R. L., Ghersa, C. M., Sanchez, R. A., and Insausti, P. 1990b. A mathematical model to predict *Sorghum halepense* (L.) Pers. seedling emergence in relation to soil temperature. Weed Research 30:91-99.

25. Berger, G. and Day, B. E. 1967. Dormancy, growth inhibition, and tuberization of nutsedge (*Cyperus rotundus* L.) as affected by photoperiods. Proceedings First Asian-Pacific Weed-Control Interchange:123.

26. Berjak, P. and Villiers, T. A. 1972a. Ageing in plant embryos. II. Age-induced damage and its repair during early germination. New Phytologist 71:135-144.

27. Berjak, P. and Villiers, T. A. 1972b. Ageing in plant embryos. III. Acceleration of senescence following artificial ageing treatment. New Phytologist 71:513-418.

28. Berjak, P. and Villiers, T. A. 1972c. Ageing in plant embryos. IV. Loss of regulatory control in aged embryos. New Phytologist 71:1069-1074.

29. Berjak, P. and Villiers, T. A. 1972d. Ageing in plant embryos. V. Lysis of the cytoplasm in non-viable embryos. New Phytologist 71:1075-1079.

30. Berry, J. A. and Raison, J. K. 1981. Responses of macrophytes to temperature. in Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H., eds. *Physiology and Biochemistry of Seeds in Relation to Germination* Volume 2. Springer-Verlag, Berlin.

31. Bewley, J. D. and Black, M. 1982. *Physiology and Biochemistry of Seeds in Relation to Germination*, Volume 2. Springer-Verlag, Berlin.

32. Bhardwaj, R. B. L. and Verma, R. D. 1968. Seasonal development of nutgrass (*Cyperus rotundus* L.) under Delhi conditions. Indian Journal of Agricultural Science 38:950-957.

33. Bierhuizen, J. F. 1973. The effect of temperature on plant growth, development and yield. in Slatyer, R. O., ed. *Plant Response to Climatic Factors*. Proceedings of the Uppsala Symposium, 1970. UNESCO (Ecology and Conservation, 5) pp 89-98.

34. Bierhuizen, J. F. and Wagenvoort, W. A. 1974. Some aspects of seed germination in vegetables. 1. The determination and application of heat sums and minimum temperature for germination. Scientia Horticulturae 2:213-219.

35. Black, C. C., Jr., Chen, I. M., and Brown, R. N. 1969. Biochemical basis for plant competition. Weed Science 17:338-344.

36. Blake, T. J. 1972. Studies on the lignotubers of *Eucalyptus obliqua* L'Herit. III. The effects of seasonal and nutritional factors on dormant bud development. New Phytologist 71:327-334.

37. Bradow, J. M. and Connick, W. J., Jr. 1988. Inhibition of cotton seedling root growth by rhizosphere volatiles. Proceedings, Beltwide Cotton Production Research Conferences. [Weed Abstracts 38:2903;1989].

38. Brown, R. F. 1987. Germination of *Aristida armata* under constant and alternating temperatures and its analysis with the cumulative Weibull distribution as a model. Australian Journal of Botany 35:581-591.

39. Brown, R. F. and Mayer, D. G. 1988a. Representing cumulative germination. 1. A critical analysis of single-value germination indices. Annals of Botany 61:117-125.

40. Brown, R. F. and Mayer, D. G. 1988b. Representing cumulative germination. 2. The use of the Weibull function and other empirically defined curves. Annals of Botany 61:127-138.

41. Burleigh, J. R., Allan, R. E., and Vogel, O. A. 1964. Effect of temperature on coleoptile elongation in eight wheat varieties and selections. Agronomy Journal 56:523-524.

42. Callaway, M. B., Phatak, S. C., and Wells, H. D. 1985. Studies on alternate hosts of the rust *Puccinia canaliculata*, a potential biological control agent for nutsedges. Plant Disease 69(11):924-926.

43. Campeglia, O. G. 1983. Control of *Cyperus rotundus* L. with glyphosate (in Spanish). Malezas 11(5):188-193. [Weed Abstracts 34:2158;1985].

44. Caseley, J. C. and Coupland, D. 1985. Environmental and plant factors affecting glyphosate uptake, movement, and activity. in Grossbard, E. and D. Atkinson, eds. *The Herbicide Glyphosate*. London, Butterworths.

45. Causton, D. R., Elias, C. O., and Hadley, P. 1978. Biometrical studies of plant growth. I: The Richards function, and its application in analyzing the effects of temperature on leaf growth. Plant, Cell, and Environment 1:163-184.

46. Chase, R. L. and Appleby, A. P. 1979a. Effect of intervals between application and tillage on glyphosate control of *Cyperus rotundus* L. Weed Research 19:207-211.

47. Chase, R. L. and Appleby, A. P. 1979b. Effects of humidity and moisture stress on glyphosate control of *Cyperus rotundus* L. Weed Research 19:241-246.

48. Chavez, R. C. and Moody, K. 1986. Ecotypic variation in Cyperus rotundus. Proceedings of the Symposium in Weed Science. Bogor, Indonesia, 10-12 April, 1984. Biotrop Special Bulletin No. 24, 123-136.

49. Chen, Y. and Katan, J. 1980. Effect of solar heating of soils by transparent polyethylene mulching on their chemical properties. Soil Science 30:271-277.

50. Chetram, R. S. and Bendixen, L. E. 1974a. Gibberellic acid plus cytokinin induced basal bulbs of purple nutsedge above ground. Weed Science 22:55-58.

51. Chetram, R. S. and Bendixen, L. E. 1974b. Phytochrome controlled basal bulb formation in purple nutsedge. Weed Science 22:269-272.

52. Chivinge, O. A. 1985. A herbicide screening trial against purple nutsedge *(Cyperus rotundus* L.) under Zimbabwean conditions. Zimbabwe Agricultural Journal 82(1):17-20.

53. Claus, J. S. and Behrens, R. 1976. Glyphosate translocation and quackgrass rhizome bud kill. Weed Science 24:149-152.

54. Claver, F. K. 1977. Comparison of two possible ecotypes of *Cyperus rotundus* L. (in Spanish). Revista de la Facultad de Agronomia, Universidad Nacional de la Plata 53:3-14. [Weed Abstracts 29:555;1980].

55. Cohen, D. 1958. The mechanism of germination stimulation by alternating temperatures. Bulletin of the Research Council of Israel, Section D. 6:111-117.

56. Cole, D. J. 1985. Mode of action of glyphosate--a literature analysis. in Grossbard, E. and Atkinson, D., eds. *The Herbicide Glyphosate*. London, Butterworths.

57. Cools, W. G. and Locascio, S. J. 1977a. Control of purple nutsedge (Cyperus rotundus L.) as influenced by season of application of glyphosate and nitrogen rate. Proceedings Southern Weed Science Society 30:158-164.

58. Cools, W. G. and Locascio, S. J. 1977b. Influence of nutrition and temperature on the germination rate of purple nutsedge (*Cyperus rotundus* L.). Abstracts Weed Science Society of America, 164.

59. Coupland, D. 1985. Metabolism of glyphosate in plants. in Grossbard, E. and Atkinson, D., eds. *The Herbicide Glyphosate*. London, Butterworths.

60. Davis, C. H. 1942. Response of *Cyperus rotundus* L. to five moisture levels. Plant Physiology 17:311-316.

61. Davis, C. H. and Hawkins, R. S. 1943. Eradication and control of nut grass. Arizona Agricultural Experiment Station Bulletin 189, 20 pp.

