ASSIMILATE ACCUMULATION AND SUGAR CONTENT DURING DEVELOPMENT AND STORAGE OF *Solanum tuberosum* L. cv. 'RUSSET BURBANK' TUBERS

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Christa E. Engelmeyer

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ABSTRACT

Engelmeyer, Christa E., M.Sc., The University of Manitoba, March 1990. Assimilate partitioning and sugar content during development and storage of *Solanum tuberosum* L. cv. 'Russet Burbank' tubers. Major Professor: Dr. M.K. Pritchard.

Growth room and field studies examined assimilate accumulation in Russet Burbank (*Solanum tuberosum* L.) tubers and determined the sugar content of tubers during development. When plants grown in controlled environment chambers were labelled with $^{14}CO_2$, the ^{14}C-content per tuber was significantly correlated to the tuber fresh weight up to 65 days after tuber initiation. The larger tubers on a plant remained the dominant sinks for assimilates during tuber bulking and a strong relationship between tuber size and carbon import was observed.

Measurement of the sugar content (sucrose, glucose, and fructose) of tubers during development in field experiments and during storage showed a lower sucrose content in the larger than average tubers when compared to the smaller than average tubers in 1988. Tubers were physiologically mature at harvest, resulting in no consistent pattern for glucose and fructose content in tubers. In 1989, tops were actively growing at harvest and there was no difference between small and large tubers for sucrose content. However, there was a higher total reducing sugar content (glucose and fructose) in small tubers indicating that the tubers were immature at harvest. The results of this experiment indicate that physiological immaturity at harvest might lead to higher reducing sugar levels in

smaller than average tubers when compared to larger than average tubers.

A split-topkill application of diquat in 1988 resulted in no consistent changes in sugar content or specific gravity of tubers during storage, likely due to the tubers being mature at harvest. However, in 1989 tubers from topkilled plants were physiologically mature at harvest and contained significantly less sucrose than the untreated controls. Tubers from the topkilled plants had a significantly lower reducing sugar content during storage when compared to tubers of untreated plants. During the same season tubers from untreated plants had significantly higher specific gravity when compared to tubers from treated plants. The desiccant, sprayed to kill the tops of the plants, enhanced chemical maturity at harvest and resulted in acceptable levels of reducing sugars during storage but did not improve specific gravity.

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1.0 INTRODUCTION

Information on the changes in carbohydrate metabolism, with emphasis on the reducing sugars, during tuber bulking in the field and during storage would help to improve post-harvest handling and storage conditions of potatoes (*Solanum tuberosum* L.). More than 27% of the total potato harvest in Canada goes into processed potato products. Russet Burbank is the major potato cultivar used in french fry processing in North America. The most important aspects of processing quality of potatoes are specific gravity, which is a reflection of the dry matter content, and the concentration of reducing sugars, which influence the frying color of the potato product.

Very little detailed information regarding the growth and development of Russet Burbank potatoes is available. In order to understand factors controlling tuber metabolism and sugar development it is important to investigate assimilate distribution into tubers. Only a few studies have been undertaken to investigate assimilate partitioning into tubers and the redistribution of assimilate between tubers. Understanding the factors controlling the carbohydrate metabolism of potato tubers could lead to further optimization of the growing conditions or to the use of alternative cultivars.

The short growing season in Manitoba can often lead to the harvest of potato plants while their vines are still green. In late maturing cultivars like Russet Burbank the tubers may not have reached full maturity and it is necessary to use vine-killing compounds to hasten harvest. Therefore, the effect of this induced senescence on sugar content of the tubers was investigated. Small tubers which are the last

to develop may contain higher levels of reducing sugars than large tubers; therefore, size might be an important factor in darkening of french fries.

This research was directed towards evaluating changes in sucrose and reducing sugar content during tuber growth and during storage period. The relationship between tuber size and sugar content was studied to better predict the acceptability of potatoes for processing. The effect of chemical vine killing compounds on processing quality was investigated in order to assist the grower in making the decisions concerning timely harvest.

