"The ecology of chufa (Cyperus esculentus sativus)"

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“The ecology of chufa (*Cyperus esculentus sativus*)”

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Summary

The purpose of this project was to investigate some elements of the ecology of chufa (Turkey Gold®), its patterns of growth and sensitivity to environmental conditions, and its potential for interacting with closely-related nutsedges co-occurring in the United States. Of particular interest was whether the potential exists for hybridization between chufa and the con-specific yellow nutsedge and, if so, what effects such hybridization could have on chufa ecology. Additionally, several experiments were conducted to determine whether extreme temperatures encountered during shipping or storage have potential for negative effects on the quality of chufa tubers.

The objectives of this research project were to:

1. Prepare a bibliography of chufa and yellow nutsedge literature whether peer-reviewed, in regional and trade journals, or in associated fields of research such as food chemistry.

2. Determine the potential for cross-pollination and genetic outcrossing between chufa and wild nutsedges. This objective was relevant because of the possibility of creating weed problems by planting chufa in natural areas.

3. Investigate the importance of competition, soil type, fertilizer, time of sowing, and the interactions between these factors on the growth and productivity of chufa.

4. Investigate the germination (sprouting) requirements and parameters of chufa. Of particular interest was to find out more about chufa sensitivity to high temperatures.

Bibliography
A partial bibliography was produced as part of this project in an attempt to review the available literature on chufa, its production, and its uses. A number of papers concerning yellow and purple nutsedges were included because of their relevance to understanding chufa biology and physiology. A concerted effort was made to locate as many international papers as possible regardless of the language of origin; however, actual copies of the magazines and journals containing them were very difficult to locate despite visits to large and excellent libraries at the University of Georgia, Clemson University, the University of California Davis, and the University of Miami. What this illustrated was that very little formal research has been or is being conducted on chufa and those few studies are being reported in regional or obscure journals.

This trend is true even for yellow and purple nutsedges which are extremely important economically to the agriculture industry. Because nutsedges are viewed as weeds, the vast majority of reports have focused on ways to eliminate or reduce their presence in crops with very little attention given to their biology other than how they take up herbicides. As a result, the biology of nutsedges as a whole is less well-known that one would expect given their world-wide importance (Holm et al. 1991).

In recent years, a growing number of high quality reports on chufa and nutsedges have emerged. These reports tend to be found in weed, agriculture, and food science journals and not in the mainstream biology or ecology journals. Thus, the research is usually very applied, but very good results have been reported on basic biology nonetheless. The most impressive recent reports (as of January 2006) have been from the Pascual and Maroto lab in Valencia, Spain, which is the location of most international commercial production and the source for Turkey Gold® used by the NWTF. Unfortunately, their reports are usually in Spanish and often published in regional journals.

The appearance of recent and high quality publications is important for another reason. In my review of the older chufa literature, I found an alarming problem: there are few good scientific papers. A number of the widely cited papers are probably not about chufa, but about yellow nutsedge, and are not very scientific. Both of these aspects are a serious problem for those interested in chufa production. For example, Mokady and Dolev (1972) report on the nutritional value of *Cyperus esculentus* and are clearly referring to chufa (grown in Israel) despite not using the cultivar designation in the Latin name. In contrast, Kelley (1990) and Kelley and Fredrickson (1991) refer to wild growing *Cyperus esculentus* as chufa and these papers are almost certainly referring to wild yellow nutsedge. Tellingly, both papers refer to chufa as a "common emergent perennial species in seasonally flooded wetlands" and the study plots in Kelley (1990) were vegetated with naturally occurring "chufa". Kelley and Fredrickson (1991) is widely cited because it is part of the Waterfowl Management Handbook produced by the US Fish and Wildlife Service. Interestingly, the drawings show chufa flowering which is highly unlikely in chufa, yet also show a rooting system that is very fibrous which is more like chufa than yellow nutsedge. However, the later drawings of the production of tubers very clearly indicate that the plant in question is yellow nutsedge and not chufa. In contrast to both of these authors, Defelice (2002) confusingly switches back and forth between chufa and yellow nutsedge in an article that appears to be about chufa from the title, but is largely about yellow nutsedge.

Therefore, unless older reports are clearly describing chufa, the accuracy of the reported data is suspect and the papers must be read carefully to determine the exact plant under investigation. As a caveat, the references used in the following report, particularly those relating to nutsedge physiology and characteristics, are mostly draw from the yellow nutsedge literature and may be only partly accurate for chufa biology.

I. The potential for cross-pollination between chufa and yellow nutsedge

Yellow nutsedge (YNS) are reported to flower when they receive 12-14 hours of daylight (Jansen 1971). We assumed that chufa would follow a similar course of development, however, it has been reported that chufa flowers only rarely under field production conditions (De Vries 1991). YNS flowers readily and produces seed although little natural reproduction is from seed and the necessity for cross-pollination (out-crossing) is not clear. The heavy dependence on asexual reproduction (tubers) is characteristic of weedy plant species. Therefore, although it seemed possible that chufa could cross-pollinate with YNS, we also recognized that plants produced from such seed would probably not be very aggressive as weeds.

To investigate the potential for crossing chufa with YNS, we planted tubers of both plants in the greenhouse and in a common garden in large pots with either different regional soils or potting soil. Both chufa and YNS were included together in several experiments and all plants over two summers were monitored for flowering. We manipulated a number of factors including soil type, soil nutrients (2 types), water availability, day length, competition (2 types), and timing of sowing. We were very successful at growing plants and producing tubers, however, over the course of two years and with over 1000 experimental plants, only one chufa plant ever flowered.

The chufa that flowered in the summer of 2003 produced 19 new tubers. These were held over the winter and sown indoors, then transplanted outdoors. All 19 tubers produced new plants. As before, YNS were sown both indoors and outdoors as potential pollinators. The main objective was to determine whether the flowering behavior of the chufa plant was a genetic trait or a particular phenotypic response. If genetic, the plants produced from the tubers were expected to flower also. However, in the summer of 2004, none of the tubers from the single flowering chufa produced another flowering plant.

The potential for cross-pollination remains a possibility. It is therefore important to understand the possible outcomes of such an event:

1. Chufa <u>do not</u> flower consistently and only rarely. The possibility of crossing with wild nutsedges is extremely low because the two species would have to distribute pollen at the same time and be within very close proximity.

2. Chufa <u>do</u> flower consistently within a family line, but <u>do not</u> cross pollinate with wild nutsedges. There should be very little concern about planting chufa in wild areas.

3. Chufa <u>do</u> flower consistently and <u>do</u> cross with wild nutsedges. Although the possibility of crossing would still be very uncommon because flowering is so rare in chufa, this outcome requires that seeds produced by the cross be grown to determine what changes in character traits may have occurred due to genetic recombination. For example, of interest is whether the resulting offspring will be more like the weedier nutsedges, if they would flower more often, and if they will produce tubers of lower nutritional quality. If chufa-nutsedge crosses flowered more often than chufa, then hybridization would create in increased potential for more genetic exchange.

After four years of observation, I conclude that the first option is almost certainly correct with the following implications: flowering is not predictable or common, the probability of outcrossing with wild nutsedges is remote, and the danger of possibly creating another weedy species by planting chufa in areas with yellow nutsedge for the purposes of game forage is extremely low. However, although one plant flowered during these experiments, I do not know why that plant flowered, and not others, given that they all grew in the same environmental conditions.

