POPULATION DYNAMICS OF YELLOW NUTSEDGE (*CYPERUS ESCULENTUS* L.)

by

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Short title

POPULATION DYNAMICS OF YELLOW NUTSEDGE (*CYPERUS ESCULENTUS* L.)

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ABSTRACT

Ph.D. DANIEL CLOUTIER Plant Science

POPULATION DYNAMICS OF YELLOW NUTSEDGE (CYPERUS ESCULENTUS L.)

The main objective of this study was to develop a model of yellow nutsedge tuber population dynamics that would, through computer simulations, help select crop management systems effective against this weed. A series of experiments were undertaken to obtain information for the model. Results indicate that all tubers died after 3.5 years. The rate of population increase depended on the original spring tuber population, and the carrying capacity of the experimental area was between 15000 and 20000 tuber m^{-2}. Emergence that was delayed for more than two months resulted in a net tuber population decrease while growth interruptions, at best, allowed the tuber population to increase to only 40 % of its potential. A corn crop reduced the tuber population to 76 % of its potential. These results were synthesized through the development of a modified Leslie matrix model. The model, when validated, was stable to changes in either matrix coefficients or input values. Applications of the model will prove to be valuable tools in developing yellow nutsedge integrated management systems.

RÉSUMÉ

Ph.D. DANIEL CLOUTIER Plant Science

DYNAMIQUE DE POPULATION DU SOUCHET COMESTIBLE (*CYPERUS ESCULENTUS* L.)

Le principal objectif de cette étude était de développer un modèle de la dynamique de population des tubercules de souchet qui puisse aider à sélectionner un système de régie culturale efficace contre celle-ci. Une série d'expériences ont été établies pour obtenir l'information requise pour développer le modèle. Le taux d'augmentation de la population dépendait des densités de tubercules au printemps, et de la capacité limite du milieu, qui était de 15000 à 20000 tubercules m^{-2} dans les parcelles expérimentales. Les délais d'émergence de plus de deux mois gardaient la population à son niveau de printemps. Les interruptions de croissance, au mieux, gardaient l'accroissement de la population à 40 % de son potentiel tandis que le maïs la réduisait à 76 % de son potentiel. L'information obtenue dans le cadre de ce projet a été synthétisée dans un modèle matriciel modifié de Leslie. Une fois validé, le modèle s'est avéré être peu sensible à des variations dans ses paramètres ou dans ses données d'entrées.

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INTRODUCTION

Yellow nutsedge (*Cyperus esculentus* L., souchet comestible) is a perennial weed indigenous to Quebec and Ontario, where it has become a prominent weed in row crops in the last two decades (Deschenes and Doyon, 1981; Doyon and Bouchard, 1981; Mulligan and Junkins, 1976). It has been reported as rapidly spreading in the United States of America and as being among the world's worst weeds (Holm et al., 1977; Mulligan and Junkins, 1976; Stoller, 1981). Yellow nutsedge is a poor competitor with other weeds, but is resistant to most herbicides. Therefore, increased weed control associated with a reduction in hand hoeing or mechanical cultivation probably favored its population increase.

Yellow nutsedge is a member of the Cyperaceae family. It is an erect herbaceous plant with solid, simple, triangular culms and with three ranked leaves. Fernald (1970) described yellow nutsedge as :

> "Perennial, bearing weak filiform stolons terminated by hard tubers; culms acutely angled, 2-9 dm high; leaves pale green, 4-9 mm wide; involucral leaves 3-9, the longest much exceeding the simple to compound yellowish to

golden-brown umbel; the latter with several erect short rays and 2-9 strongly ascending longer ones; spikelets strongly flattened, mostly 4-ranked along the wing-angled rachis, obtuse, strongly flattened, 0.5-3.0 cm long; scales thin, yellowish- or golden-brown, oblong, obtuse or a little mucronate, distinctly nerved, scarious at tip, 2.2-3 mm long; rachilla with adnate narrow hyaline scales; style 3-cleft; achenes lustrous, trigonous, ellipsoid or narrowly obovoid, rounded at summit, 1.2-1.5 mm long."

Several biotypes have been characterized and found to differ in various attributes such as; herbicide sensitivity to atrazine, 2,4-D, linuron, and metribuzin (Costa and Appleby, 1976; Hauser, 1968; McCue, 1982); morphology (Costa and Appleby, 1976; Fernald, 1970; Lorougnon, 1969; Matthiesen, 1976; Stoller, 1981); photoperiod response (Matthiesen, 1976); tuber composition (Matthiesen, 1976; Matthiesen and Stoller, 1978; Stoller and Weber, 1975); overwinter tuber survival (Matthiesen, 1976; Stoller and Weber, 1975); and diverse growth attributes such as size, phenology, rate of growth, and tuber and shoot number (Costa and Appleby, 1976; Hauser, 1968; Matthiesen, 1976; Phillips, 1979, 1980, 1981; Stoller, 1981; Yip, 1978; Yip and Sweet, 1978).

Yellow nutsedge is a weed of both tropical and temperate climates that is found on all continents, in all American states, and in Ontario, Quebec, New Brunswick, and Nova Scotia. Since yellow nutsedge is more troublesome in tropical areas, cold has been suggested as limiting its range (Holm et al., 1977; Mulligan and Junkins, 1976; Stoller, 1981). Yellow nutsedge occurs both in natural habitats and agricultural fields in Canada. Its natural habitat in Quebec and Ontario is mostly riparian, but it is also found in bogs and marshes. Yellow nutsedge grows on a wide range of soil types and in a wide range of soil moisture conditions. Its growth is severely reduced by shading, but greatly increased by fertilizing (Barko and Smart, 1978,1979; Mulligan and Junkins, 1976; Stoller, 1981).

Yellow nutsedge overwinters as tubers and seeds only. In the spring, the germinating seed or tuber respectively produce a coleoptile or a shoot with a negative geotropic response. Once the soil surface is reached, a basal bulb is formed a few centimeters below the soil surface. As the bulb is formed, the internodes in that region shorten. The meristems for roots, rhizomes, leaves, and a single flower stalk are in the basal bulb. The basal bulb produces a shoot that may flower. A few weeks after the formation of the basal bulb, rhizomes are produced. In the course of a growing season, 16 rhizomes or more can be produced from a single basal bulb (Jansen, 1971). Their tips either differentiate into another basal bulb or a tuber. These secondary bulbs can produce rhizomes with tips that differentiate either into a basal bulb or a tuber. This cycle can be repeated several times. The differentiation into basal bulb or tuber is regulated by several factors of which photoperiod is considered to be the most important. However, environmental conditions, interference from other plants, and field management techniques also affect differentiation. Long days are reported as favoring basal bulb formation, but some yellow nutsedge biotypes are reportedly unaffected by photoperiod (Matthiesen, 1976; Mulligan and Junkins, 1976; Stoller, 1981).

Tubers are spherical in shape and consist of short internodes at the rhizome tip where starch accumulates and rhizomes enlarge (Bendixen, 1973). Tubers are white when initiated but they darken as they mature. They are dark brown to brownish black at maturity (Stoller, 1981). A proportion of the tubers are dormant at maturity but chilling, washing, or scarification increases their germination (Thomas, 1967). Tubers are most dormant at the end of the summer and least in the spring and early summer (Stoller, 1981).

There are between 4 to 7 buds on a tuber and most of them can sprout and establish a plant (Bendixen, 1973; Thullen and Keeley, 1975). There can be several sprouts produced at the same time and tubers will resprout if the original sprouts are destroyed. However, the vigor of subsequent sprouts is greatly reduced (Thullen and Keeley, 1975).

Tubers are reported as remaining viable from 1.5 to 4 years or more in the soil depending on the cropping system, the tuber size, and the depth of the tuber in the soil (Stoller and Wax, 1973; Thullen and Keeley, 1981). Tuber viability increased with tuber size (Thullen and Keeley, 1975) and increased with tuber depth in the soil (Bell et al., 1962; Stoller, 1981). Tubers are found to a depth of 46 cm in the soil but 85 to 97 % of the tubers are in the top 15 cm (Bell et al., 1962; Friesen and Hamill, 1977; Tumbleson and Kommedahl, 1961). Most shoots observed in the field (56 to 95 %) arise from tubers in the top 10 to 15 cm (Bell et al., 1962, Stoller and Wax, 1973; Tumbleson and Kommedahl, 1961).

A yellow nutsedge inflorescence can produce up to 1500 seeds that are dormant at maturity and have 50 to 95 % viability. However, the number of seeds found in field populations is very variable and often no seeds are produced. This, in conjunction with the fact that there are no reported cases of seedlings found in fields, has convinced most researchers that tubers are the only means through which yellow nutsedge is perpetuated in already established infestations (Mulligan and Junkins, 1976; Stoller, 1981).

Yellow nutsedge is reported to reduce corn and soybean yield through allelopathy (Drost and Doll, 1980) and to enhance the growth of soil denitrifier microorganisms which result in less available nitrogen to crops (Volz, 1977). Yellow nutsedge is considered to lack competitiveness although it can reduce corn yield by up to 79 % (Parochetti, 1974; Simkins and Doll, 1980; Stoller, 1981; Stoller et al., 1979) and soybean yield by 87 % (Simkins and Doll, 1980; Wax et al., 1972) when allowed to grow unchecked. Competition for moisture is reported as being the factor which causes the greatest crop losses although the response varies with yellow nutsedge density and environmental conditions (Stoller, 1981; Stoller et al., 1979). Yellow nutsedge is also host to several organisms that attack crops (Mulligan and Junkins, 1977).

There are several effective control measures used against yellow nutsedge, but very few can directly kill tubers. When the tubers are sprouting, destroying the sprouts has some indirect effect which is either to induce the tubers to become dormant (Stoller, 1981) or to cause resprouting (Stoller et al., 1972). The latter exhausts the food reserves of tubers through repeated action, or at least delays yellow nutsedge emergence until the crop is sufficiently established to withstand interference (Stoller, 1981; Stoller et al., 1972; Taylorson, 1967). The control methods used against yellow nutsedge can be classified into several categories such as mechanical, chemical, biological, and cultural control methods.

Tillage is reported as being efficient against yellow nutsedge infestations. It kills seedlings already produced and exposes some tubers to environmental extremes (cold or desiccation). Cultivation can provide excellent control of yellow nutsedge, but must be repeated frequently to be effective. Thullen and Keeley (1975) recommended a 4-week interval between cultivations for optimum control. If tuber longevity is taken into account, cultivations should be done for at least two years to effectively reduce yellow nutsedge tuber population levels. This has been recommended for purple nutsedge control (<u>Cyperus rotundus</u> L.) (Thullen and Keeley, 1975). Cultivation in crops is sometimes reported as being as efficient as the use of herbicides (Stoller et al., 1979).

Several herbicides provide some control of yellow nutsedge (Table 1.1). They gave between 75 to 98 % control of yellow

Table 1.1. Selective herbicides currently recommended in eastern Canada against yellow nutsedge in corn.

Herbicide[a] name	Chemical name	Mode of application
Alachlor	2-chloro-N-(2,6-diethylphenyl)-N-(methoxymethyl)acetamide	preplanting incorporated
Atrazine	6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine	any stage
Bentazon	3-(1-methylethyl)-(1H)-2,1,3-benzothiadiazin-4(3H)-one 2,2-dioxide	post - emergence
Butylate	S-ethyl bis(2-methylpropyl)carbamothioate	preplanting incorporated
EPTC	S-ethyl dipropyl carbamothioate	" "
Metolachlor	2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxy-1-methylethyl)acetamide	" "
Vernolate	S-propyl dipropylcarbamothioate	" "

[a] The herbicides common names and chemical names follow that of the Weed Science Society of America (Anonymous, 1983).

nutsedge in the experimental area yearly between 1982 and 1984 (Watson, pers. comm.). They perform well although their effectiveness depends on soil type and environmental conditions. Their period of activity varies between 2 to 8 weeks or more, and their efficacy against yellow nutsedge is sometimes erratic (Stoller, 1981).

Currently, there are no biological control agents that are actively used against yellow nutsedge in field infestations. Several organisms have been reported to attack yellow nutsedge (Mulligan and Junkins, 1976) and research is currently being conducted on two promising organisms. The organisms are a weevil, <u>Bactra verutana</u> Zeller; and a rust, <u>Puccinia canaliculata</u> (Schw.) Lagerh.. Both organisms naturally control the weed too late in the season and at too low a level to prevent crop yield reductions and tuber production. A solution is to multiply these organisms in laboratories or greenhouses and to release them early in the growing season in order to maximize their effect on yellow nutsedge (Frick and Wilson, 1978; Phatak et al., 1983; Stoller, 1981).

Crop rotations are recommended to suppress yellow nutsedge. Yellow nutsedge is considered a poor competitor and very sensitive to shade. Therefore, crops that rapidly develop a canopy could contribute to controlling yellow nutsedge (Jordan-Molero, 1978; Keeley and Thullen, 1978; Patterson, 1982). Crops such as alfalfa are reported to have few problems with yellow nutsedge after the year of establishment (Bendixen and Stroube, 1977). The main benefit of crop rotation as a method to control yellow nutsedge is that different control measures can be used in different crops, therefore allowing some flexibility in choosing the control methods. Most cropping systems tested were very successful and reduced yellow nutsedge populations by over 90 % in three years (Keeley et al., 1979, 1983). These systems involved the use of cultivation with or without herbicides, plus alfalfa, barley, corn, cotton, potatoes, and soybeans.

Increasing the crop density or decreasing the space between crop rows is reported to decrease yellow nutsedge growth (Bell et al., 1962; Ghafar and Watson, 1983b). Other cultural practices such as early planting so that the crop is already established when yellow nutsedge emerges can be used (Ghafar and Watson, 1983a). Also, delayed planting can allow yellow nutsedge to emerge and be killed before the crop is planted (Stoller, 1981).

These different control methods vary in effectiveness and they all suffer from the fact that they rarely afford season long control. The control methods available are most effective in corn and soybeans and will usually prevent yield losses, but will not totally control yellow nutsedge during the growing season. Either some plants will become established because they escaped control, or the control measure used will lose effectiveness during the growing season, allowing some plants to become established. Furthermore, given yellow nutsedge tuber longevity, the infestations will resurge the following year and control methods must be repeated yearly. If a control program is applied for less than four years, or if there is any lessening of the pressure on yellow nutsedge, this weed will often reach its original infestation level within one or possibly two growing season (Lapham et al., 1985).

In general, yellow nutsedge infestations have rarely been successfully reduced for a significant length of time in Quebec because the control methods :

- are costly,
- must be applied for a number of years,
- require close attention for herbicide application and monitoring of the weed's stage of growth in some cases,
- are not flexible (few effective measures possible in few crops), and
- knowledge and control methods are incomplete for a proper control of yellow nutsedge.

In view of these problems, it is suggested that an integrated management program would be more cost effective and flexible (Getz and Guttierez, 1982; Miller, 1982) against yellow nutsedge. An integrated management program means that every available control method against yellow nutsedge should be considered, alone or in combination. The life cycle stages when yellow nutsedge is most susceptible to control would be identified and taken into consideration. The factors limiting yellow nutsedge growth and the crop management techniques that can best exploit yellow nutsedge weaknesses would also be identified and considered.

Since tubers can not be killed directly by most available control techniques and since some tubers will remain dormant and viable for over four years, yellow nutsedge infestations could not be destroyed within one year. Therefore, yellow nutsedge control must be planned for several years to manage infestations so that they are either reduced to, or stabilized at, a non-detrimental level since eradication is impossible for all practical purposes.

The tubers are the survival units of yellow nutsedge and, as such, should be used as the basic units through which the success of any control program can be assessed. Since they are viable for several years and maintain yellow nutsedge infestations in cultivated fields, it is suggested that tuber demography should be used as the cornerstone in the development of any yellow nutsedge management program.

There are two main approaches that could be considered in the development of integrated yellow nutsedge management programs: an empirical approach or a systematic approach. The empirical approach would consist of intuitively selecting and testing new treatments, or treatment combinations, to control yellow nutsedge by selecting control methods that were reported as being good to excellent against yellow nutsedge or against other weeds. Afterwards, the promising combinations would be further evaluated. The systematic approach would consist of using a model of yellow nutsedge tuber population dynamics and, through simulations, selecting the treatments or treatment combinations that showed promising results against yellow nutsedge. Subsequently, the effectiveness of the treatment combinations would be verified in the field.

The modeling of yellow nutsedge tuber population dynamics is suggested because the number of experiments that would be required to develop a yellow nutsedge management program using the empirical approach would be too large for practical undertaking. Furthermore, the treatment combinations that could be the most efficient against yellow nutsedge might not be tested if the number of treatments was reduced. For example, if 6 dates of seeding, 6 seeding densities, 8 crop species, 2 fertilizer regimes, 4 harvest dates, 3 types of tillage machinery, and 12 different combinations of control techniques (such as 1 or 2 cultivations, at selected time intervals, at a range of dates, with different herbicides and application rates and so on) were considered, this would give over 80,000 possible combinations. This example is simplified but the implications remain in that it is impossible to allocate enough resources to test even a fraction of the possible combinations in the field. Some combinations could be eliminated immediately for lack of potential, but that would still leave far too many treatments. Furthermore, these tests would have to be done for several years, which increases their cost and the difficulty in justifying them. However, it would be easy and economical, using computer simulations, to examine every possible treatment combination, for 5, 10 or more years. Therefore, it is suggested that the use of a yellow nutsedge tuber population dynamics model would replace most of the empirical work required to provide the data needed for the elaboration of integrated yellow nutsedge management strategies.

The main objective of this research project is to develop a yellow nutsedge tuber population dynamics model that could be used in the selection of yellow nutsedge management programs. An appropriate type of model, such as will be used in this project, is a modified Leslie matrix. Its properties have already been demonstrated in general demographic work (Pielou, 1977; Usher, 1972) and in the study of weed populations (Mortimer, 1983; Watson, 1985).

There is a large volume of data available on yellow nutsedge in the literature, but the data originated from areas with different growing conditions and were likely taken on different biotypes. Therefore, sufficient data must be collected on local infestations to allow proper estimation of the parameters required in the development of a yellow nutsedge tuber population model.

Certain information was required before proceeding to the development of the model. Therefore, more specific objectives, which are presented in separate sections, were :

- to assess the importance of plant parts other than tubers in yellow nutsedge population dynamics,
- to determine tuber size distribution,
- to determine tuber longevity,
- to determine the depth of tuber production in the soil,
- to ascertain the effect of density on tuber production,
- to determine changes in tuber number with time,

- to assess the effect of delayed emergence on tuber numbers,

- to assess the effect of interrupted growth on tuber numbers, and

- to determine the effect of corn on tuber production.

The thesis is arranged with information on the separate experiments presented initially, followed by parameter estimations of the model and model development.

Section 2

GENERAL MATERIALS AND METHODS

2.0. Introduction :

Field experiments were conducted over a 3 year period, 1981 to 1983, in a research area located at Macdonald College, Ste-Anne-de-Bellevue, Quebec (45°26'N, 73°56'W). The soil was a St-Amable loamy sand with a pH of 5.9, 3.4% organic matter, and an average of 300 kg/ha of P_2O_5 and 400 kg/ha of K_2O. The soil preparation consisted of plowing in the fall, a spring tillage, followed by a fertilizer application of 5-20-20 which was incorporated with a harrow. Details of the field operations are presented in Table 2.1.

Silage corn (cv. COOP-S-265) was planted at a density of 66,667 plants/ha with a spacing of 75 cm between and 20 cm within the row. A starter fertilizer (18-46-0) was applied at the rate of 30 kg/ha over the seeds at planting and 150 kg/ha of 34-0-0 was side dressed when corn was at the 4- to 6-leaf stage and again 3 weeks later. The corn yield was not determined, but in all years of the study, corn growth was normal and the plants had a height of over 1.5 m.

The experimental area had been infested by yellow nutsedge for several years and the infestation was uniform at the start

Table 2.1. General field operations in the experimental area.

Year	Fertilizer[a] rate (Kg/Ha)	Last tillage date	Seeding date
1981	360	May 14	May 19
1982	480	May 13	May 14
1983	360	May 14	May 14

[a] A 5-20-20 fertilizer that was applied prior to seeding.

of the research project. All other weeds were removed manually as they appeared. During the second and third years of the study, dicamba was applied over the experimental area at a rate of 0.6 kg/ha in the week after the last tillage to assist in broadleaf control.

Treatments involving hoeing consisted of using a hoe to cut any shoots that were visible. The soil of the plots was disturbed in only the top 3 cm. The rototiller used in the course of this project consisted of a plot rototiller that worked the soil to a depth of 10 to 15 cm.

2.1 Sampling methodology :

Yellow nutsedge growth and development was assessed both by above and underground sampling. Quadrats (25 by 25 cm) placed at random were used to delineate the aboveground sampling site. Sampling consisted of clipping the shoots at ground level. The underground sampling was done using the soil sampler described by Gutman and Watson (1980). The sampler dimensions were 15 by 15 by 15 cm and it was used at random within the area where the aboveground sample had previously been taken. All plots had guard rows or the equivalent on every side. Paths were utilized within larger plots in order not to disturb sampling areas.

Shoots were dried to constant weight in an oven at 55 C. The soil samples were washed by running water as described by Gutman and Watson (1980). The material retained in the sieve was dried to a constant weight in a forced air oven kept at 45 to 50 C. Afterwards, the tubers were counted, dried again in an oven, and weighed.

2.2 Statistical analysis :

Several variables were measured and were then used to calculate ratios. The aboveground variables measured were number of shoots and shoot biomass per m^2. The underground variables consisted of number and dry weight of tubers separated into two size classes, smaller or greater than 3.97 mm. The values are reported on a m^2 basis and to a depth of 15 cm in the soil unless otherwise stated.

The total number of tubers and the total tuber dry weight were obtained by combining the data from the two size classes. Some ratios were calculated to obtain a measure of the contribution of the smaller tubers to the total tuber population. Tuber number ratio was the number of small tubers divided by the total number of tubers and the tuber dry weight ratio was the dry weight of the small tubers divided by the total tuber dry weight (Table 2.2). Dry weight expressed on an area basis will be referred to as biomass. Since the overall objective is directed at yellow nutsedge management through its tubers, only tuber data will be used in developing a yellow nutsedge tuber population dynamics model, the aboveground data will not be presented or analysed in the present study.

Analyses of variance were done on the variables or ratios

Table 2.2. Parameters and ratios used throughout this research project.

Variable	Description
Tuber number	: Total number of tubers (small+large)[a]
Tuber number ratio	: Number of small tubers / total number of tubers
Tuber biomass	: Total dry weight of tubers (small+large) (g m^{-2})[b]
Tuber biomass ratio	: Biomass of small tubers / total tuber biomass

[a] Small tubers were smaller than 3.97 mm and large tubers were larger than 3.97 mm.

[b] Tuber data was expressed per m^2 to a depth of 15 cm in the soil except when otherwise reported.

using the Statistical Analysis System (SAS; Anonymous, 1985). Samples and data sets were tested for homogeneity of variances, nonadditivity, and normality using programs accompanying the book by Sokal and Rohlf (1981). Homogeneity of variance was tested using Hartley's F_{max}-test, Bartlett's test for homogeneity of variances, and the Scheffe-Box test. Tukey's test was used to test for nonadditivity. Normality was tested using the Kolmogorov-Smirnov test for goodness of fit. No data transformations were required to analyse the data used in this thesis.

Polynomial regressions can misrepresent data by unrealistic behavior such as negative values or overshooting and decreasing values before the true maximum is reached. Therefore, regressions were only fitted to data that was used in the modeling development of yellow nutsedge tuber population dynamics and the other variables were described by the standard error of the means and compared through the least significant difference at the 5 % level of probability (LSD 0.05). Although the LSD is less appropriate than the regression analysis, it is sufficient for the intended purpose of discussion.

Whenever possible, single degrees of freedom components at the 5 % level of significance were used in the analysis of variance to select the polynomial levels that would be retained to calculate the regression. Afterwards, the regression equations were calculated using the means.

Section 3

IMPORTANCE OF PLANT PARTS OTHER THAN TUBERS IN YELLOW NUTSEDGE POPULATION DYNAMICS

3.0 Introduction :

The main objective of the research on yellow nutsedge at Macdonald College is the development of an integrated yellow nutsedge management program. Although tubers are considered as the sole means of perpetuation for yellow nutsedge in the field, the potential of achenes; rhizomes and basal bulbs in contributing to the regeneration of yellow nutsedge populations must be assessed in order not to neglect what could be significant factors in yellow nutsedge population dynamics.

Yellow nutsedge is a perennial weed which has perfect flowers, is wind pollinated, and is self-incompatible (Mulligan and Junkins, 1976). Reports on the number of achenes it produces in the field vary widely from none (Mulligan and Junkins, 1976) to 605 million per hectare (Hill et al., 1963) with a wide range of percentage germination (Table 3.1).

This variability is reportedly associated with the fact that in some areas, infestations are clones of yellow nutsedge

Table 3.1. Reported yellow nutsedge seed production and germination.