2.0 LITERATURE REVIEW

2.1 Assimilate Partitioning

2.1.1 Plant growth

Solanum tuberosum is a tuber bearing plant which is usually propagated vegetatively. Because potatoes are widely grown the world over as a food staple, the environmental factors affecting growth and development of tubers are of major concern. Moorby and Milthorpe (1978) specified three major phases of growth within any given potato crop. The first growth phase is from planting to the establishment of a leaf area of 200-300 cm^2. At this time the plant depends on substrate from the mother tuber for growth. The second phase is the beginning of autotrophic growth in which haulm production predominates. The third major phase is the period of tuber growth during which time the haulm contributes photosynthate to tuber bulking then gradually senesces and dies.

2.1.2 Tuber development

Potato plants produce numerous rhizomes and rhizome branches, each of which can initiate tubers over a long period of time (Moorby and Milthorpe, 1978). The tuberization process begins with the swelling of the apical end of the rhizome followed by cell division and enlargement in the inner and outer parenchyma tissue, which in turn gives rise to the early growth of the tuber tissue (Mares and Marschner, 1980). Final size of tubers over 30 to 40 g fresh weight is mainly the result of an increase in cell volume (Reeve et al., 1973; Peterson et al., 1985).

However, Plaisted (1957) and Engels and Marschner (1987) found that the formation of new storage cells and the storage of photosynthates occurred simultaneously up until the end of the growing period, although cell enlargement was the main mode of growth for tubers of the sizes mentioned above.

In general, only tubers formed during the first two weeks of tuber initiation grow to a marketable size. Even though new tubers are constantly formed they are usually resorbed after this time period (Moorby and Milthorpe, 1978). Krijthe (1955) and Plaisted (1957) determined that the tubers which were induced first had the fastest growth rate and that these were also the largest at maturity. Moorby (1968) suggested that the larger tubers do not necessarily grow faster than the smaller tubers but that tubers appeared to grow in turn, with the tuber growing most actively at any one time obtaining the greatest supply of available substrate. Engels and Marschner (1986) found that the growth rate of a tuber was determined by the time of tuber initiation, the first tubers initiated had the advanced growth. The rate of tuber growth appeared to be relatively constant once it was established (Moorby and Milthorpe, 1978). Mares and Marschner (1980) determined that for any particular potato plant, tubers exhibit a variety of growth rates ranging between 0 and 4 to 5 g fresh weight per tuber per day up until the end of the growing season.

Tuber growth follows the pattern of a sigmoid curve. The rate of bulking is exponential for the first two to three weeks, but then becomes almost linear. Near the time of maturity the rate of photosynthesis declines due to increased leaf age. Under environmental influence plants begin to senesce and tuber growth slows down, until it

finally stops (Moorby, 1970; Moorby and Milthorpe, 1978; Wurr, 1977). During the initial phase of growth, factors such as the position of the tuber on the plant and the competition for assimilates between the haulm and the tuber mainly determine tuber growth rate (Engels and Marschner, 1986). Engels and Marschner (1986) also observed that in the later stages of tuber growth, when sink strength was increasing, the strength of the competition for assimilates among tubers was dominated by intrinsic factors such as sink size, represented by the weight of the tuber itself, and sink activity, represented by the rate of starch synthesis.

2.1.3 Sink strength in relation to tuber size

A single potato stem may bear tubers with a wide range of sizes, but the causes of such variation are not well understood (Wurr, 1977). Substantial portions of photosynthate are delivered to the potato storage organs, the tubers. Moorby (1970) in his study on tranlocation of carbohydrates with the potato cultivar Arran Pilot estimated that 90% of the dry matter that moves into the tubers is dependent on current assimilation. Ten percent of the dry weight of tubers comes from the transfer of previously assimilated material (Moorby and Milthorpe, 1978). Soon after tuber initiation, Moorby (1968) found a two to three fold increase in the assimilation of $^{14}CO_2$ and a doubling of the proportion of assimilates exported from the leaves to the tubers. Therefore, tuber initiation leads to a re-orientation of assimilate distribution in the plant. Different sized tubers have different sink strengths, which means that at different stages of development tubers

vary in their ability to "attract" photo-assimilates (Dwelle, 1985). The supply of photosynthate is limited, therefore the individual tubers have to compete among themselves, which results in differential growth rates (Gregory, 1965; Mares and Marschner, 1980).