It is my opinion that the original development of chufa as an agricultural cultivar represents a genetic abnormality. Although not investigated in this project, I believe that chufa represents a polyploid version of yellow nutsedge (which itself is likely to be a paleopolyploid) that is generally incapable of flowering and producing viable seed or, if it does, it is reproductively isolated from wild nutsedge (Stebbins 1940). Polyploidy is a recognized characteristic of up to 70% of all angiosperms, virtually all grasses, and is often related to highly clonal growth patterns (Stebbins 1940). In the case of chufa, polyploidy has resulted in a fast-growing plant with short rhizomes and fibrous roots. Other favored characteristics have been selected by chufa growers over the years, such as large but short-lived tubers with higher carbohydrate and lipid content than normally found in wild nutsedges. Lastly, it is my opinion that a careful morphological and karyotype examination of chufa would probably result in a new species designation rather than the current subspecies designation.

II. Factors affecting germination and viability of tubers

a. Germination temperature

One factor in growing chufa is the need to know the best time to sow the tubers without exposing them to factors that could reduce production in the field. For example, if chufa is sown when temperatures are low and germination is suppressed, the tubers will remain dormant in the soil and exposed to predation and attack by fungi. In contrast, sowing tubers after spring temperatures are high enough for germination would mean delaying growth and production of new tubers. Obviously, to maximize production, sowing should coincide with the appropriate growing conditions.

Studies on nutsedges have reported that germination is initiated at temperatures at or above 20^{o}C (about 70^{o}F), but optimal germination occurs when temperatures alternate in a natural day/night pattern (Holt & Orcutt 1996, Miles et al. 1996). (Technically, chufa tubers do not germinate, but sprout as the dormant meristems become activated.) We verified this sprouting response in chufa by sowing 476 tubers in several locations with different average and alternating temperatures. Tubers were sown in 1” x 6” plastic seedling tubes and placed in three environments: a growth chamber with controlled temperatures, ambient (shaded) conditions outdoors, and a greenhouse. The results after 14 days were:

Temperature	Emergence	Location
10^{o}C(50^{o}F) night/20^{o}C(68^{o}F) day	0%	Growth chamber
15^{o}C(59^{o}F) night/25^{o}C(77^{o}F) day	30%	Growth chamber
~20^{o}C(70^{o}F) night/~25^{o}C(80^{o}F) day	60%	Greenhouse
~20^{o}C(70^{o}F) night/~30^{o}C(86^{o}F) day	80%	Outdoors

Chufa did not emerge well or only very slowly when nighttime temperatures were below 68^{o}F (20^{o}C), but grew readily at any combination of temperatures over 68^{o}F. Germination was greatest at the highest daytime temperature. The response of chufa to temperature is very similar to that of YNS. The best germination was close to that reported for Turkey Gold (83%) in part because we chose tubers randomly rather than intentionally picking out large or healthy looking samples. All tubers were weighed before the experiment and non-germinating tubers were not different in weight from germinating tubers. Also, of the several soil types we used, none had any effect on germination.

b. Temperature sensitivity among chufa accessions

In an experiment to measure more precisely the temperature requirements of two accessions of chufa (Georgia chufa and Turkey Gold®), tubers were wetted in Petri dishes and held for ten days at different temperatures. We chose three constant temperatures: 20^{o}C (68^{o}F), 25^{o}C (77^{o}F), and 30^{o}C (86^{o}F), and two fluctuating temperatures: (25^{o}C day - 15^{o}C night and 30^{o}C day - 20^{o}C night). The two fluctuating combinations had the same average as the two lower constant temperatures. We looked at how quickly 50% of the tubers sprouted under these conditions and found that Turkey Gold® emerged more rapidly at cooler temperatures than did the Georgia population. However, both populations emerged best at the lower fluctuating temperature and did not differ. These results were consistent with other yellow nutsedge studies. At the highest temperature (30^{o}C), many tubers were attacked by fungi and bacteria and this treatment was discarded.

In summary, there is a definite temperature preference in chufa and noticeable response variation among the different chufa accessions. Some implications are obvious: sprouting at low temperatures suggests that some accessions could be used in cooler parts of the country. However, early emergence also implies that such chufa could be more competitive for light because it would grow and establish sooner than other weedier species and would be less suppressed by neighbors. The chufa literature indicates that earlier sowing leads to greater tuber production (Thullen & Keeley 1987) and therefore earlier emerging chufa should be more productive.

c. The effect of extreme temperatures on chufa tuber viability

Commercial chufa sellers related the concern that low germination rates in some Turkey Gold® chufa could be the result of elevated temperatures during shipping. We conducted three experiments to better understand the effect of high temperature on tuber viability. As a preliminary study, we exposed five samples (250 tubers each) to 24 hour or 168 hour (1 week) periods of elevated temperature [approximately 40^{o}C (104^{o}F), 50^{o}C (122^{o}F) and 60^{o}C (140^{o}F)] to simulate the conditions that may be encountered during overseas shipping. We then planted the 1250 tubers in potting soil in plastic seedling tubes at constant 22^{o}C. Private tests showed 83% emergence of Turkey Gold® tubers, but in this experiment we recorded only 68% emergence which is likely a result of the temperature conditions.

We found a trend toward loss of tuber viability at higher temperatures, but it was not statistically strong. Emergence at the highest temperatures (60^{o}C for 1 day) was significantly lower than the control (68% vs 58%), but when all data were considered together the trend was not highly significant. Had the control emergence been nearer to the private test values, all temperatures tested would probably have shown a significant decrease in tuber viability.

After some discussion we continued this testing in a different way. Fully dried tubers are less likely to be affected by temperature extremes because the embryos are fully dormant. The absence of cellular water may prevent them from being damaged during heat exposure. Embryos are activated when water is absorbed into the tissues. Therefore, we repeated the above tests with tubers that had a slightly higher water content to investigate whether tuber damage is a direct result of heat or to a combination of heat and moisture.

As a preliminary study, twenty samples of 100-200 tubers were allowed to gain about 10-12% moisture by weight, then subjected to a short heat pulse. Half of the samples were in plastic bags to retain the moisture, half were in plastic bags but were allowed to dry as they heated. Unfortunately, we did not have tight control over the temperature which ranged from 60-80^{o}C depending on the location of the samples in the drying oven. As a consequence, the moist tubers were held at a somewhat cooler temperature than the drying tubers.

The results suggest that extreme heat plus additional moisture can greatly increase tuber mortality. A control sample of tubers germinated at 84% as expected for Turkey Gold®. However, tubers that remained moist while heated to about 60^{o}C germinated at only 31%. Tubers that were allowed to dry as they heated to greater than 60^{o}C germinated at 12%. Thus, heat and moisture do appear to have a detrimental effect on tuber survival, but a fully controlled experiment was needed to determine the exact relationship.

Therefore, we treated 100 samples of 50 tubers (4500 total) in several ways. First, ten true controls were neither heated not allowed to absorb moisture. A second set of controls were heated at each temperature only. Eighty samples were allowed to increase their mass by absorbing water in humid conditions and the increase ranged from 4.5% to 18%. Half of the higher moisture samples were heated for 96 hours (4 days) at about 40^{o}C and half for the same length of time at about 60^{o}C. All samples were then sown in the greenhouse (ambient temperatures) by placing all 50 tubers from each sample in a 4" pot containing potting soil and allowed to germinate.

The 10 true control samples germinated at an average of 92% which was higher than stated standards. Samples used as temperature controls showed about 82% emergence at 40^{o}C and about 75% for 60^{o}C. We conclude from these results that high temperatures up to 60^{o}C (140^{o}F) have very little impact on chufa viability when the tubers are kept dry.