Experimental location	Number of seeds per inflorescence			% germination			Reference
	Min.	Max.	Mean	Min.	Max.	Mean	
California	26	692	228	1	78	55	Thullen and Keeley (1979)
New York	12	3238	555	0	84	25	Kelley (1950)
Maine	104	2010	485	2	95	67	Justice and Whitehead (1946)
Massachusetts				43	51	46	Hill et al. (1963)
Northeast. U.S.				29	84	53	Bell et al. (1962)
Northeast. U.S.				1	331	16	Bell and Larssen (1960)

and therefore infertile. Achene production would accordingly depend on cross-pollination with other genotypes and thus be dependent on distance and environmental conditions at the time of pollination (Mulligan and Junkins, 1976). Furthermore, within a stand, the number of flowering individuals is reported to decrease with increased density, which could further reduce the number of inflorescences and, consequently the potential number of achenes produced (Hill et al., 1963). The growth of yellow nutsedge is affected by shading and fewer inflorescences would be produced in situations where there is a closed canopy later in the growing season, such as in a field crop (Bell et al., 1962; Jordan-Molero and Stoller, 1978; Keeley and Thullen, 1978; Patterson, 1982).

However, despite yellow nutsedge's great potential to produce viable achenes, the achenes' contribution to established infestations is considered minimal, if not negligible, since there are no reports of seedling development in field situations. This fact has lead several researchers to state that yellow nutsedge reproduces mostly, if not exclusively, by tubers (Hauser, 1968; Mulligan and Junkins, 1976 ; Stoller, 1981; Thullen and Keeley, 1979).

The vegetative spread and propagation of yellow nutsedge begins with rhizomes which originate from basal bulbs. These rhizomes differentiate into either a tuber or a basal bulb at their apex. Since these rhizomes have occasionally been found to branch (Jansen, 1971; Lorougnon, 1969; Wills et al., 1980), they must have potentially active buds at their nodes and therefore could have regenerative abilities, as do rhizomes of other weed species (Kigel and Koller, 1985).

The basal bulb is formed from the meristematic cells of the rhizome apex and produces secondary rhizomes, leaves, roots, and the flowering stalk; and it is considered as being the principal site of initiation of vegetative growth for yellow nutsedge (Wills et al., 1980). Up to 15 rhizomes can originate from the same bulb and produce more basal bulbs (daughter shoots) or tubers.

Tillage operations are part of most field management practices and therefore could contribute to multiplying yellow nutsedge by cutting and/or spreading its rhizomes, basal bulbs, or achenes. The following experiments were undertaken to evaluate the potential of achenes, rhizomes and basal bulbs in contributing to the regeneration of yellow nutsedge populations.

3.1. Materials and methods :

Flower heads were collected when yellow nutsedge shoots had all senesced (late September). Twenty samples were taken both in 1983 and 1984 and each sample consisted of twenty flower heads collected from pure stands. The flower heads were stored in the dark at room temperature until May 1985 when the inflorescences were threshed, and the achenes were collected and counted. They were then placed on two layers of moistened filter paper in petri dishes. The dishes were covered, kept constantly moist and placed in a growth cabinet with a diurnal temperature 24 C / 18 C and a 14 hour photoperiod. Germinating achenes were removed and counted when shoots reached 5 mm in length. The experiment was terminated after 6 weeks.

Rhizomes were taken at random from pure yellow nutsedge stands (Aug. 3, 1983), cut in 7 to 10 cm long segments with at least 2 nodes. Each segment was then placed in waxed cardboard boxes, covered with sand, and transferred to a seed germinator cabinet (20 boxes with 10 rhizomes each). The boxes were 12 cm by 12 cm and were 4 cm high. The temperature was 28 C for 8 hours of light, and 20 C during the dark period. The soil was kept moist at all times. The boxes were observed for plant regeneration during a 4 week period.

Basal bulbs of healthy green plants were taken from pure stands of yellow nutsedge (Aug. 3, 1983). Shoots were cut 1.5 cm above the bulb collar and rhizomes connected to the bulb were cut 1.5 cm from it. The bulbs were then placed in waxed cardboard boxes (10 boxes with 20 bulbs each). The boxes were placed under the same conditions as described for the rhizomes. They were observed for plant regeneration during a 4 week period.

3.2. Results and discussion :

There was an average of 3.05 achenes/inflorescence based on inflorescences collected in 1983 with extremes of 0.2 to 10.4 achenes. The average germination rate was 24 % with extremes of 0 and 50 %. More than twice as many achenes were produced in 1984, with 6.4 achenes/inflorescence and extremes of 1.3 to 25.7 achenes. The average germination rate was 25 % with a minimum of 3 % and a maximum of 53 % (Table 3.2).

The difference in achene production could probably be attributed to differences in environmental factors. The number produced is clearly less than that reported for yellow nutsedge in the United States (Table 3.1) but the germination rate is well within that of recorded reports. The number of achenes produced here is probably lower because the plant is at its northern limit, and therefore growing under sub-optimal conditions. Furthermore, since yellow nutsedge requires cross-pollination, it is possible that a scarcity of different genotypes exists in the area, thus limiting the number of flowers fertilized (Mulligan and Junkins, 1976). The achenes that did not germinate could have been dormant (Justice and Whitehead, 1946) but no effort was made to determine this.

The contribution of yellow nutsedge achenes to already established infestations is probably minimal. Under the present experimental conditions, approximately 40 inflorescences m^{-2} were produced, each yielding an average of 4.7 achenes, therefore generating 200 achenes m^{-2}. Contrasted to this, over 15000 tubers m^{-2} were produced in the same area (Section 7). Furthermore, Stoller (1981) states that the achenes produce small and non-vigorous seedlings that do not survive in cultivated fields. However, achene contribution to dispersal in time and space could potentially be highly

Table 3.2. Production and germination rate of achenes of yellow nutsedge at Ste-Anne-de-Bellevue, Quebec, in 1983 and 1984.

	1983		1984	
sample[a] number	achene number	germination (%)	achene number	germination (%)
1	94	2	44	30
2	125	15	99	33
3	116	48	93	41
4	14	0	36	28
5	47	19	351	11
6	208	13	260	15
7	136	0	143	10
8	33	15	81	21
9	35	14	74	22
10	67	30	48	46
11	22	27	178	33
12	22	41	135	32
13	4	50	26	4
14	25	44	92	10
15	4	25	49	14
16	5	40	48	33
17	21	24	109	24
18	61	16	99	53
19	99	30	515	3
20	72	24	53	43
means	61	24	127	25

[a] Each sample consisted of 20 inflorescences.

significant.

Mulligan and Junkins (1976) found achenes on an herbarium specimen that were still viable 56 years after the plant had been collected. Under field conditions, in an experiment on the longevity of buried seeds, Goss (1924) reported that yellow nutsedge achenes had a 5 to 17 % germination rate after 20 years in the soil. From these observations, and considering that some of the achenes are probably dormant, the potential of yellow nutsedge achenes in perpetuating the species through time is important, and stresses the fact that field infestations could recur, after being totally controlled, without re-introduction of seeds or tubers in the field.

Another, and possibly more important, function of the achenes is the establishment of new populations through dispersal in space (Hill et al., 1963). They are probably dispersed by water or by animals associated with their natural habitat. The natural habitat occurs along the shores of rivers, streams, lakes, and in bogs and marshes (Barko and Smart, 1978; Mulligan and Junkins, 1976). In the experimental area, it was observed that once senesced, the rachis tended to break easily, allowing it to be carried some distance.

The rhizomes and basal bulbs did not show any vegetative growth during the course of the experiment, which concurs with the findings of Orsenigo (1953). The rhizomes and the basal bulbs do not accumulate starch and therefore have a reduced possibility of regenerating the plant if they are severed from the original tuber or rhizome that produced them (Jansen, 1971; Wills et al., 1980). Stoller et al. (1972) found that plants cut below the basal bulb and transplanted, or that plants transplanted without the mother tuber, could grow, although to a much lesser extent than intact plants.

The contribution of yellow nutsedge achenes to established infestations is probably negligible since they are produced in low numbers, they have relatively low germination rates, and there is no evidence of seedling establishment in the field. Achene production can therefore be neglected when considering yellow nutsedge management systems. However, achenes can be an important factor in spreading yellow nutsedge across short or great distances, either by farm machinery or other means. Therefore, preventive control measures should be considered in order to restrict spread of yellow nutsedge to new areas as achenes.

Rhizomes and basal bulbs do not regenerate yellow nutsedge on their own and therefore do not contribute in maintaining yellow nutsedge populations. The use of tillage or other field operations can be considered without running the risk of multiplying the plant by cutting its rhizomes or basal bulbs.

Section 4

TUBER SIZE DISTRIBUTION

4.0 Introduction :

Tubers are considered as the main, if not sole, means of propagation for yellow nutsedge populations in fields (Mulligan and Junkins, 1976; Stoller, 1981). Tuber shape is generally spherical although it may vary considerably. Tuber size and weight vary between (Keeley and Thullen, 1970; Matthiesen and Stoller, 1978; Stoller and Wax, 1973; Stoller, Nema, and Bhan, 1972; Stoller and Weber, 1975; Thullen and Keeley, 1975; Tumbleson and Kommedhal, 1961), and within yellow nutsedge populations (Ghafar and Watson, 1983a,b). Tuber size and weight are probably regulated by both genetic and environmental factors.

There are several characteristics associated with differences in tuber size and weight. The number, size, and rate of production of shoots are proportional to tuber weight and size (Stoller et al., 1972; Stoller and Wax, 1973; Thullen and Keeley, 1975; Vilumajo, 1979). Tuber longevity is correlated to tuber weight and size (Thullen and Keeley, 1975).

Furthermore, susceptibility to atrazine is inversely related to tuber weight (Vilamajo, 1979). The number of buds found on tubers and tuber sprouting and re-sprouting rate, on the other hand, are not related to tuber size or weight (Thullen and Keeley, 1975).

The above properties are important for yellow nutsedge population dynamics and therefore tuber size and weight should be considered in studies of yellow nutsedge and the assessment of management systems. Therefore, the following sampling was undertaken to determine the tuber size distribution of yellow nutsedge in the field population of the experimental site.

4.1 Materials and methods :

Sampling was conducted in late fall (October, 1983) with randomly assigned sampling sites located in pure yellow nutsedge stands. All yellow nutsedge shoots were dead at the time of sampling. Using a shovel, soil was removed to a depth of 15 cm. The samples were washed and kept in cold storage (4 C) until the tubers were sorted by size and weighed. Size here is used to refer to the smallest diameter of a tuber. The tubers were then dried to a constant weight in a convection oven kept at 55 C, sorted by size, and weighed again. Fourteen sieves of different diameters were used to sort the tubers by size. These sieves were in imperial units (64 th of inch). The sizes have been converted to mm throughout this study, which explains the fractional measures of the size classes

(Table 4.1).

4.2 Results and discussion :

There were 3096 tubers in the sample taken from the field. The fresh tuber distribution is presented in Table 4.1. Fresh tubers had a mean size of 5.96 mm and a median of 5.88 mm (Table 4.2). Their distribution was skewed to the right (positive g1 value) and was platykurtic (negative g2 value)(Sokal and Rohlf, 1981). The fresh tuber sizes were not normally distributed at the 5% significance level (D_{max} value, Sokal and Rohlf, 1981). The average tuber fresh weight was 110 mg with extremes of 4 and 462 mg. These values were similar to values observed in other areas (Table 4.3) and the sizes are comparable to that reported by Tumbleson and Kommedahl (1961).

The dry tubers had a mean size of 4.86 mm and a median of 4.82 mm. The values for the different size classes are found in Table 4.1 and the statistics in Table 4.4. The dry tuber size distribution was skewed to the right and platykurtic, but followed a normal distribution. The average dry weight was 66 mg with extremes of 2 and 384 mg, which corresponded to values reported elsewhere (Table 4.3).

Since the dry tubers' size distribution was found to be normal and since all tuber measurements in this thesis were done on dry tubers, the relation between dry tuber size and weight was evaluated. The data and the calculated regression are illustrated in Figure 4.1. The relation was quadratic and

Table 4.1. Size and weight of tubers of yellow nutsedge sampled from the field in the fall of 1983.

Tuber size		Fresh tubers		Dry tubers	
		Number	Mean weight	Number	Mean weight
64 th inch	(mm)		(mg)		(mg)
3	1.191	0	0	16	2
5	1.984	20	4	90	5
7	2.778	93	10	301	13
9	3.572	248	22	473	24
11	4.366	427	39	623	41
13	5.159	543	64	598	65
15	5.953	526	94	494	92
17	6.747	469	134	312	130
19	7.541	392	177	131	168
21	8.334	230	243	44	235
23	9.128	94	291	10	309
25	9.922	37	353	3	282
27	10.716	16	383	1	384
29	11.509	1	462	0	0

Table 4.2. Statistics of yellow nutsedge fresh tuber size distribution.

	Statistic	Standard error	Confidence limits (95%)	
Mean	5.956	.029	5.893	6.010
Median	5.884	.037	5.810	5.957
Variance	2.775			
G1[a]	.18	.04	.10	.27
G2[a]	-.34	.09	-.51	-.17
D_{max}[b]	.024			

[a] Moment statistics.
[b] Kolmogorov-Smirnov test-statistic D.

Table 4.3. Reported fresh and dry weight of yellow nutsedge tubers.

Location	Tuber Fresh weight (mg)	Tuber Dry weight (mg)	Reference
Oregon	240		Costa and Appleby, 1976
Quebec		49-71	Ghafar and Watson, 1983a
California	16-338		Keeley and Thullen, 1970
Georgia	350-530	158-233	Matthiesen and Stoller, 1978
Illinois	150	88	" "
Maryland	710	404	" "
Minnesota	70	31	" "
Oklahoma	230	129	" "
Illinois	61-294		Stoller et al., 1972
Illinois	50-120		Stoller and Wax, 1973
Illinois	255	135	Stoller and Weber, 1975
Georgia	862	538	" "
California		157-662	Thullen and Keeley, 1975
Minnesota	160-285		Tumbleson and Kommedhal, 1961

Table 4.4. Statistics of yellow nutsedge dry tuber size distribution.

	Statistic	Standard error	Confidence limits (95%)	
Mean	4.865	.026	4.813	4.916
Median	4.822	.033	4.757	4.887
Variance	2.172			
G1[a]	.17	.04	.08	.25
G2[a]	-.24	.09	-.41	-.06
D_{max}[b]	.013			

[a] Moment statistics.

[b] Kolmogorov-Smirnov test-statistic D.

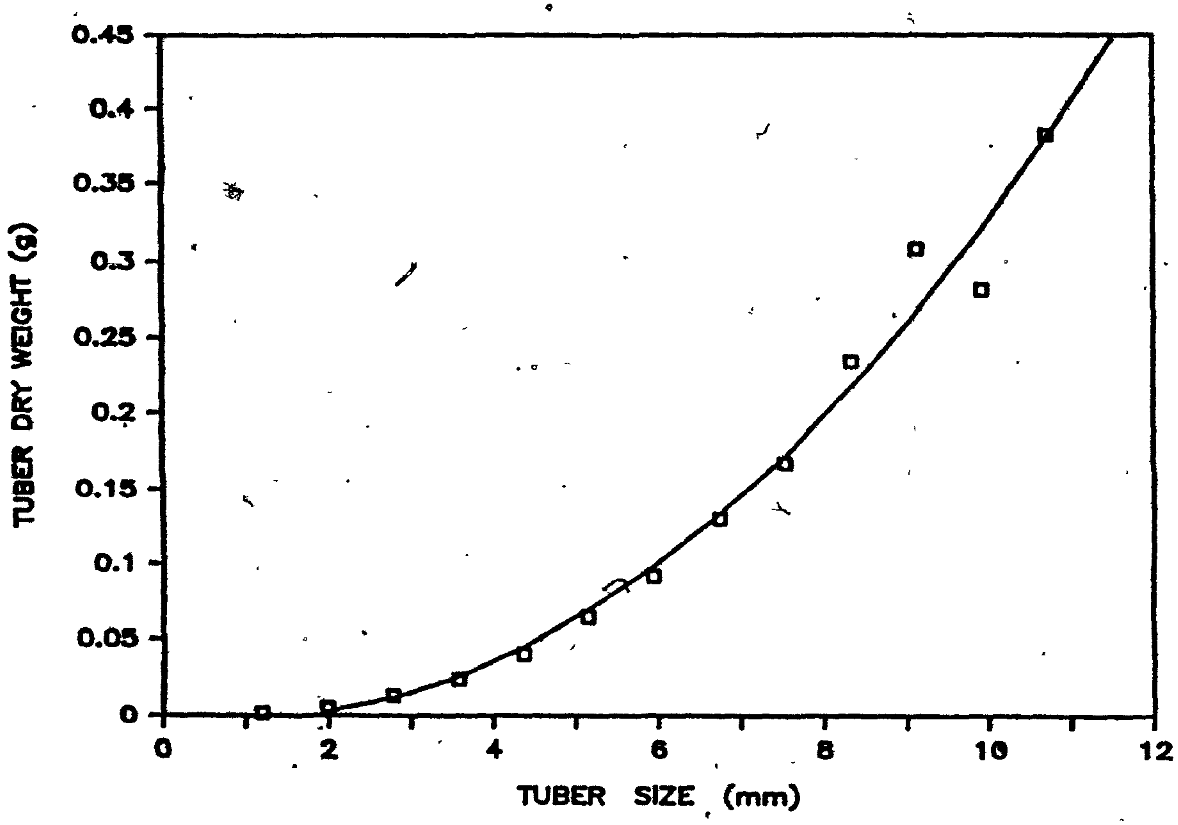


Figure 4.1. Yellow nutsedge tuber dry weight in relation to tuber size. Where the regression is $Y = 0.003 - 0.008X + 0.004X^2$ ($R^2 = 0.98$, $Pr = 0.005$) and where Y = the tuber dry weight in g, X = tuber size in mm, R^2=coefficient of determination and Pr = significance level.

significant at 0.001 %. Identical results were obtained for the fresh tubers. Therefore, since there was a close relation between the tuber size and weight, these two terms were used interchangeably throughout the rest of this study.

Tuber sorting and weighing by size was found to be extremely labor intensive, therefore it was decided that tubers would be sorted in only 2 sizes, small and large. This allowed the compilation of ratios of small tubers to overall tuber number or weight and thereby permitted the observation of tuber population shifts towards smaller or larger tubers.

As stated above, the mean and median size of dry tubers was 4.86 and 4.82 mm, respectively, and they were both in the same size class (Table 4.1). If this class was selected to sort tubers into small or large categories, shifts in the ratio could be detected, although biologically negligible shifts in tuber size would have occurred around the mean. Therefore, the contiguous size class would be more appropriate, since it would be less sensitive to small shifts in size but would indicate important shifts towards smaller or larger tubers. Arbitrarily, the smaller size class (4.37 mm) was chosen to separate the tubers in sizes, where tubers greater than or equal to 3.97 mm were considered as large tubers and those smaller than 3.97 mm as small tubers. Keeley and Thullen (1970) used a similar size (4 mm) for tuber studies. The advantage of choosing the smaller size class was that the ratios calculated gave an immediate percentage measure of the proportion of the small tubers in the sample.

In the present sample, the number of dry tubers smaller than 3.97 mm was 880 and the ratio of small tubers to total tuber number was 0.2842. The total dry weight of the small tubers was 16.076 g and the total tuber weight was 202.859 g. The ratio of small tuber dry weight to total tuber dry weight was 0.079247.

Section 5

YELLOW NUTSEDGE TUBER LONGEVITY

5.0 Introduction :

Tubers are considered as the only means by which yellow nutsedge persists in cultivated fields (Stoller, 1981). Under temperate conditions, the tubers overwinter and reestablish yellow nutsedge the following spring. Most of the tubers sprout the first spring but some remain dormant. Tubers are reported to lose viability rapidly with a 62 % to 86 % reduction the first year (Bell et al., 1962; Doty, 1973; Stoller and Wax, 1973). However, in some instances, viabilities of 1 to 8 % have been reported after 4 years or more (Thullen and Keeley, 1981).

Tuber depth in the soil, tuber size, and environmental conditions affect the length of time tubers remain viable. Tuber longevity increases with depth (Bell et al., 1962; Stoller, 1981), and with tuber size (Thullen and Keeley, 1975) while an increase in soil moisture conditions results in a decrease in longevity (Thullen and Keeley, 1981).

Tuber longevity has an important function in the population dynamics of yellow nutsedge since it determines the level of the residual tuber population, and therefore determines the resilience of yellow nutsedge infestations. Consequently, tuber longevity must be taken into account, along with the tuber production potential, in the development of an integrated yellow nutsedge management program.

Available information on tuber longevity is scattered through numerous reports and is difficult to integrate into a descriptive and predictive model. Furthermore, the growing conditions and yellow nutsedge biotype(s) in each of the experiments were different. Therefore, the present experiments were undertaken to estimate tuber cohort (tubers of the same age) longevity and to estimate the tuber pool (tuber bank) longevity in an already infested area. The objectives were : 1) to assess the importance of tuber depth and size on longevity, and 2) to obtain a descriptive and predictive regression of yellow nutsedge tuber longevity as a function of time.

5.1 Materials and methods :

Two types of experiments were conducted to achieve these objectives. The first consisted of burying tubers of known age and following their survival through time (tuber cohort longevity). The second group of experiments consisted of following the survival of established yellow nutsedge tuber populations in time while preventing the formation of new tubers (tuber bank longevity).

Tuber cohort longevity :

In the fall of 1981, after all yellow nutsedge shoots had died (November), soil samples were taken from the top 15 cm of a field infested with a pure stand of yellow nutsedge. The samples were washed and tubers were sorted and counted. Tubers that were pale brown, fully formed, and appeared healthy were placed in polypropylene mesh envelopes, to which sand was added, and buried in plots in a field previously free of yellow nutsedge. The experimental field had a soil texture and structure similar to that of the field of tuber origin.

The experiment was planned for five years and during the growing seasons, all vegetation was destroyed as it appeared. Eight tuber sizes were used, 1.6, 2.4, 3.2, 4.0, 4.8, 5.6, 6.3, and 7.1 mm, and were buried at three different depths, 6, 13, and 19 cm. The number of tubers in each envelope of a specific size are presented in Table 5.1. The difference in tuber number was due to tuber availability, and the uneven size classes were due to conversion from the imperial to the metric system of measure. Because of the limited number of tubers, tubers of size 1.6, 3.2, 4.8, and 6.3 mm were only sampled in the spring while the other sizes were only sampled in the fall. Ten 2 by 2 m plots were used and the experiment was not replicated. A peg was placed at the center of each plot and the envelopes were placed at 15 cm intervals along diagonals from the peg to each plot corner. Envelopes of the same tuber size were buried along the same diagonal with the ones that

Table 5.1 Number of tubers placed in individual envelopes for the tuber cohort longevity experiment.

Tuber size (mm)	Tuber number	Time of sampling [a]
2.0	14	spring
2.8	55	fall
3.6	95	spring
4.4	100	fall
5.2	100	spring
6.0	100	fall
6.7	65	spring
7.5	30	fall

[a] Refers to the time at which the specific tuber size was sampled during the experiment.

were buried at 6 cm closest to the peg and at 19 cm farthest from the peg. There were five diagonals of each tuber sizes and, every year, one was taken out at random and tuber viability was assessed.

At the time of retrieval, tubers and sand from the envelopes were placed in waxed cardboard boxes (12 cm by 12 cm by 4 cm high) and placed in a seed germinator cabinet. In the cabinet, the temperature during the eight hour day was set at 28 C and the night temperature was 20 C. The sand was kept moist and sprouting tubers were counted and removed as they were observed. After 4 weeks, ungerminated tubers remaining in the boxes were taken out and examined, those tubers that were firm and pale inside were counted as viable.

Since there were no replications, a multiple regression analysis was performed on the percentage of viable tubers as a function of time, tuber size, and soil depth. There were 9, 8, and 3 levels of these factors, respectively. The regression analysis was done using single degree of freedom components up to the cubic level for main effects and interactions. The balance of the levels were used for experimental error. Components significant at the 5 % level were retained to calculate the multiple regression polynomial equation.

Tuber bank longevity :

Two experiments were initiated to determine the longevity of yellow nutsedge tubers in natural field infestations. One experiment was established in an area where yellow nutsedge had been actively growing for over four years and the other experiment was established in an area that was previously infested by yellow nutsedge, but had been under alfalfa for the last three years. They were designated as young and old tuber populations, respectively. It was assumed that the soil tuber bank consisted of a pool of tubers of all ages in the first experiment while it consisted chiefly of older tubers in the second one. The purpose was to determine how long the tuber population would remain viable in the soil when the production of any new tubers was prevented.

The methodology was the same for both experiments. The experiments were established in the spring of 1982 and consisted of keeping the ground of the experimental area bare, by hoeing, in order to prevent any tuber production. Each experiment consisted of 3 plots 6 m by 5 m subdivided into subplots of 1 m by 1 m. Every 6 months, spring and fall, for three years, two subplots were randomly chosen and sampled per plot. The sampling was done using a 25 by 25 cm quadrat and consisted of removing the soil in 5 cm layers, down to 30 cm. The samples were processed according to the procedure described in Section 2.

5.2 Results and discussion :

The results for each series of experiments are first discussed separately after which general conclusions are drawn from this section.

Tuber cohort longevity :

The effects of time, soil depth and tuber size on tuber survival were tested for significance through multiple regression analysis and a polynomial was fitted to the significant terms. Placement depth of the envelopes in the soil was not found to have any statistically significant effect on yellow nutsedge tuber survival while tuber size, time, and their interaction were found to significantly affect tuber survival. Increase in tuber depth is considered to improve tuber survival (Stoller, 1981), but the soil gradient in the experiment was probably too small to significantly affect tuber survival. Also, the handling of the experimental material before burial could have removed any effect that depth of placement might have had on tuber survival.