Engels and Marschner (1987) indicated that there were three factors which could limit tuber growth rate: the source, which supplies the photosynthate; the sink, which is the storage capacity of tubers; and the pathway, which is the capacity of the phloem for photosynthate transport. After investigating these three factors, they found that for the cultivar Ostara during the stage of linear growth, tuber bulking was limited only by the capacity of the plant to supply assimilates, not by the pathway or the sink. Engels and Marschner (1987) concluded from their work that the supply of photosynthates was the limiting factor during tuber bulking. Therefore, carbon assimilation and partitioning are the two most significant factors affecting potato yield.

In studies concerned with the relationship between the sink size and the sink strength, Moorby (1968) found a poor correlation between tuber fresh weight and ^{14}C-photosynthate import 20 h after a ^{14}C-labelling of photosynthate. This correlation was improved when the tubers were harvested five weeks after the foliage was exposed to $^{14}CO_2$. Recent evidence presented by Oparka (1985) and Engels and Marschner (1986) suggests that the largest tubers on a plant are always the most dominant sink for assimilates during the tuber bulking period.

Oparka (1985), using the cultivar Maris Piper, found a good correlation ($r=0.95$, $P<0.01$) between tuber fresh weight and ^{14}C-content, two weeks after tuber initiation in field grown potatoes. However, the correlation became slightly more variable 2 months after tuber

initiation ($r=0.80$, $P<0.01$). He suggested that there was a strong positive correlation between tuber size and carbon import. Engels and Marschner (1986) found for the cultivar Ostara a significant positive relationship ($r=0.87$, $P<0.01$) between ^{14}C-content per tuber and tuber fresh weight 14 days after tuber initiation. Engels (1983) indicated that this relationship was due to the simultaneous occurrence of cell division and storage of assimilates in the tuber during the early stages of tuber development. The ^{14}C-concentration per unit fresh weight of tuber tissue (sink activity) was not correlated with the tuber fresh weight. While the parameters which influence sink strength of tubers are already set at tuberization, Engels and Marschner (1986) concluded that the weight of the tuber itself is the factor which influences the photosynthate import. Therefore, tuber fresh weight, the sink size, must be the factor which has the greatest influence on sink strength.

2.2 Sugar Content of Potato Tubers

Although sugars constitute a small fraction of the dry matter in potato tubers, usually up to 3%, they are particularly important because they result in browning of chips and french fries during the frying process. Sugar content is closely related to the color produced during the processing procedure (Talburt et al., 1987). Upon frying, the aldehyde groups of the reducing sugars, glucose and fructose, react non-enzymatically with the amino groups of amino acids present in the tubers. This reaction is called the Maillard reaction (Maillard, 1912). High reducing sugar levels during the frying process result in a dark brown or even black color, along with a bitter taste, both of which are

undesirable in the final fried product. Sucrose does not participate in the browning of processed products directly but it serves as a substrate for reducing sugar production via the storage activated enzyme invertase (Pressey, 1969). The maximum permissible reducing sugar level in tubers used for french frying is about 4.0 to 5.0 mg per gram fresh weight (van Es and Hartmans, 1987), while about 3.5 mg per gram fresh weight is the upper limit for the non-reducing disaccharide sucrose.

2.2.1 Sugar content during tuber bulking

Carbohydrates are translocated from leaves to tubers as sucrose. Oparka et al. (1988) stated that sucrose was the predominant sugar translocated from leaves to tubers in the potato plant and that it was rapidly converted to starch after it entered the tuber. Smith (1977) found high sucrose levels in freshly harvested immature tubers and concluded that sucrose enters young tubers faster than it can be converted to reducing sugars or starch. Several days after harvest this sucrose was converted to reducing sugars. Therefore, high sucrose levels at harvest can lead to high levels of post-harvest reducing sugars. Sucrose and the reducing sugars, glucose and fructose, were initially at high levels in newly-formed tubers; however, levels declined continuously during the growing season, reaching their lowest levels at the time of final harvest (Sowokinos, 1973; Burton, 1978; Morrell and Rees, 1986). Nelson and Sowokinos (1983) studied the prediction of processing quality and concluded that sucrose levels measured during early tuber development, about two months after planting

when differences are greatest among cultivars, will determine whether or not the stored potatoes will produce an acceptable processed product.