For the temperature treatments, we used regression analysis to test whether moisture content affected the survival of tubers. We found a significant and strong effect that was highly dependent on both moisture content and temperature. As moisture increased, tuber viability decreased significantly but linearly after being held at 40^{o}C **(Fig. 1a)**. However, at 60^{o}C, viability decreased dramatically to near zero even at relatively low moisture content **(Fig. 1b)**. At 6% moisture, emergence was as high as 80% at 40^{o}C, but was nearly zero for most samples at 60^{o}C.

Summary- Our experiments demonstrated that chufa tubers are highly resistant to elevated temperatures when they are maintained in a dry state. However, the same temperatures can greatly reduce viability when tubers are allowed to increase moisture content through contact with humid air. It is possible that reduced germination of tubers that have been shipped from international ports may be the result of a combination of extreme conditions experienced in transit. International and domestic tubers, however, could still be exposed to lethal conditions if stored improperly in, for example, metal sheds exposed to direct summer sun and ambient humidity. Care should be taken to avoid these conditions.

III. Emergence variation among different chufa accessions

Early emergence results in a longer growing season and increases production accordingly. Early emergence also has been associated with higher competitive ability because plant size is directly related to the ability to dominate in the struggle for light or soil resources. Physiologically, the ability to grow earlier in the season implies a differential sensitivity to temperature among populations. Populations (accessions) showing such characteristics might be preferred for earlier production of tubers in the field.

Three Spanish accessions of Turkey Gold ® with possible early-sprouting characteristics were tested against the standard Turkey Gold® accession. This was done at ~22C (late spring) and in potting soil. We found that one sample (S-I) did show ~60% sprouting in only 5 days and all three accessions were faster than Turkey Gold (~15%). However, after 7 days, Turkey Gold sprouting was not different (>30%) from two of the accessions, but still much lower than S-I (~75%).

We ranked the accessions S-I > S-CH > S-V > Turkey Gold after 5 days, but S-I > S-CH = S-V = Turkey Gold after 7 days. A small sample of the tubers produced from each accession was kept in the greenhouse over the winter and, in early spring 2004, all remaining samples were watered at the same time and the rank order was very clearly S-CH > S-I > S-V. This result indicated that timing of emergence in these accessions is closely related to temperature and, therefore, the order of emergence may depend on the particular growing season. In 2005, single pots with multiple tubers from each original accession were watered simultaneously and the emergence order was S-CH > S-V and S-I did not emerge.

Overall, there seems to be the possibility of developing early emerging chufa cultivars. The importance of which can be seen in the section below concerning tuber production when emergence is delayed. However, germination in nutsedges is somewhat temperature sensitive as indicated above (Holt & Orcutt 1996, Miles et al. 1996). Because shoot production is from a meristem and not from an embryo, growth is initiated by warm temperatures and accelerates as temperatures rise. It is the temperature sensitivity that most likely sets early emerging types apart. If the weather warms quickly, all chufa cultivars are likely to emerge quickly with no particular differences among them. The early emerging types are more likely to be effective when spring temperatures rise slowly and their ability to grow at somewhat lower temperatures is more advantageous.

IV. Chufa tuber persistence in the soil

As part of the regular course of experimentation, subsets of each experiment were held over the winter for observation the following spring. Pots from summer 2003 experiment with all treatments represented were allowed to resume growth in spring 2004. The result was that only 54% of the pots containing tubers grew chufa in the second year and all pots containing yellow nutsedge survived. There was no effect of fertilization in the previous year (but sample size was small), and the presence of yellow nutsedge had a minor negative effect on whether chufa survived. The same set of pots showed no survival of chufa in spring 2005 with nearly complete survival of yellow nutsedges. Although not investigated, these results suggest that chufa tubers may be more susceptible to the decomposing actions of bacteria and fungi and this may be related to differences in the biochemical composition of chufa tubers compared to nutsedge tubers. (Note: a set of 60 chufa in pots were grown in 2008, with and without fertilizer and without competition. Thirty pots were harvested in late winter and all had large numbers of tubers. The other 30 pots were allowed to overwinter under ambient conditions. Only two of the 30 pots sprouted chufa plants in the spring 2009.)

V. Effects of competition, fertilizer, and delayed sowing on chufa production

A number of factors influence the growth of any plant in the field. The primary factors are the availability of resources, the intensity of competition for resources, and the length of the growing season. Working in combination, these factors can have very negative effects on chufa production, but it may also be possible to manipulate one factor to reduce the effects of another. For example, increased nutrient availability by adding fertilizer may alleviate the negative effects of competition from neighboring plants. On the other hand, if competing plants gain a disproportionate benefit from additional nutrients, the addition of fertilizer may result in reduced production from chufa. The second outcome will almost certainly be true if neighbor plants begin growing before the chufa emerge.

In experiments investigating competitive effects and cumulative impacts of resources, it is important to make regular harvests to understand how plant response changes over the course of the growing season. Such experiments require large numbers of replicates and this restricts the number of treatment factors that can be included. We conducted a series of experiments in which we were able to examine the effects of competition, fertilization, and delayed sowing independently and in combination.

Experimental designs- In the first experiment, chufa tubers were sown outdoors in 1-gallon pots with one quart of red clay at the bottom. These pots were used as a reasonable compromise between field conditions (maximal space but low control over soil conditions) and laboratory conditions (restricted rooting space but high experimental control). To test the importance of soil type, four South Carolina soils were used to fill the pots: Prosperity (Piedmont soil; sandy loam with clay and some rocks), Aiken and Pelion (Fall Line soil; sandy loam), Summerville (Low Country soil; silty loam). In mid-June 2002, 320 pots were sown with chufa such that 160 grew alone and 160 grew with competition from a wild nutsedge plant. An additional 160 pots contained nutsedge only. Pelleted slow-release fertilizer was added at the time of sowing. Beginning one month after sowing, chufa tubers were harvested every two weeks from mid-July to October (8 harvests) and aboveground plant material was also collected in the first six harvests.

In the second experiment the following year, chufa tubers were sown outdoors in 1-gallon pots filled with Aiken topsoil (sandy loam) and fertilized every two weeks beginning one month after sowing (25 June) with either RackMax™ or Schultz Plant Food. Both nutrient solutions were applied at the recommended rate (0.2 ml/gal for RackMax™ and 3.0ml/gal for Schultz), but availability may have been affected by rain. RackMax™ is promoted as a supplement that increases forage quality and promotes rapid weight gain in deer.

The objectives of this experiment were to determine
1. if supplemental nutrients resulted in more rapid growth and tuber production in chufa,
2. if leaf nitrogen (as a surrogate for palatability) of chufa is increased by fertilization, and
3. if either nutrient supplement promoted growth more effectively.

The timing of emergence is very strongly correlated with competitive ability in plants (Ross & Harper 1972). Early emerging plants tend to be more competitive because of the advantage of early growth and have better growth and higher survival. In combination with the nutrient addition experiment described above, we planted wild yellow nutsedge (YNS) in competition with chufa under normal and fertilized conditions. To test the effects of the timing of emergence, we planted chufa tubers at the same time as the YNS, 2 weeks later, or 4 weeks later. In this way, the chufa emerged at the same time as the YNS or after the YNS had a chance to establish in the pots. Planting began on 21 May. Replicates of these treatments were harvested four times at two week intervals and total of 258 pots were planted.

a. Soil type
Chufa tubers emerged at about 85% regardless of the soil type. As the plants grew, there were no observable differences among the four soil types for either tuber number or tuber mass. For the analyses reported below, data from the different soil types were combined. We did not pursue further chemical descriptions of the four soil used because part of the rationale for using fertilizer as a treatment was to overcome any major differences in soil nutrient capacity among the soil types.

b. Competition
Chufa vegetative biomass was positively and linearly related to tuber production which reached a peak of about 50 tubers per plant by September **(Fig. 2a)**. Maximal tuber mass was about 14 grams per plant and was reached by last September, two weeks after tuber numbers peaked **(Fig. 2b)**. There was very little reduction in average tuber mass due to competition. Average tuber mass reached about 0.3 g/tuber at the 5th harvest and remained steady indicating that the initiation of new tubers may be linked to the size of existing tubers **(Fig. 2c)**.