The multiple regression polynomial of the percentage of the original tubers that remained viable through time is plotted in Figure 5.1. The number of viable tubers decreased over time, with smaller tubers decreasing more rapidly than the larger ones. Approximately 1.4 % of the original tubers were still viable after 3.5 years, but none were viable after 4 years. These results are in agreement with data reported by Stoller (1981). There were no compilation or analyses done on tuber number ratio or tuber weight since the material was originally sorted fresh and would not be comparable to the data obtained throughout the rest of this project.

The description and prediction of tuber survival is required in the development of a yellow nutsedge tuber

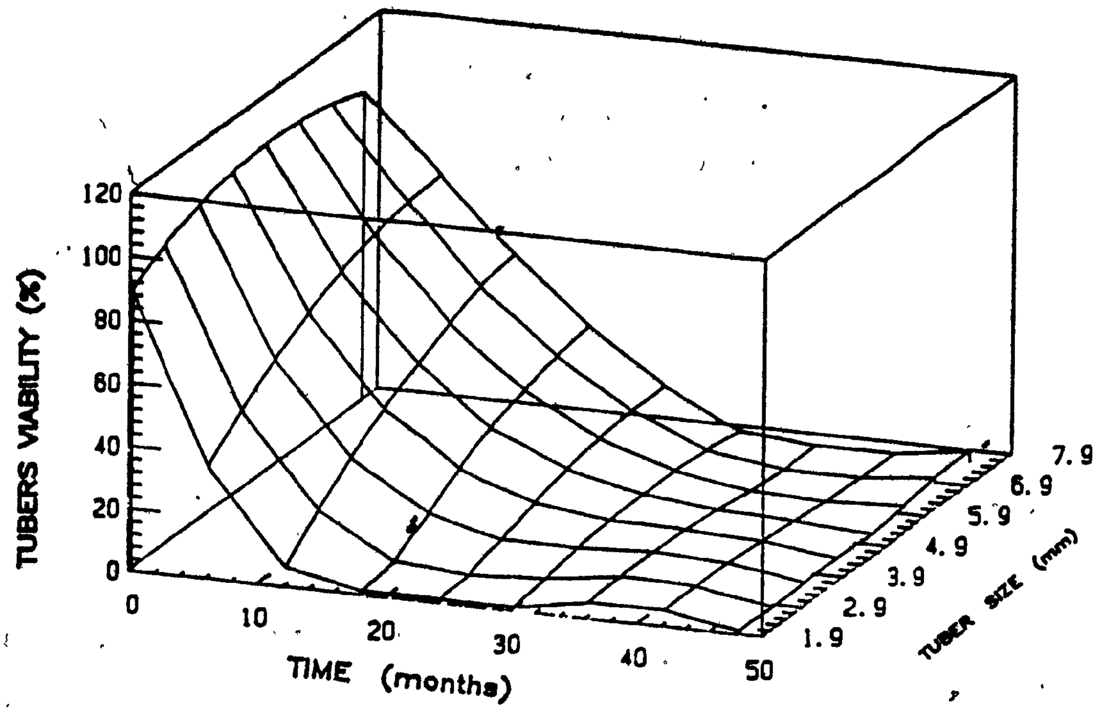


Figure 5.1. Multiple regression polynomial of the effect of time and tuber size on yellow nutsedge tuber cohort viability. The percentage values are expressed as a function of the tuber number originally used.

population dynamics model. Therefore, a regression was fitted to the changes in tuber number (averaged over the different tuber sizes) through time (Figure 5.2 and Table 5.2). The regression curve had a good fit ($R^2 = 0.99$) and described the tuber survival very well with only a small percentage of tubers still viable after three years and none after four years.

Tuber bank longevity:

The percentage of viable tubers was significantly affected by both the tuber depth and by the length of time the tubers were present in the soil. Also for both the young and the old tuber populations, the interaction of depth and time had a significant effect. Regressions for both tuber populations are plotted in Figure 5.3. As for the tuber cohort, the percentage of viable tubers decreased over time. There was one exception after 6 months. In the young tuber population at the 25 to 30 cm soil depth, the number of tubers increased above the original level. This increase is not confirmed by the data means (Appendix 1) and therefore could be attributed to the behavior of the regression. Another exception to the general decrease in viability over time was found in the old tuber population where the percentage of viable tubers increased at the last date of sampling. Referring to the data means (Appendix 1), this was confirmed but difficult to explain except that perhaps some new tubers were produced. Another possibility might be that the variability of the population present caused the apparent increase.

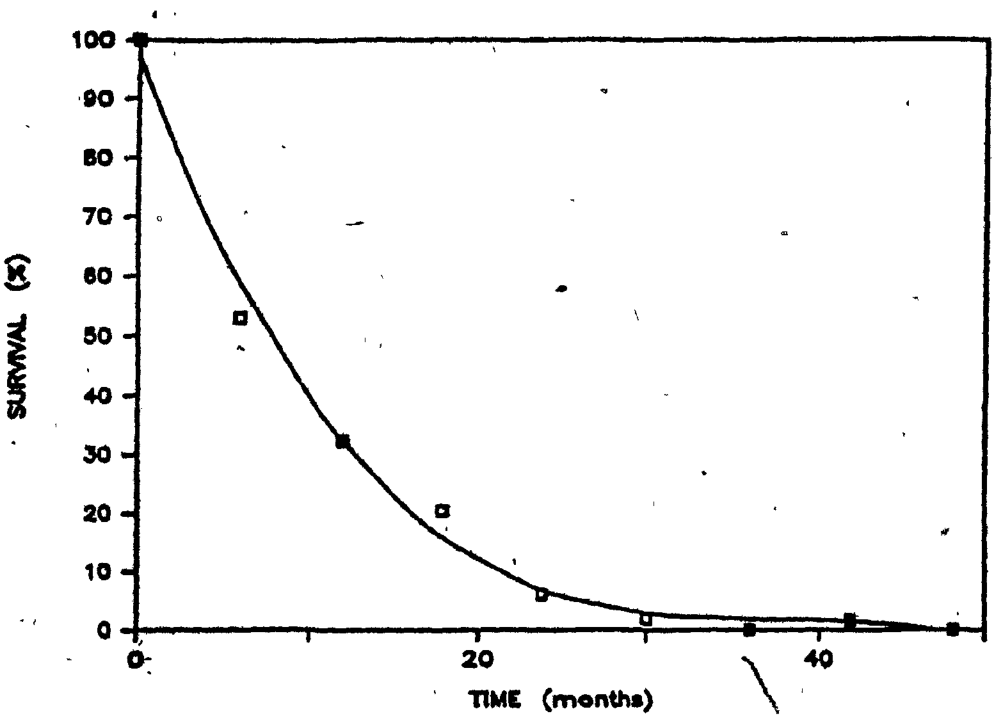
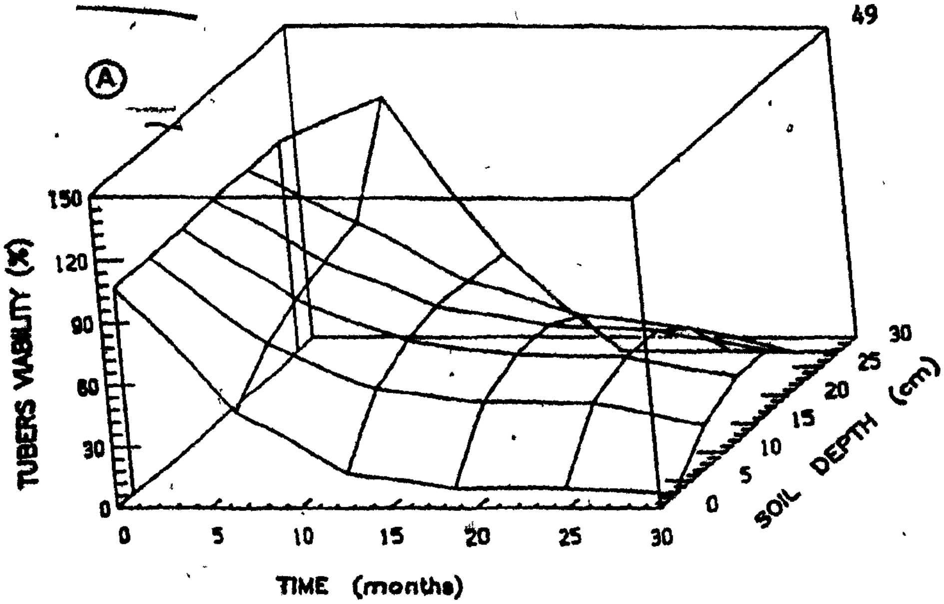


Figure 5.2. Regression of yellow nutsedge tuber cohort viability in time. The percentage values are expressed as a function of the number of tubers originally used.

Table 5.2. Regression coefficients of various factors on yellow nutsedge tuber number.

Experiment	Regression equations	R^2	Pr.
Tuber cohort longevity:			
Multiple regression	$Y = 65 + 14.6S - 1.4S^2 - 13T + 0.6T^2 - 0.006T^3 + 1.04ST + 0.03S^2T - 0.07ST^2 + 0.001ST^3$	0.97	0.001
Simple regression	$Y = 97 - 7.5T + 0.2T^2 - 0.002T^3$	0.99	0.001
Tuber bank longevity:			
Young tuber population:	$Y = 1361 - 246T + 9.2T^2 - 0.004T^4 + 180D - 14.3D^2 + 0.22D^3 + 10.2TD - 0.56T^2D + 0.0097T^3D$	0.86	0.001
Old tuber population:	$Y = 204 - 39T + 3T^2 - 0.007T^4 + 0.00016T^5 + 0.7D^2 - 0.001D^4 + 0.004D^2T$	0.47	0.007
Combined regression as a function of depth:	$Y = 92 - 5.7T + 0.11T^2$	0.89	0.05

Where Y = Percentage of the initial number of tubers
S = Tuber size in cm
T = Time in months
D = Soil depth in cm
R^2 = coefficient of determination
Pr = level of significance of the regression



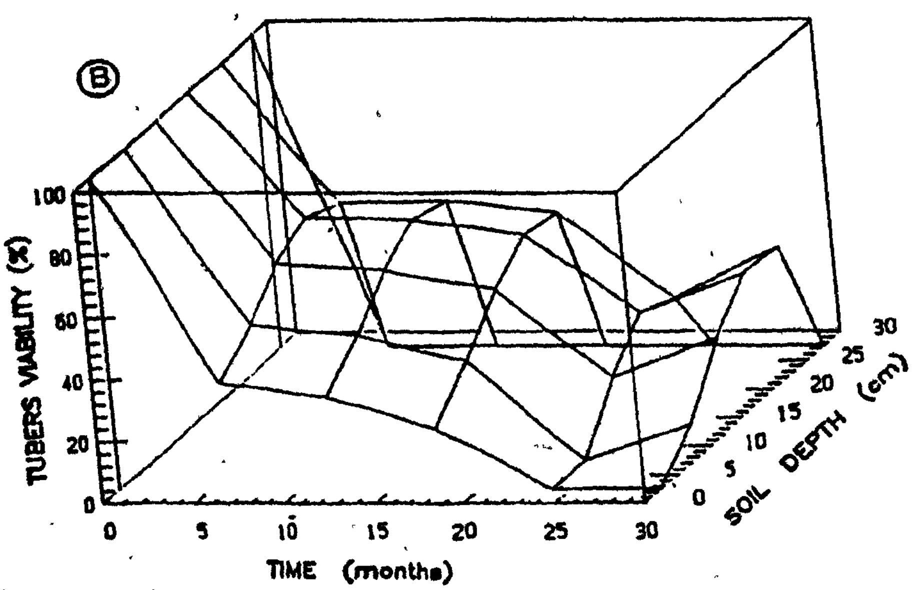


Figure 5.3. Multiple regression polynomial of the effect of time and soil depth on yellow nutsedge tuber bank viability. The values are expressed as a function of the regression values at the first sampling time.

A. Young tuber bank population.
B. Old tuber bank population.

Tubers that were either in the 0 to 5 cm or 25 to 30 cm soil layer had a more rapid decrease in viability than tubers between these two layers. These trends were more marked for the old tuber population (Figure 5.3). Tubers closer to the soil surface are more subject to sprouting and are more exposed to environmental and biological factors, therefore they would be expected to have a more rapid decline in viability. Data reported by Bell et al. (1962) and Stoller and Wax (1973) confirm this hypothesis. However, there are no reports mentioning such a decrease for tubers at a greater depth. The decrease was most marked 18 months after the beginning of these two experiments. A possible explanation might be that the natural sprouting of tubers was more important at the greater depth. Since this is a part of the soil profile that is the least disturbed by normal field operations, the tuber population of that soil layer might have a greater inherent sprouting than those closer to the surface and therefore a greater mortality since all above-ground growth was destroyed, which eventually translated into tuber death through exhaustion of food reserves.

Since tuber population viability in time was the information to be used in the development of the yellow nutsedge tuber population dynamics model, the soil depth effect was averaged over for each time of sampling. The mean number of tubers viable in both yellow nutsedge tuber populations are plotted in Figure 5.4A. Tuber number differed between the populations sampled and therefore tuber viability in time was

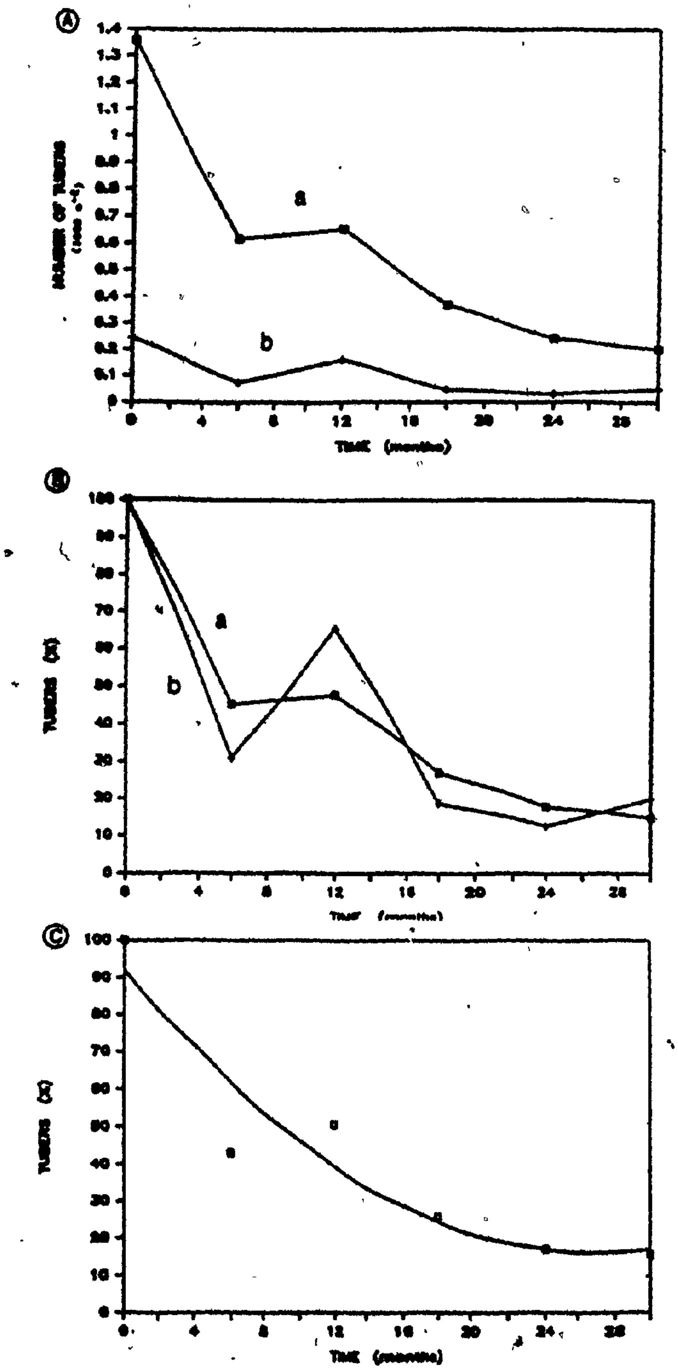


Figure 5.4. Yellow nutsedge tuber bank population viability in time. Where a = young tuber bank and b = old tuber bank.

A. Mean tuber number m^{-2} measured at six month intervals in both tuber bank populations.
B. Values of A expressed as percentage of the first sampling time.
C. Regression of the changes in time of the percentage of viable tubers fitted to the combined data of the tuber bank populations.

plotted as percentage in order to have a common basis of comparison (Figure 5.4B). The main difference between the two tuber populations seemed to be in the number of tubers present in the soil since, on a percentage basis, both populations decreased in a similar way. The difference between experiments might have been only in the number of tubers, rather than in the tubers' ages, which could not be verified. Therefore, a regression was fitted to their combined data (Table 5.2 and Figure 5.4C). The percentage of viable tubers decreased by 60 % after the first year and by over 80 % after the second year, which is similar to values reported in the literature (Stoller, 1981).

The proportion of small tubers to the total number of tubers (tuber number ratio) was significantly affected only by the depth of the tubers in the soil. The means and their standard errors as a function of the depth in the soil are plotted in Figure 5.5 along with their respective LSD. Tuber number ratio behaved similarly for both the young and the old tuber populations.

The proportion of small tubers to the total number of tubers was between 20 to 35 % near the surface of the soil while it increased to 50 % at the 10 to 15 cm depth layer. The proportion of small tubers decreased steadily at greater depths to form 1 to 20 % of the total number of tubers found at the 25 to 30 cm layer. The only statistically significant differences were between the tuber number ratio in the 10 to 15 cm layer and the 25 to 30 cm layer (Figure 5.5). These results

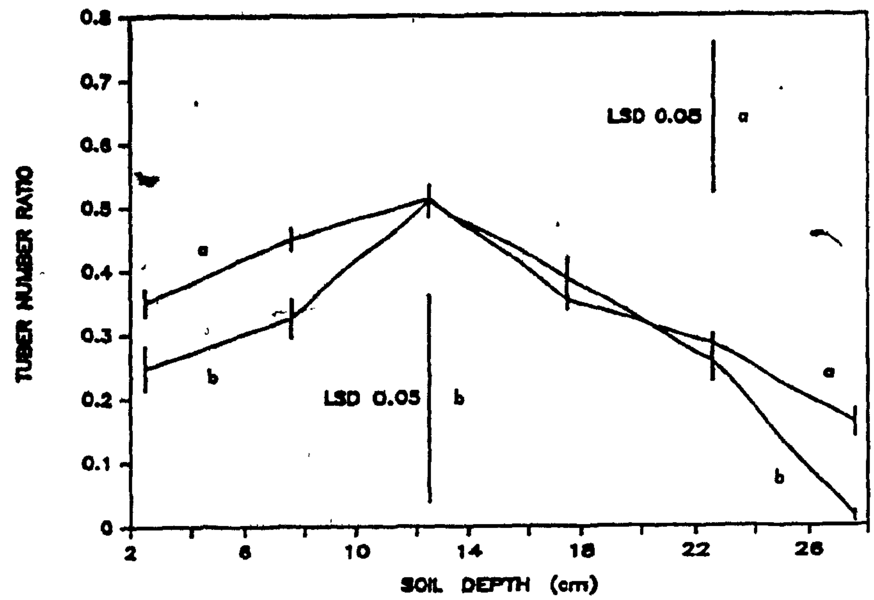


Figure 5.5. Means and standard deviations of changes in tuber number ratio of both tuber bank populations as a function of tuber depth in soil. Where a = young tuber bank and b = old tuber bank.

indirectly indicate that larger tubers are produced at greater depth or that small tubers died more rapidly at the greater depth.

Tuber longevity was not affected by tuber size in these experiments since tuber number ratio was not significantly affected by the length of time the tubers were present in the soil. This is in contradiction with observations made in the tuber cohort experiment and that which had been reported by Thullen and Keeley (1975). However, Stoller and Wax (1973) did not observe any differences in longevity between small and large tubers. Tubers of different weights were used by these researchers which makes comparisons difficult. Therefore, both trends reported might be true, depending on the size of the tubers used. The lower limit of the size class used to separate small from large tubers in this research project may have included tubers which were too large in the smaller size class selected, thereby masking some responses that could be attributed to differences in tuber size.

Tuber dry weight and tuber dry weight ratio followed exactly the same trends and had the same statistically significant factors as the tuber number and the tuber number ratio, respectively. Therefore, they are not discussed, but their means are presented in Appendix 1 along with LSD values. The means of the tuber numbers are also presented in Appendix 1.

Two regression curves are presented to describe yellow nutsedge tuber survival in time, one for tuber cohort longevity (Figure 5.2) and one for tuber bank longevity (Figure 5.4C). However, only one regression should be used in the model development, therefore either one of the two regressions must be dropped or they must be combined. Both regressions, with their 95 % confidence intervals, are plotted in Figure 5.6. They are relatively similar for the first two years with only a 10 % difference in survival in favor of the tuber bank experiment. This difference might be attributed to inherent variability in the biological material, to the greater depth of the tuber bank population, or to the production of tubers in the tuber bank experiments. However, since the confidence intervals overlap, it might be assumed that they did not differ significantly. The regression from the tuber cohort experiment was retained for use in the model development of yellow nutsedge tuber population dynamics since it was conducted for a longer period of time and had a greater coefficient of determination. Furthermore, its regression had a greater level of significance and seemed to correspond more closely to observations made by other researchers on other yellow nutsedge populations (Stoller, 1981).

The two series of experiments were subject to a decrease in tuber viability in time but had opposite responses to the other factors tested. There were no significant differences in viability due to tuber size in the tuber bank experiment while there was a decrease in viability with a decrease in tuber sizes in the tuber cohort experiment. Tuber depth in soil did

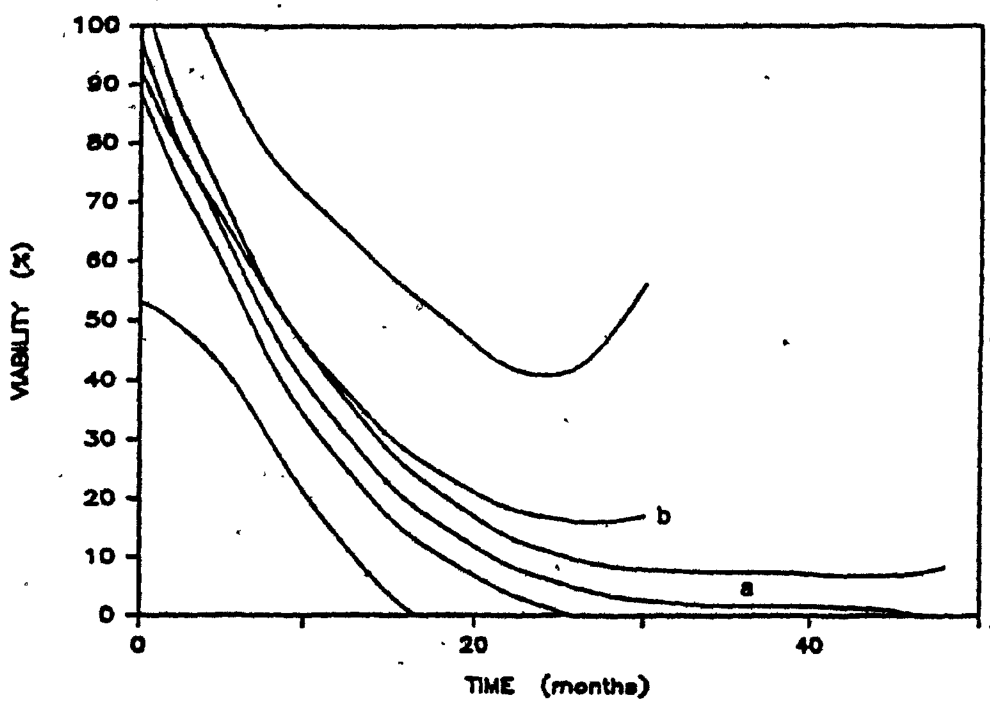


Figure 5.6. Proportion of the tuber cohort and combined tuber bank population that survived over time. Where a = tuber cohort and b = combined tuber bank. The other curves are the 95 % confidence intervals of the regressions.

not significantly affect tuber viability in the latter but did in the former experiment. These opposite results demonstrate the variability of yellow nutsedge and the need for further investigations of tuber longevity to clarify important factors in yellow nutsedge tuber survival and to quantify them. Ideally, it would be more advantageous to conduct such experiments in a site where yellow nutsedge was planted and allowed to multiply for one year only (tuber cohort) and sampled regularly thereafter, while the production of new tubers would be prevented. This method would result in minimal tuber disturbance in contrast to the use of envelopes which involved considerate manipulation of the tubers when they were buried.

Section 6

YELLOW NUTSEDGE GROWTH IN TIME

6.0 Introduction :

Yellow nutsedge infestations are re-established every spring by tuber sprouting. Since tubers are reported as being the sole means of perpetuating yellow nutsedge infestations in agricultural fields, the initiation of tuber production has been included in phenological observations made on this weed. The variation in phenology of yellow nutsedge (Table 6.1) could be attributed to several factors, two of the most important being biotypes and environmental conditions (Fernald, 1970; Hauser, 1968; Matthiesen, 1976; Stoller, 1981; Yip, 1978).