62. Deat, M. 1975. Trials for chemical control of *Cyperus rotundus* L. in fibre crops (cotton, kenaf, roselle) (in French). Coton et Fibres Tropicales 30:419-425. [Weed Abstracts 26:1266;1977].

63. Deuber, R. and Forster, R. 1977. Control of *Cyperus rotundus* L. with glyphosate (in Portuguese). Revista de Agricultura, Piracicaba, Brazil 52:183-190. [Weed Abstracts 29:1079;1980.

64. Devine, M. D., Bandeen, J. D., and McKersie, B. D. 1983. Temperature effects on glyphosate absorption, translocation, and distribution in quackgrass (*Agropyron repens*). Weed Science 31:461-464.

65. Doll, J. and Piedrahita, W. 1975. Systems for controlling *Cyperus rotundus* using 2,4-D and glyphosate (in Spanish). Sociedad Colombiana de Control de Malezas y Fisiologia Vegetal "COMALFI". Resumenes de los Trabajos en el VII Seminario, Bogota 37-38. [Weed Abstracts 26:405;1977.

66. Doll, J. D. and Piedrahita, W. 1982. Effect of glyphosate on the sprouting of *Cyperus rotundus* L. tubers. Weed Research 22:123-128.

67. Ebert, T. A. 1980. Estimating parameters in a flexible growth equation, the Richards function. Canadian Journal of Fisheries and Aquatic Science 37:687-692.

68. Edwards, T. I. 1932. Temperature relations of seed germination. Quarterly Review of Biology 7:428-443.

69. Egley, G. H. 1983. Weed seed and seedling reductions by soil solarization with transparent polyethylene sheets. Weed Science 31:404-409.

70. Egley, G. H. 1990. High-temperature effects on germination and survival of weed seeds in the soil. Weed Science 38:429-435.

71. Ekern, P. C. 1965. The evapotranspiration of pineapple in Hawaii. Pineapple Research Institute Technical Report 109.

72. Ekern, P. C. 1966. Evaporation from bare low humic latosol in Hawaii. Journal of Applied Meteorology 5(4):431-435.

73. Ekern, P. C. 1967. Soil moisture and soil temperature changes with the use of black vapor-barrier mulch and their influence on pineapple (*Ananas comosus* (L.) Merr.) growth in Hawaii. Soil Science Society of America Proceedings 31:270-275.

74. El Saeed, E. A. K. 1967. The smothering effect of *Dolichos lablab* L. Weed Research 7:68-69.

75. El-Masry, R. and Rehm, S. 1976. The effects of growth regulators and herbicides on purple nutsedge (*Cyperus rotundus* L.) II. Effect of dicamba on basal bulb formation. Z. Acker- und Pflanzenbau 143:312-321.

76. El-Masry, R. and Rehm, S. 1977. The effects of growth regulators and herbicides on purple nutsedge (*Cyperus rotundus* L.) IV. Effects of glyphosate and morphactin on the viability of tubers. Z. Acker- und Pflanzenbau 144:259-267.

77. El-Masry, R., Awad, F., and Ibrahim, S. A. 1980. Growth and cations content of purple nutsedge (*Cyperus rotundus* L.) as affected by soil characteristics. Agrochimica 24:501-507.

78. Elmore, C. D., Brown, M. A., and Flint, E. P. 1983. Early interference between cotton (*Gossypium hirsutum*) and four weed species. Weed Science 31:200-207.

79. Erez, A., Couvillon, G. A., and Hendershott, C. H. 1979. Quantitative chilling enhancement and negation in peach buds by high temperatures in a daily cycle. Journal of the American Society for Horticultural Science 104(4):536-540.

80. Evans, H. C. 1987. Fungal pathogens of some subtropical and tropical weeds and the possibilities for biological control. Biocontrol News and Information 8(1):7-30. [Weed Abstracts 36:2245;1987].

81. Evans, R. A., Easi, D. E., Book, D. N., and Young, J. A. 1982. Quadratic response surface analysis of seed germination trials. Weed Science 30:411-416.

82. Freund, R. J., Littel, R. C., and Spector, P. C. 1986. *SAS System for Linear Models*. SAS Institute, Inc., Cary, North Carolina.

83. Frick, K. E. 1976. Purple nutsedge (*Cyperus rotundus* L.): A case for augmentation. Proceedings IV International Symposium on Biological Control of Weeds 145-151.

84. Frick, K. E. and Chandler, J. M. 1978. Augmenting the moth (*Bactra verutana*) in field plots for early-season suppression of purple nutsedge (*Cyperus rotundus*). Weed Science 26:703-710.

85. Frick, K. E., Williams, R. D., and Wilson, R. F. 1978. Interactions between *Bactra verutana* and the development of purple nutsedge (*Cyperus rotundus*) grown under three temperature regimes. Weed Science 26:550-553.

86. Friedman, T. and Horowitz, M. 1971. Biologically active substances in subterranean parts of purple nutsedge. Weed Science 19:398-401.

87. Gamboa, W. and Vandermeer, J. 1988. Root and shoot competition in *Phaseolus vulgaris* and *Cyperus rotundus* in Nicaragua. Tropical Ecology 29:21-25.

88. Garcia-Huidobro, J., Monteith, J. L., and Squire, G. R. 1982a. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. and H.) I. Constant temperature. Journal of Experimental Botany 33:288-296.

89. Garcia-Huidobro, J., Monteith, J. L., and Squire, G. R. 1982b. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. and H.) II. Alternating temperature. Journal of Experimental Botany 33:297-302.

90. Gastal, M. F. Da C. and Castela, C. R. 1982. Allelopathic influence of *Cyperus rotundus* L. on *Glycine max* (L.) Merrill (in Portuguese). in Anais, II seminario nacional de pesquisa de soja. Volume II. [Weed Abstracts 35:352;1986].

91. Gill, H. S., Bhatia, R. K., Sandhu, K. S., and Mehra, S. P. 1982. Ecological studies on Cyperus rotundus L. in Abstracts of papers, annual conference Indian Society of Weed Science, pp. 47-48. [Weed Abstracts:3904;1984].

92. Glaze, N. C. 1987. Cultural and mechanical manipulation of *Cyperus* spp. Weed Technology 1:82-83.

93. Gomez, C. and Cruz, R. 1975. Chemical and mechanical control of *Cyperus rotundus* (in Spanish). Sociedad Colombiana de Control de Malezas y Fisiologia Vegetal "COMALFI." Resumenes de los Trabajos en el VII Seminario, Bogota 38-39. [Weed Abstracts 26:406;1977].

94. Gossett, B. J., Stephens, R. L., and Gillingham, J. T. 1975. Response of purple nutgrass to glyphosate. Proceedings Southern Weed Science Society 28:146.

95. Grinstein, A., Katan, J., Abdul-Razik, A., Zeydan, O., and Elad, Y. 1979. Control of *Sclerotium rolfsii* and weeds in peanuts in by solar heating of the soil. Plant Disease Reporter 63(12):1056-1059.

96. Hammerton, J. L. 1968. Nutgrass in Panama: First impression. Pesticide Articles and News Summaries (C) 14:339-345.

97. Hammerton, J. L. 1974. Experiments with *Cyperus rotundus* L. I. Growth and development and effects of 2,4-D and paraquat. Weed Research 14:365-369.