In this experiment, chufa plants with competition grew and produced tubers at the same rate as those without competition suggesting that chufa was relatively insensitive to the presence of wild yellow nutsedge plants.

Common garden experiment 2002.

In the second experiment, vegetative productivity was again linearly related to tuber production. Although shoot biomass and tuber mass were not as high as the first experiment, the relationship between the two variables was the same **(Fig 3a,b)**. These results clearly indicate the importance of large plant size for tuber production.

Common garden experiment 2003.

However, in contrast to the first experiment, both chufa tuber number and mass were significantly reduced by competition **(Fig 4a,b)**. When planted at the same time, both tuber number and mass were reduced by about 33% and delays to sowing exacerbated the effects and led to reductions of >80%.

c. Competition and fertilizer

A review of previous research on chufa and YNS suggested that fertilizer does not have a consistent effect on tuber production (Killinger & Stokes 1949, Pascual et al. 2000). However, if leaf palatability and N content do increase with fertilization, the results may not always be positive as chufa may become more attractive as a forage species and defoliation by herbivores will reduce overall tuber production.

Plants grown with Schultz' produced greater tuber mass and more tubers than either those with RackMax™ or those without any fertilizer **(Fig. 5a-d)**. (The results were somewhat inconsistent between the two harvests, but second harvest data are shown.) Tuber mass and tuber number were greater for the Schultz treatment for all three planting dates and production in the 4-week-delay treatment was greater than the control plants with no planting delay. Fertilizer applied that that concentration was therefore very effective at increasing tuber production in chufa. It is worth noting that production in the control pots was reduced by >50% with a 4-week delay, but was almost three times greater in fertilized pots compared to control pots **(Fig 5a,c)**.

In addition, when competition was present, Schultz fertilizer maintained production at or above control levels. However, production dropped quickly and dramatically when sowing was delayed regardless of the fertilizer application. These results probably indicate that the negative effects of competition are made worse by fertilizer and this implies that wild nutsedges respond faster than chufa in the presence of fertilizer. These results are not unexpected as weedy species typically respond faster and to a greater degree to fertilizer than do agricultural plants.

One unexpected result was that average mass of tubers in these treatments did not decrease with delayed sowing in competition or no competition experiments **(Fig. 5e,f)**. The reason for this is not clear, but it suggests that plants invest a relatively fixed amount of resources in mature tubers and this does not change even when the plants are under stress. And because the tuber numbers decrease a similar amount, these results also imply that new tubers are being initiated at a steady rate as other tubers mature.

While the addition of fertilizer did contribute to greater tuber production in chufa, there is also the possibility that an increase in leaf nitrogen could lead to an increase in herbivory. Because plant size is so important to tuber production **(Fig 3a,b)**, any herbivory will likely decrease tuber production. To test this effect of fertilizer, leaf samples from plants grown without competition were analyzed for total nitrogen content (Clemson University Agricultural Extension). All samples showed very low nitrogen content, but plants that received fertilizer had higher nitrogen content than those that did not. (The RackMax™ treatment was statistically higher than control plants, but not different than the Schultz treatment.). Because the nitrogen levels of these samples were so low, they do not support the contention that leaf palatability went up with fertilization.

d. Competition and delayed emergence
The effects of delayed sowing appear to be very negative **(Figs. 4 and 5)**. Tuber mass and number consistently decreased as sowing delays increased. This clearly shows the competitive impact that established vegetation can have on newly emerging vegetation and this result widely recognized in ecological and agricultural reports. These results also appear to contradict the first outdoor experiment described in section V.b.

However, in these results, there were two components to consider. First, production is reduced with delayed sowing because the chufa plants have a shorter growing season and less time to produce biomass and tubers. Thus, chufa plants will produce fewer tubers with delayed sowing regardless of the presence of competitors. The response was linear **(Fig 4a,b)** with a 40% decrease in both tuber number and tuber mass between the controls and the 4-week-delay treatment.

Second, the response to competitors was negative and resulted in a 33% drop in tuber number and mass, but it may be that additional decreases were due to the delay only, not competition, as seen in the linear response across the sowing treatments **(Fig. 4a,b)**. The interpretation of the response cannot be clearly made from these data: 1) the response was uniform indicating no additional negative effects of competitors with delayed sowing or 2) there was a 33% decrease in the controls but a 67% decrease in late sowing treatments indicating an additional effect of competitors on top of the sowing delay. The response of yellow nutsedge to chufa indicated that chufa had a negative effect on the nutsedge also.

Summary- The results indicate that tuber production in chufa does not appear to be sensitive to soil type, but that nutrient additions can increase tuber production. The increase in production is most likely tied to aboveground vegetative biomass such that the larger the plant, the more tubers are produced. Therefore, from a production perspective, management techniques that enhance growing conditions are likely to be beneficial. Similarly, early sowing leads to a longer growing season which is correlated with higher production. Lastly, early emergence increases production because competing vegetation will not be as well established and will therefore have less impact on growing conditions.

These caveats are pertinent to chufa production because chufa is classified as a C_4 plant meaning that it has a biochemical pathways associated with photosynthesis that is temperature sensitive. Therefore, chufa does not grow well until average temperatures are above about 20^oC or 68^oF whereas C_3 plants are capable of growing throughout the winter and early spring months. As a result, regardless of the timing of emergence of chufa in the late spring, it will always be faced with competitive conditions unless management techniques have reduced the surrounding vegetation. In addition, C_4 plants are often shade sensitive and it is this aspect more than nutrient competition that is likely to have the largest effect throughout the growing season.

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Figure captions

Fig. 1: Emergence (sprouting) of chufa tubers after storage for 96 hours at ~40°C and at ~60°C. The linear regressions were highly significant ($P<0.001$) and indicate no negative effect of temperature alone. However, there was a fairly predictable decrease in viability as moisture content increased at 40°C and a very rapid decrease in viability as moisture content increased at 60°C.

Fig. 2: Tubers production (mean ± 1se) over the course of a growing season in 1-gallon pots. There was no effect of competition on chufa tuber numbers or tuber mass per plant. Mass per tuber peaked earlier in the season than tuber number or total tuber mass.

Fig. 3: The relationship between the size of the vegetative portion of the plant and the number and mass of tubers produced by that plant. The linear regression in both graphs is highly significant ($P<0.001$) indicating that larger plants are more productive than small plants.

Fig. 4. The negative effect of planting delay on tuber production in chufa (mean ± 1se). In both graphs, the effect of delay and the presence of competitors were statistically significant.

Fig. 5. The effects of fertilizers, planting delay, and competition on tuber production in chufa (mean ± 1se). Despite significant positive effects of fertilizer and negative effects of both delayed sowing and competition (Figs a-d), there were no consistent changes in mean tuber mass related to any treatment (Figs. e-f).

Figure 1a.