Sowokinos (1973) found that the sugar content of potatoes during tuberization and at the time of lifting was largely dependent on cultivar, even when the different cultivars were grown in the same environments. Furthermore, factors such as planting date, growing location, soil fertility, cultural practice, and disease and environmental stresses during tuber development can influence the sugar levels at harvest. Iritani (1981) found that for Russet Burbank, processing quality factors such as sugar content, types of sugar, and sugar distribution were heavily influenced by stress conditions such as high and low temperature, low moisture, and fertility imbalance during the growing period. This same author also found that these stresses not only lead to malformed tubers but can also result in the development of so called "sugar ends", where the reducing sugar content of one end of the tuber is high relative to the remainder of the tuber, leading to uneven french fry color.

Iritani and Weller (1977) reported that in Washington the high sucrose content of early harvested Russet Burbank tubers gradually decreased with later sampling dates until about the middle of September when it was at a minimum level. The reducing sugar content of immature tubers, sampled nine weeks after planting, was found to be very low (1.5% of dry weight) compared to sucrose (5.8% of dry weight). The authors used the dinitro-phenol method to analyze the sugars.

The stage of maturity at time of harvest will influence both the processing quality and the storability of the tubers. The initial levels of reducing sugars and sucrose at the time of harvest is affected

by maturity. Immature tubers contain more sugars than mature tubers (van Es and Hartmans, 1987). Tubers for processing can be left in the field until the crop has finished sizing and has reached full maturity. Maturity is defined as the point at which tubers have reached maximum starch and minimum sugar content (Burton, 1966). In areas with a short growing season like Manitoba, this is not always possible.

2.2.2 Sugar content during tuber storage

Once the rhizome connection between the tuber and the rest of the plant is broken, tuber carbohydrate metabolism may change considerably (Oparka et al.,1988). During storage the starch in the tubers is frequently converted to an undesirably high concentration of sugars, usually as a result of stress brought on by unfavorable storage conditions such as high or low storage temperatures. One important factor influencing sugars in tubers is the storage temperature (Iritani and Weller, 1977). The accumulation of reducing sugars from starch reserves is of critical importance for the processing industry, and therefore, these changes in metabolism after harvest and during storage have been the focus of much attention.

Ideal storage temperatures for potatoes about to be processed into French fries is considered to be about 10 to 11°C (Smith, 1977). The usual commercial practice is to store the tubers at or around 10°C until they are used for processing. The Manitoba production guide for potato growers (Manitoba Agriculture, 1986) recommended two weeks of post-harvest storage at temperatures of 15°C. After this initial two week period the temperature should be dropped gradually to 10°C for long term

storage. The recommended humidity level is 90%. Some of the local growers in Manitoba may store tubers at temperatures of 7-8°C to reduce respiration rates and minimize storage losses. Nelson and Sowokinos (1983) mentioned that at a storage temperature of 10°C ± 1°C, healthy well ventilated tubers should not be affected by the process of heat or cold-induced starch degradation.

The most important factor influencing the content of reducing sugars during storage and hence the suitability for processing, is the cultivar. Van Vliet and Schriemer (1960) showed that the differences in maximum reducing sugar levels ranged from 5.9 mg to 26.5 mg per gram fresh weight when 12 different cultivars were stored at 2°C over a period of two months after harvest. The sucrose content varied from 4.3 mg to 14.9 mg per gram fresh weight. Dwelle and Stallknecht (1978) showed for the cultivar Russet Burbank that the reducing sugar and sucrose levels were lowest at 10°C compared to lower storage temperatures. Their research was conducted over two years. During the first year the sugars declined between December and May, but stayed relatively constant during the second year of the storage study. The authors stressed that even within a single cultivar any generalization concerning sugar levels is difficult.

2.2.3 Sugar content as influenced by chemical topkill

Destruction of the haulm by chemical means, while it is still actively engaged in photosynthesis, is sometimes necessary because of the restricted length of the growing season. Proper vine killing allows tubers to reach physiological and physical maturity prior to harvest.

Sugar content will reach the lowest possible level, and the cork formation in the periderm during the maturation period minimizes skinning and bruising during harvest and transport. Rowberry and Johnston (1966) found that for late-maturing potatoes, timely vine-killing is essential for proper skin-set.