Despite numerous articles on yellow nutsedge tuber production, there are few reports that describe tuber population variation in time, and the ones that do are based solely on experiments done in containers (Kogan and Gonzalez, 1979; Phillips, 1980).

Information on qualitative and quantitative tuber population changes in the course of a growing season is required before consideration of a long term yellow nutsedge

Table 6.1. Yellow nutsedge phenology.

Stage	Date	Reference
Tuber sprouting	March April in Georgia	Taylorson, 1967
	Late April in Illinois	Jordan-Molero and Stoller, 1978
	Early May in Illinois	Stoller, 1981
	May 7 to 10 in Illinois	Stoller and Wax, 1973
	Mid-May to early June in Ontario	Mulligan and Junkins, 1976
	May in Ohio	McCue, 1982
Tuber initiation	June 17 in Ontario	Mulligan and Junkins, 1976
	Late July in Illinois	Jordan-Molero and Stoller, 1978
	August in Illinois	Stoller, 1981
Flowering	Early July in Ontario	Mulligan and Junkins, 1976

management program. Therefore, the following experiments were initiated to provide detailed information on tuber population variations in time in a natural field infestation. Furthermore, regression equations of soil tuber population changes in the summer must be included in the intended model of yellow nutsedge tuber population dynamics to provide information on tuber population behavior during the course of a growing season.

6.1 Materials and methods :

Field experiments were conducted for three years, 1981 to 1983. General details are presented in Section 2. The experimental designs were randomized complete blocks with two treatments; yellow nutsedge growing alone or yellow nutsedge growing with corn. The plots were 6 m long by 12.75 m wide and all received the same treatments of starter fertilizer at planting, and nitrogen side dressing later in the season. In plots of yellow nutsedge growing alone, stakes indicated where the corn row would theoretically be, in order to ensure proper placement of fertilizer and sampling quadrats. Two paths 0.75 m wide by 12.75 m long were delineated in each plot by ropes laid across the plots so that only a given fraction of the plot area would be used to circulate within the plots when hand pulling other weeds or sampling was required. Sampling areas were delineated both by where the corn rows were, or should have been (0.75 m), and by the ropes that were laid down to give lengths of 1.5 m, resulting in 39 sampling areas per plot.

With the exceptions of the first and the last samplings of the season, all samplings were conducted in the plots where yellow nutsedge was growing alone. At approximately every two weeks, three sampling areas were selected at random within each of the three replications. Within these sampling areas, three samples were taken, giving a total of 27 samples per sampling date. The sampled areas were in the equivalent of between row spaces (where no fertilizer had been applied directly after planting) and, once sampled, an area was not sampled again. The first sampling of the season was conducted in both treatments, while the last sampling of the season was also done in the two treatments, and both on rows and between rows (or their equivalent). Only the data collected between rows in yellow nutsedge growing alone is presented in this section. The remainder of the data are discussed in the section on the effect of corn on yellow nutsedge growth (Section 11). Regressions were fitted to the tuber population variation in time and plotted. Other variables were plotted with their means and the least significant difference at the 5 % level of probability (LSD 0.05) when applicable.

6.2. Results and discussion :

Yellow nutsedge started emerging during the first two weeks of May in the experimental area. Tubers were initiated during the second or third week of June, while flowering started on the last week of June or first week of July. These observations correspond to those reported under similar growing conditions (Table 6.1).

A cubic regression was fitted to the tuber population as it changed during the 1981 season, while quadratic curves were fitted to the tuber population for the other two years of the project (Figure 6.1). The spring tuber population increased every year of the project (Figure 6.1). This could be attributed to the fact that no control measures were used against yellow nutsedge in the experimental area, thereby allowing the yellow nutsedge tuber population to increase.

In 1981, the number of tubers started to increase earlier and more rapidly than the other years (Figure 6.1). It was the only year where a maximum was apparent while the number of tubers increased steadily for the other two years. These differences could be due to the fact that the rate of increase of a smaller spring tuber population was several times that of a more dense population (Section 7). The carrying capacity for the experimental area was determined to be 15000 tubers m^{-2} although the 1983 data had passed that limit, ending the season at 20000 tubers m^{-2}. More measurements taken over a wider range of spring tuber population levels for several years and covering a wider range of environmental conditions would be required to more accurately determine which is the true carrying capacity of the population in the experimental area. However, since 20000 tubers m^{-2} were obtained at a spring value of 4000 to 5000 tubers m^{-2} in Section 7, the measured value was probably a delayed population response and the true carrying

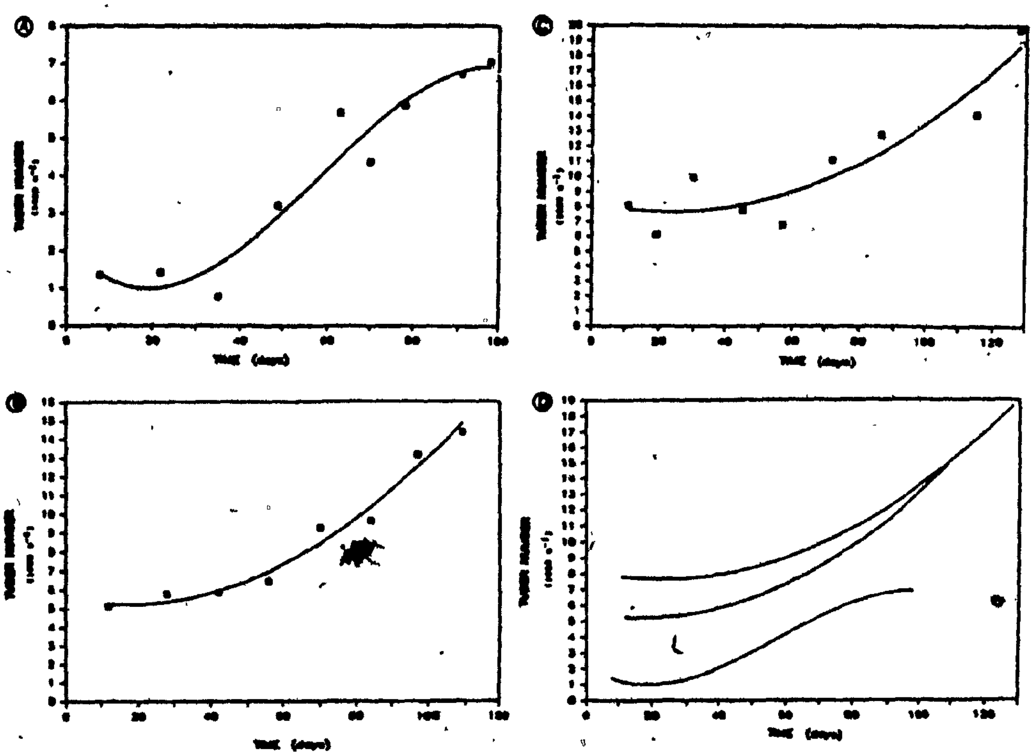


Figure 6.1. Variation in tuber population of yellow nutsedge during the season. Where Y = number of tubers, X = number of days after emergence, R^2 = coefficient of determination, Pr = significance level.

A. 1981 growing season, $Y = 2227 - 139X + 4.34X^2 - 0.025X^3$ ($R^2 = 0.97$, $Pr > 0.002$).
B. 1982 growing season, $Y = 5558 - 39X + 1.15X^2$ ($R^2 = 0.98$, $Pr > 0.0001$).
C. 1983 growing season, $Y = 8228 - 48X + 1.01X^2$ ($R^2 = 0.87$, $Pr > 0.002$).
D. Combined yearly curves of yellow nutsedge tuber population changes in time.

capacity was probably in the 15000 tuber m^{-2} range in the experimental area.

The data of the three years were not pooled since the spring tuber populations levels differed, a factor which has been found to affect the rate of increase of the tuber population (Section 7). Consequently, the data collected for the three years were considered as describing the behavior of three different populations and pooling the three years would only have increased data variability.

The proportion of small tubers to the total number of tubers (tuber number ratio) varied widely in 1981 but remained relatively stable in 1982 and 1983. As expected, there was a sharp increase in the proportion of small tubers when yellow nutsedge started to produce tubers (between 40 and 60 days), followed by a decline to a ratio near that of the initial spring one later in the season (Figure 6.2). The increase can probably be attributed to the initiation of a large number of tubers at the same time followed by an increase in the size of these tubers later in the season. However, in 1982 and 1983, the ratio of tuber number remained stable and was not statistically affected by sampling date in 1983, indicating perhaps that proportionally fewer tubers were produced and that they increased in size continuously as they were produced (Figure 6.2). The yearly differences observed could be related to the greater rate of tuber number increase at low population levels, although, more work is required to clarify this situation. The ratio of tuber number (0.28) reported in

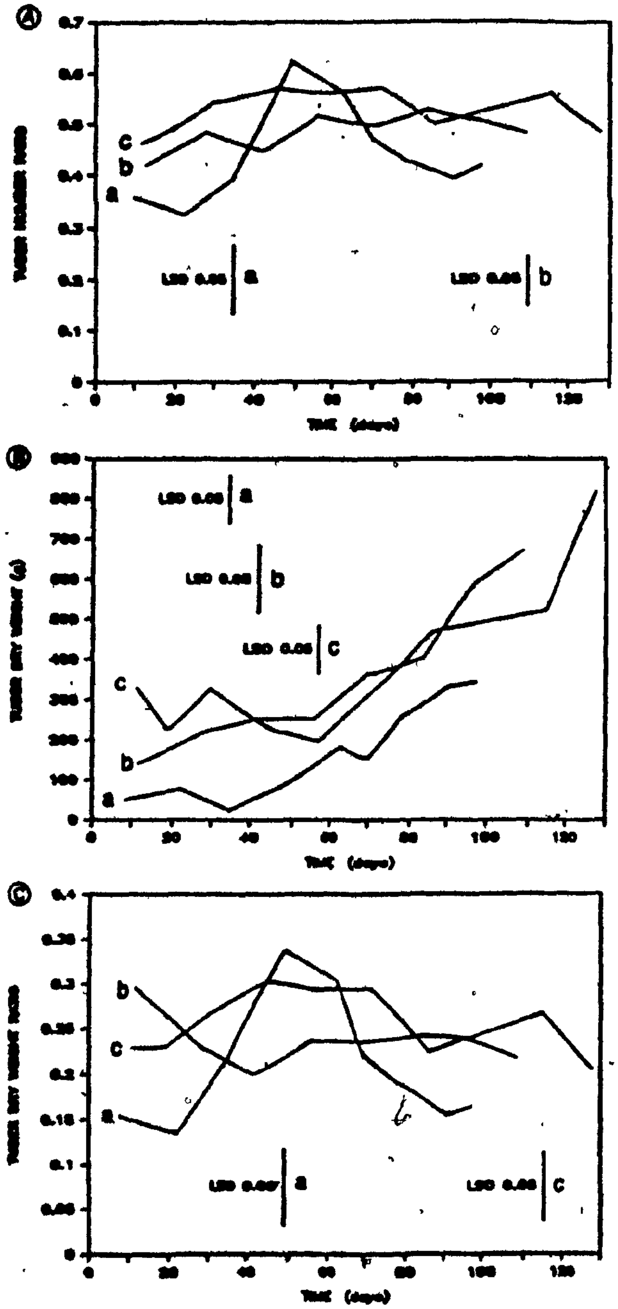


Figure 6.2. Changes in tuber number ratio, tuber dry weight, and tuber dry weight ratio of yellow nutsedge during the growing season. Where a = 1981 samples, b = 1982 samples, c = 1983 samples.

A. Proportion of small tubers to the total number of tubers (tuber number ratio).
B. Tuber dry weight of the total number of tubers.
C. Proportion of small tuber dry weight to the total tuber dry weight (tuber dry weight ratio).

Section 4 ("Tuber size distribution") as the standard for the experimental area is clearly inferior to the ratios plotted in Figure 6.2, which seem to be in the range of 0.3 to 0.6. This could be explained partly by the fact that data reported in Section 4 were from samples taken in the late fall of 1983, when all yellow nutsedge aboveground tissues had senesced. However, in the experiments reported here, final sampling occurred before complete senescence and as such, it is probable that tuber size continued to increase later in the season, consequently reducing the proportion of small tubers. If this was the case, the tuber number ratio would have been closer to that reported in Section 4.

The total tuber dry weight and the contribution of small tuber dry weight to total tuber dry weight (tuber dry weight ratio) are presented in Figure 6.2. The product-moment correlation coefficients ranged from 0.93 to 0.99 between tuber number and dry weight, and between the two ratios, showing the close relationship among these variables. Therefore, data on tuber dry weight is not discussed further since they follow trends similar to tuber number and tuber number ratio, respectively.

The functions describing yellow nutsedge tuber number changes during the growing season are used in the model development of yellow nutsedge tuber population dynamics in a subsequent section.

Section 7

DENSITY EFFECT ON YELLOW NUTSEDGE

7.0 Introduction :

Yellow nutsedge is a perennial weed which reproduces almost exclusively by tubers (Mulligan and Junkins, 1976; Stoller, 1981). Therefore, tuber production is the most important variable in population dynamics studies since the number of tubers determine whether yellow nutsedge populations increase, decrease, or remain stable in time.

Although the biology of yellow nutsedge has been extensively studied, there are few reports on tuber production potential in the field. A single tuber planted in the field has been reported to produce from 32 to 2700 tubers in one growing season (Hauser, 1968; Lapham, 1985; Phillips, 1979, 1980, 1981; Tumbleson and Kommedahl, 1961). These values are indicative of reproductive potential, but are rarely, if ever, observed in a field situation where several factors contribute to maintaining yellow nutsedge population levels within certain limits. The limiting factors regulating field plant populations can be grouped in three broad categories : biotic, abiotic, and field management practices.

One of the biotic factors that affects populations is intraspecific interference. Yellow nutsedge intraspecific interference has been investigated in pots or tiles but not unrestrained in the field (McCue, 1982; Philips, 1979; Williams, 1981). The present experiment was undertaken to measure the reproductive potential of yellow nutsedge in the field as a function of its spring tuber population. The first objective was to obtain a mathematical function that would allow the prediction of fall tuber populations from spring tuber population estimates. The second objective was to quantify the carrying capacity of the experimental area as measured by the number of tubers produced in the fall.

7.1 Materials and methods :

There were no experimental plots established specifically to meet the objectives stated above. Instead, the data needed were extracted from the various experiments conducted during the three years of this project (1981 to 1983). The values used were obtained from plots where yellow nutsedge was growing freely in pure stands, and where spring and fall tuber sampling had been conducted. The respective spring and fall tuber values were paired and, subsequently, a regression analysis was performed to fit the data.

7.2 Results and discussion :

The number of tubers produced in the fall, as a function of the number of tubers observed in the spring, is plotted in Figure 7.1A. The number of tubers measured in the fall increased continuously when the number of tubers present in the soil in the spring was less than 5000 tubers m^{-2}. However, for spring populations above 5000 tubers, the number of tubers observed in the fall remained relatively constant at approximately 15000 tubers m^{-2}(Figure 7.1A).

The type of response observed here corresponds to general principles of population dynamics with populations increasing rapidly at low densities until the carrying capacity of the particular site is reached (Begon and Mortimer, 1981; Silvertown, 1982). This type of response is best described by Richards function which is a generalization of the logistic function (Causton and Venus, 1981). Such a function was fitted to the data (Figure 7.1A) but, although the fit was excellent (R^2 =0.90), this curve was not used to describe the data for two reasons. First, the present data overshot the calculated carrying capacity between 3000 and 5000 spring tubers and then decreased to the carrying capacity (Figure 7.1A). This type of behavior could be attributed to the effect of time delay in the population response to intraspecific interference and therefore would not be properly described by the Richards function (Elseth and Baumgardner, 1981). The second reason was that this type of function is nonlinear which is statistically intractable and therefore could not be used for the intended simulations (Causton and Venus, 1981; Draper and Smith, 1981). However, the carrying capacity was clearly defined as 15206

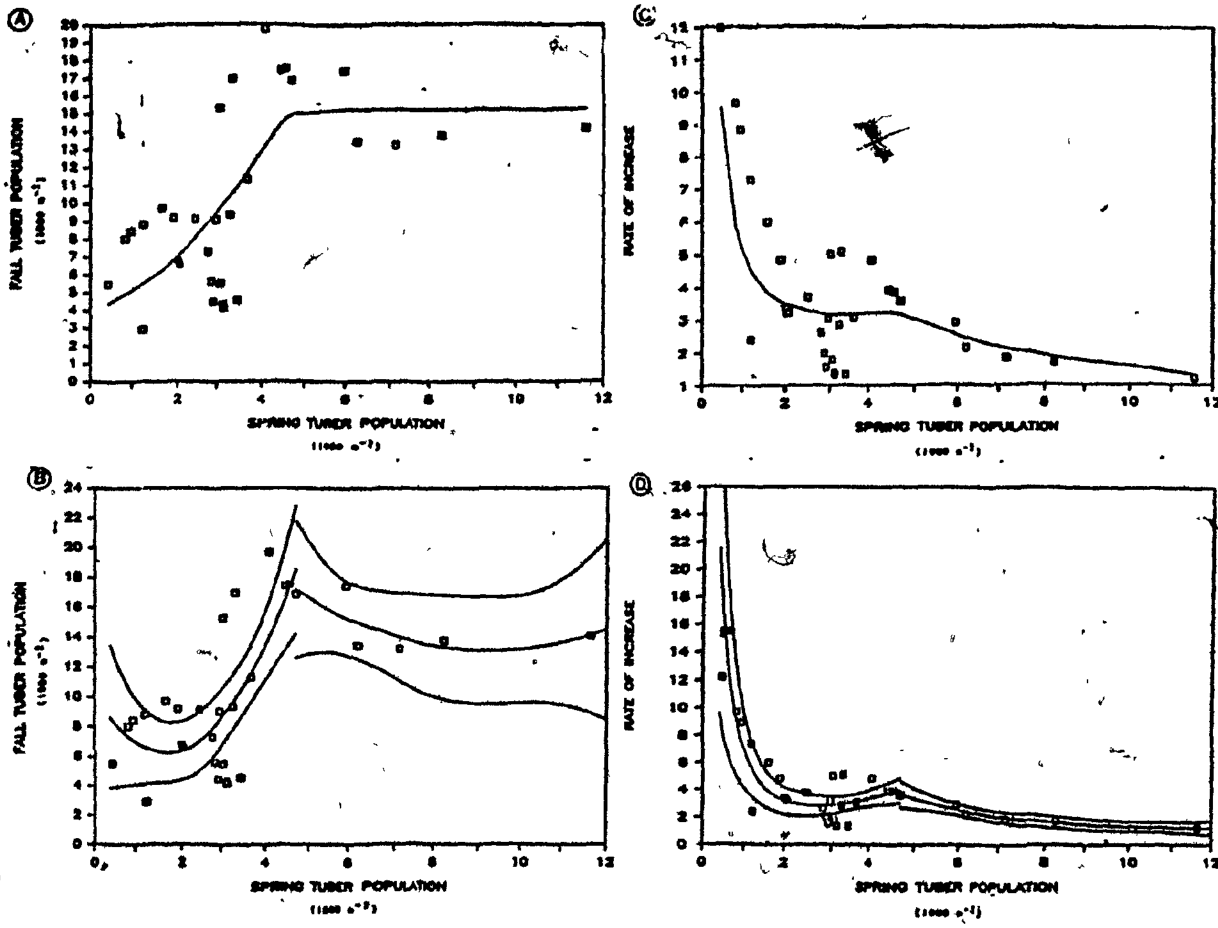


Figure 7.1 Yellow nutsedge fall tuber population as a function of the spring tuber population.

A. Richards function.
B. Segmented quadratic polynomial regressions plotted with their 95 % confidence interval. The equation for the first segment is $Y = 10297 - 4.72X + 0.0014X^2$ and the equation for the second segment is $Y = 29909 - 3.62X + 0.00019X^2$ where Y= number of tubers counted in the fall on a m^{-2} basis and X = number of tubers found in the spring soil samples.
C. Rate of increase of yellow nutsedge tuber population, from the Richards function.
D. Rate of increase of yellow nutsedge tuber population, from the polynomial regressions.

tubers m^{-2} to a depth of 1[illegible] cm for the experimental area while Lapham et al. (1985) reported a carrying capacity of 10400 tubers m^{-2} to a depth of 20 cm in Zimbabwe. The difference could probably be attributed to the difference in biotypes and growing conditions.

Polynomial regression analyses were conducted on the collected data but the selected curves were either unrealistic (with maxima or minima at various densities) or afforded a poor fit (very low coefficient of determination). Therefore, to obtain a more realistic and better fit, the data were analysed as two different segments as suggested by Hunt (1982). The data were separated at a spring tuber level of 4700 m^{-2} and polynomial regressions were fitted to both data sets. The curves were separated at the value of 4700 tubers m^{-2} since this value corresponded to the threshold beyond which the carrying capacity was reached (according to the Richards function illustrated in Figure 7.1A). Quadratic curves were retained for both segments, giving an overall fit of 50 % (Figure 7.1.B). The second segment had no significant regressions but nevertheless a curve was fitted to cover the spring tuber density range. In this case, the quadratic curve was selected since it was more significant than the linear curve and improved the fit by 30 %. Theoretically, a straight line was expected and would probably have occurred if there were more data points for this segment.

The data presented here can be used to illustrate the tuber population rate of increase by dividing the observed or calculated fall tuber population by the spring tuber population. The advantage of this data manipulation is that it gives an immediate measure of the rate of population increase. This has been done and is illustrated in Figure 7.1.C and Figure 7.1.D. The rate of increase was more than 12 fold at the lowest spring densities but decreased sharply to become relatively stable at spring densities above 5000 tubers m^{-2}.

From the population rate of increase, the control effort required to stabilize a known population can be calculated. The % of control is obtained by subtracting the inverse of the rate of increase from 1. For example :

2000 spring tubers and a rate of increase of 12.
1/12= 0.08,
1 - 0.08 = 0.92
0.08 * (12 * 2000) = 2000 (rounded figures)

therefore, if the population is prevented from producing 92 % of the projected number of tubers, there will not be any increase in tubers for the given area. The values decrease with the decrease in the rate of population increase. Therefore, the control effort required to stabilize the yellow nutsedge population decreases as the spring tuber population increases.

The mathematical functions identified in this section provide a tool to predict rate of population increase in pure stands of yellow nutsedge. These are only rough approximations since several other factors such as winter survival, tuber longevity, and growing conditions should be taken into account to more accurately predict population increase. Furthermore, in cropping situations, the level of yellow nutsedge populations must be considered since crop yields can be reduced by stable but high populations (Stoller, 1981).

Section 8

YELLOW NUTSEDGE TUBERS DISTRIBUTION IN THE SOIL

8.0 Introduction :

Yellow nutsedge infestations are maintained in field crops through their tubers and therefore, tuber population levels must eventually be reduced to control yellow nutsedge. Yellow nutsedge tubers are distributed through the soil profile to depths extending to 46 cm and therefore part of the tuber population is beyond the reach of most control methods (Bell et al., 1962; Tumbleson and Kommedahl, 1961).

The majority of shoots (56 to 95 %) arise from tubers in the top 10 to 15 cm of the soil, although in some cases tubers from the 30 cm depth produce 3 to 39 % of the observed shoots in the field (Bell et al., 1962; Stoller and Wax, 1973; Tumbleson and Kommedahl, 1961). A tuber was found to produce shoots even when placed 80 cm deep in a greenhouse experiment (Tumbleson and Kommedahl, 1961). Yellow nutsedge was reported to have 67 to 83 % of its tubers in the top 10 cm in the soil, 85 to 97 % in the top 15 cm, and 0 to 1 % beyond 30 cm in the soil (Bell et al., 1962; Friesen and Hamill, 1977; Tumbleson and Kommedahl, 1961).

Although several reports have been made on yellow nutsedge tuber number distribution in the soil, the changes in tuber sizes as a function of soil depth were never studied. Furthermore, biotypes and growing conditions have been reported to affect yellow nutsedge growth response (Matthiesen, 1976; Stoller, 1981) and therefore results from elsewhere could not automatically be extended to the yellow nutsedge population of the present experimental area. However, this information would be useful in determining the most effective cultivation or tillage depth, and herbicide depth placement for the experimental area.

The present experiment was undertaken to establish yellow nutsedge tuber number, size, and dry weight distribution in the soil profile.

8.1 Materials and methods :

This experiment was conducted in the plots of the experiments presented in Section 6 "Yellow nutsedge growth in time". Therefore, only details specific to the current trial are presented here.

The experiment consisted of using a 25 by 25 cm quadrat to sample yellow nutsedge tubers to a depth of 30 cm in increments of 5 cm. The sampling sections were ; 0-5, 5-10, 10-15, 15-20, 20-25, and 25-30 cm. The sampling was conducted in pure stands of yellow nutsedge. Areas sampled corresponded to those between corn rows in the experiments of Section 6. These areas had not received localized fertilizer applications. There were two replications and the experiment was carried for two years. Sampling took place August 31, 1982, and September 13, 1983. The samples were processed according to the procedure presented in Section 2.

Analyses of variance were conducted each year and when statistically warranted, data of both years were combined. Only standard error of the means and LSD are used in this section since they are not required for the modeling of yellow nutsedge tuber population dynamics.