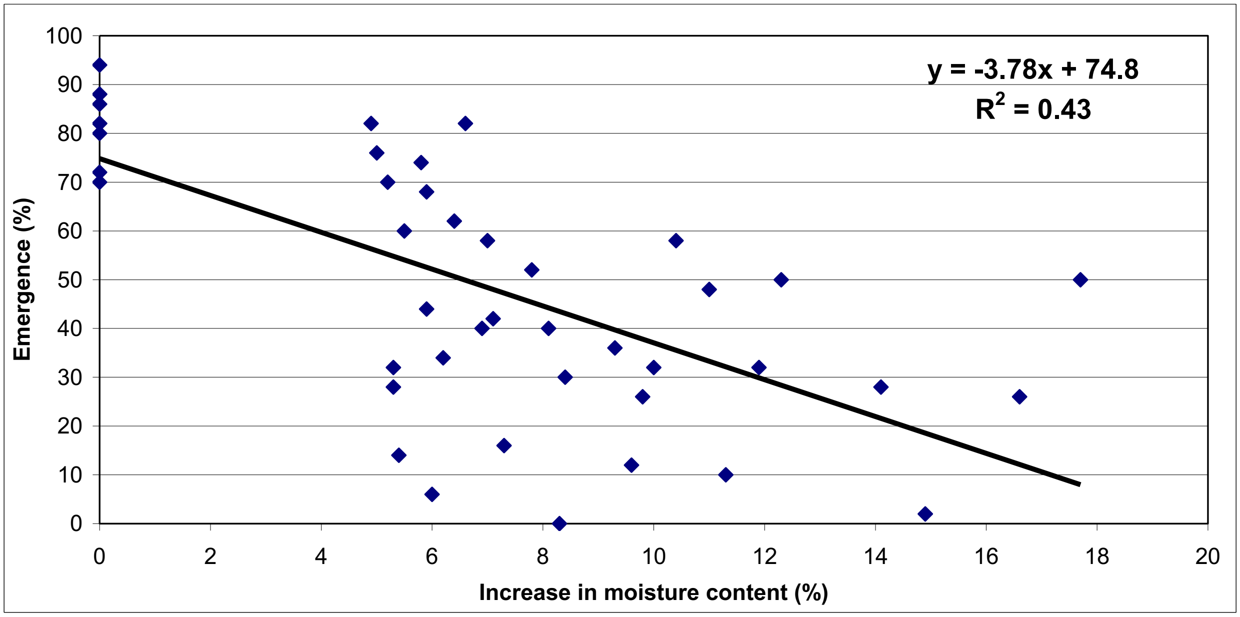


Figure 1b.

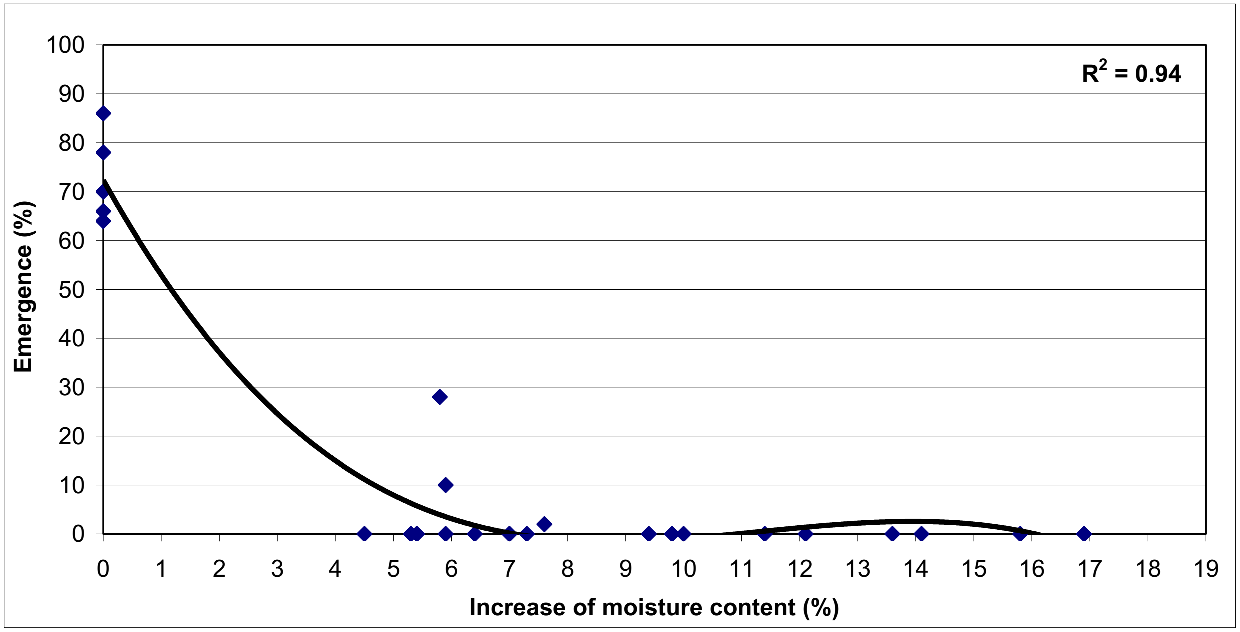
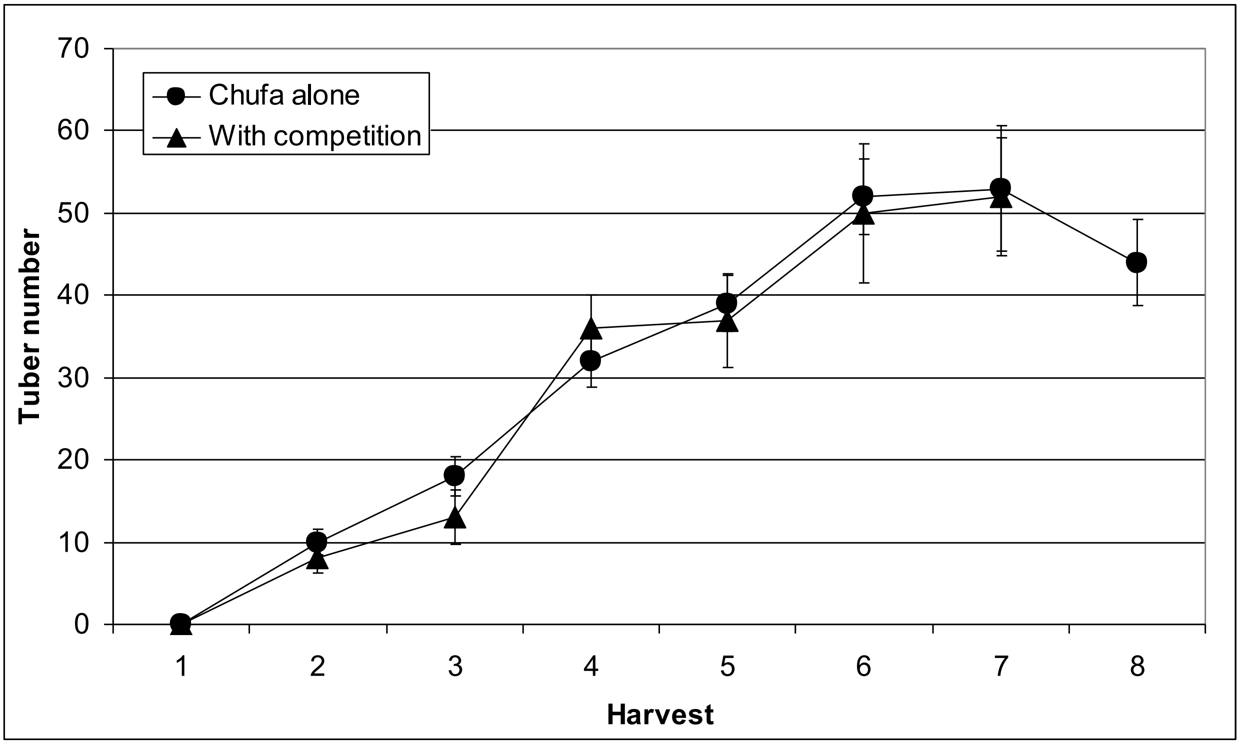


Figure 2a.