One important consideration related to vine killing is the prevention of any significant yield reduction by ensuring that the topkill application is timed properly. Premature destruction of the haulm prior to harvest will be more likely to reduce yield than affect the processing quality of the crop (Twiss, 1963). If vine destruction is done rapidly, there is no translocation of photoassimilates from the leaves to the tubers, and hence, no increase in dry matter (Smith, 1987). Therefore, in fast-killed vines there may be a yield reduction. Research reported by Schaupmeyer et al. (1989) showed that the marketable yield of Russet Burbank tubers from diquat-killed plots, where vines died slowly, was significantly higher than the yield from plots where the vines had been cut. This difference however, only occurred in a single season. This study does indicate that slowly-killed vines may still have been contributing to tuber bulking, while vines that had been cut were unable to make such a contribution.

In Manitoba, there is a substantial processing industry. Processing quality of potatoes grown under climatic conditions found in Manitoba tends to be very high, mainly because of high total dry weight, which is largely the result of high starch content. Russet Burbank is the major cultivar used for making french fries in Manitoba. Russet Burbank often requires a long season to reach maturity. Harvesting is often delayed as long as possible to allow maximum yield and to minimize

reducing sugar levels. Not much is known about how topkill influences the changes in sucrose and reducing sugars during the time of lifting.

In 1978 Iritani and Weller came to the conclusion that Russet Burbank tubers which were allowed to mature in the ground, accumulated less reducing sugars during storage than tubers dug shortly after vine-kill. They also found that sucrose levels were not influenced by vine killing.

Walsh (1988, personal communication) investigated topkilling effects on sucrose levels of Russet Burbank potatoes. He found if tubers had not reached optimum maturity at time of harvest the tubers from untreated controls had slightly higher sucrose ratings than tubers from plants that had been topkilled. Walsh (1988, personal communication) speculated that if tubers are immature at the time of topkill, conversion of sucrose to starch is increased. Therefore if topkill is used, the sucrose content of immature tubers is low. In the control plants the foliage was still intact and sucrose continued to be transported to the tubers. Based on his research, Walsh (1988, personal communication) recommended a split application of chemical topkill for processing potato growers. This split application would allow for a slow top death and would optimize the balance between physiological and physical tuber quality.

The only work done on the influence of topkill on the reducing sugar levels was by Grassert (1979). He found that chemical topkill applied two weeks prior to harvest led to significantly higher levels of reducing sugars compared to an untreated control. This study however, did not include Russet Burbank.

2.2.4 Specific gravity as influenced by chemical topkill

High specific gravity potatoes are preferred for processing as french fries (Smith, 1977). Early work by Rowberry and Johnston (1966) on the influence of topkill on specific gravity showed that vine killing generally decreased yield and specific gravity of tubers when compared to untreated plants. Yields were decreased only if the vines were killed too early in the season, before the tubers had finished sizing.

Walsh (1988, personal communication) found specific gravity to be significantly higher in the untreated controls than in vine killed treatments of Russet Burbank. Halderson et al. (1988) also showed that specific gravity was generally highest in tubers from untreated tops in Russet Burbank. The difference was not, however, always significant. The various experiments undertaken to investigate the influence of topkill on yield, sugar levels, and specific gravity of Russet Burbank potatoes show that the results are variable and differ from season to season.

3.0 MATERIALS AND METHODS

3.1 Growth Room Studies

3.1.1 Single stem plant production

Russet Burbank tubers were planted in moist Metromix 200. Once the rooted sprouts had reached a length of about 20 cm (5 to 6 leaf stage), the single stems were transplanted into 76 cm diameter plastic bags containing the commercial potting media Metromix 200. The large sized plastic bags were used in order to allow unrestricted growth of rhizomes and tubers. Axillary buds were removed from the plants every three days to reduce branching. The plants were fertilized with liquid fertilizer 20:20:20 ($N:P_2O_5:K_2O$) at the time of transplanting and again 10 days after tuber initiation. During the course of the experiment the plants were kept in a growth chamber at 16 hour daylength, 20/17°C day/night temperature and at a photosynthetically active photon flux density (PPFD) at the top of the plant canopy of about 280 $\mu E\ m^{-2}\ s^{-1}$.