98. Hammerton, J. L. 1975a. Experiments with *Cyperus rotundus* L. II. Effects of some herbicides and growth regulators. Weed Research 15:177-183.

99. Hammerton, J. L. 1975b. Experiments with *Cyperus rotundus* L. III. Seasonal variations in growth. Weed Research 15:339-348.

100. Harrington, G. T. 1923. Use of alternating temperatures in the germination of seeds. Journal of Agricultural Research 23:295-332.

101. Harrington, J. F. 1963. The effect of temperature on the germination of several kinds of vegetable seeds. Proceedings of the 16th Horticultural Congress, Vol. 2. pp 435-441.

102. Hauser, E. W. 1962a. Establishment of nutsedge from space-planted tubers. Weeds 10:209-212.

103. Hauser, E. W. 1962b. Development of purple nutsedge under field conditions. Weeds 10:315-321.

104. Hendricks, S. B., and Taylorson, R. B. 1976. Variation in germination and amino acid leakage of seeds with temperature related membrane phase change. Plant Physiology 58:7-11.

105. Hendricks, S. B., and Taylorson, R. B. 1978. Dependence of phytochrome action in seeds on membrane organization. Plant Physiology 61:17-19.

106. Hendricks, S. B., and Taylorson, R. B. 1979. Dependence of thermal responses of seeds on membrane transitions. Proceedings of the National Academy of Science of the U.S.A. 76:778-781.

107. Henson, I. E. and Little, E. C. S. 1969. Penetration of polyethylene film by the shoots of Cyperus rotundus. Pest Articles and News Summaries 15(1):64-66.

108. Heydecker, W. 1977. Stress and seed germination: An agronomic view. in Khan, A. A., ed. *The Physiology and Biochemistry of Seed Development, Dormancy and Germination*. Elsevier/North Holland, Amsterdam.

109. Hildebrand, D. M. 1985. Soil solar heating for control of damping-off fungi and weeds at the Colorado State Forest Service nursery. Tree Planters' Notes 36(1):28-34.

110. Holm, L. G., Plucknett, D. L., Pancho, J. V., and Herberger, J. P. 1977. *The World's Worst Weeds*, pp. 8-24. The University Press of Hawaii, Honolulu.

111. Horowitz, M. 1965. Data on the biology and chemical control of the nutsedge (*Cyperus rotundus*) in Israel. Pesticide Articles and News Summaries (C) 11:389-416.

112. Horowitz, M. 1972a. Effects of frequent clipping on three perennial weeds, *Cynodon dactylon*, (L.) Pers., *Sorghum halepense* (L.) Pers., and *Cyperus rotundus* L. Experimental Agriculture 8:225-234.

113. Horowitz, M. 1972b. Growth, tuber formation and spread of *Cyperus rotundus* L. from single tubers. Weed Research 12:348-363.

114. Horowitz, M. and Givelberg, Assia. 1982. Effect of high temperatures on germination and dormancy of *Solanum nigrum* seeds. Phytoparasitica 10(4):279-280.

115. Horowitz, M., Regev, Y., and Herzlinger, G. 1983. Solarization for weed control. Weed Science 31:170-179.

116. Horowitz, M. and Taylorson, R. B. 1983. Effect of high temperatures on imbibition, germination, and thermal death of velvetleaf (*Abutilon theophrasti*) seeds. Canadian Journal of Botany 61:2269-2276.

117. Horowitz, M. and Taylorson, R. B. 1984. Hardseededness and germinability of velvetleaf (*Abutilon theophrasti*) as affected by temperature and moisture. Weed Science 32:11-115.

118. Hsu, F. H., Nelson, C. J., and Chow, W. S. 1984. A mathematical model to utilize the logistic function in germination and seedling growth. Journal of Experimental Botany 35:1629-1640.

119. Hunt, R. 1979. Plant growth analysis: The rationale behind the use of the fitted mathematical function. Annals of Botany 43:245-249.

120. Hunt, R. 1982. *Plant Growth Curves: The Functional Approach to Plant Growth Analysis*. Edward Arnold, London.

121. Ito, M. F., Pizzinato, M. A., and Paulo, E. M. 1988. Occurrence of *Ustilago* sp. on purple nutsedge (Cyperus rotundus L.) (in Portuguese). Summa Phytopathologica 14(1-2):29. [Weed Abstracts 38:107;1989].

122. Jacobsohn, A., Greenberger, A., Katan, J., Levi, M. and Alon, H. 1980. Control of egyptian broomrape (*Orobanche aegyptiaca*) and other weeds by means of solar heating of the soil by polyethylene mulching. Weed Science 28:313-316.

123. Jahns, T. 1983. Germination of common weed seeds at cultural depths as affected by soil solarization. MS Thesis. California State University, Fresno.

124. Jangaard, N. O., Sckerl, M. M., and Schieferstein, R. H. 1971. The role of phenolics and abscisic acid in nutsedge tuber dormancy. Weed Science 19:17-20.

125. Jaworski, E. G. 1973. Mode of action of n-phosphonomethylglycine: inhibition of aromatic amino acid biosynthesis. Journal of Agricultural and Food Chemistry:1195-1198.

126. Jennings, P. R. and de Jesus, J., Jr. 1964. Effect of heat on breaking seed dormancy in rice. Crop Science 4:530-533.

127. Jha, P. K. and Sen, D. N. 1980. Drought avoidance by *Cyperus rotundus*. Folia Geobotanica et Phytotaxonomica 15:387-394.

128. Jha, P. K. and Sen, D. N. 1985. Adaptation and survival strategies in *Cyperus rotundus* L. - a perennial weed of pantropical distribution. Folia Geobotanica et Phytotaxonomica 20:281-289.

129. Jong, S. K., Brewbaker, J. L., and Lee, C. H. 1982. Effects of solar radiation on the performance of maize in 41 successive monthly plantings in Hawaii. Crop Science 22:13-18.

130. Jordan, T. N. 1977. Effects of temperature and relative humidity on the toxicity of glyphosate to bermudagrass (*Cynodon dactylon*). Weed Science 25:448-451.

131. Justice, O. L. and Whitehead, M. D. 1946. Seed production, viability, and dormancy in the nutgrasses *Cyperus rotundus* and *C. esculentus*. Journal of Agricultural Research 73:303-318.

132. Karssen, C. M. 1982. Seasonal patterns of dormancy in weed seeds. in Khan, A. A., ed. *The Physiology and Biochemistry of Seed Development, Dormancy and Germination*. pp 243-270. Elsevier, Amsterdam.

133. Katan, J. 1981. Solar heating (solarization) of soil for control of soilborne pests. Annual Review of Phytopathology 19:211-236.

134. Katan, J., Greenberger, A., Alon, H. and Grinstein, A. 1976. Solar heating by polyethylene mulching for the control of diseases caused by soil-borne pathogens. Phytopathology 66:683-688.

135. Katan, J., Grinstein, A., Greenberger, A., Yarden, O., and DeVay, J.E. 1987. The first decade (1976-1986) of soil solarization (solar heating): a chronological bibliography. Phytoparasitica 15(3):229-255.

136. Kawabata, O. and DeFrank, J. 1990. Suppressing rhizome growth and tuber formation in purple nutsedge by paclobutrazol. HortScience 25:106.