8.2 Results and discussion :

All variables were significantly affected by soil depth in both years with the exception on the tuber number ratio in 1982. The number and dry weight of tubers were pooled over both years. However, the tuber number ratio and tuber dry weight ratio could not be pooled because they lacked homogeneous variances.

The number of tubers decreased significantly with increases in soil depth (Figure 8.1A). Of the total number of tubers, 65 % were found in the top 10 cm, 84 % in the top 15 cm, and 94 % in the top 20 cm of the soil profile. These values are similar to earlier reports (Bell et al., 1962; Friesen and Hamill, 1977; Tumbleson and Kommedahl, 1961).

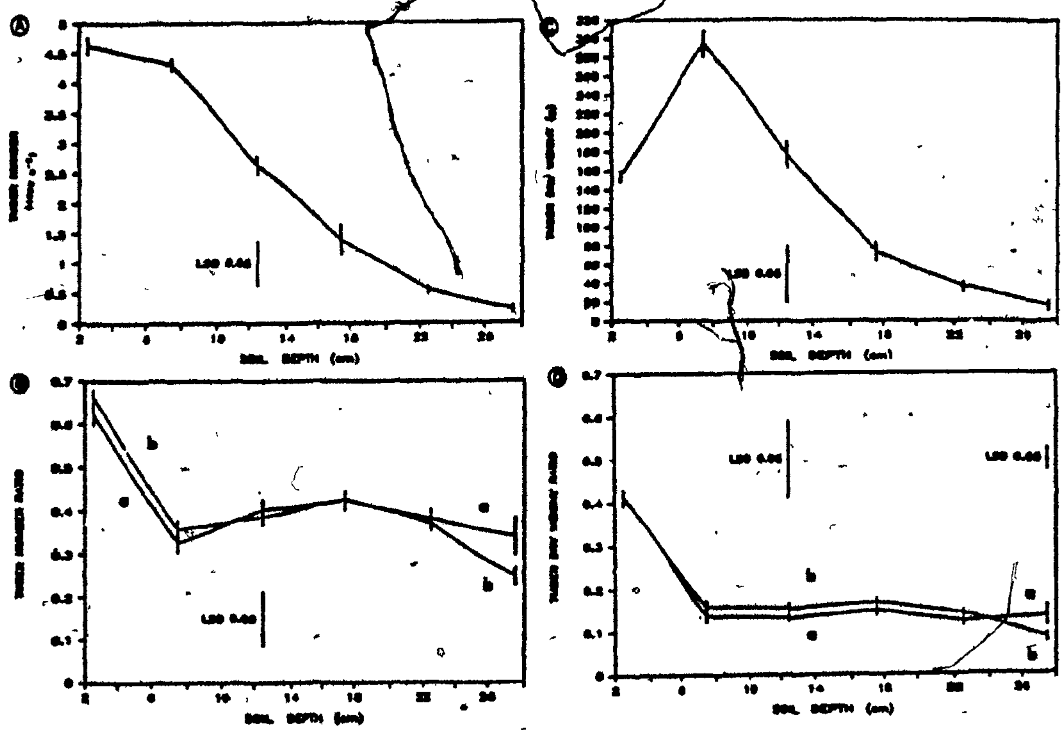


Figure 8.1. Changes in yellow nutsedge tuber attributes as a function of soil depth. Where a = 1982 data and b = 1983 data.

A. Tuber number
B. Tuber number ratio
C. Tuber dry weight
D. Tuber dry weight ratio

These results indicate that the sampling depth used throughout this research project accounted for approximately 84 % of the total soil tuber population.

Tuber number ratios (proportion of small tubers to the total number of tubers) were not pooled over the years and their means and standard errors are plotted in Figure 8.1B along with the LSD for 1983. Similar values were measured in both years. Only the 1983 data are discussed as the 1982 values were not significantly affected by soil depth.

The greatest proportion of small tubers was closest to the soil surface (0 to 5 cm) where they constituted 66 % of the total number of tubers. The next soil section (5 to 10 cm) had almost 50 % fewer small tubers than the first one. The small tubers in the sections from 5 to 25 cm deep formed between 36 to 43 % of the total number of tubers. In the section between 25 and 30 cm, the tuber number ratio was 0.25.

The proportion of small tubers decreased as the depth increased. The last tuber number ratio was approximately that which was reported as being the standard ratio in Section 4 (0.28). The present sampling took place before all the yellow nutsedge shoots senesced and it is expected that over time the ratio continued to decrease until it reached a level of approximately 0.28 in most soil sections. The greater proportion of small tubers encountered closest to the soil surface might be attributed to the fact that the tubers in that section were the most immature and still increasing in size.

As the depth increased, the level of maturity was increasing and so the ratio was decreasing, close to the hypothesized standard value of 0.28 in the 25 to 30 cm section. Further work is required to determine if the ideas advanced here can be observed in field situations.

The combined tuber dry weight means and their standard errors are plotted in Figure 8.1C along with their LSD. They followed trends similar to tuber number with the exception of the 0 to 10 cm sections. Tuber dry weight doubled between the 0 to 5 cm section and the following section (5 to 10 cm). Afterwards, total tuber dry weight decreased as the soil depth increased. When mean tuber dry weight was compiled (Table 8.1), the heaviest mean tuber dry weight was found in the deepest section of the soil profile, while the lightest tubers were found in the section closest to the soil surface. These values tend to strengthen the hypothesis that tubers found in the section closest to the soil surface were immature at the date of sampling.

Tuber dry weight ratios (proportion of small tuber dry weight to the total tuber dry weight) for 1982 and 1983 are plotted in Figure 8.1D. Means are shown with their standard errors and LSD. They follow trends similar to that of the tuber number ratio with the greatest proportion of dry weight contributed by the small tubers in the section closest to the soil surface (0 to 5 cm). The ratio then decreased to a relatively constant value for the other soil sections (5 to 30 cm) with a further slight decrease in ratio for the 1983 data.

Table 8.1. Mean tuber dry weight as a function of soil depth.

Soil depth sections (cm)	Mean tuber dry weight (g)
0 - 5	0.0334
5 - 10	0.0683
10 - 15	0.0673
15 - 20	0.0533
20 - 25	0.0633
25 - 30	0.0738

The greatest proportion of small tubers closest to the soil surface could be considered as confirming that the tubers in that soil section were immature although, as stated above, further work is required to corroborate the hypothesis advanced.

The observations reported in this section should be considered in the development of yellow nutsedge management programs. The majority of tubers were encountered within the plowing layer (top 15 to 20 cm) and the top 10 cm was the area experiencing the greatest loss in viability (Section 5 and Mulligan and Junkins, 1976; Phillips, 1981b; Stoller and Wax, 1973). Therefore, tillage operations that could expose more tubers to winter cold or other weather extremes would contribute to the decrease of yellow nutsedge tuber populations. Spring plowing could perhaps contribute to decreasing yellow nutsedge tuber populations since plowing the soil in the fall might protect tubers from the cold by burying them. Another possibility might be to stop tuber maturation at dates similar to the dates at which the experiments of this section were sampled. This would tend to stop further tubers from maturing, and then the tubers in the top 5 cm could be buried down at 20 cm or more by choosing a combination of tillage techniques and equipment. Over 60 % of the tubers in the top 5 cm of soil were small and that soil layer represented 34 % of the total number of tubers in the soil profile. Therefore, their burial could result in a decrease in the number of tubers sprouting since 56 to 95 % of the shoots arise from the top 10 to 15 cm in the soil (Bell et al., 1962). Such a practice, if possible, could be used every three to four years, given the longevity of yellow nutsedge tubers, and could contribute to reducing yellow nutsedge tuber populations.

There is little, if any, information on the effect of these suggested practices and therefore they must be fully investigated before any suggestions concerning their use could be made or even considered at the field level.

Section 9

EFFECT OF DELAYED EMERGENCE ON YELLOW NUTSEDGE GROWTH

9.0 Introduction :

Crop management practices that delay weed emergence are usually beneficial for the crop and detrimental to the weed. Weeds that have their emergence delayed in most crops cause less crop yield reductions and probably have a reduced growth because of both a shortened growing season and greater competition from the crop (Zimdahl, 1980). Cultivation and herbicides that have a residual activity of at least a few weeks are among the available practices that can be used to delay weed emergence. In the case of yellow nutsedge, it has been reported that a delay of 4 weeks in emergence resulted in a tuber population decrease of 50 to 90 % in the field or in containers (Jordan-Molero and Stoller, 1978; Keeley and Thullen, 1975). A lesser reduction in tuber production (13 %) was found in the present experimental area when corn planting and, consequently, land preparation was delayed three weeks (Ghafar and Watson, 1983a).

The present experiments were undertaken to quantify the effect of delayed emergence on yellow nutsedge tuber production and to derive a regression curve that could be used in the elaboration of a model of yellow nutsedge tuber population dynamics. This model could then be used to evaluate and identify efficient yellow nutsedge management systems through simulations.

9.1 Materials and methods :

An experiment was repeated four times in 1982 and 1983. The experimental design was a randomized complete block with three replications. The plots were 1.5 m by 1.5 m in 1982. In 1983, two experiments had this plot size while the other two had plot sizes of 2 m by 1.5 m. There were eight treatments in 1982 and nine treatments in 1983. In 1982, the treatments consisted of preventing yellow nutsedge emergence for 0, 2, 4, 6, 8, 10, 12, and 14 weeks from the start of the experiment, after which yellow nutsedge was allowed to grow freely. In 1983, the treatment added increased the emergence delay time to 16 weeks. In each treatment, hoeing was used to keep the ground bare. Hoeing was undertaken at least once weekly and at the last day of a treatment. Each year, in two of the experiments, a rototiller was used on the last day of a treatment instead of the hoe. In 1983, one of the wider plots was tilled, while the other was hoed on the last date of treatment. Rhizomes were cut regularly between plots with a narrow blade at the end of a hoe.

The experiments were sampled on September 2, 1982 and September 22, 1983. Three samples were taken per plot and the sampling procedure described in Section 2 was followed. Regressions were fitted to the number of tubers in the soil as a function of delayed emergence of yellow nutsedge. The tuber number ratios were pooled where applicable and were plotted with the standard error of their treatment means. The least significant differences at the 5 % level of probability (LSD 0.05) were used when appropriate. As in the preceding section, tuber dry weight and tuber dry weight ratio followed the same trends as the tuber number. Consequently, these data are presented in Appendix 2 and are not discussed further.

9.2 Results and discussion

Yellow nutsedge growth after hoeing or tillage is first expressed through the production of shoots. Therefore, data on shoot production are presented, since they, better than tuber attributes, illustrate yellow nutsedge growth after delayed emergence. The combined data on shoot number m^{-2} within years could not be analysed due to heterogeneity of variance. Since no consistent trends could be observed between plots hoed or tilled at the last day of treatment, the data were pooled for each year for the purpose of the present discussion. The mean number of shoots m^{-2} produced after delayed emergence are presented in Table 9.1, with their standard errors.

Some shoots were produced by yellow nutsedge even when it

Table 9.1. Yellow nutsedge shoot production after a delayed emergence.

Time of delayed emergence (days)	Shoot number m^{-2}	Standard error of the mean	Time of delayed emergence (days)	Shoot number m^{-2}	Standard error of the mean
1982			1983		
0	1710	62.8	0	1616	127.7
14	1601	53.8	18	1697	91.4
28	1090	50.7	31	1524	48.2
42	855	46.1	46	1040	31.3
56	919	36.3	58	516	64.2
70	162	21.5	72	77	14.1
84	56	7.3	87	20	5.4
98	1	0.7	100	8	2.1
			115	12	4.1

was only allowed to emerge in mid-August or early September (Table 9.1). These shoots were produced either by resprouted or newly sprouted tubers (Bendixen, 1973; Thullen and Keeley, 1975). Since there were no consistent differences between hoed or tilled plots, and because hoeing barely disturbed the top 3 cm of the soil, most of the shoot production could probably be attributed to innate tuber sprouting in time. These results show that yellow nutsedge tubers sprouted continuously during both summers. Some researchers have observed that tubers initiated new shoots until mid-July in Illinois (Jordan-Molero and Stoller, 1978; Stoller and Wax, 1973). Under the experimental conditions of the present study, yellow nutsedge produced new shoots from tubers for a much longer period of time. As a result of delayed emergence, green shoots were found in larger quantities in treatments where yellow nutsedge had more recently emerged. However, in the present case, it is difficult to determine to what extent hoeing or tilling did affect sprouting. Therefore, more specific experiments are required to clarify this aspect.

Tuber populations of each experiment had regressions fitted to them and the parameter values are presented in Table 9.2. The regressions fitted to the number of yellow nutsedge tubers measured after a delayed emergence are plotted in Figure 9.1A and 9.1B for 1982 and 1983, respectively. The parallel lines are used to represent spring tuber population levels. The spring population levels were similar for both years, 3158 tubers m^{-2} in 1982 and 3112 tubers m^{-2} in 1983.

Table 9.2. Regression coefficients of the effect of delayed emergence on the number of tubers produced by yellow nutsedge.

Experiment number	Roto-tilling	Regression equations	R^2	Pr.
Figure 9.1 A:				
1. 1982	NO	$Y = 11064 - 231X + 1.39X^2$	0.97	0.001
2. 1982	NO	$Y = 11581 - 255X + 1.57X^2$	0.99	0.001
3. 1982	YES	$Y = 8990 - 158X + 0.89X^2$	0.98	0.001
4. 1982	YES	$Y = 10866 - 257X + 1.69X^2$	0.94	0.001
Figure 9.1 B:				
1. 1983	NO	$Y = 10398 + 317X - 9.9X^2 + 0.05X^3$	0.92	0.003
2. 1983	NO	$Y = 7883 + 563X - 26X^2 + 0.3X^3 - 0.001X^4$	0.95	0.008
3. 1983	YES	$Y = 13276 - 227X + 1.1X^2$	0.99	0.001
4. 1983	YES	$Y = 7655 + 213X - 6.4X^2 + 0.04X^3$	0.90	0.006
Figure 9.1 C:				
1982 combined experiments		$Y = 10625 - 225X + 1.39X^2$	0.98	0.001
1983 combined experiments		$Y = 9501 + 313X - 14X^2 + 0.2X^3 - 0.0005X^4$	0.99	0.001
Figure 9.1 D:				
Combined 1982 and 1983 experiments		$Y = 11537 - 184X + 0.83X^2$	0.80	0.001

Where Y = the number of tubers.
X = numbers of days of delay in emergence.
R^2 = coefficient of determination.
Pr. = level of significance of the regression.

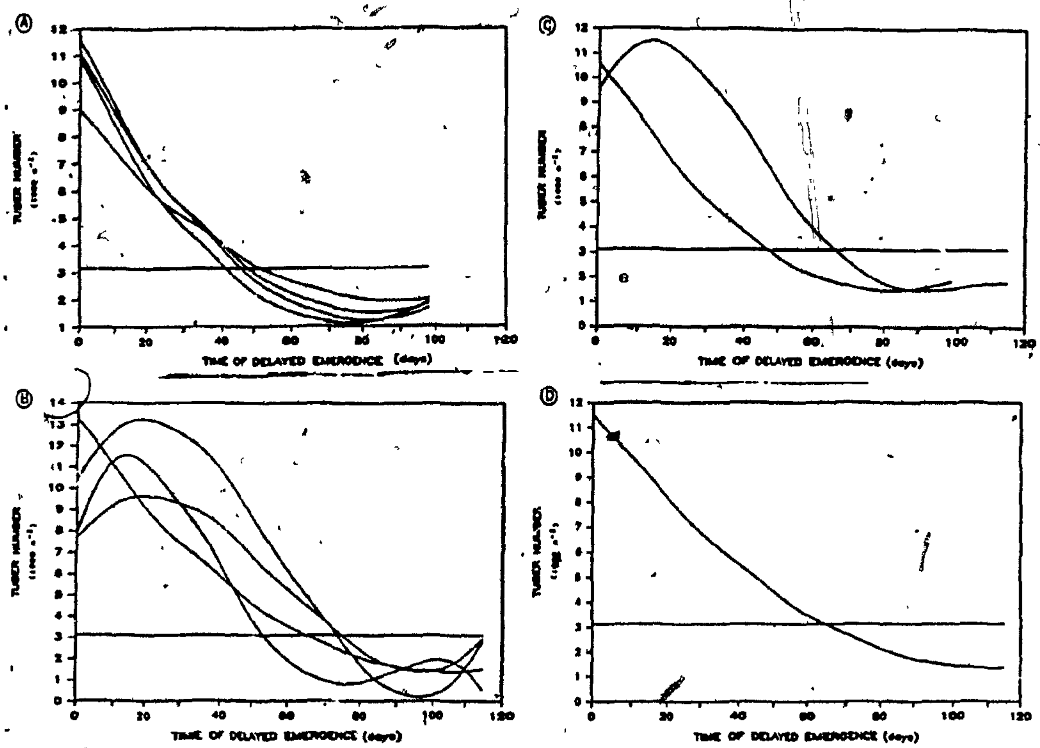


Figure 9.1. Effect of delayed emergence on yellow nutsedge tuber population in 1982 and 1983.

A: 1982 experiments regressions.
B: 1983 experiments regressions.
C: Regressions on the combined data for each year.
D: Regression on the combined data of both years.

The line parallel to the abscissa represents the spring tuber population. The regression equations are presented in Table 9.2.

All the regressions were quadratic in 1982 while two were cubic, one was quadratic, and one was quartic in 1983 (Table 9.2). All quadratic regressions in 1982 showed a decrease in yellow nutsedge tuber population with an increase in the length of time yellow nutsedge emergence was delayed. In 1982, the original spring tuber population level was reached when yellow nutsedge emergence was delayed until the first week of July (approximately 50 days after the start of the experiment). The number of tubers fell below the original spring population level when emergence was further delayed.

In 1983, the three experiments which did not have a quadratic response had an increase in tuber numbers if yellow nutsedge emergence was delayed for the first two weeks of the experiments while the fourth experiment had a response similar to that reported for the 1982 experiments. The original spring tuber population level was reached in the last two weeks of July in 1983 (65 to 80 days after the start of the experiments) after which tuber population fell below the spring population level.

The data collected on the number of tubers produced in experiments conducted the same year were pooled and statistically analysed. The tuber production response in 1982 differed little between experiments (Figure 9.1A) while in 1983, the response was more variable (Figure 9.1B) and did not theoretically allow pooling of the data since there was a statistically significant effect due to the experiments themselves in 1983. The difference between years might be attributed to differences in environmental conditions or spring tuber population level, although this latter factor varied little between years (3158 vs 3112 tubers m^{-2}). The variations in the 1983 experimental results could have been caused by differences in spring tuber population levels and/or soil heterogeneity. Since the ultimate purpose of this section was to obtain functions describing and predicting yellow nutsedge tuber population as affected by delayed emergence, the data of each year's experiments were combined, although this was only statistically warranted for the 1982 data, and had regressions fitted to them. The regression parameter values are presented in Table 9.2 while the functions are plotted in Figure 9.1C.

The observations on the four regressions curves made for each year were still applicable for the pooled data. There was a decrease in tuber number in 1982 with the increase in the length of time yellow nutsedge was delayed. Tuber numbers increased in 1983 when yellow nutsedge growth was delayed for the first three weeks. Still in 1983, the tuber number was the same when yellow nutsedge emergence was delayed three weeks or not delayed at all (Figure 9.1C). The tuber population reached the spring tuber population level after 50 days of delayed emergence in 1982 (first week of July) and after 70 days of delayed emergence in 1983 (fourth week of July) (Figure 9.1C).

The difference in tuber production level between the two years was more obvious when both were combined in the same figure (Figure 9.1C). Differences could probably be attributed to environmental conditions although small variations in spring tuber density might have had an effect. However, the cause of the differences can not be easily pinpointed with the available data and a descriptive and predictive regression curve is required in the elaboration of the model of yellow nutsedge tuber population dynamics. Therefore, since no discriminating factors could be used to decide which regression curve to use, the data of both years were pooled to obtain one regression that would describe and predict yellow nutsedge tuber production when emergence was delayed. Regression parameters are presented in Table 9.2 and are plotted in Figure 9.1D.

When both years data were pooled, the increase in tuber number after three weeks of delayed emergence observed in 1983 was smoothed out. The tuber population reached the pooled spring tuber population level (3135 tubers m^{-2}) when yellow nutsedge emergence was delayed until the third week of July (65 days after the start of the experiments). When emergence was delayed beyond that time, there was an actual decrease in tuber number compared to the spring tuber population level.

These data suggest that any delay in yellow nutsedge emergence would reduce tuber production, and if yellow nutsedge emergence was delayed to the end of July, the tuber population would be stabilized at the spring population level or would decrease. However, it should be noted that these results were obtained by samplings that took place before recently emerged yellow nutsedge shoots had senesced or were killed by the frost. Therefore, more growth may have occurred after the final samplings.

In the context of a yellow nutsedge management program, growth would have to be prevented after the final sampling dates of these experiments in order to obtain results comparable to the current trial. A delay in yellow nutsedge emergence could be produced by the use of a residual herbicide, by cultivating, by delayed planting, by fallowing, or by a combination of these practices. They should be considered in the development of yellow nutsedge integrated management systems.

There were no significant differences in the proportion of small tubers to total tuber number (tuber number ratio) between the experiments in 1982, according to the combined analysis of variance. Therefore, the data of the four experiments of 1982 were pooled into one data set of which the means are plotted in Figure 9.2A, with their standard errors and the LSD (0.05).

The proportion of small tubers was at its lowest in 1982 when yellow nutsedge emergence was either not delayed or only delayed for the first two weeks of the experiment. The tuber number ratio then increased to reach its maximum when emergence was delayed until mid-July. The proportion of small tubers decreased thereafter until the first week of August and subsequently increased again. The variation between the maximum and minimum tuber number ratio was approximately 10 %. The smallest ratio observed when yellow nutsedge emergence was only slightly delayed might be attributed to the fact that yellow nutsedge had time to complete its development in the available growing period. However, the ratio was greater than

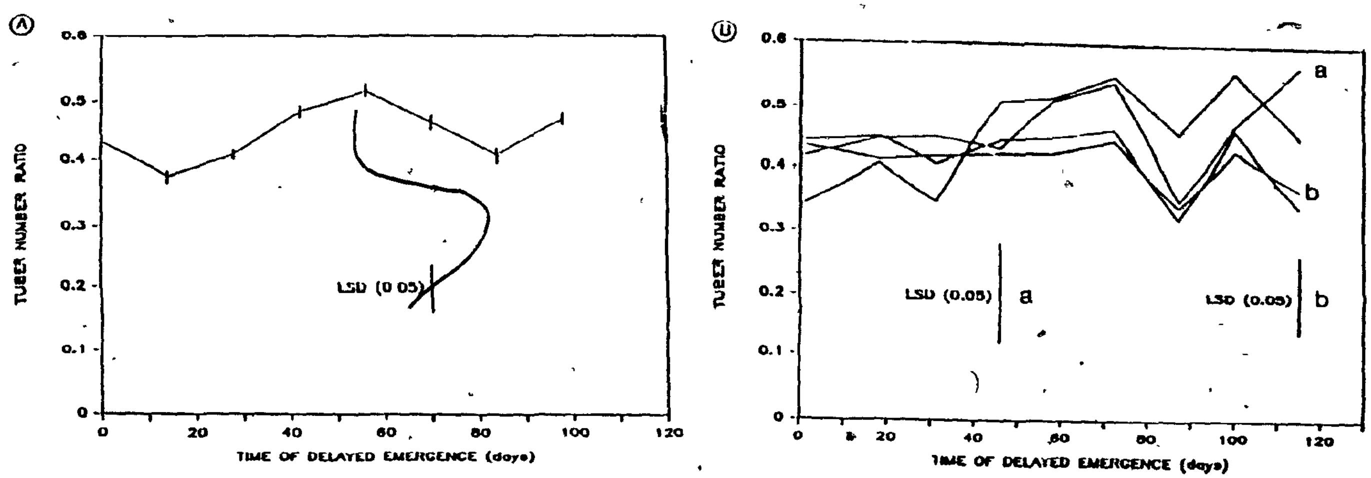


Figure 9.2. Effect of delayed emergence on the tuber number ratio of the tubers produced in 1982 and 1983. Where a and b refer to two experiments where tuber number ratio was significantly affected by the period of delayed emergence.

A: Combined tuber number ratio for the experiments conducted in 1982.

B: Tuber number ratios for the 1983 experiments.

the typical yellow nutsedge tuber number ratio (0.28) reported in Section 4. This high ratio (Figure 9.2A) would probably decrease given time because some plants were still maturing and increasing the size of their tubers after the sampling took place.

Up to 50 % of the tubers were small when yellow nutsedge was allowed to emerge in early July, most probably because the tubers that had been initiated were still increasing in size when they were sampled. This period with its greatest proportion of small tubers was followed by a 10 % decrease in tuber number ratio in treatments where yellow nutsedge had been prevented from emerging until early August (Figure 9.2A). This decrease could be due to the fact that very few tubers had had time to be produced (Figure 9.1) before the sampling period. In fact, the lowest number of tubers was observed in a yellow nutsedge population that had been allowed to emerge in that period, indicating that few, if any, new tubers had been initiated. The ratio observed was probably that of the residual tuber population, although it can not be ruled out that yellow nutsedge might have been triggered into producing a few, large tubers when they were initiated in early August. The increase in the tuber number ratio that occurred in late August might be explained by the fact that yellow nutsedge could have been induced to produce tubers by environmental conditions prevalent at the time (Bell et al., 1962; Bendixen, 1970). Although a larger number of new tubers were initiated, they did not have time to mature before the sampling date.