3.1.2 Labelling of photosynthates using ^{14}C

Experimental procedures were similar to those reported by Oparka (1985). There were 6 labelling dates at 10 day intervals starting 14 days after tuber initiation. Tuber initiation was determined by inspection of developing rhizomes for swelling of the tips. Three plants were labelled at each date for 3 hours, starting at 1100 h during which time the plants were enclosed in clear plastic bags. The bags were then removed and tubers were harvested 21 hours later. The labelling solution was made by diluting 500 µL $Na_2{}^{14}CO_3$ with a

radioactive concentration of 74 MBq/mL in 5 mL H_2O, so that the radioactive concentration was 7.4 MBq/mL. 1.85 MBq $Na_2{}^{14}CO_3$ (250 µL) was used per plant for the first three labelling dates. A slightly higher dosage of 2.22 MBq was used for the three remaining dates to prevent excessive dilution of the label with increasing tuber size (Oparka, 1985). The labelled solution of $Na_2{}^{14}CO_3$ was placed in a glass vial, which was tied to the stem of the plant. $^{14}CO_2$ was liberated from $Na_2{}^{14}CO_3$ by addition of excess 75% lactic acid.

3.1.3 Determination of ^{14}C-content of tubers

After the labelling period the tubers were harvested and weighed, then put immediately into a freezer (-20°C). Once frozen, the tubers were freeze-dried for four days. The dry weight of the individual freeze-dried tubers was determined and they were then stored in sealed plastic bags at room temperature for later analysis. The tuber material was ground into powder, and two-100 mg subsamples per tuber were combusted in a Packard Biological Sample Oxidizer, Model B306. Packard Combusto Cones were used to burn the samples in the oxidizer and oxidized material was collected in Packard Cytoscint scintillation liquid. The ^{14}C-content was determined using a Beckman LS 1701 liquid scintillation system. Each sample was counted for ten minutes. The total ^{14}C-content of each tuber was based on the following formula:

$$^{14}C \text{ content/tuber (dpm)} = (^{14}C \text{ content / g (dpm/g dry weight))} \times \text{(tuber weight (g dry weight))}$$

3.2 Field Studies 1988 and 1989

The site for both field experiments was at Graysville, Manitoba, in a grower's field (Almasippi loamy fine sand). In the summers of 1988 and 1989 potatoes were planted on May 12th and 15th respectively. Both plantings were on wheat stubble at a row spacing of 97 cm, with 41 to 45 cm between hills. In 1988 the crop was fertilized on July 15th with an initial foliar application of 5% Cu and 2.5% Zn at 2.8 L/ha and followed by a second foliar application of 28:0:0 at 23 L/ha. In 1989 the field was fertilized at planting time with 17:20:0 at a rate of 37 kg/ha. The potatoes were cultivated and hilled as needed. After harvest the tubers were stored for two weeks at 15°C, then the temperature was decreased slowly, at a rate of 1°C per week, to 8°C for long term storage at 90% relative humidity.

3.2.1 Experiment I: Sugar content of small and large tubers

The trial was designed as a factorial experiment in a randomized complete block design, with four replications. There were 17 sampling dates in the first year and 9 in the second year; these and the two tuber sizes represented the two factors in the experiment. The treatments were the biweekly sampling dates. Tuber initiation started in mid July, approximately 60 days after planting. In 1988 final harvest for storage took place on September 22 and on September 20 in 1989. The tubers were put into storage after harvest. Sampling for sugar content of the tubers started two weeks after tuber initiation (July 28, 1988 and July 26, 1989) and continued every two weeks until

harvest. During storage, biweekly sampling was continued until February 27, 1989. In the second year tubers were sampled biweekly, but only until November 15, 1989. Ten plants were harvested per replication, per sampling date, then bulked together. The average tuber weight was calculated as follows:

$$\frac{\text{total weight of tubers}}{\text{number of tubers}} = \text{average tuber weight}$$

Samples were separated into larger than average tuber weight (=large) and smaller than average tuber weight (=small). Five small and five large tubers were then taken at random for sugar analysis. To measure variability between plants, the average tuber weight of each individual plant for each plot on every sampling date was determined.

The five tubers used for sugar analysis were peeled, weighed, and passed through an Olympic fruit and vegetable juicer (Model No. 1000), which was rinsed afterwards three times with 90 mL H_2O. The collected juice was then stirred and left to settle at 4°C. 15 mL of the juice were removed with a pipette from the center of the sample after approximately 1 hour and frozen at -20°C until analyzed.