137. Kawabata, O. and DeFrank, J. 1991. Enhancing activity of glyphosate and sulfosate on purple nutsedge parent tubers by paclobutrazol. Abstracts, Weed Science Society of America (in press).

138. Keeley, P. E. 1987. Interference and interaction of purple and yellow nutsedges (*Cyperus rotundus* and *C. esculentus*) with crops. Weed Technology 1:74-81.

139. Khan, R. A., Ahmad, S. and Hussain, S. 1973. Effects of pre-sowing high temperature stress on seedling emergence and yield of seed cotton. Experimental Agriculture 9:9-14.

140. Kiatsoonthorn, V., Ueki, K., and Komai, K. 1985. Differences in phenotypic characters of purple nutsedge collected from various soil moisture habitats in Thailand. Proceedings Asian-Pacific Weed Science Society 11:406-412.

141. Klevorn, T. B. and Wyse, D. L. 1984. Effect of soil temperature and moisture on glyphosate and photoassimilate distribution in quackgrass (*Agropyron repens*). Weed Science 32:402-407.

142. Koller, D. 1972. Environmental control of seed germination. in Kozlowski, T. T., ed. *Seed Biology*, Volume II. pp 2-101. Academic Press, New York.

143. Komai, K. and Ueki, K. 1975. Polyphenolic substances in *Cyperus rotundus* L. and *Cyperus serotinus* Rottb. Proceedings Asian-Pacific Weed Science Society 5:71-77.

144. Komai, K. and Ueki, K. 1977. Physiological function of polyphenolic substances in germination of purple nutsedge tubers (in Japanese). Weed Research, Japan 22:193-198. [Weed Abstracts 27:3780;1978].

145. Komai, K. and Ueki, K. 1980. Plant-growth inhibitors in purple nutsedge (*Cyperus rotundus* L.) (in Japanese). Weed Research, Japan 25:42-47. [Weed Abstracts 27:2130;1978].WRONG DATE FOR WEED ABSTRACTS

146. Komai, K. and Ueki, K. 1981. Geographical variation of essential oils in tubers of purple nutsedge. Proceedings Asian-Pacific Weed Science Society 8:387-389.

147. Komai, K. and Ueki, K. 1982. Effect of shoot-cutting treatment on the regrowth ability and carbohydrate contents of purple nutsedge (*Cyperus rotundus* L.) tubers (in Japanese). Weed Research, Japan 27:272-277. [Weed Abstracts 33:202;1984].

148. Komai, K., Iwamura, J., Kiatsoonthorn, V., and Ueki, K. 1983. Geographical variation of *Cyperus rotundus* L. and ecological properties. Proceedings Asian-Pacific Weed Science Society 9:66-70.

149. Komai, K., Iwamura, J., and Ueki, K. 1977. Isolation, identification, and physiological activities of sesquiterpenes in purple nutsedge tubers (in Japanese). Weed Research, Japan 22:14-18. [Weed Abstracts 27:1078;1978].

150. Komai, K., Osaki, K., and Ueki, K. 1978. Geographical variation of essential oils in tubers of purple nutsedge (in Japanese). Weed Research, Japan 23:160-164. [Weed Abstracts 28:4150;1979].

151. Komai, K., Tang, C. S., and Nishimoto, R. K. 1991. Chemotypes of *Cyperus rotundus* in Pacific rim and basin: Distribution and inhibitory activities of their essential oils. Journal of Chemical Ecology 17:1-8.

152. Kondap, S. M., Ramakrishna, K., Bhoji Reddy, G., and Rao, A. N. 1982. Investigations on the competitive ability of certain crops against purple nutsedge (Cyperus rotundus L.). Indian Journal of Weed Science 14(2):124-126.

153. Kramarovsky, E. and Salvador, C. 1976. Chemical control of *Cyperus rotundus* L. (in Spanish). Trabajos y Resumenes, III Congreso Asociacion Latinoamericana de Malezas "ALAM" y VIII Reunion Argentina de Malezas y su Control "ASAM", Mar del Plata. ASAM 4:212-216. [Weed Abstracts 28:3584;1979].

154. Kydrev, T. G., and Kolev, V. M. 1962. Thermal treatment of dry wheat seeds and its effect on the plants. AIBS Translation, soviet Plant Physiology 8:460-463.

155. Landsberg, J. J. 1977. Some useful equations for biological studies. Experimental Agriculture 13:273-286.

156. Laude, H. M., Shrum, J. E., Jr., and Biehler, W. E. 1952. The effect of high soil temperatures on the seedling emergence of perennial grasses. Agronomy Journal 44:110-112.

157. Leach, C. M. 1956. The effects of carbon tetrachloride, air, and water at 158 F on the microflora and germination of clover seed. Phytopathology 46:637-638.

158. Lehle, F. R. and Putnam, A. R. 1982. Quantification of allelopathic potential of sorghum residues by novel indexing of Richards' function fitted to cumulative cress seed germination curves. Plant Physiology 69:1212-1216.

159. Levitt, J. 1980. *Responses of Plants to Environmental Stresses, Vol. I: Chilling, Freezing, and High Temperature Stress.* Academic Press, New York.

160. Loustalot, A. J., Muzik, T. J., and Cruzado, H. J. 1954. Studies on nutgrass (*Cyperus rotundus* L.) and its control. Bulletin United States Department of Agriculture, Puerto Rico 52, 30 pp.

161. Lucena, J. M. and Doll, J. 1976. Growth-inhibiting effects of *Cyperus rotundus* L. on sorghum and soybeans (in Spanish). Revista COMALFI 3:241-256. [Weed Abstracts 26:2700;1977].

162. Lyr, H., Hoffman, G., and Richter, R. 1970. On the chilling requirement of dormant buds of *Tilia platyphyllos* Scop. Biochemie und Physiologie der Pflanzen 161(2):133-141. [Biological Abstracts 52(8):45563; 1971].

163. Magalhaes, A. C. 1967. Observations on the influence of light on the growth of purple nutsedge, *Cyperus rotundus* L. (in Portuguese). Bragantia 26:131-142. [Weed Abstracts 19:1211;1970].

164. Magalhaes, A. C. and Franco, C. M. 1962. Toxicity of *Canavalia ensiformis* to Cyperus rotundus (in Portuguese). Bragantia 21:53-58. [Weed Abstracts 13:1451;1964].

165. Magambo, M. J. S. and Terry, P. J. 1973. Control of purple nutsedge (*Cyperus rotundus*) with glyphosate. Proceedings 4th Asian-Pacific Weed Science Society Conference 191-194.

166. Mahrer, Y. 1979. Prediction of soil temperatures of a soil mulched with transparent polyethylene. Journal of Applied Meteorology. 18:1263-1267.

167. Mahrer, Y. and Katan, J. 1981. Spatial soil temperature regime under transparent polyethylene mulch: numerical and experimental studies. Soil Science 131:82-87.

168. Martinez, E. and Pulver, E. 1975. The effects of repeated glyphosate treatments on nutsedge control in some fruit trees (in Spanish). Sociedad Colombiana de Control de Malezas y Fisiologia Vegetal "COMALFI". Resumenes de los Trabajos en el VII Seminario, Bogota 35. [Weed Abstracts 26:651;1977].

169. Mayer, A. M. and Polyakoff-Mayber, A. 1963. *The Germination of Seeds*. Pergamon Press, New York.

170. Mayton, E. L., Smith, E. V., and King, D. 1945. Nut grass eradication studies: IV. Use of chickens and geese in the control of nut grass, *Cyperus rotundus* L. Journal of the American Society of Agronomy 37:785-791.