This explanation is supported by the observed increase in tuber number when yellow nutsedge was allowed to emerge in mid-August or later (Figure 9.1A).

The tuber number ratio data could not be pooled in 1983 because of significant differences among the experiments. Therefore, the ratios of each of the four experiments are plotted in Figure 9.2B. Two of the experiments were significantly affected by the delay in yellow nutsedge emergence and, therefore, their LSD at the 5 % level of probability are presented with the data. Standard errors of the means were not shown to leave the figure uncluttered.

In 1983, the tuber number ratio followed the same trends observed in 1982. The treatment added in 1983 (emergence delayed until early September) produced a decrease in tuber number ratio when compared to the previous treatment response. This result was probably due to the samples being constituted solely of the residual tuber population since the growth period was too short for the initiation and development of new tubers.

Tuber number ratio observations corroborated what has been reported on the number of tubers, in that, ideally, yellow nutsedge emergence should be delayed until late August to have smaller tubers and to reduce tuber number. Yellow nutsedge that was only allowed to emerge in July produced the greatest proportion of small tubers, although in a greater number than if its emergence had been delayed until later. However, it can not be assumed that there would not be more tubers or an increase in tuber size after the date at which the experiments were sampled. This fact, and the results of the current experiments must be taken into consideration in the elaboration of a yellow nutsedge management program.

Section 10

EFFECT OF GROWTH INTERRUPTIONS ON YELLOW NUTSEDGE TUBER POPULATION

10.0 Introduction :

Yellow nutsedge growth and tuber population level can be reduced by delayed emergence incurred through crop management systems. Delayed planting and cultivation are two methods which have had some degree of success in reducing tuber production by 10 to 90 % (Ghafar and Watson, 1983a; Jordan-Molero and Stoller, 1978; Keeley and Thullen, 1975). Delayed emergence could even reduce yellow nutsedge tuber population from year to year if the weed was delayed for a sufficiently long period of time (Section 9). Residual herbicides could also act to delay emergence thereby reducing tuber production. However, implementing some or all of those techniques to delay yellow nutsedge emergence could be both costly and relatively inefficient.

The effect of interrupting yellow nutsedge growth through one or two field operations, such as cultivation or perhaps the application of a herbicide, might be economical and effective in developing an integrated yellow nutsedge management program. Accordingly, the present project was initiated in order to assess the potential effects of either single or double interruptions of yellow nutsedge growth. Regression equations were used to describe and predict the effectiveness of such operations so that these control techniques could be integrated into the model of yellow nutsedge tuber population dynamics.

10.1 Materials and methods :

The experimental design was a randomized complete block repeated three times with five treatments in 1982 and seven treatments in 1983. The plots were 2 m long and 1.5 m wide. Details of times of tillage are presented in Table 10.1. The treatments consisted of allowing yellow nutsedge to grow freely during the summer and, at a particular treatment date, tilling the plot, after which yellow nutsedge was again allowed to grow freely. At 4 week intervals, two plots were tilled and 6 to 8 days later, one of these plots was tilled again. A rototiller crossed the plots twice the first time they were tilled, and, if there was a second time, the rototiller made only one pass since yellow nutsedge growth was not as dense after the first tillage. The experiment was sampled August 26, 1982 and September 27, 1983. Three samples were randomly taken in each plot following the sampling procedure described in Section 2.

This was a factorial experiment where the main effects were the date of tillage and the frequency of tillage (once or

Table 10.1. Effect of growth interruptions on yellow nutsedge tuber number ratio, total tuber dry weight, and tuber dry weight ratio in 1982 and 1983.

Treatment number	Time of interruption[a]	Number of tillage operations[b]	Tuber number ratio	Standard error +/-	Tuber dry weight ($g\ m^{-2}$)	Standard error +/-	Tuber dry weight ratio	Standard error +/-
1982								
1	0	1	0.53	0.009	178	44	0.25	0.003
2	36	1	0.49	0.049	74	13	0.29	0.041
3	42	2	0.58	0.026	65	8	0.32	0.039
4	56	1	0.59	0.052	43	7	0.37	0.055
5	63	2	0.54	0.034	82	10	0.26	0.027
1983								
1	0	1	0.54	0.014	766	21	0.22	0.010
2	18	1	0.57	0.012	433	30	0.25	0.010
3	26	2	0.57	0.010	573	17	0.25	0.008
4	46	1	0.57	0.010	310	16	0.26	0.010
5	53	2	0.57	0.020	218	11	0.28	0.013
6	80	1	0.59	0.012	246	18	0.29	0.014
7	86	2	0.60	0.024	224	17	0.31	0.019
LSD 0.05					203			

[a] The time of interruption refers to the number of days from the start of the experiment.

[b] 1 = Tilled at one date only.
2 = Tilled a second time 6 to 8 days after the first date.

twice). Consequently, both main effects and interactions were tested in an analysis of variance. When the date of tillage was found to have significantly affected yellow nutsedge tuber population, a regression was fitted to the number of tubers in relation to the time of tillage.

10.2 Results and discussion :

The frequency of tillage did not significantly affect any of the yellow nutsedge tuber parameters measured and there were no significant interactions between the frequency of tillage and the date of tillage. It would appear therefore that a second tillage gave no additional benefits in yellow nutsedge control under the conditions of this study.

In 1982, no statistically significant differences were found for any of the measured variables between the different times of tillage. The mean tuber population for each treatment time with their standard errors and with the 1982 spring tuber population level are plotted in Figure 10.1. The means of the tuber number ratio, the total tuber dry weight, and the tuber dry weight ratio are presented in Table 10.1, with their standard errors.

In 1983, the number of tubers and the total tuber dry weight were significantly affected by the time of tillage. The 1983 tuber population response to the time of interruption was best described by a quadratic polynomial regression. The regression of tuber population is plotted in Figure 10.1 along

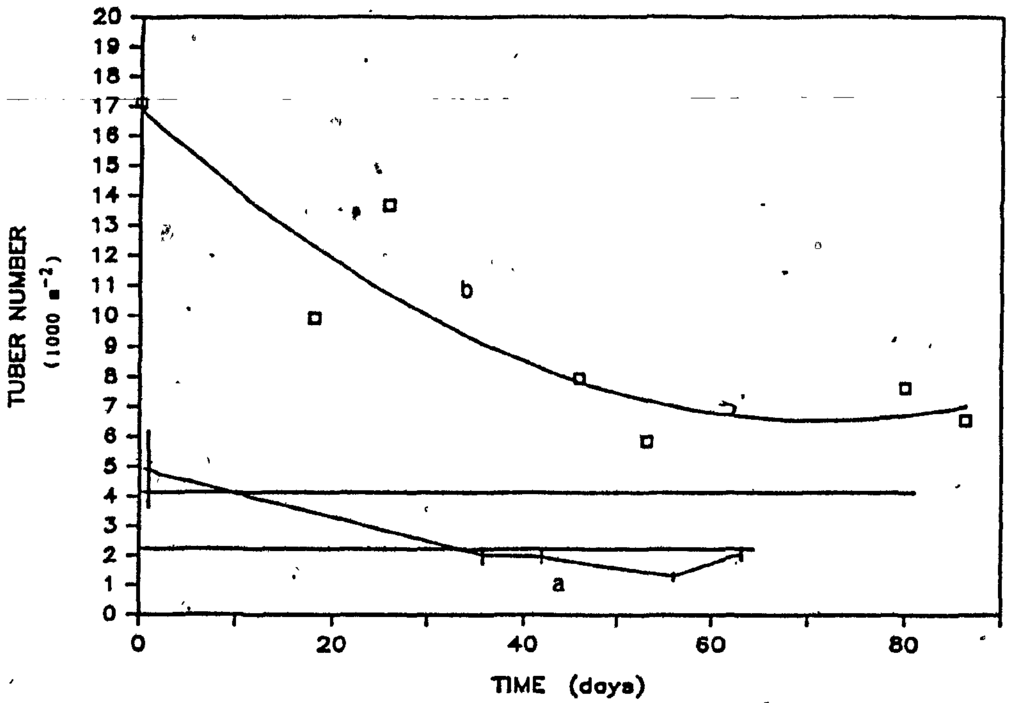


Figure 10.1. Effect of the time of interruption on yellow nutsedge tuber population in 1982 and 1983. Where the regression is $Y = 16880 - 291X + 2X^2$ ($R^2 = 0.83$, Pr = 0.03), the parallel lines represent the spring tuber populations, a = 1982 means and their standard errors, b = 1983 regression, Y = fall tuber population, X = time of the last tillage, in days, R^2 = coefficient of determination, Pr = level of significance.

with the 1983 spring tuber population level. The interruption of yellow nutsedge growth at any of the dates did not produce a decrease in the tuber population below the spring tuber population level for 1983. The lowest population, according to the regression, was 1.6 times that of the spring tuber population.

The total tuber dry weight had a response similar to that of the tuber number and, therefore, will not be discussed further. The means of the total tuber dry weight are presented in Table 10.1 with their standard errors and the least significant difference at the 5 % level of probability. The mean tuber number ratio and mean tuber dry weight ratio are also presented in Table 10.1, along with the standard error of their means. The ratios were not significantly affected by the time or frequency of tillage and, as in Section 9, they were greater than the values that were presented as being the population values in Section 4. The discussion on differences in ratios presented in the previous section applies here.

The difference in results observed between the two years of the experiment might be attributed to the differences in spring tuber population, to the differences in sampling date, or to the differences in growing conditions between the two years. The 1982 spring tuber population was approximately half that of 1983 and the number of tubers observed in the season decreased below that of the spring tuber level starting at the first tillage date. In 1983, the most effective treatment had a tuber population at least 1.6 times greater than the spring tuber population level. The sampling was conducted one month earlier in 1982 than in 1983 and might have been done before possible treatment differences were fully expressed. The difference in growing conditions might also have had an effect on the response of the yellow nutsedge tuber population to treatments. It is most likely that any differences in response resulted from a combination of these factors.

It would seem that interruptions of yellow nutsedge growth did not reduce the tuber population by as much as delays in emergence (Section 9). However, in 1983, a single tillage in July or August decreased yellow nutsedge tuber population by 60 %. Although very promising as a control strategy, these experiments would have to be repeated for several years in order to verify that these results are consistent, particularly considering that no significant differences were observed in 1982. If the results obtained in 1983 were obtained in subsequent experiments, the inclusion of these treatments in the planning of yellow nutsedge population management programs would be most important since a single tillage operation could replace several tillage operations, depending on the time in the season. Therefore the cost of control could be reduced and the range of crop management programs increased and made more flexible.

Section 11

EFFECT OF CORN ON YELLOW NUTSEDGE GROWTH

11.0 Introduction :

Yellow nutsedge growth was observed primarily in pure stands throughout most of this study in order to have a uniform basis for growth comparisons between several crop management systems. There have been reports on the effect of different control measures used in corn against yellow nutsedge (Dixon et al., 1980; Keeley et al., 1983; Parochetti, 1974; Stoller et al., 1971), but there are no reports on the effect of the corn crop on yellow nutsedge. Therefore, in order to be able to assess the effectiveness of different weed control measures, the effect of corn alone on yellow nutsedge had to be determined.

Ghafar and Watson (1983a,b) and Simkins and Doll (1980) reported that yellow nutsedge growth was greater within corn rows than between corn rows. One of the explanations offered was that the fertilizer applied close to the crop row stimulated yellow nutsedge growth. These observations raised the problem of accurately assessing yellow nutsedge growth in corn in the field. The following experiments were conducted to qualify and quantify the effect of corn on yellow nutsedge.

11.1 Materials and methods :

Since this experiment was an integral part of the main experiment of the project, it has been previously described in chapter 6, "Yellow nutsedge growth in time", and only a brief treatment outline of the procedure is presented here. There were two treatments, yellow nutsedge growing in pure stands or yellow nutsedge growing with corn, which were replicated three times. The crop management system was the same in both treatments with starter fertilizer (30 kg/ha of 18-46-0) applied at seeding and nitrogen side dressing applied close (10 to 20 cm) to the corn row or where a corn row would have been in pure stands of yellow nutsedge. The nitrogen side dressing was applied to the left of the rows only, at a rate of 150 kg/ha of 34-0-0 at two different dates (see the general materials and methods for further details). This experiment was conducted for the three years of the project, 1981 to 1983.

Yellow nutsedge was sampled at the end of the growing season in each of the three years. In the fall of 1982 and fall of 1983, yellow nutsedge was sampled on the corn rows and between the corn rows. For the pure stands of yellow nutsedge, samples were taken in the equivalent areas. Nine samples were taken in each location (on the row and between the row) in all replicates of all treatments. All values are reported on a m^2 basis. In the fall of 1983, transects samples were taken across rows in order to measure the variation from row to row, in 15 cm gradients, resulting in five quadrats of 15 by 15 cm from row to row, since the spacing was 75 cm between corn rows. Three transects were taken in each replicate of each treatment.

A fire destroyed part of the samples that had been taken in the fall of 1983. Therefore, a subsequent sampling was done to collect tuber data in one replication. No statistical analyses were performed on tuber data for that sampling date.

Data were analysed considering two sets of factors: yellow nutsedge growth in pure stands or with corn (treatments) and yellow nutsedge growth on or between corn rows or their equivalent (locations). Furthermore, the interaction between treatments and locations was tested. Transect data was used to compare the two treatments, and subsequently, regression curves were fitted to them.

11.2 Results and discussion :

The effects of growing with corn is presented first and is followed by the effects of growing on or between the rows. Finally, the transect results are discussed.

11.2.1 Treatment effects :

Tuber number was reduced significantly by corn in 1983 only. Similar trends existed for 1982, however. For both years, yellow nutsedge produced an average of 23.7 % fewer tubers when growing with corn, with extremes of 9.4 and 50.9 %.

However, in 1981 the number of tubers in both treatments was similar (a 0.5 % difference). The ratio of the number of smaller tubers to the total number of tubers was significant in the fall of 1983 only, but trends were similar for the other years. The smaller tubers constituted a greater proportion of the total tuber population when yellow nutsedge was growing in corn. Although there was wide variation, the smaller tubers' contribution to the total number of tubers was, on average, 20.5 % more in the corn treatment (Table 11.1).

The total biomass of tubers was consistently, although not always significantly, greater in plots where yellow nutsedge was growing alone. On average, the total tuber dry weight m^{-2} was 48.5 % greater with extremes of 12.3 and 89 %. The ratio of small tuber dry weight to total tuber dry weight was, on average, 45 % greater for yellow nutsedge growing in corn. There are only two cases where the differences are statistically different but the trend was consistent.

The differences in response from year to year and within the same year demonstrated the variability of yellow nutsedge. This, associated with fluctuations of the environmental conditions from year to year, compounded the difficulties in quantifying the effect of growing in corn. However, some general trends were identified. For example, the number of tubers was reduced by 24 % and their mean dry weight was reduced by 23 %. Their size was also reduced.

Only one replication was sampled on September 19, 1983 for

Table 11.1. Effect of corn absence or presence on yellow nutsedge growth.[a]

Sampling date	Treatment[b]	Tuber number (m^{-2})	Tuber[c] number ratio	Total tuber biomass (gm^{-2})	Tuber[d] biomass ratio
Fall 1981	1	6692	0.411	330	0.158
(Aug. 20)	2	6725	0.488	284	0.217
		n.s.	n.s.	n.s.	n.s.
Fall 1982	1	13282	0.483	622	0.216
(Aug. 30)	2	12145	0.502	554	0.228
		n.s.	n.s.	n.s.	n.s.
Fall 1983	1	14433	0.476	639	0.199
(Sept. 6)	2	12004	0.612	376	0.324
		*	*	**	*
Fall 1983	1	13403	0.440	615	0.178
(Sept. 12)	2	11717	0.572	397	0.299
		**	**	**	**
Fall 1983	1	19973	0.485	843	0.205
(Sept. 19)	2	13233	0.589	446	0.310
		n.a.	n.a.	n.a.	n.a.

[a] The codes and abbreviations used here are; n.s. for not significant; n.a. for not available; * for significant at the 5 % level; ** for significant at the 1 % level.

[b] The two treatments are: 1- yellow nutsedge growing alone, and 2- yellow nutsedge growing with corn.

[c] Small tuber number over total tubers number.

the underground data. This might help in explaining the difference in magnitude observed between the various sampling dates in 1983.

11.2.2 Location effect :

Effects of sampling locations on yellow nutsedge growth are shown in Table 11.2. There were 6.8 % more tubers produced between the rows in 1982 while 2.8 and 5.4 % less tubers were produced between the rows in 1983. The proportion of smaller tubers relative to the total number of tubers was greater between the rows for both years. Smaller tubers contributed, on average, 9.8 % more to the total number of tubers between the rows than on the rows, with extremes of 6.9 and 15.4 %.

The biomass of tubers was invariably greater on the corn rows or their equivalent. The tuber biomass was 13.4 % more on the rows. The small tubers' portion was 17.9 % greater for yellow nutsedge growing between the rows than on the rows.

Yellow nutsedge growing on the corn row or its equivalent produced tubers 15 % heavier than yellow nutsedge growing between the rows or their equivalent. A similar number of tubers was produced on the row or between but the proportion of smaller tubers was 10 % greater between rows and their contribution to tuber biomass was 18 % greater than within the rows.

There were no significant interactions between the treatments (yellow nutsedge growing alone or with corn) and the

Table 11.2. Yellow nutsedge growth on or between corn rows or their equivalent.[a]

Sampling date	Location[b]	Tuber number (m^{-2})	Tuber[c] number ratio	Total tuber biomass (gm^{-2})	Tuber[d] biomass ratio
Fall 1982	1	13159	0.509	585	0.233
(Aug. 20)	2	12269	0.476	590	0.211
		n.s.	n.s.	n.s.	n.s.
Fall 1983	1	12873	0.583	446	0.296
(Sept. 6)	2	13564	0.505	569	0.227
		n.s.	n.s.	n.s.	n.s.
Fall 1983	1	16370	0.556	609	0.273
(Sept. 19)	2	16836	0.519	681	0.242
		n.a.	n.a.	n.a.	n.a.

[a] The codes and abbreviations used here are; n.s. for not significant; n.a. for not available; * for significant at the 5 % level; ** for significant at the 1 % level.

[b] The two sites are: 1- between corn rows or their equivalent, and 2- on the corn rows or their equivalent.

[c] Small tuber number over total tubers number.

sampling location (on the row or between). However, some trends could be discerned despite the variability of the material under study. Generally, yellow nutsedge growth was superior when growing in pure stands; and, whether growing with corn or alone, superior when growing in close proximity to where the nitrogen side dressing had been applied.

11.2.3 Transects :

Data from the transects taken across rows in yellow nutsedge growing with corn or the equivalent area in yellow nutsedge growing alone were used to compare the treatments (Table 11.1, Sept. 12, 1983). All the variables measured were significantly affected by corn. Regressions were fitted on each treatment. Means were used to calculate the regressions because of the great variability of the data. For the same reason, regressions that were significant up to the 7 % level were kept to illustrate the trends expressed by the data.

Variables are plotted in Figure 11.1 A-D with their significant regressions where applicable. These regressions and their parameters are presented in Table 11.3. For every graph, the first and last observation start and finish exactly on the row.

<u>Yellow nutsedge growing in pure stands</u> :

Significant linear regressions were fitted on the number of tubers produced as a function of their distance from the left side of the row (Table 11.3; Figure 11.1A). The number of

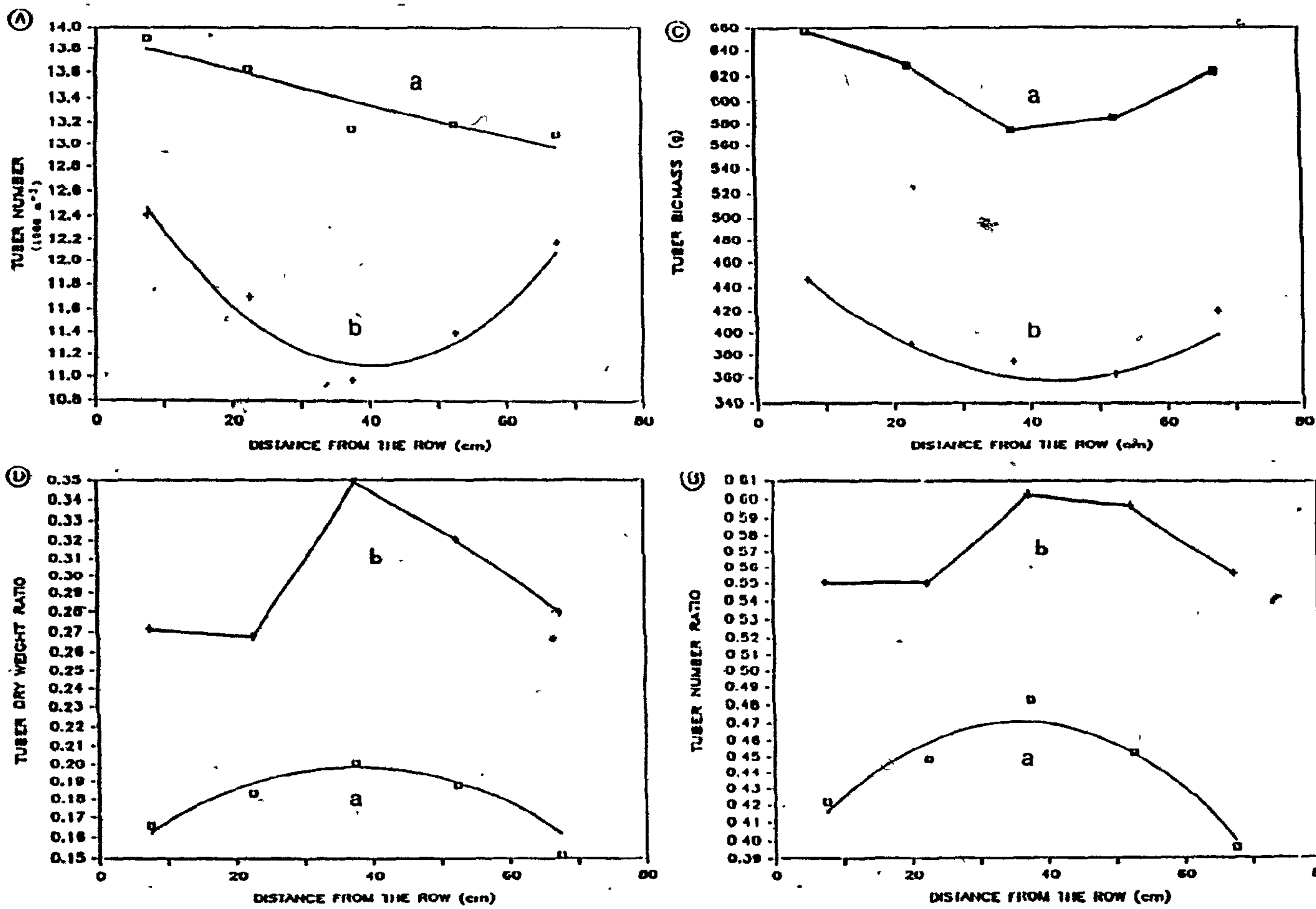


Figure 11.1. Growth variations along transects taken in yellow nutsedge growing in pure stands or with corn. Where a = pure stand and b = with corn.

A. Number of tubers.
B. Tuber number ratio.
C. Tuber biomass.
D. Tuber dry weight ratio.

Table 11.3. Regression equations of yellow nutsedge variables in transects taken in yellow nutsedge growing in pure stands or with corn.

Variable	Treatment[a]	Equation[b]	R^2 [c]	Pr[d]
Tuber number	1	$Y = 13906 - 13.8*X$	0.83	0.03
Ratio of tuber number	1	$Y = 0.382 + 0.005*X - 0.00007*X^2$	0.93	0.07
Ratio of tuber weight	1	$Y = 0.142 + 0.003*X - 0.00004*X^2$	0.95	0.05
Tuber number	2	$Y = 13183 - 104*X + 1.3*X^2$	0.95	0.06
Tuber dry weight	2	$Y = 489 - 6.06*X + 0.07*X^2$	0.95	0.05

[a] Yellow nutsedge growing, 1- in a pure stand, 2- with corn.
[b] Y is the dependent variable and X is the distance on the transect, starting at the left of the row.
[c] Coefficient of determination.
[d] Level of significance.

tubers was greatest close to that side of the transect. At the 75 cm distance, the number of tubers was reduced by 6 %.

The ratios of tuber number and tuber biomass also had significant regressions. Both regressions were quadratic with the greatest proportion of small tubers being located in the middle of the transects, which was between rows. A possible explanation might be that nutrients were more limiting there (Figure 11.1 B,D).

The tuber dry weight did not significantly change on the transect in pure stands of yellow nutsedge (Figure 11.1 C).

Yellow nutsedge growth with corn :

Significant regressions could only be fitted to tuber number and tuber biomass when yellow nutsedge was growing with corn. The regressions were quadratic and were fitted to the means of these variables (Table 11.3; Figure 11.1 A,C). Their minima occurred in the third and fourth sampling sites of the transects (Figure 11.1 A,C). This is probably where there was the least amount of nutrients in the transects. None of the other variables followed any significant patterns along the transects.