3.2.2 Experiment II: Influence of desiccant spray on sugar levels

The trial was designed as a split plot with six replications. There were two main plots, top-killed and control, and seven subplots, represented by sampling dates. Sampling started on August 26 in 1988 and on August 29 in 1989, and was undertaken once a week until final harvest for storage. The plants were topkilled on September 6 and 13 in

both 1988 and 1989 with a split application of diquat at a rate of 700 g a.i./ha. Final harvest dates were September 16, 1988 and September 19, 1989. Tubers were sampled out of storage every two weeks until October 28 in 1988 and October 31 in 1989. Five plants per plot were harvested at each sampling date, bulked together, and the average tuber weight was determined. Five tubers of approximate average weight were taken from each replication and juice was extracted in the same way as for experiment I.

3.2.3 Determination of sugars by HPLC

A modification of the high-performance liquid chromatography (HPLC) method of Wilson et al. (1981) was used to determine sucrose, glucose, and fructose content of the potato tubers. A Beckman gradient liquid chromatograph system (model 322) equipped with a pump (model 100A) solvent metering system, an Altex sample injector (model 210), and an Altex 156 refractive index detector were utilized. The carbohydrate analysis column was an Aminex HPX-87P (300 x 7.8 mm) (Bio-Rad Laboratories (Canada) Ltd., Mississauga, Ontario) with a mobile phase of redistilled, filtered, degassed H_2O, at a flow rate of 0.6 mL/min, and a column temperature of 85°C. The detector signal was recorded on a Spectra Physics SP4100 computing integrator.

The frozen potato juice samples were thawed and a 10 mL portion was transferred into a centrifuge tube. 10 mL MeOH were added and the sample mixed on a vortex. The sample was then centrifuged at 27,000 g for 5 minutes. The supernatant was collected and a 10 mL aliquot was dried on a roto-evaporator at 45°C, and redissolved in 10 mL

redistilled, filtered H_2O. Samples were then filtered through a 2.5 cm glass micro-fibre filter (0.7 µM pore size) connected to a syringe and 5 mL of this filtered solution was passed through a Sep-Pak, of which 50 µL were finally injected for HPLC-analysis.

Standards were prepared prior to each day's HPLC-analysis by dissolving 100 mg each of sucrose, glucose, and fructose in 25 mL H_2O. 10 mL of this solution was then handled in the same manner as the potato juice samples described above. The actual sugar content of each five tuber sample was calculated by the following formula:

(area sugar sample/area standard) x (mg/mL of standard) x
(vol.sample juice/sample fwt) = sugar conc (mg/g fwt)

In this way quantification of each of the sugars was accomplished by comparing peak area of the samples to peak area of the standard since peak area was directly proportional to concentration of the standard.

3.2.4 Determination of specific gravity

Tubers used for sugar determination in experiment II were also analyzed for specific gravity. The potatoes were weighed in air then weighed in water that was at room temperature. The formula used to calculate specific gravity (SG) was as follows:

SG = [(weight(g) in air)/(weight(g) in air - weight(g) in water)]

3.3 Statistical Analysis

Experiment I (Sugar content of small and large tubers) was analyzed as a factorial experiment in a randomized complete block design and experiment II (Influence of desiccant spray on sugar levels) as a split plot design. Data from 1988 and 1989 were analyzed separately for both of the field experiments. The general linear model procedure of the Statistical Analysis System (SAS, 1985) was used for all analyses of variance. The regression procedure of SAS (1985) was utilized to calculate simple linear regression analysis for the labelling study.

4.0 RESULTS AND DISCUSSION

4.1 Investigation of Assimilate Partitioning in Potato Tubers

Russet Burbank potato plants grown in a growth room were labelled with $^{14}CO_2$ at six different times during tuber bulking. The first labelling took place approximately 14 days after tuber initiation and was repeated five more times at 10 days intervals. The time span given for the experiment was designed to reflect the length of seasonal growth in the field.

The distribution of tuber weights over the duration of the experiment (Table 1) clearly shows that as early as two weeks after initiation there was wide variation in tuber weights within three plants.

Table 1. Weight distribution of tubers from potato plants grown in the growth room for the labelling experiment.