171. Meissner, R., Nel, P. C., and Smit, N. S. H. 1982. The residual effect of Cyperus rotundus on certain crop plants. Agroplantae 14:47-53.

172. Mercado, B. L. 1979. Monograph on *Cyperus rotundus* L. BIOTROP Bulletin no. 15, 63 pp.

173. Mohamed-Saleem, M. A. and Fawusi, M. O. A. 1983. A note on the effects of tropical weed decomposition on seed germination and seedling growth of some agricultural crops. Agriculture, Ecosystems, and Environment 10:347-352.

174. Moore, F. D., III and Joliffe, P. A. 1987. Mathematical characterization of seed mortality in storage. Journal of the American Society for Horticultural Science 112(4):681-686.

175. Moosavi-Nia, H. and Dore, J. 1979a. Factors affecting glyphosate activity in *Imperata cylindrica* (L) Beau. and *Cyperus rotundus* L. I. Effect of soil moisture. Weed Research 19:137-143.

176. Moosavi-Nia, H. and Dore, J. 1979b. Factors affecting glyphosate activity in *Imperata cylindrica* (L) Beau. and *Cyperus rotundus* L. II: effect of shade. Weed Research 19:321-327.

177. Morinaga, T. I. 1926. Effect of alternating temperatures upon the germination of seeds. American Journal of Botany 13:141-158.

178. Muzik, T. J. and H. J. Cruzado. 1953. The effect of 2,4-D on sprout formation in *Cyperus rotundus*. American Journal of Botany 40:507-512.

179. Nelson, E. A., and Lavender, D. P. 1979. The chilling requirement of western hemlock seedlings. Forest Science 25(3):485-490.

180. Nelson, Larry A. 1989. A statistical editor's viewpoint of statistical usage in horticultural science publications. HortScience 24(1):53-57.

181. Nussbaum, E. S., Wiese, A. F., Crutchfield, D. E., Chennault, E. W., and Lavake, D. 1985. The effects of temperature and rainfall on emergence and growth of eight weeds. Weed Science 33:165-170.

182. Okafor, L. I. and DeDatta, S. K. 1974. Competition between weeds and upland rice in monsoon Asia. Philippine Weed Science Bulletin 1:39-45.

183. Okafor, L. I. and DeDatta, S. K. 1976. Competition between upland rice and purple nutsedge for nitrogen, moisture, and light. Weed Science 24:43-46.

184. Onwueme, I. C. 1974. Retardation of hypocotyl growth by prior heat stress in seedlings of cowpea, melon and tomato. Journal of Agricultural Science 83:409-413.

185. Onwueme, I. C. 1975a. Changes in imbibition rate of okra (*Hibiscus esculentus*) seeds following high temperature treatments. Phyton 33:139-142.

186. Onwueme, I. C. 1975b. Enhancement of okra (*Hibiscus esculentus*) seedling growth and emergence by heat stress conditions. Journal of Agricultural Science 85:233-239.

187. Onwueme, I. C. and Adegoroye. 1975. Emergence of seedlings from different depths following high temperature stress. Journal of Agricultural Science 84:525-528.

188. Onwueme, I. C. and Atakoumi, A. K. 1975. Yield of *Celosia* and *Amaranthus* as affected by high temperature stress. Phyton 33:143-147.

189. Onwueme, I. C. and Laude, H. M. 1972. Heat-induced growth retardation and attempts at its prevention in barley and wheat coleoptiles. Journal of Agricultural science 79)331-333.

190. Onwueme, I. C. and Lawanson, A. O. 1975. Chlorophyll accumulation in cowpea (*Vigna*) and melon (*Colocynthis*) cotyledons as influenced by prior heat stress and seedling age. Phyton 33:69-73.

191. Onwueme, I. C., Laude, H. M., and Huffaker, R. C. 1971. Nitrate reductase activity in relation to heat stress in barley seedlings. Crop Science 11:195-200.

192. Orcutt, D. R. and Holt, J. S. 1990. Temperature thresholds for bud sprouting in perennial weeds and seed germination in cotton. Abstracts Weed Science Society of America 30:47.

193. Palmer, R. D. and Porter, W. K., Jr. 1959. The metabolism of nut grass (*Cyperus rotundus* L.) I. The influence of various oxygen and carbon dioxide levels upon germination and respiration. Weeds 7:481-489.

194. Parker, C. 1985. Growth patterns in Cyperus rotundus. Proceedings 1985 British Crop Protection Conference--Weeds, Volume 1:387-394.

195. Parker, C. and Dean, M. L. 1972. The effect of some plant growth regulators on the sprouting of *Cyperus rotundus* and its response to herbicides. Proceedings 11th British Weed Control Conference, 744-751.

196. Parker, C., Holly, K., and Hocombe, S. D. 1969. Herbicides for nutgrass control--conclusions from ten years of testing at Oxford. Pest Articles and News Summaries 15(1):54-63.

197. Patterson, D. T. 1982. Shading responses of purple and yellow nutsedges (*Cyperus rotundus* and *C. esculentus*). Weed Science 30:25-30.

198. Phatak, S. C., Sumner, D. R., Wells, H. D., Bell, D. K., and Glaze, N. C. 1983. Biological control of yellow nutsedge with the indigenous rust fungus *Puccinia canaliculata*. Science 219:1446-1447.

199. Phatak, S. C., Callaway, M. B., and Vavrina, C. S. 1987. Biological control and its integration in weed management systems for purple and yellow nutsedge (*Cyperus rotundus* and *C. esculentus*). Weed Technology 1:84-91.

200. Pitelli, R. A., Durigan, J. C., and Benedetti, J. J. 1983. Inter- and intraspecific competition studies in *Glycine max* (L.) Merrill and *Cyperus rotundus* (L.) in greenhouse conditions (in Portuguese). Planta Daninha 6(2):129-137. [Weed Abstracts 34:3054;1985].

201. Pollock, B. M. 1972. Effects of environment after sowing on viability. in Roberts, E. H., ed. *Viability of Seeds*. Chapman and Hall, London.

202. Ponchio, J. A. De R., Favarin, J. L., Louro, M. P., Portugal Junior, A., Minami, H., and Victoria Filho, R. 1984. Competition between purple nutsedge (*Cyperus rotundus* L.) and summer squash (*Cucurbita moschata* L.) cv. Menina Brasileira (in Portuguese). Solo 76(1):5-10. [Weed Abstracts 34:458;1985].

203. Pothecary, B. P. and Thomas, W. D. 1968. Control of Cyperus rotundus in the Sudan Gezira. Pest Articles and News Summaries 14(3):236-240.

204. Powell, C. L., Caldwell, K. I., Littler, R. A., and Warrington, I. 1988. Effect of temperature regime and nitrogen fertilizer level on vegetative and reproductive bud development in *Cymbidium* orchids. Journal of the American Society for Horticultural Science 113(4):552-556.

205. Powles, S. B., Charman, N., and Poole, F. 1988. Solar heating (solarization) of the soil surface: effect on weed control, and yield of *Phaseolus vulgaris*. Plant Protection Quarterly 3:31-35.

206. Pullman, G. S., DeVay, J. E., and Garber, R. H. 1981. Soil solarization and thermal death: A logarithmic relationship between time and temperature for four soilborne plant pathogens. Phytopathology 71:959-964.