The variability of yellow nutsedge associated with the changing response from season to season (Ghafar and Watson, 1983,a,b) does not allow generalizations based on so few years data. However, some important findings did emerge from these experiments although the exact quantification of the effects investigated was difficult.

Corn did reduce yellow nutsedge tuber production by 24 % over the three years of the experiments. Smaller and lighter weight tubers were produced when yellow nutsedge was growing in corn rather than alone. Tubers produced between rows were reduced in size and number probably because less nutrients were available there. The variability expressed in the different samplings done within the same year indicated that yellow nutsedge must be considered as a highly variable, heterogeneous biological material.

Tuber numbers showed dissimilar trends in the transects taken across rows in corn or in yellow nutsedge growing alone. Significant regressions were fitted to the number of tubers produced in both treatments. A straight line was fitted to the number of tubers which constantly decreased across rows in yellow nutsedge growing alone, while a quadratic curve was fitted to the number of tubers produced across rows in corn. The minimum number of tubers occurred in the middle of the transects, midway between corn rows. The difference in response can probably be attributed to the presence of corn which shaded yellow nutsedge and mobilized the fertilizer that was applied at planting or as side dressing (Keeley and Thullen, 1978; Volz, 1977).

Section 12

MODEL OF YELLOW NUTSEDGE TUBER POPULATION DYNAMICS

12.0 Introduction :

Yellow nutsedge is a perennial weed propagated primarily through its tubers in field infestations (Stoller, 1981). It has become the worst weed problem in the American corn belt and new infestations are continuously appearing (Stoller, 1981). Most row crop weed control methods and competitive crops are successful in preventing this weed from reducing yields, and/or in decreasing the level of infestation of yellow nutsedge (Keeley et al., 1979,1983; Simkins and Doll, 1979; Stoller et al., 1979). Despite these effective control measures, yellow nutsedge infestations keep increasing in number and size.

Long term success in controlling yellow nutsedge has never been achieved for two reasons. Firstly, there are no measures that provide season-long control, and secondly, there is a lack of understanding of the mechanisms that regulate its populations. Successful control of yellow nutsedge can best be achieved through an increased comprehension of the life cycle of yellow nutsedge and its population dynamics rather than by simply hoping to increase the length of the control period.

The research effort of this thesis was aimed at expanding the knowledge of yellow nutsedge tuber population dynamics, and incorporating this knowledge into a model. This section presents the selected model, its parameter estimations, its verification, and its validation.

12.1 Model development :

Plant population processes can be presented as a simple algebraic equation that describes the change in numbers of a population between two points in time :

$$N_{t+1} = N_t + B - D + I - E \qquad (1)$$

where N is the number of individuals
t is time
B is the number of new individuals produced between t and t+1 (fecundity)
D is the number of individuals that died between t and t+1 (mortality)
I is the number of individuals that immigrated into the area (considered negligible for yellow nutsedge)
E is the number of individuals that emigrated from the area (considered negligible for yellow nutsedge)

Since most studies cannot include the entire population of a species, this equation is usually based on densities rather than absolute numbers and N is expressed either on a m^{-2} or another area basis (Mortimer and Begon, 1981; Silvertown, 1982). Equation 1 is very general and must be converted to a form that can reflect the complexities of plant populations in the field (Mortimer and Begon, 1981). Sagar and Mortimer's (1976) diagrammatic life-table incorporates the diversities pertaining to plant life cycles. Briefly, the plant population is broken down in classes of plant stages (seeds, buds, seedlings, and adults) for which numbers are assessed at the beginning and end of each time period. Such a description can be further refined by the incorporation of classes of intermediate growth stages or size of plants (Caswell and Werner, 1978; Law, 1983; Werner and Caswell, 1977). The mortality and fecundity of each of the classes change with their age. It is a simple matter to express in algebraic terms the changes in numbers of individuals changing class. For example :

$$t_{n+1} = t_n * p_1 * p_2 * p_3 * p_4 * p_5 * f \qquad (2)$$

where p = the proportion of the individuals that reach the next stage.

t_{n+1} = the number of seeds at time n+1
t_n = the number of seeds at time n
p_1 = seeds that survive
p_2 = seeds that germinate
p_3 = individuals that establish seedlings
p_4 = individuals that survive to maturity
p_5 = individuals that survive to produce seeds
f = number of seeds produced

This is a simplified example, but the principles remain the same for more complex situations where fecundity and surviving proportions might change with density, growth stage and individual size as a function of time. As the number of equations and classes increase, so do the algebraic expressions, and they become increasingly difficult to manage. Matrix algebra allows the use of the same equations but in a more compact and simpler form (Usher, 1972) such as :

$$A * a_t = a_{t+1} \qquad (3)$$

where a_t is a column vector representing the population stage structure at time t, and where A is a matrix representing the proportion of individuals changing class (surviving) and the production of new individuals (fecundity). It is called a transition matrix. For example, an annual plant species could be simply expressed as :

$$a_t = \begin{bmatrix} \text{number of seeds} \\ \text{number of seedlings} \\ \text{number of mature plants} \end{bmatrix}$$

and

$$A = \begin{bmatrix} 0 & 0 & 12 \\ 0.33 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix} = \begin{bmatrix} F & F & F \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{bmatrix}$$

where F = production of seeds
and p = the proportion of individuals changing class.

The first matrix row, last element, represents the fecundity (each mature plant produces 12 seeds).
The second row, first element, represents the proportion of seeds that produce seedlings (33 % produce seedlings, the rest die).
The third row, second element, represents the proportion of seedlings that produce mature plants (50 % produce mature plants, the rest die).

An example with numbers would be as follows :

if $a_t = \begin{bmatrix} 100 \\ 0 \\ 0 \end{bmatrix}$ seeds, no seedlings, no mature plants

therefore,

$$a_{t+1} = \begin{bmatrix} 200 \\ 0 \\ 0 \end{bmatrix}$$

where the time interval could be one year. The basis of this model is a set of recurrence equations which are solved in a stepwise fashion (iterations) as illustrated below.

first step

$$a_{z+1} = \begin{bmatrix} 0 \\ 33.3 \\ 0 \end{bmatrix} \begin{matrix} = \\ = \\ = \end{matrix} \begin{bmatrix} (0*100+0*0+12*0) \\ (0.33*100+0*0+0*0) \\ (0*100+0.5*0+0*0) \end{bmatrix} \begin{matrix} \text{seeds} \\ \text{seedlings} \\ \text{mature plants} \end{matrix}$$

second step

$$a_{z+2} = \begin{bmatrix} 0 \\ 0 \\ 16.7 \end{bmatrix} \begin{matrix} = \\ = \\ = \end{matrix} \begin{bmatrix} (0*0+0*33.3+12*0) \\ (0*0+0*33.3+0*0) \\ (0*0+0.5*33.3+0*0) \end{bmatrix} \begin{matrix} \text{seeds} \\ \text{seedlings} \\ \text{mature plants} \end{matrix}$$

third step

$$a_{z+3} = \begin{bmatrix} 200 \\ 0 \\ 0 \end{bmatrix} \begin{matrix} = \\ = \\ = \end{matrix} \begin{bmatrix} (0*0+0*0+12*16.7) \\ (0*0+0*0+0*16.7) \\ (0*0+0.5*0+0*16.7) \end{bmatrix} \begin{matrix} \text{seeds} \\ \text{seedlings} \\ \text{mature plants} \end{matrix}$$

A property of the matrix model used here is that

$$A*a= \lambda *a \tag{4}$$

where λ is a latent root and a the latent vector associated with λ. The latent root that has the greatest absolute value in an unrestricted environment is called the finite rate of increase. In the example above, $\lambda = 2$. Therefore, the number of seeds doubles at every time interval. A population that has a $\lambda > 1$ is increasing while a population where $\lambda = 1$ is stable. If $\lambda < 1$ then the population is decreasing.

The matrix model used above is referred to as a modified Leslie matrix (Mortimer, 1983; Usher, 1972). Modified Leslie matrix models have been used in several plant population studies where the plant stages were generally separated in classes such as seeds, seedlings, immature plants, mature plants, flowering plants, with bud production in the case of perennials, and with size classes in some cases (Caswell and Werner, 1978; Law, 1983; McMahon and Mortimer, 1980; Mortimer, 1983; Werner and Caswell, 1977). These models are frequently used because they are simple, compact, and have well known properties (Usher, 1972).

The models using modified Leslie matrices rely on demographic studies to obtain estimates of the parameters used in the matrix. However, in the experimental area of this study, yellow nutsedge shoot density was often between 1000 and 2000 shoots m^{-2} which made the number of individuals at different plant stages very difficult to follow. Since yellow nutsedge is a perennial weed which persists in field crops through its tubers, a model relying on tuber demography would be a more appropriate tool for use in the selection of yellow nutsedge management programs. Due to the importance of field infestations, tuber population dynamics was studied on an area rather than an individual basis to maximize available research resources. Therefore, the working model suggested for this project is a modified Leslie matrix that uses tuber age classes to predict tuber population dynamics.

The proposed modified Leslie matrix model is :

$$A = \begin{bmatrix} F & F & F & F \\ p & 0 & 0 & 0 \\ 0 & p & 0 & 0 \\ 0 & 0 & p & 0 \end{bmatrix}$$

where F = tuber production
and p = proportion of tuber within one age class changing to the next age class.

with a class vector a = $\begin{bmatrix} \text{tubers 0 - 1 year old} \\ \text{tubers 1 - 2 years old} \\ \text{tubers 2 - 3 years old} \\ \text{tubers 3 - 4 years old.} \end{bmatrix}$

This model was used to integrate the information collected in the course of this project pertaining to yellow nutsedge tuber cohort longevity, tuber production in time, tuber density effect, and the effects of growth interruptions or delays on tuber production. Regressions were calculated for each of the factors and used in model building and simulations. The regressions, converted to percentages for use and uniformity, are presented in Table 12.1.

The only tuber demographic work conducted during this research project was that on tuber longevity where a tuber cohort was buried for set periods of time after which their viability was evaluated. A regression was fitted to the tuber longevity through time (Table 12.1) and subsequently was used to compile a life-table for yellow nutsedge (Table 12.2). The life-table data were compiled from the regression equation rather than the actual data. Life-tables are usually more elaborate than the one in Table 12.2, but only the data needed for the purpose of the present work have been shown.

Cold is reported as limiting yellow nutsedge distribution and causing tuber death (Mulligan and Junkins, 1976; Stoller, 1981). Therefore, the age classes of the transition matrix were separated into summer and winter groups, yielding two

Table 12.1. Functions used to determine the expected number of tubers in time in the modified Leslie matrix model.

Function	Regression equation[a]	Section[b]
Tuber production in time :		
if the number of tubers is		6
< 3540 then	$Y = 165 - 10X + 0.3X^2 - 0.002X^3$	
> 3540 and < 6515 then	$Y = 106 - 0.6X + 0.02X^2$	
> 6515 then	$Y = 101 - 0.6X + 0.01X^2$	
Growth delay in time :	$Y = 352 - 6X + 0.03X^2$	7
Growth interruption in time :	$Y = 406 - 7X + 0.05X^2$	8

[a] These regressions were derived in the respective sections of this thesis and are presented here as a percentage of their respective spring tuber populations.
[b] Refers to the sections of this thesis where the functions were derived.

Table 12.2. Simplified life table of yellow nutsedge derived from the regression on tuber longevity.

Tuber age class (months)	Proportion[a] of tubers surviving (%)	Mortality rate	Proportion[b] of tubers surviving to the next age class
0- 6	97.26680[c]	0.396590	0.603409
6-12	58.69176	0.450912	0.549087
12-18	32.22688	0.516504	0.483495
18-24	15.58154	0.585076	0.414923
24-30	6.465142	0.599837	0.400162
30-36	2.587109	0.359588	0.640411
36-42	1.656813	0.164889	0.835110
42-48	1.383622	1	0

[a] Derived from the regression equation presented in Table 5.2.
[b] Values used in the transition matrices.
[c] A precision of six decimals was used in the model and the values are presented here.

transition matrices for the model.

The two transition matrices are :

Summer transition matrix (SU) :

$$SU = \begin{bmatrix} F & F & F & F \\ 0.55 & 0 & 0 & 0 \\ 0 & 0.41 & 0 & 0 \\ 0 & 0 & 0.64 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad \begin{array}{l} \text{classes} \\ \text{0.5-1 year} \\ \text{1.5-2 year} \\ \text{2.5-3 year} \\ \text{3.5 + year} \end{array}$$

Fall transition matrix (FA) :

$$FA = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0.60 & 0 & 0 & 0 \\ 0 & 0.48 & 0 & 0 \\ 0 & 0 & 0.40 & 0 \\ 0 & 0 & 0 & 0.84 \end{bmatrix} \quad \begin{array}{l} \text{classes} \\ \text{0-0.5 year} \\ \text{1-1.5 year} \\ \text{2-2.5 year} \\ \text{3-3.5 year} \end{array}$$

where the classes are the age of the tubers,
and F = tuber production function.

The tuber production function (F) was used to calculate the number of new tubers and was based on the total number of tubers in the summer age class vector rather than individual classes. The functions are presented in Table 12.1.

Yellow nutsedge tuber production in time was studied for three years and a regression was fitted for each year due to the difference in the spring tuber population levels (Section 6). The function used in the model was also selected according to the spring tuber population level. The densities shown in Table 12.1 were determined by the mean distance between the confidence intervals of the regressions.

Several assumptions were made in developing this model, namely that :

- all tubers have died after a period of 3.5 years.
- tubers of any age class and the plants that they produce all have the same vigor.
- the carrying capacity of the area was set at 20000 tubers
- when a function was used to simulate tuber production beyond the last date to which the regression was fitted, the value of the last date was used.

The section on density effect on yellow nutsedge concluded by stating that the carrying capacity of the experimental area was 15000 tubers m^{-2} (Section 7). The regression fitted to the tuber production in time, however, showed that yellow nutsedge produced more than 19000 tubers m^{-2} at the end of the growing season (Section 6), and several samples contained more than 20000 tubers m^{-2}. Therefore, in order to prevent an underestimation of the potential of the experimental area, the carrying capacity was set at 20000 tubers m^{-2}.

12.2 Simulation conditions :

The functions presented in Table 12.1 were used to simulate some of the control methods available for yellow nutsedge.

The growth interruption experiment was conducted in order to obtain a function that was equivalent to plowing or cultivating at different times during the growing season. Only the 1983 regression was used since the 1982 experiment was not significantly affected by the interruption in growth (Section 10).

The growth delay experiment was conducted to obtain a function equivalent to applying a herbicide or cultivating. Cultivation or herbicide activity acts by killing actively growing parts of yellow nutsedge such as roots, rhizomes, or shoots, but they rarely kill the tubers (Stoller, 1981). Therefore, delaying yellow nutsedge emergence by hoeing (Section 9) can be considered as equivalent to the effect of cultivation, with yellow nutsedge tubers resprouting or sprouting immediately after the treatment, since there is no residual activity. The same reasoning can be applied to herbicides except that some of them do have a residual activity. However, selective herbicides in use in crops such as corn have a short residual activity, of the order of 4 to 9 weeks, depending on environmental conditions (Dixon et al., 1980; Obrigawitch et al., 1980; Stoller, 1981). Therefore, delayed emergence resulting from either hoeing or herbicide use would be comparable for simulation purposes.

The common approach to modeling weed populations with Leslie matrices has been; to simulate the unrestricted population growth, to determine λ, and from this to ascertain the level of control required to stabilize or reduce the population level (Mortimer, 1983). The formula can be expressed as $H = 100 (\lambda - 1/ \lambda)$ where H is the percentage of control required to stabilize the weed population. Usher (1972) presented H as the level of harvest possible without causing any population decrease. The level of control has usually been introduced in the simulations as a set value. For example, "containment may be achieved if 73.7% of all adults are annually killed" (Mortimer, 1983).

The present simulations were conducted using a similar approach, although instead of simulating a set level, control was presumed to be achieved through delayed emergence. Effectively, yellow nutsedge control levels reported throughout the literature (Dixon et al., 1980; Obrigawitch et al., 1980; Stoller, 1981) refer more to a delayed emergence than a set percentage of plants killed. The activity of most soil applied herbicides declines with time and eventually allows emergence. Sub-lethal herbicide levels might affect yellow nutsedge growth, but it was assumed that the delayed emergance experiments (Section 9) had effects similar to residual herbicide activity and consequently, the regression for delayed emergence was used.

Corn was found to decrease yellow nutsedge tuber production by an average of 24 % with extremes of 9 and 51 % (Section 11). A decreased tuber number of 10 to 20 % was assumed for the simulations of yellow nutsedge growing with corn.

Spring cereals were presumed harvested in early August, which corresponded to the last period of interrupted growth of yellow nutsedge. Cereals were considered to further decrease yellow nutsedge tuber production so that no new tubers were produced during that year. A similar reasoning was applied to winter cereals although they are generally considered as more competitive than spring cereals and are harvested earlier.

Alfalfa was considered to have little effect on yellow nutsedge during the year of establishment when no herbicides were used. Yellow nutsedge tuber production was arbitrarily set as being reduced by 95 % in subsequent years since some yellow nutsedge growth probably occurred.

12.3 Simulations :

Only a limited number of situations were simulated, and computer aided simulations were conducted for a period of 25 years. Three basic situations were simulated, followed by two simple cropping systems. The three basic situations were; yellow nutsedge having unrestricted growth, interrupted growth, and delayed emergence. They were conducted first on a pure stand of yellow nutsedge, followed by yellow nutsedge growing in corn. The cropping systems used were; alfalfa + corn, and corn + cereals.

12.3.1 Simulations in a pure stand of yellow nutsedge :

Unrestricted growth of yellow nutsedge in time was simulated with an initial population of 1 tuber per 10 m^2. The tuber population increased rapidly and reached carrying capacity within 11 years (Figure 12.1A). The oscillation apparent in all graphs are due to winter mortality. λ would be 1.32 if there was not a carrying capacity of 20000 tubers m^{-2}. Generally, λ was 0.58 for the winter period while it was 2.29

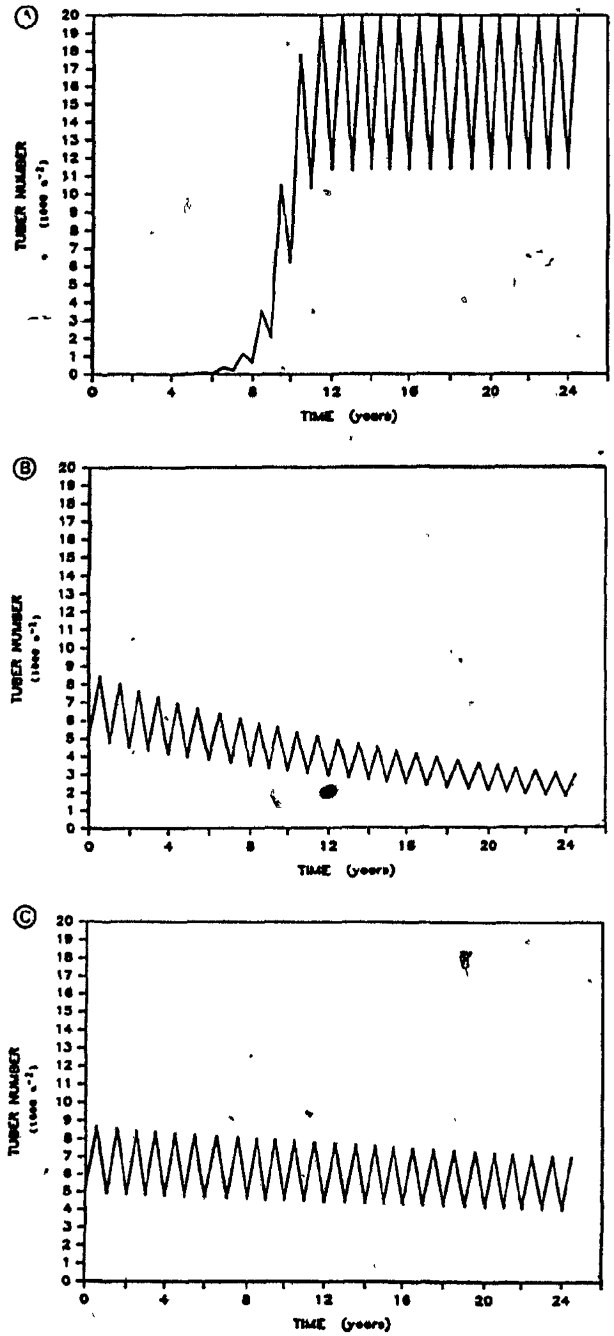


Figure 12.1 Simulation of the changes in the tuber population of yellow nutsedge with time under some conditions.

A. Unrestricted growth with an initial population of 1 tuber per 10 m^2.

B. Growth interruption after 86 days from an initial population of 5000 tubers m^{-2}.

C. Delayed emergence of 38 days. Initial population was 5000 tuber m^{-2}.

in yellow nutsedge growing alone with no restrictions, or 1.72 under the constraints of the carrying capacity. The proportion of tubers in a particular age class was, on average, approximately 75 %, 17 %, 3 %, and 1 % for first, second, third, and fourth year tubers, respectively.

Growth was determined as being interrupted at 86 days (August 8) since that was the date by which a cereal crop might be harvested or a green manure crop plowed under. The initial tuber population was 5000 tubers in the spring tuber age class of 0.5 to 1 year old. Yellow nutsedge's tuber population decreased by 4 % every year (λ= 0.96) (Figure 12.1B). The number of tubers produced in the summer was sufficient to increase the tuber population level but winter mortality caused a yearly decrease.

Yellow nutsedge tuber population was found to decrease when emergence was delayed for 38 days in a pure stand of yellow nutsedge (Figure 12.1C). That period corresponded to a minimum period of herbicide activity that would stabilize the population (taking in consideration tuber winter death). The 38 day delay actually caused a 0.84 % yearly decrease in tuber population (λ= 0.9916). This situation represented the effects of an average herbicide remaining active for several weeks. A longer delay would have reduced the population while a shorter delay would have allowed the population to increase. The initial tuber population was 5000 tubers in the spring tuber age class of 0.5 to 1 year old.

12.3.2 Simulations of yellow nutsedge growing with corn :

Simulations with the same conditions as above were repeated with the added effect of the corn crop on yellow nutsedge growth. Corn was assumed to decrease yellow nutsedge tuber production by either 10 or 20 %.

The tuber population that started with 1 tuber 10 m^{-2} reached carrying capacity after 13 or 22 years when corn reduced tuber production by 10 or 20 %, respectively. λ was 1.22 for the 10 % reduction in tuber number by corn while it was 1.05 for the 20 % reduction, with no carrying capacity limit.

Growth interruptions in August, with a tuber number reduction of 10 or 20 % attributed to corn, had a λ of 0.86 and 0.76, respectively, while it was 0.96 when yellow nutsedge's growth in a pure stand was interrupted. It appears that the more competitive the crop is, the faster the yellow nutsedge tuber population decreases. Other crops, such as cereals or green manure, would probably reduce yellow nutsedge growth more.

Yellow nutsedge emergence had to be delayed for 33 days to be stabilized when there was a 10 % reduction in tuber production. The same effect was obtained with a delay of 27 days when the reduction in tuber number was 20 %. The delay period required to stabilize a yellow nutsedge population decreased with the increased reduction in tuber production from the crop.

12.3.3 Crop simulations :

It is possible to simulate a wide combination of field operations and dates. However, for the purposes of this section, simulations of two crop management systems with one variation each were undertaken to illustrate examples of model applications. Variations simulated situations where herbicide or crop would accidently have no effect on yellow nutsedge for the period of a year.

The first system selected consisted of a cycle of 2 years corn (with a delay of 30 days used for herbicide effect) followed by 2 years cereals, for 25 years (Figure 12.2A). The variation consisted of the first system, but with no herbicide control in the first year of every second corn cycle (years 5, 13, 21)(Figure 12.2B). The tuber population increased under corn in the summer but winter mortality was greater than the increase, thereby reducing tuber population (Year 1 and 2, 5 and 6). The decrease was more severe under cereals where yellow nutsedge did not produce new tubers. There were no traces of the yellow nutsedge tuber population after 8 years of this cropping system. The lack of control situation had a greater tuber population under corn in years 5 and 6 (Figure 12.2B) . However, the tuber population still disappeared after 8 years. Such a rapid population decline can be attributed to the fact that the excellent control provided by the cereals compensated for the period of no control under corn.