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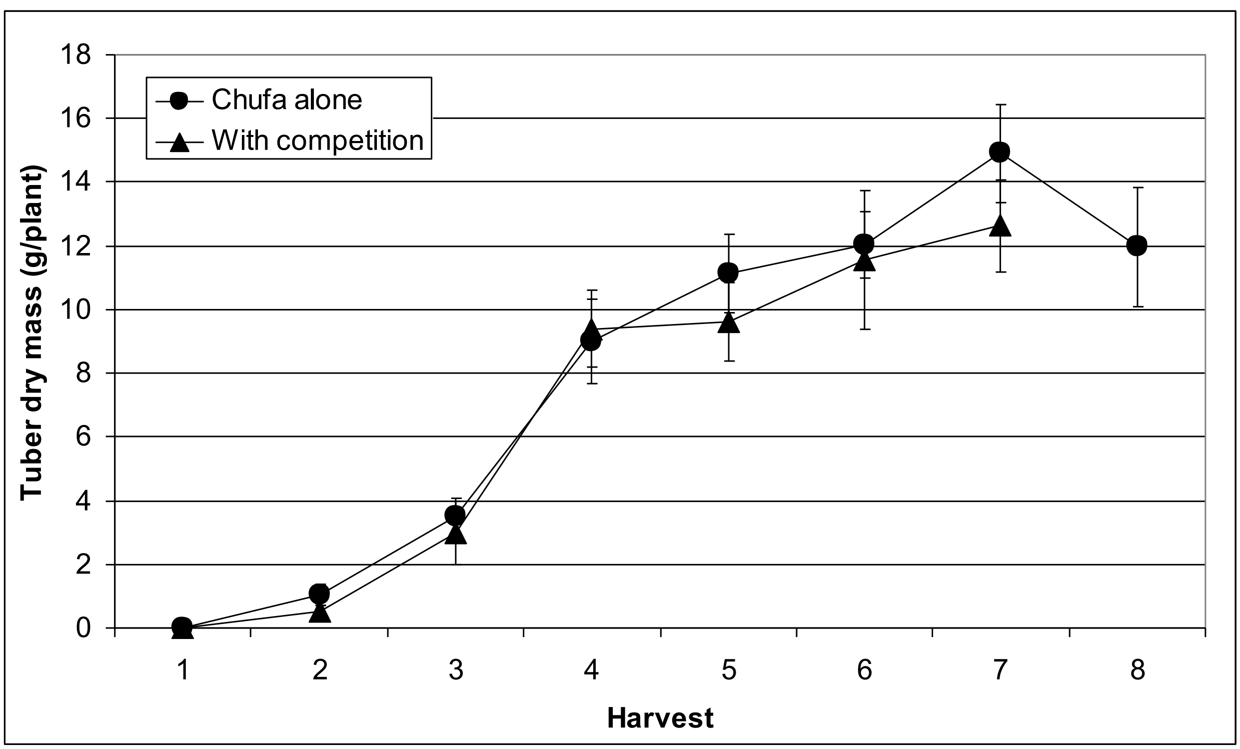
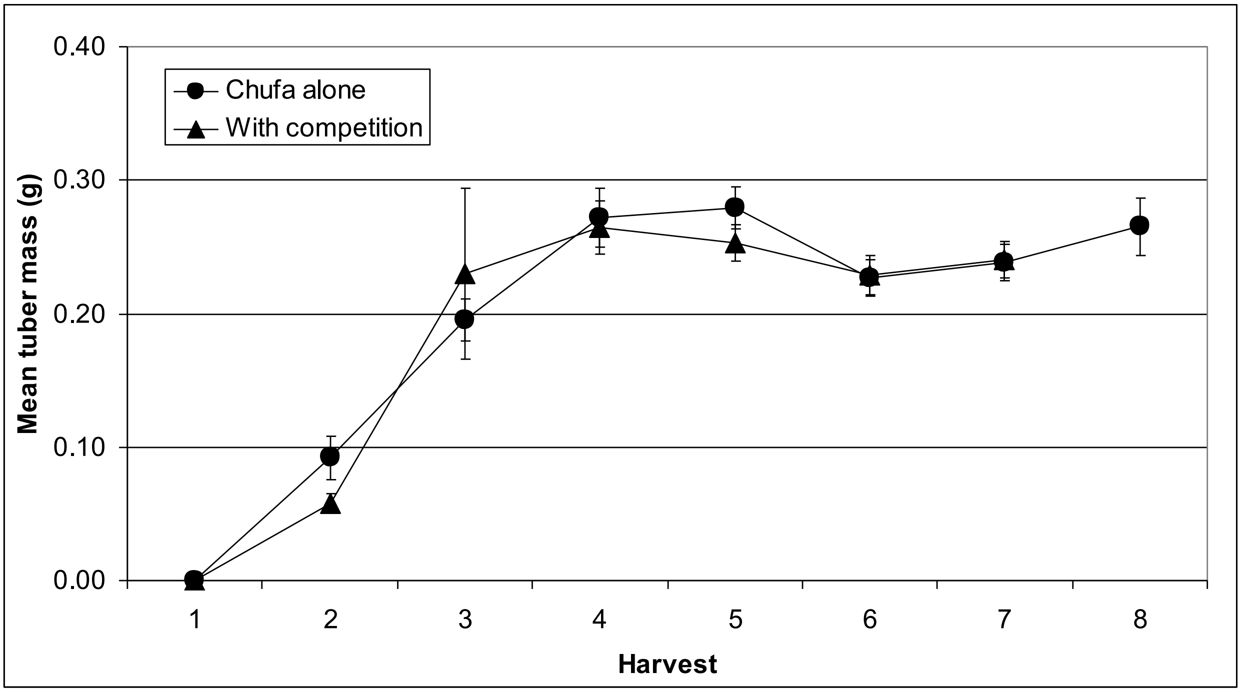


Figure 2c.



Chufa alone
With competition
Mean tuber mass (g)
0.40
0.30
0.20
0.10
0.00
1
2
3
4
5
6
7
8
Harvest

Figure 3a.