207. Purea, M. 1985. A preliminary investigation into economising the use of glyphosate by using urea as a synergist in the Cook Islands. Alafua Agricultural Bulletin 10(1):9-11.

208. Quimby, P. C., Jr. and Frick, K. E. 1985. Evaluation of herbicide-coated larvae of *Bactra verutana* [Lep. Tortricidae] to control nutsedges [Cyperus rotundus L. and *C. esculentus* L.]. Entomophaga 30(3):287-292.

209. Quinlivan, B. J. 1961. The effect of constant and fluctuating temperatures on the permeability of the hard seeds of some legume species. Australian Journal of Agricultural Research 12:1009-1022.

210. Quinlivan, B. J. 1966. The relationship between temperature fluctuations and the softening of hard seeds of some legume species. Australian Journal of Agricultural Research 17:625-631.

211. Ragone, D. and Wilson, J. 1988. Control of weeds, nematodes, and soil-borne pathogens by soil solarization. Alafua Agricultural Bulletin 13:13-20.

212. Ranade, S. and Burns, W. 1925. The eradication of *Cyperus rotundus* L. Memoirs of the Department of Agriculture in India, Botanical Series 13:99-192.

213. Rao, J. S. 1968. Studies on the development of tubers in nutgrass and their starch content at different depths of soil. Madras Agricultural Journal 55:18-23.

214. Rees, A. R. 1972. *The Growth of Bulbs*. Academic Press, London.

215. Rehm, S. and El-Masry, R. 1976. The effects of growth regulators and herbicides on purple nutsedge (*Cyperus rotundus* L.) I. The effect on sprout and root formation of dormant tubers. Z. Acker- und Pflanzenbau 143:98-108.

216. Rehm, S. and El-Masry, R. 1977. The effects of growth regulators and herbicides on purple nutsedge (*Cyperus rotundus* L.) III. The combined effect of morphactin CME 73170 P and Dicamba. Z. Acker- und Pflanzenbau 144:215-221.

217. Richards, F. J. 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10:290-300.

218. Rincker, C. M. 1954. Effect of heat on impermeable seeds of alfalfa, sweet clover, and red clover. Agronomy Journal 46:247-250.

219. Rincon, D. J. and Warren, G. F. 1978. Effect of five thiocarbamate herbicides on purple nutsedge (*Cyperus rotundus*). Weed Science 26:127-131.

220. Roberts, E. H., and Ellis, R. H. 1982. Physiological, ultrastructural and metabolic aspects of seed viability. in Khan, A. A., ed. *The Physiology and Biochemistry of Seed Development, Dormancy and Germination*. Elsevier/North Holland, Amsterdam.

221. Rochecouste, E. 1956. Observations on nutgrass (*Cyperus rotundus* L.) and its control by chemical methods in Mauritius. Proceedings Ninth Congress International Society of Sugar Cane Technologists, 319-329.

222. Romanowski, R. R., Jr. and Nakagawa, Y. 1967. Chemical weed control with vegetable crops in Hawaii. Proceedings First Asian-Pacific Weed Control Interchange 99-102.

223. Ronoprawiro, S. 1971. The effect of drying on the survival of the nutgrass tubers (*Cyperus rotundus* L.). Proceedings 1st Indonesian Weed Science Conference 101-105.

224. Rubin, B. and Benjamin, A. 1983. Solar heating of the soil: Effect on weed control and on soil-incorporate herbicides. Weed Science 31-819-825.

225. Rubin, B. and Benjamin, A. 1984. Solar heating of the soil: Involvement of environmental factors in the weed control process. Weed Science 32:138-142.

226. Sale, P. J. M. 1979. Growth of potatoes (*Solanum tuberosum* L.) to the small tuber stage as related to soil temperature. Australian Journal of Agricultural Research 30:667-675.

227. Salisbury, F. B. and Ross, C. W. 1978. *Plant Physiology*. Wadsworth, Belmont, California.

228. Sanborn, S. M., Wyman, J. A., and Chapman, R. K. 1982. Threshold temperature and heat unit summations for seedcorn maggot development under controlled conditions. Annals of the Entomological Society of America 75:103-106.

229. Satorre, E. H., Ghersa, C. M., and Pataro, A. M. 1985. Prediction of *Sorghum halepense* (L.) Pers. rhizome sprout emergence in relation to air temperature. Weed Research 25:103-109.

230. Sauerborn, J., Linke, K. H., Saxena, M. C., and Koch, W. 1989. Solarization; a physical control method for weeds and parasitic plants (*Orobanche* spp.) in Mediterranean agriculture. Weed Research 29:391-397.

231. Scherp, L. A. 1975. A review of some factors affecting the performance of glyphosate. Proceedings of the New Zealand Weed and Pest control Conference 28:165-168.

232. Schimpf, S. D., Flint, S. D., and Palmblad, I. G. 1977. Representation of germination curves with the logistic function. Annals of Botany 41:1357-1360.

233. Schreiber, M. M. 1982. Modeling the biology of weeds for integrated weed management. Weed Science 30:13-16.

234. Scott, S. J., Jones, R. A., and Williams, W. A. 1984. Review of data analysis methods for seed germination. Crop Science 24:1192-1199.

235. Shamsi, S. R. A., Al-Ali, F. A., and Hussain, S. M. 1978. Temperature and light requirements for the sprouting of chilled and unchilled tubers of the purple nutsedge, *Cyperus rotundus*. Physiologia Plantarum 44:193-196.

236. Shetty, S. V. R., Sivakumar, M. V. K., and Ram, S. A. 1982. Effect of shading on the growth of some common weeds of the semi-arid tropics. Agronomy Journal 74:1023-1029.

237. Shiam, R., Sirohi, H. S., Rashmi, Km. R., and Malik, P. L. 1987. Effects of gibberellic acid, maleic hydrazide, copper sulfate and streptomycin on growth, flowering, and tuber formation of Cyperus rotundus L. Indian Journal of Forestry 10(2):126-131.

238. Siegel, S. M. 1950. Effects of exposures of seeds to various physical agents. I. Effects of brief exposures to heat and cold on germination and light-sensitivity. Botanical Gazette 112:57-70.

239. Siegel, S. M. 1953. Effects of exposures of seeds to various physical agents. II. Physiological and chemical aspects of heat injury in the red kidney bean embryo. Botanical Gazette 114:297-312.

240. Siegel, S. M. and Carrol, P. 1975. Permeability-viability relations in plant damage: A note on alpha-amylase leakage and growth inhibition in bean embryos. Plant and Cell Physiology 16:1151-1155.

241. Sierra, J. N. 1973. Some aspects of the biology of purple nutsedge *Cyperus rotundus* L. Proceedings Second Indonesian Weed Science Conference 71-86.

242. Simon, E. W. 1974. Phospholipids and plant membrane permeability. New Phytologist 73:377-420.

243. Sinha, T. D. and Thakur, C. 1967. Control of nutgrass weed by cultivation. Indian Journal of Agronomy 12:121-125.

244. Siriwardana, G. 1986. Low rates of glyphosate for management of *Cyperus rotundus* L. Ph D Dissertation, University of Hawaii, Honolulu.

245. Siriwardana, G. and Nishimoto, R. K. 1987. Propagules of purple nutsedge (*Cyperus rotundus*) in soil. Weed Technology 1:217-220.