The second cropping system consisted of a cycle of four

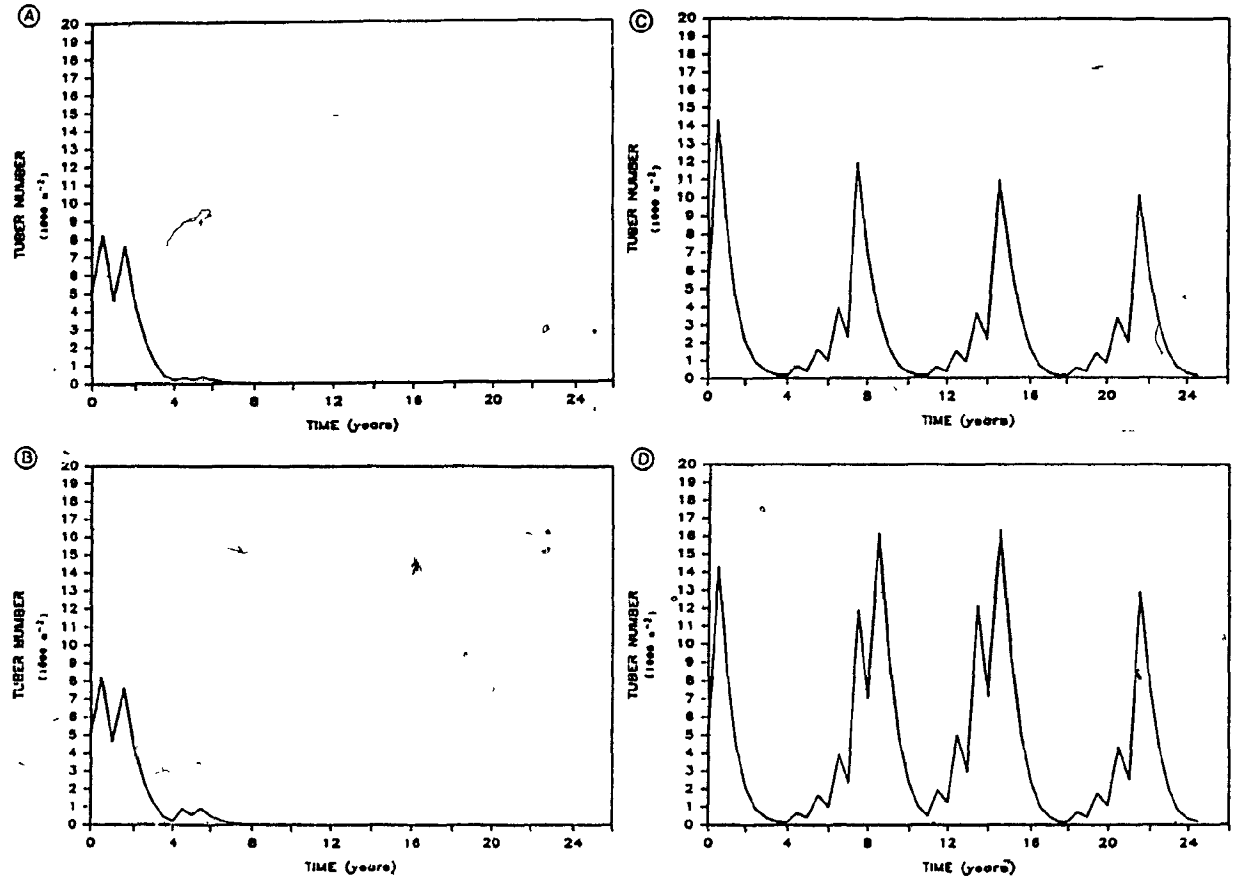


Figure 12.2 Simulation of some cropping systems and their effect on the tuber population with time.

A. Corn-cereal crops on a 2 years-2 years cycle, starting with corn.
B. Corn-cereal crops on a 2 years-2 years cycle, starting with corn, but with no control of yellow nutsedge in year 5, 13, and 21.
C. Alfalfa-corn crops on a 4 years-3 years cycle, starting with alfalfa.
D. Alfalfa-corn crops on a 4 years-3 years cycle, starting with alfalfa, but with no control of yellow nutsedge in year 9.

years alfalfa followed by three years corn for 25 years. Alfalfa did not reduce tuber production the year of establishment but controlled tuber production by 95 % in subsequent years. Corn controlled yellow nutsedge for 30 days and reduced tuber production by 20 %. The simulation began with alfalfa and 5000 tubers. The tuber population greatly increased the year of establishment but rapidly decreased afterwards, until corn was planted (Figure 12.2C). The population increased under corn but decreased after alfalfa was established. The overall population trend was a decrease in time with increases in tubers the year of alfalfa establishment or of corn growth. When yellow nutsedge was not controlled in year 9 (system 2, variation), the population greatly increased (Figure 12.2D) and took 10 years to decrease to the level of the second cycle of the simulation in Figure 12.2C.

In all simulations (Figure 12.2), tuber population decreased rapidly when there was some yellow nutsedge control either by herbicides or crops. Such a response was expected since most publications on cropping systems against yellow nutsedge report a reduction in yellow nutsedge population within a relatively short time (Keeley et al., 1979, 1983; Stoller et al., 1979).

These simulations illustrate that a vigorous crop can contribute to yellow nutsedge control. It is important to note that even if herbicides show a long period of residual activity, the vigor of the crop should not be neglected as a component of yellow nutsedge control.

12.4 Model sensitivity :

Sensitivity analysis allows for the identification of parameters that require more precise determination or those that are more likely to cause erroneous model behavior. Briefly, the method consists of changing the internal parameters of the model to determine the amplitude of their effect upon the output (Caswell, 1978; Caswell and Werner, 1978; Sargent, 1982). The sensitivity parameter is $d\lambda / d a_{i,j}$ where $da_{i,j}$ represents a change in a coefficient of the transition matrix and $d\lambda$ is the change in the intrinsic rate of increase.

The sensitivity of the transition matrices coefficients was tested for the three general functions used to depict tuber number variations in time (growth in time, interrupted growth, and delayed growth). Two levels of variation were used for each coefficient , 10 % and 25 %. Results are presented in Table 12.3.

Coefficients of the transition matrices are not particularly sensitive to changes in their coefficients (Table 12.3). A sensitivity coefficient of 1 means that the model response is proportional to the changes. Sensitivity coefficients with absolute values smaller than 1 reflect a smaller change than the change in the matrix coefficient value; while absolute values greater than 1 indicate that the coefficient caused a change greater than its change in value.

Table 12.3. Sensitivity coefficients of the transition matrices.

Simulations conditions	Transition matrix coefficient	Coefficients variation			
		+10%	-10%	+25%	-25%
1 tuber 10 m^{-2}					
	F_{21}	1.063	1.062	1.064	1.061
	F_{32}	0.219	0.212	0.224	0.207
	F_{43}	0.032	0.032	0.032	0.031
	F_{54}	0.011	0.011	0.012	0.011
	S_{21}	-0.052	-0.050	-0.054	-0.049
	S_{32}	-0.009	-0.009	-0.009	-0.009
	S_{43}	0.004	0.004	0.004	0.004
	S_{54}	0	0	0	0
interrupted after 86 days					
	F_{21}	0.698	0.697	0.700	0.696
	F_{32}	0.201	0.194	0.208	0.188
	F_{43}	0.042	0.042	0.043	0.041
	F_{54}	0.020	0.020	0.020	0.020
	S_{21}	-0.046	-0.043	-0.048	-0.041
	S_{32}	-0.009	-0.008	-0.009	-0.008
	S_{43}	0.006	0.007	0.006	0.006
	S_{54}	0	0	0	0
delayed 38 days					
	F_{21}	0.756	0.754	0.757	0.753
	F_{32}	0.205	0.197	0.212	0.192
	F_{43}	0.041	0.040	0.041	0.039
	F_{54}	0.018	0.018	0.018	0.018
	S_{21}	-0.047	-0.045	-0.049	-0.043
	S_{32}	-0.009	-0.009	-0.009	-0.009
	S_{43}	0.006	0.006	0.006	0.006
	S_{54}	0	0	0	0

Sensitivity coefficients of changes in tuber number over time are presented in Table 12.4 where unrestricted growth refers to growth in time as opposed to delayed or interrupted growth. Sensitivity coefficients are greater for tuber production functions than for transition matrices. These results are expected since any changes in tuber production will have immediate effects on λ. Mortimer (1983) reported similar trends for bud production in Agropyron repens (L.) Beauv.. The sensitivity coefficients of the interrupted or delayed growth function are more than double that of the unrestricted growth (4.6 and 4.1 opposed to 1.4, respectively). Their magnitude is still within reasonable limits, but indicates that the growth interruption and growth delay functions might be the weakest elements in the model.

The matrix model used here could be qualified as a "robust" model, since slight variations in the matrix coefficients will have few consequences on the overall model performance.

12.5 Model verification :

Model verification is often defined as ensuring that the model behaves as intended. There is no set of rules regulating verification, but the main step involves ensuring that the computer programs used in the simulations perform as intended (Sargent, 1982).

The computer program results used for the simulations were

Table 12.4 Sensitivity coefficients of the tuber production functions.

Coefficient variation	Growth in time		
	Unrestricted	Interrupted	Delayed
-10%	1.376	4.633	4.125
+10%	1.378	-2.626	-2.001
-25%	1.372	2.448	4.024
+25%	1.379	-0.445	-0.160
-50%	1.036	1.707	1.653
+50%	1.381	0.284	0.455

tested and verified by conducting the calculations manually on some of the data used in the simulations. The logic of the program and the algorithms used were thoroughly traced for errors in code implementation. Data extremes were used in some of the simulations to verify that safeguards placed in the program performed effectively to prevent erroneous results. There is great confidence that the program used for the simulations performed as intended.

12.6. Model validation :

A definition of validation is " ... the substantiation that a computerized model within its domain of applicability possesses a satisfactory range of accuracy consistent with the intended application of the model" (Lewandowski, 1982).

Data were not collected to statistically validate the model because of the labour intensive aspect of this project. Since the purpose of the modeling effort in this thesis was to provide a tool for use in the development of yellow nutsedge management programs, it was intended that such programs would be used to validate the results of the simulations.

Validation techniques used in this study were sensitivity, face validity, traces, and historical data validation (Sargent, 1982). Sensitivity analysis has already been used in this section (Section 12.4) to judge if the model was relatively stable to changes in its parameters.

Face validity consisted in asking other researchers knowledgeable about yellow nutsedge whether the model's output was reasonable. The model's logic and input-output was considered adequate by three fellow researchers involved with yellow nutsedge.

Traces involved following the fate of the different components of the model in the computer program to determine if the model's logic and the program were coherent. This work was conducted while verifying the model, and has been presented in the section on model verification (Section 12.5).

The historical data validation consisted of verifying the model through data or results available in the literature. There were several reports on yellow nutsedge growth in time or on the effect of a delayed or interrupted growth if the assumptions presented in Section 12.2 were accepted. They consisted of equating the effect of cultivation or herbicide on growth delay while growth interruptions would be equated to plowing or cultivating. Although the literature abounded with reports on yellow nutsedge control by herbicides or cultivation, reports where spring and fall tuber population were sampled are very rare. Only two such reports were used. One of these covered the effect of crop rotations on yellow nutsedge (Keeley et al., 1983), while the other one examined the control of yellow nutsedge in corn (Stoller et al., 1979).

Keeley et al. (1983) reported a 47 to 76 % decrease in tubers during the first experimental year and 75 to 90 % after the second year. These values were of the same magnitude as the perfect control values from the model where tuber population decreased by 67 % after a year (Table 12.2, 0-6 to 12-18 months) and by 93 % after two years (Table 12.2, 0-6 to 24-30 months).

The study by Stoller et al. (1979) allowed the calculation of a finite rate of increase. Control plots where yellow nutsedge grew freely had a λ of 6.3, while it was 5.1 in this research project at tuber densities below 3540 tubers m^{-2}. Tuber mortality rate was 74 % in their treatments with no yellow nutsedge growth while it was 80 % in this study (Table 12.2, 12-18 to 24-30 months).

The validations conducted with the available data confirm the adequacy of the model. The model is therefore considered validated for the purpose of this study. Model validation is a continuous process and should not be considered as completed by this project. However, the model is judged as satisfactory for present purpose, and is not rejected. Furthermore, as previously mentioned, yellow nutsedge management programs tested or adopted after completing the simulations should be used to further validate the model and to improve upon it.

Section 13

SUMMARY AND CONCLUSIONS

The main objective of this study was to develop a model of yellow nutsedge tuber population dynamics that could, through computer simulations, be used to assist in the selection of crop management systems that would reduce yellow nutsedge populations. A large volume of data on yellow nutsedge was available in the literature, but as it originated from several areas with different growing conditions, and since there was considerable variability between biotypes, the range in the type of data collected made their quantitative use both impracticable and unreliable. Consequently, data had to be collected locally to obtain parameter estimates and functions of tuber population changes in time required for model development, and to fill gaps in the knowledge of yellow nutsedge population dynamics.

Tubers and achenes were found to be the only means through which yellow nutsedge was propagated in the study area since rhizomes and basal bulbs were not able to regenerate the plant (Section 3). The production of achenes (approximately 200 m^{-2}) was considered negligible as compared to the production of tubers (approximately 15000 m^{-2}). Tubers can, therefore, be considered as the main means through which yellow nutsedge infestations are propagated in field infestations. Achenes might be important for dispersal through time, since they remain viable for up to 20 years in the soil (Goss, 1924), or through space, due to their small size.

The importance of tubers in maintaining infestations in field crops warranted using tubers exclusively rather than the whole plant life cycle in the modeling effort. Tubers had two attributes, size and longevity, that were relevant to the study of tuber population dynamics.

In this study, tuber size and dry weight were found to be closely related and could be used interchangeably (Section 4). The sizes of the dry tubers were normally distributed with a mean of 4.86 mm. From that distribution, two arbitrary size classes (small and large, based on 3.97 mm) were used to measure all samples. The proportion of small tubers was 28 % that of the total number of tubers (Section 4).

Tuber longevity and plant vigor reportedly increased with tuber size (Stoller et al., 1972; Stoller and Wax, 1973; Thullen and Keeley, 1975). Smaller tubers buried in the field were found to lose viability faster than larger tubers, while the last tubers died in the period between 3.5 and 4 years after burial (Section 5).

Tuber initiation started in mid-June and the rate of tuber population increase depended on the original spring tuber population (Sections 6 and 7). Up to 20000 tuber m^{-2} were found in fall samples although, the site most likely had a carrying capacity of between 15000 and 20000 tubers m^{-2}. The majority of tubers were in the top 15 cm (86 %), but some tubers were found to a depth of 30 cm in the soil profile. The proportion of small tubers was approximately 60 % of the total number of tubers in the top 5 cm of the soil (Section 8).

Yellow nutsedge tuber population levels did not increase compared to that of the initial spring level when its emergence was delayed for more than two months (Section 9). Growth interruptions were not as successful as delayed emergence in preventing tuber population increase but they required less labor. At best, yellow nutsedge growth interruptions allowed the tuber population to only increase by 60 % compared to 400 % when yellow nutsedge was allowed to grow freely (Section 10).

The corn crop, compared to yellow nutsedge growing in a pure stand, decreased the fall tuber population by 24 % through interference with yellow nutsedge growth. Tubers size and dry weight were also reduced when yellow nutsedge grew in corn. Approximately 10 % more tubers were produced on the corn row than between rows due to fertilizer placement (Section 11).

Regression equations of tuber population changes in time were derived from data obtained in the course of this research project. They provided coefficient estimates or tuber production functions that were used in the modified Leslie matrix model presented in Section 12. The model was found to be valid in that it described realistic behavior of the tuber population in time. The model, furthermore, exhibited a desirable characteristic in that it was not particularly sensitive to changes in either parameters or input values.

Limitations mentioned concerning yellow nutsedge studies conducted elsewhere apply equally to this project. The data collected does not necessarily apply directly to other areas due to the differences in yellow nutsedge biotypes and growing conditions. Trends exhibited by data collected in various experiments within this project and by the model simulations should, however, provide qualitatively usable information, to aid in the selection of yellow nutsedge management programs.

Section 14

CONTRIBUTIONS TO KNOWLEDGE

The biology, ecology, and control of yellow nutsedge have been extensively studied, but there were several areas that had to be clarified before the information could be synthesized in a compact and quantitative form, such as the model presented in Section 12. The following are considered to be contributions to original knowledge:

1. Since viable seeds were found in the experimental area, they might have a more important function than previously believed in Canadian populations (Mulligan and Junkins, 1976).

2. This is only the second research report where rhizome and basal bulbs were tested for their ability to regenerate yellow nutsedge. The first report was made by Orsenigo (1953). Rhizomes and basal bulbs cannot regenerate yellow nutsedge.

3. The size or weight of yellow nutsedge tubers have often been reported in the literature (Table 4.3). This is the first time that the size of yellow nutsedge tubers were

sampled to obtain their distribution and weight.

4. Tuber longevity has been reported to range from 1.5 years to 4 years (Doty, 1973; Stoller and Wax, 1973). There were a few instances where tuber cohorts of a set age were sorted by size and buried (Thullen and Keeley, 1975), but this is the first instance where longevity was studied on an extensive number of tuber sizes.

5. This is the first study of yellow nutsedge tuber production in time in an already established infestation in the field. There are several reports on yellow nutsedge growth in time, but they were all conducted in containers (Kogan and Gonzalez, 1979; Phillips, 1980).

6. The carrying capacity for yellow nutsedge was reported by Lapham et al. (1985) to be 10411 tubers m^{-2} in Zimbabwe. The present report is the first North American report of yellow nutsedge carrying capacity which was between 15000 and 20000 tuber m^{-2}.

7. This is the first report made on tuber distribution in the soil that includes tuber size as a variable. Particularly interesting is the fact that small tubers constituted 66 % of the total number of tubers in the top 5 cm of the soil in the experimental plots (Section 8). Furthermore, the top 5 cm contained 34 % of the total number of tubers in the soil profile.

8. This is the first time that delayed emergence experiments

were conducted and equated to the effect of herbicides applied to the soil. This approach opens new avenues in simulations in that it allows quantification of the time value which leads to be a better understanding and more accurate expression of weed control, as opposed to using a simple percentage of repression.

9. The effect of control methods used in corn against yellow nutsedge are frequently reported, but the effect of the crop itself on yellow nutsedge has never been investigated. Corn was found to reduce yellow nutsedge tuber production by 24 % on average.

10. a. Modified Leslie matrix models have been used to model weed population dynamics, but this is the first time that such a model only considers propagules (tubers) instead of the various aspects of the plant's life cycle.

b. Lapham et al. (1985) did present a model of yellow nutsedge population dynamics based on a demographic study, but only intraspecific competition was available as a function. The present model is the most elaborate model ever developed for yellow nutsedge.

c. Although such models have been used before (Mortimer, 1983), this is possibly the most comprehensive weed model presented in that it integrates propagule longevity, propagule production as a function of density, the effect of delayed emergence (soil applied herbicide), and the effect of growth interruptions (plowing or cultivation).

Section 15

SUGGESTIONS FOR FUTURE RESEARCH

1. Tuber longevity should be determined in undisturbed populations in the field. The design should consist of planting tubers and allowing yellow nutsedge to grow for one year. Any tuber production should be prevented in subsequent years and the viability of the tuber population assessed.

2. Since the majority of tubers are in the top 15 cm with 66 % of the small tubers in the top 5 cm, the effect of various tillage techniques and different equipment on the dispersal of tubers in the soil profile should be further investigated, as should their effect on winter tuber mortality.

3. Stochastic (probabilistic) simulations should be conducted with the model to obtain a more realistic population behavior. Herbicides effectivity should have some probability associated with their use (such as "25 % probability of delaying yellow nutsedge emergence 10 days

only, 50 % for 20 days..."). The confidence interval of the regressions already utilized could be used.

4. The economic aspects of using the various control techniques against yellow nutsedge should be assessed. To determine the crop returns assessed with alternative control methods. Most of these values could be expressed as linear programming equations with constraints. The most economical alternatives could then be identified by maximization.

APPENDICES

Appendix 1. Effect of time and soil depth on mean tuber number, tuber number ratio, tuber dry weight and tuber dry weight ratio of yellow nutsedge.

Time (months)	Tuber depth (cm)	Tuber number (m^{-2})	Tuber number ratio	Tuber dry weight (gm^{-2})	Tuber dry weight ratio	Tuber number (m^{-2})	Tuber number ratio	Tuber dry weight (gm^{-2})	Tuber dry weight ratio
		----- young tuber population -------				-------- old tuber population ------			
0	2.5	1946.7	0.39			98.7	0.42	2.6	0.17
0	7.5	1619.2	0.42			157.3	0.57	3.6	0.37
0	12.5	2344.0	0.51	65.4	0.25	448.0	0.55	9.7	0.40
0	17.5	1536.0	0.39	74.8	0.15	616.0	0.69	11.9	0.45
0	22.5	626.7	0.27	37.7	0.09	96.0	0.47	4.2	0.18
0	27.5	113.3	0.32	7.3	0.09	42.7	0.18	3.2	0.04
6	2.5	218.7	0.38	6.4	0.18	29.3	0.37	0.8	0.14
6	7.5	856.0	0.46	33.6	0.27	50.7	0.53	1.3	0.44
6	12.5	1097.6	0.59	39.8	0.33	133.3	0.54	3.0	0.37
6	17.5	1017.6	0.40	54.6	0.15	160.0	0.74	2.3	0.47
6	22.5	281.6	0.31	18.4	0.14	72.0	0.43	2.7	0.19
6	27.5	99.2	0.33	5.5	0.15	5.3	0.00	0.0	
12	2.5	270.7	0.32	8.1	0.18	6.7	0.67	0.2	0.20
12	7.5	878.7	0.51	26.0	0.26	32.0	0.43	1.2	0.33
12	12.5	1402.7	0.56	51.9	0.23	310.7	0.55	9.0	0.37
12	17.5	768.0	0.23	46.1	0.07	492.0	0.77	9.2	0.56
12	22.5	486.7	0.34	31.4	0.09	101.3	0.42	5.5	0.14
12	27.5	90.7	0.33	5.6	0.19	13.3	0.00	0.8	0.00
18	2.5	120.0	0.61	3.3	0.35	2.7	0.00	0.0	
18	7.5	750.7	0.56	22.5	0.31	106.7	0.67	1.7	0.47
18	12.5	760.0	0.53	32.5	0.24	104.0	0.70	2.6	0.56
18	17.5	464.0	0.35	26.7	0.13	50.7	0.67	1.7	0.37
18	22.5	98.7	0.31	6.7	0.16	8.0	0.00	0.5	0.00
18	27.5	10.7	0.00	1.0	0.00	0.0		0.0	
24	2.5	80.0	0.44	2.7	0.31	2.7	0.00	0.0	
24	7.5	413.3	0.45	14.0	0.25	40.0	0.57	1.1	0.43
24	12.5	497.3	0.38	21.2	0.20	101.3	0.62	2.9	0.37
24	17.5	280.0	0.27	17.4	0.11	34.7	0.33	1.7	0.20
24	22.5	157.3	0.34	12.8	0.11	0.0		0.0	
24	27.5	16.0	0.00	1.0	0.00	0.0		0.0	
30	2.5	58.7	0.39	1.5	0.18	0.0		0.0	
30	7.5	240.0	0.45	12.0	0.22	18.7	0.80	0.3	0.57
30	12.5	496.0	0.53	20.5	0.28	141.3	0.73	2.1	0.55
30	17.5	304.0	0.48	17.4	0.18	93.3	0.60	1.6	0.43
30	22.5	93.3	0.38	7.1	0.21	24.0	0.83	0.5	0.74
30	27.5	5.3	0.00	0.6	0.00	13.3	0.00	0.2	0.00
LSD 0.05			0.23	22.9	0.18		0.32	3.9	0.35

Appendix 2: Effect of delayed emergence on the tuber dry weight and tuber dry weight ratio of yellow nutsedge.

Variable name	1982 experiments number 1: Tuber dry weight (g)	1: Tuber dry weight ratio	2: Tuber dry weight (g)	2: Tuber dry weight ratio	3: Tuber dry weight (g)	3: Tuber dry weight ratio	4: Tuber dry weight (g)	4: Tuber dry weight ratio
Time of allowed emergence (days)								
0	534.2	0.19	453.6	0.20	689.4	0.16	646.8	0.16
14	549.6	0.14	388.6	0.13	637.4	0.10	421.5	0.17
28	279.1	0.19	256.4	0.19	316.2	0.15	178.5	0.16
42	136.7	0.24	140.5	0.20	146.0	0.23	74.4	0.29
56	88.1	0.25	143.1	0.24	82.1	0.28	86.2	0.27
70	63.0	0.17	73.2	0.25	45.9	0.28	81.9	0.23
84	114.6	0.15	106.4	0.17	56.5	0.21	76.9	0.22
98	62.7	0.29	92.2	0.18	63.4	0.25	68.9	0.24
LSD (0.05)	100.6	0.10	109.8	N.S.	93.8	0.12	114.7	N.S.

	1983 experiments number 1: Tuber dry weight (g)	1: Tuber dry weight ratio	2: Tuber dry weight (g)	2: Tuber dry weight ratio	3: Tuber dry weight (g)	3: Tuber dry weight ratio	4: Tuber dry weight (g)	4: Tuber dry weight ratio
0	543.5	0.14	747.1	0.15	487.4	0.10	436.9	0.12
18	811.6	0.13	506.2	0.16	732.9	0.13	516.4	0.14
31	595.2	0.16	444.2	0.14	488.0	0.11	567.6	0.17
46	468.9	0.16	288.5	0.17	143.4	0.22	328.7	0.15
58	425.7	0.16	173.3	0.18	114.4	0.21	158.8	0.23
72	31.3	0.25	94.8	0.21	81.5	0.29	182.3	0.26
87	45.0	0.16	81.2	0.13	59.1	0.23	60.6	0.15
100	73.3	0.21	49.7	0.2[illegible]	29.2	0.36	106.7	0.22
115	101.1	0.16	105.6	0.14	45.4	0.17	89.9	0.34
LSD (0.05)	206.9	0.08	220.1	N.S.	123.0	0.12	204.7	0.10

Where N.S. stands for no significant effects attributable to the delay of emergence.

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