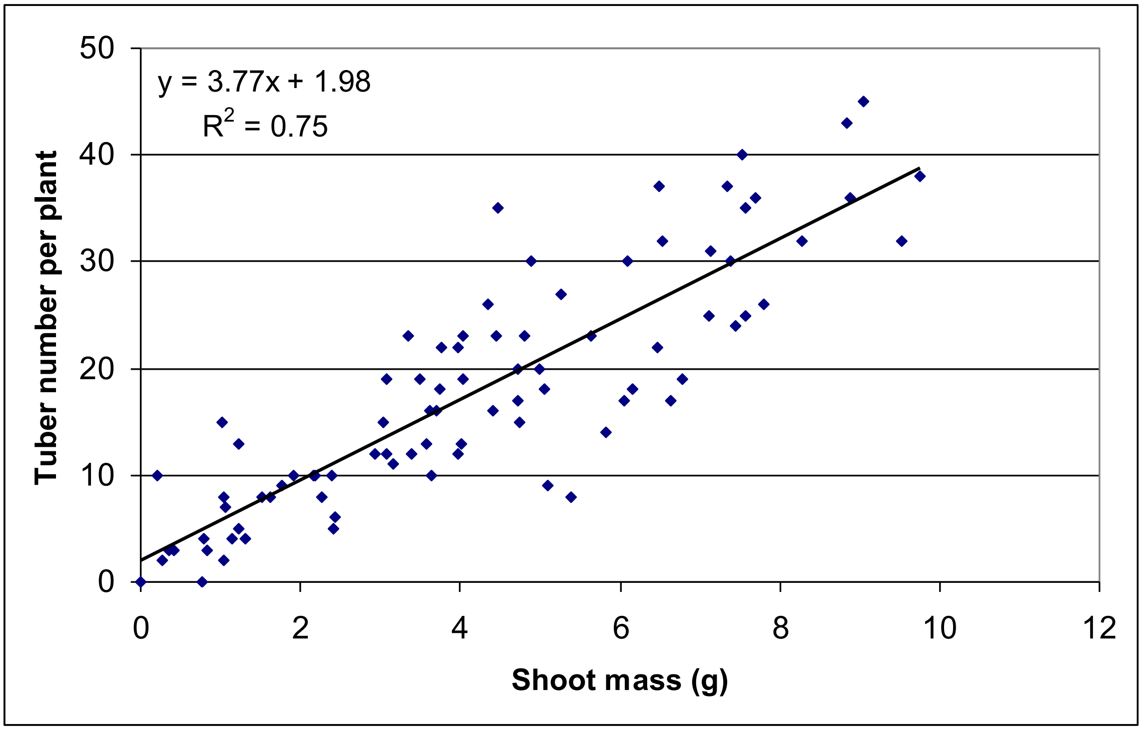


Figure 3b.

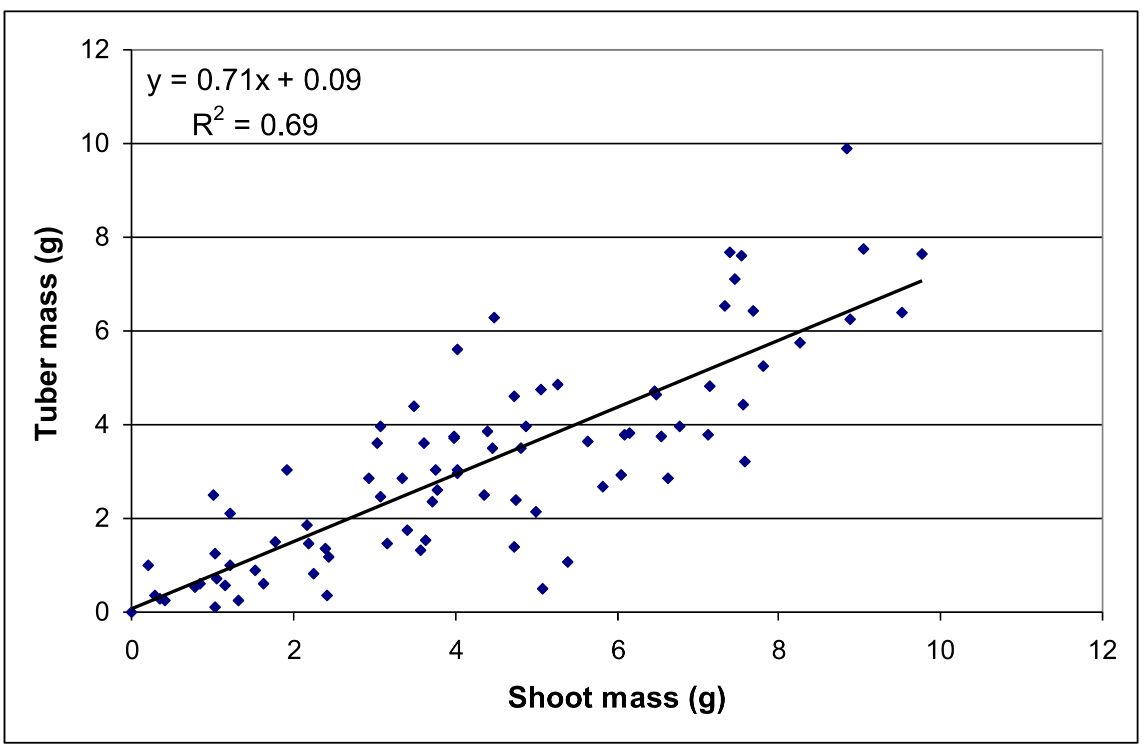


Figure 4a.

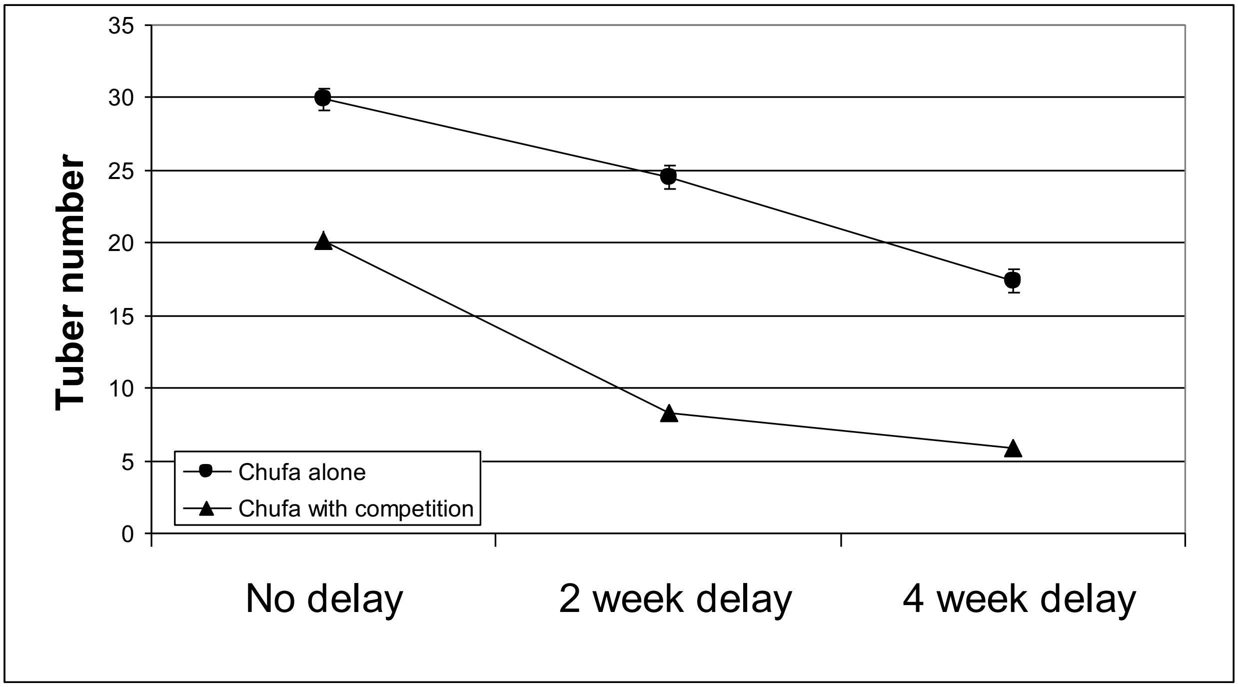


Figure 4b.