246. Smid, D. and Hiller, L. K. 1981. Phytotoxicity and translocation of glyphosate in the potato (*Solanum tuberosum*) prior to tuber initiation. Weed Science 29:218-223.

247. Smith, E. V. and Fick, C. L. 1937. Nut grass eradication studies. I. Relation of the life history of nut grass, *Cyperus rotundus* L., to possible methods of control. Journal of the American Society of Agronomy 29:1007-1013.

248. Smith, E. V. and Mayton, E. L. 1938. Nut grass eradication studies: II. The eradication of nut grass, *Cyperus rotundus* L., by certain tillage treatments. Journal of the American Society of Agronomy 30:18-21.

249. Smith, E. V. and Mayton, E. L. 1942. Nut grass eradication studies: III. The control of nut grass, *Cyperus rotundus* L., on several soil types by tillage. Journal of the American Society of Agronomy 34:151-159.

250. Sprague, V. G. 1943. The effects of temperature and day length on seedling emergence and early growth of several pasture species. Proceedings, Soil Science Society of America 8:287-294.

251. Sprankle, P., Meggitt, W. F., and Penner, D. 1975a. Rapid inactivation of glyphosate in the soil. Weed Science 23:224-228.

252. Sprankle, P., Meggitt, W. F., and Penner, D. 1975b. Adsorption, mobility, and microbial degradation of glyphosate in the soil. Weed Science 23:229-234.

253. Sprankle, P., Meggitt, W. F., and Penner, D. 1975c. Absorption, action, and translocation of glyphosate. Weed Science 23:235-240.

254. Staker, E. V. 1925. The effect of dry heat on alfalfa seed and its adulterants. Journal of the American Society of Agronomy 17:32-40.

255. Standifer, L. C. 1980. Control of nutsedge with repeated applications of glyphosate. Proceedings Southern Weed Science Society 33:297. (Abstract)

256. Standifer, L. C. and Chin, H. F. 1969. The use of corn as a competitive crop for economical control of purple nutsedge (*Cyperus rotundus*). Proceedings 2nd Asian-Pacific Weed Control Interchange 190-197.

257. Standifer, L. C., Jr., Normand, W. C., and Rizk, T. 1966. An effect of light on basal bulb formation of purple nutsedge (*Cyperus rotundus*). Proceedings 19th Southern Weed Conference 550-552.

258. Standifer, L. C., Wilson, P. W., and Porche-Sorbet, R. 1984. Effects of solarization on soil weed seed populations. Weed Science 32:569-573.

259. Stapleton, J. J. and DeVay, J. E. 1986. Soil solarization: a non-chemical approach for management of plant pathogens and pests. Crop Protection 5(3):190-198.

260. Stapleton, J. J., and Garza-Lopez, J. G. 1988. Mulching of soil with transparent (solarization) and black polyethylene films to increase growth of annual and perennial crops in southwestern Mexico. Tropical Agriculture (Trinidad) 65(1):29-33.

261. Steinrucken, H. C. and Amrhein, N. 1980. The herbicide glyphosate is a potent inhibitor of 5-enolpyruvylshikimic acid-3-phosphate synthase. Biochemical and Biophysical Research Communications 94(4):1207-1212.

262. Stevens, C., Khan, V. A., Okoronkwo, T., Tang, A.-Y., Wilson, M. A., Lu, J., and Brown, J. E. 1990. Soil solarization and Dacthal: influence on weeds, growth, and root microflora of collards. HortScience 25(10):1260-1262.

263. Stewart, G. 1926. Effect of color of seed, of scarification, and of dry heat on the germination of alfalfa seed and some of its impurities. Journal of the American Society of Agronomy 18:743-760.

264. Stimart, D. P., and Ascher, P. D. 1981. Development responses of *Lilium longiflorum* bulblets to constant or alternating temperatures *in vitro*. Journal of the American Society for Horticultural Science. 106(4):450-454.

265. Stoller, E. W. 1981. Yellow nutsedge basal bulb development. Proceedings North Central Weed Control Conference 36:18.

266. Stoller, E. W. and Sweet, R. D. 1987. Biology and life cycle of purple and yellow nutsedges (*Cyperus rotundus* and *C. esculentus*). Weed Technology 1:66-73.

267. Suwunnamek, U. and Parker, C. 1975. Control of *Cyperus rotundus* with glyphosate: the influence of ammonium sulphate and other additives. Weed Research 15:13-19.

268. Suzuki, K., Hiroese, K., and Kawase, K. 1988. Studies on weed control in a citrus orchard. III. Control of broad leaf perennial weeds (in Japanese). Bulletin of the Fruit Tree Research Station, B (Okitsu), Japan 15:21-34. [Weed Abstracts 38:675;1989].

269. Swarbrick, J. T. and Dominiak, B. C. 1975. Nutgrass (*Cyperus rotundus*) suppression with polythene film. Proceedings Asian-Pacific Weed Science Society 4:195-196.

270. Swietlick, D. 1989. Adjuvants affect the efficacy of glyphosate on selected perennial weeds. HortScience 24(3):470-472.

271. Tapke, V. F. 1924. Effects of the modified hot-water treatment on germination, growth, and yield of wheat. Journal of Agricultural research 28:79-98.

272. Taylorson, R. B. 1969. Photocontrol of rough cinquefoil seed germination and its enhancement by temperature manipulation and KNO_3. Weed Science 17:144-148.

273. Taylorson, R. B., and Hendricks, S. B. 1972a. Interactions of light and a temperature shift on seed germination. Plant Physiology 49:127-130.

274. Taylorson, R. B., and Hendricks, S. B. 1972b. Phytochrome control of germination of *Rumex crispus* L. seeds induced by temperature shifts. Plant Physiology 50:645-648.

275. Taylorson, R. B., and Hendricks, S. B. 1977. Dormancy in seeds. Annual Review of Plant Physiology 28:331-354.

276. Taylorson, R. B., and Hendricks, S. B. 1979. Overcoming dormancy in seeds with ethanol and other anesthetics. Planta 145:507-510.

277. Teo, C. K. H. and Nishimoto, R. K. 1973. Cytokinin-enhanced sprouting of purple nutsedge as a basis for control. Weed Research 13:118-121.

278. Teo, C. K. H., Bendixen, L. E., and Nishimoto, R. K. 1971. Benzyl adenine induced sprouting in purple nutsedge tubers. Proceedings North Central Weed Control Conference 26:85-86.

279. Teo, C. K. H., Bendixen, L. E., and Nishimoto, R. K. 1973. Bud sprouting and growth of purple nutsedge altered by benzyladenine. Weed Science 21:19-23.

280. Teo, C. K. H., Nishimoto, R. K., and Tang, C. S. 1974. Bud inhibition of *Cyperus rotundus* L. by inhibitor B or abscisic acid and the reversal of these effects by N-6-benzyladenine. Weed Research 14:173-179.

281. Teo, C. K. H., Zandstra, B. H., and Nishimoto, R. K. 1973. Purple nutsedge (*Cyperus rotundus*): Its biology and control. Proceedings Asian-Pacific Weed Science Society Conference 4:184-190.

282. Terry, P. J. 1985. Efficacy of glyphosate for weed control in the tropics and sub-tropics. in Grossbard, E. and D. Atkinson, eds. *The Herbicide Glyphosate*. London, Butterworths.

283. Tipton, J. L. 1984. Evaluation of three growth curve models for germination data analysis. Journal of the American Society for Horticultural Science 109(4):451-454.

284. Toole, E. H., Toole, V. K., Borthwick, H. A., and Hendricks, S. B. 1955. Interaction of temperature and light in germination of seeds. Plant Physiology 30:473-478.

285. Toole, V. K. 1973. Effects of light, temperature and their interactions on the germination of seeds. seed science and technology 1:339-396.

286. Torres, M. and Frutos, G. 1989. Analysis of germination curves of aged fennel seeds by mathematical models. Environmental and Experimental Botany 29:409-415.

287. Toth, J. and Smith, L. W. 1979. *Cyperus rotundus* control with glyphosate. Proceedings Asian-Pacific Weed Science Society Conference 7:67-69.

288. Totterdell, S., and Roberts, E. H. 1980. Characteristics of alternating temperatures which stimulate loss of dormancy in seeds of *Rumex obtusifolius* L. and *Rumex crispus* L. Plant, Cell, and Environment 3:3-12.

289. Tripathi, R. S. 1967. Ecology of *Cyperus rotundus* L. II. Tuber sprouting in relation to temperature. Proceedings National Academy of Sciences, India (B) 37:409-412.

290. Tripathi, R. S. 1969a. Ecology of *Cyperus rotundus* L. III. Population of tubers at different depths of the soil and their sprouting response to air drying. Proceedings National Academy of Sciences, India (B) 39:140-142.

291. Tripathi, R. S. 1969b. Ecology of *Cyperus rotundus* L. IV. Effect of two different temperatures on growth and reproduction. Proceedings National Academy of Sciences, India (B) 39:161-163.

292. Tripathi, R. S. 1969c. Ecology of *Cyperus rotundus* L. V. Reproduction by seeds. Proceedings National Academy of Sciences, India (B) 39:164-168.

293. Tumbleson, M. E. and Kommedahl, T. 1962. Factors affecting dormancy in tubers of *Cyperus esculentus* L. Botanical Gazette 123:186-189.

294. Turner, P. E. T. 1985. Nutgrass competition and control in cane fields. Sugar Cane 4:1-7. From Abstracts on Tropical Agriculture 11,54011. [Weed Abstracts 35:2906;1986].

295. Ueki, K. 1969. Studies on the control of nutsedge (*Cyperus rotundus* L.): On the germination of a tuber. Proceedings 2nd Asian-Pacific Weed Control Interchange 355-369.

296. Uhlinger, R. D. 1970. Germination of heat treated seeds of *Philadelphia lewisi* Pursh. Journal of the American Society for Horticultural Science 95:307-310.

297. Villamayor, F. G., Jr. 1983. Effect of Cyperus rotundus L. on the growth and yield of cassava. Radix 5(2):10. [Weed Abstracts 35:3205;1986].

298. Villapudua, J. R. and Munnecke, D. E. 1986. Solar heating and amendments control cabbage yellows. California Agriculture, pp. 11-13.

299. Vora, A. B. and Patel, M. K. 1975. Effect of heat treatment and GA feeding on seedling growth of mung. Current Science 44:749-750.

300. Wagenvoort, W. A., and Bierhuizen, J. F. 1977. Some aspects of seed germination in vegetables. II. The effect of temperature fluctuation, depth of sowing, seed size, and cultivar, on heat sum and minimum temperature for germination. Scientia Horticulturae 6:259-270.

301. Wagenvoort, W. A., and Van Opstal, N. A. 1979. The effect of constant and alternating temperatures, rinsing, stratification and fertilizer on germination of some weed species. Scientia Horticulturae 10:15-20.

302. Waggoner, H. D. 1917. The viability of radish seeds (*Raphanus sativus* L.) as affected by high temperatures and water content. American Journal of Botany 4:299-313.

303. Waldecker, M. A. and Wyse, D. L. 1985. Soil moisture effects on glyphosate absorption and translocation in common milkweed (*Asclepias syriaca*). Weed Science 33:299-305.

304. Wanjura, D. F., Buxton, D. R., and Stapleton, H. N. 1970. A temperature model for predicting initial cotton emergence. Agronomy Journal 62:741-743.

305. Warrington, I. J. and Kanemasu, E. T. 1983. Corn growth response to temperature and photoperiod I. Seedling emergence, tassel initiation, and anthesis. Agronomy Journal 75:749-754.

306. Wiese, A. M., and Binning, L. K. 1987. Calculating the threshold temperature of development for weeds. Weed Science 35:177-179.

307. William, R. D. 1976. Purple nutsedge: Tropical scourge. HortScience 11:357-364.

308. William, R. D. and Warren, G. F. 1975. Competition between purple nutsedge and vegetables. Weed Science 23:317-323.

309. Williams, R. D. 1978. Photoperiod effects on the reproductive biology of purple nutsedge (*Cyperus rotundus*). Weed Science 26:539-542.

310. Williams, R. D. 1982. Growth and reproduction of *Cyperus esculentus* L. and *Cyperus rotundus* L. Weed Research 22:149-154.

311. Williams, R. D., Quimby, P. C., Jr., and Frick, K. E. 1977. Intraspecific competition of purple nutsedge (*Cyperus rotundus*) under greenhouse conditions. Weed Science 25:477-481.

312. Wills, G. D. 1969. Factors affecting germination and growth of nutsedge. Proceedings Southern Weed Science Society 22:336.

313. Wills, G. D. 1975. Effect of light and temperature on growth of purple nutsedge. Weed Science 23:93-96.

314. Wills, G. D. 1987. Description of purple and yellow nutsedge (*Cyperus rotundus* and *C. esculentus*). Weed Technology 1:2-9.

315. Wills, G. D. and Briscoe, G. A. 1970. Anatomy of purple nutsedge. Weed Science 18:631-635.

316. Wills, G. D. and McWhorter, C. G. 1985. Effect of inorganic salts on the toxicity and translocation of glyphosate and MSMA in purple nutsedge (*Cyperus rotundus*). Weed Science 33:755-761.

317. Wood, A. and Paleg, L. G. 1974. Alteration of liposomal membrane fluidity by gibberellic acid. Australian Journal of Plant Physiology 1:31-40.

318. Wood, A., Paleg, L. G., and Spotswood, T. M. 1974. Hormone-phospholipid interaction: A possible hormonal mechanism of action in the control of membrane permeability. Australian Journal of Plant Physiology 1:167-169.

319. Yoshihara, T. and Ekern, P. C. 1977. Solar radiation measurements in Hawaii. Hawaii Natural Energy Institute, University of Hawaii, Honolulu.

320. Zaenudin, M. S. 1988. Control of purple nutsedge (Cyperus rotundus L.) in preparing land for cacao. Weedwatcher 6-7:6.

321. Zandstra, B. H. 1976. Herbicidal activity and translocation of glyphosate in *Cyperus rotundus* L. Ph D Dissertation, University of Hawaii, Honolulu.

322. Zandstra, B. H. and Nishimoto, R. K. 1975. Effect of undisturbed soil period on glyphosate control of *Cyperus rotundus* L. Proceedings 5th Asian-Pacific Weed Science Society Conference 5:130-133.

323. Zandstra, B. H. and Nishimoto, R. K. 1977. Movement and activity of glyphosate in purple nutsedge. Weed Science 25:268-274.

324. Zandstra, B. H., Teo, C. K. H., and Nishimoto, R. K. 1974. Response of purple nutsedge to repeated applications of glyphosate. Weed Science 22:230-232.