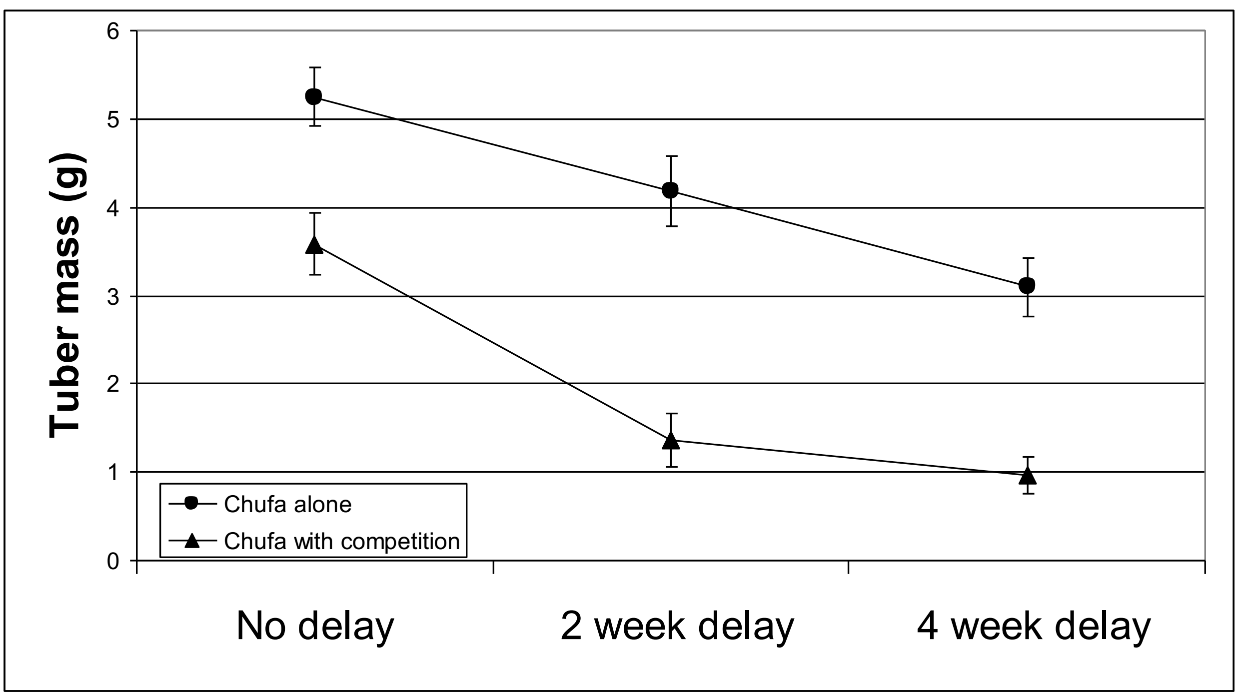
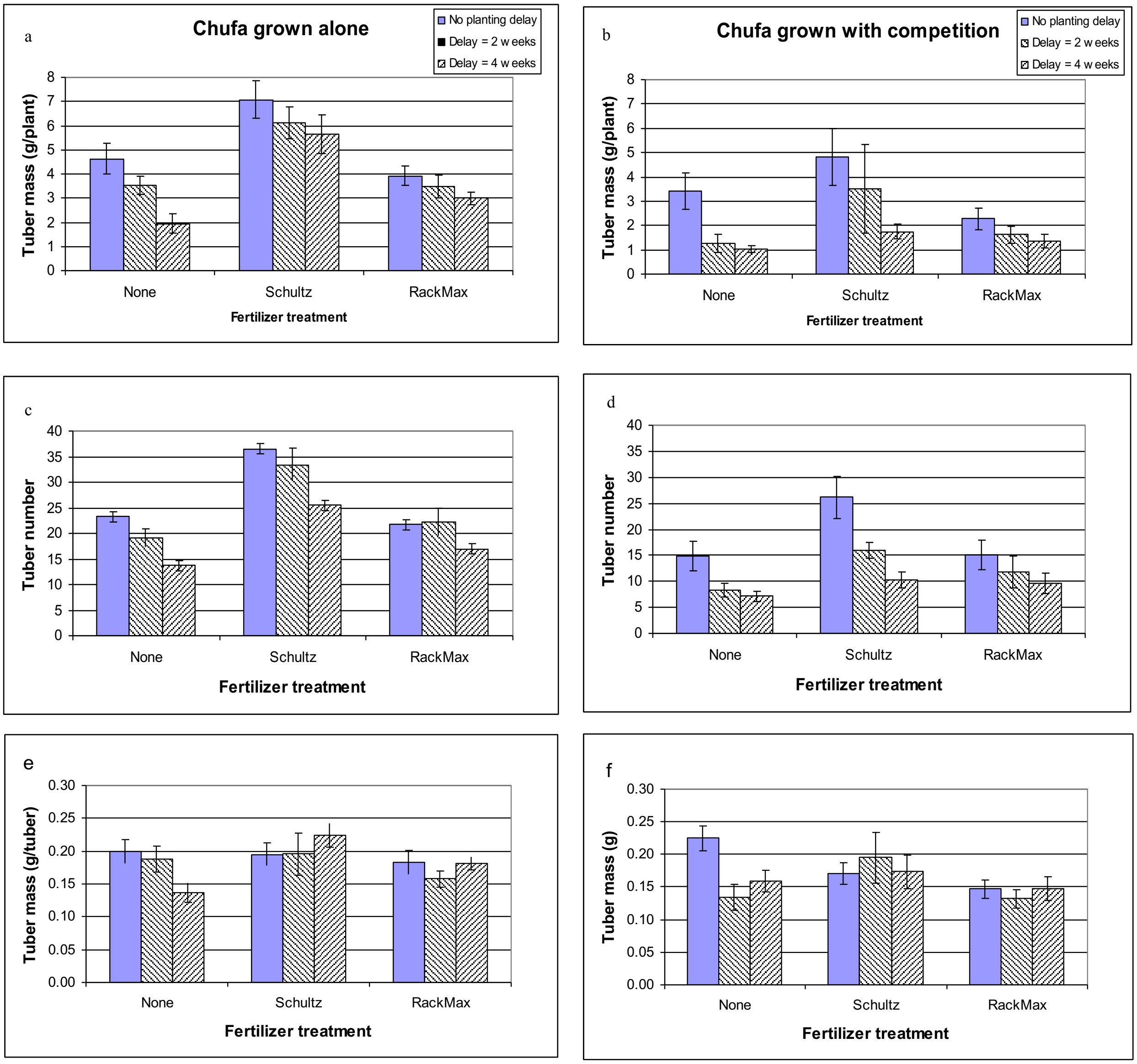


Figure 5.


a
Chufa grown alone
No planting delay
Delay = 2 w eeks
Delay = 4 w eeks
Tuber mass (g/plant)
0
1
2
3
4
5
6
7
8
None
Schultz
RackMax
Fertilizer treatment
b
Chufa grown with competition
No planting delay
Delay = 2 w eeks
Delay = 4 w eeks
Tuber mass (g/plant)
0
1
2
3
4
5
6
7
8
None
Schultz
RackMax
Fertilizer treatment
c
Tuber number
0
5
10
15
20
25
30
35
40
None
Schultz
RackMax
Fertilizer treatment
d
Tuber number
0
5
10
15
20
25
30
35
40
None
Schultz
RackMax
Fertilizer treatment
e
Tuber mass (g/tuber)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
None
Schultz
RackMax
Fertilizer treatment
f
Tuber mass (g)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
None
Schultz
RackMax
Fertilizer treatment