	Days after Tuber Initiation					
	14	24	35	45	55	65
No. of Tubers (3 plants)	33	42	36	44	39	31
Largest Tuber(g)	34.0	56.3	96.8	129.3	221.5	306.0
Smallest Tuber(g)	0.3	0.2	0.8	0.6	1.1	0.5
Average Weight(g)	11.1	11.8	43.0	45.5	61.4	77.2

Engels and Marschner (1986) proposed that these differences in tuber weight can be attributed to variation in the time of tuber induction, coupled with the differential growth rates of the individual tubers. Therefore, the variation in weight observed in this experiment could be explained by both longer duration of growth and higher growth rates.

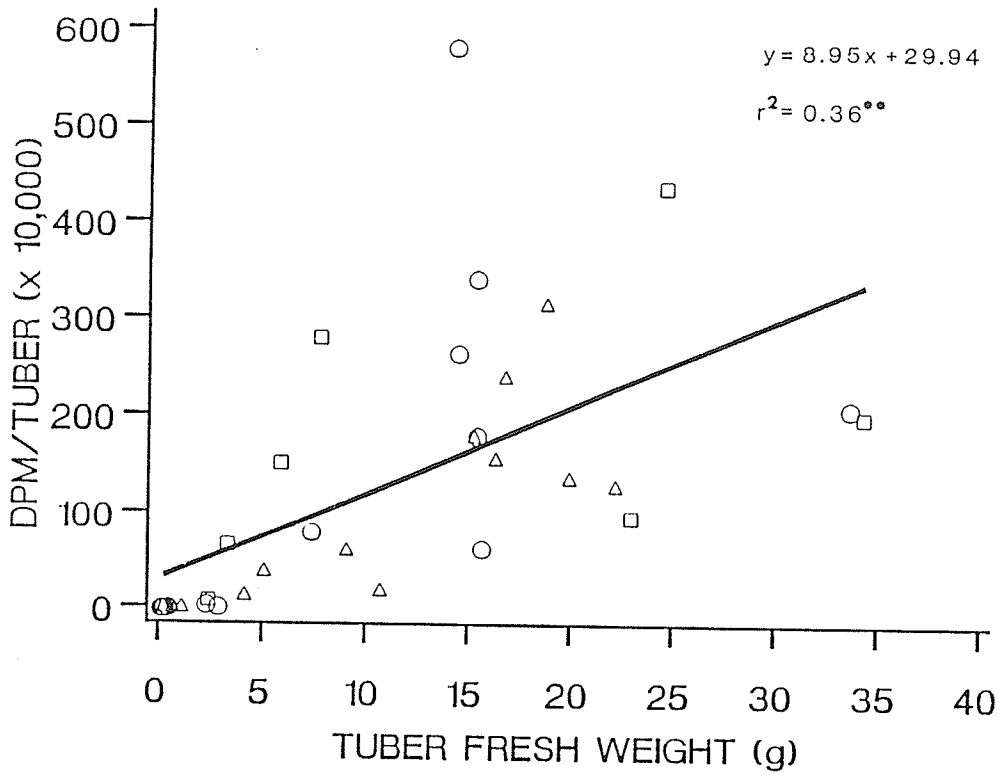
4.1.1 Relationship between ^{14}C-accumulation per tuber and tuber fresh weight

Changes in the pattern of assimilate partitioning to different sized tubers on a single stem plant were examined in relation to tuber weight. There was a positive relationship between assimilate accumulation per tuber and tuber weight. ^{14}C-content of tubers 20 hours after the haulm was labelled showed a significant positive relationship with the tuber fresh weight at each labelling date (Fig. 1 to 3). These findings coincide with those of Engels and Marschner (1986) who also found a positive relationship between tuber fresh weight and ^{14}C-content of tubers sampled 14 days after tuber initiation. Therefore, it would appear that the weight of the tuber itself may play an important role in the competition among tubers for assimilates.

The freeze drier failed during the processing of the tubers from the last labelling date (65 days after tuber initiation). The recovery of radioactivity from these tubers was lower than that obtained from the other samples. However, the regression results did not appear to be greatly affected by this problem.

Fig. 1. Relationship between ^{14}C-content of tubers and tuber fresh weight for potato plants labelled with $^{14}CO_2$ fourteen and twenty-four days after tuber initiation (○ , □ , △ , = tubers from three individual plants).

FOURTEEN DAYS AFTER TUBER INITIATION



TWENTY-FOUR DAYS AFTER TUBER INITIATION

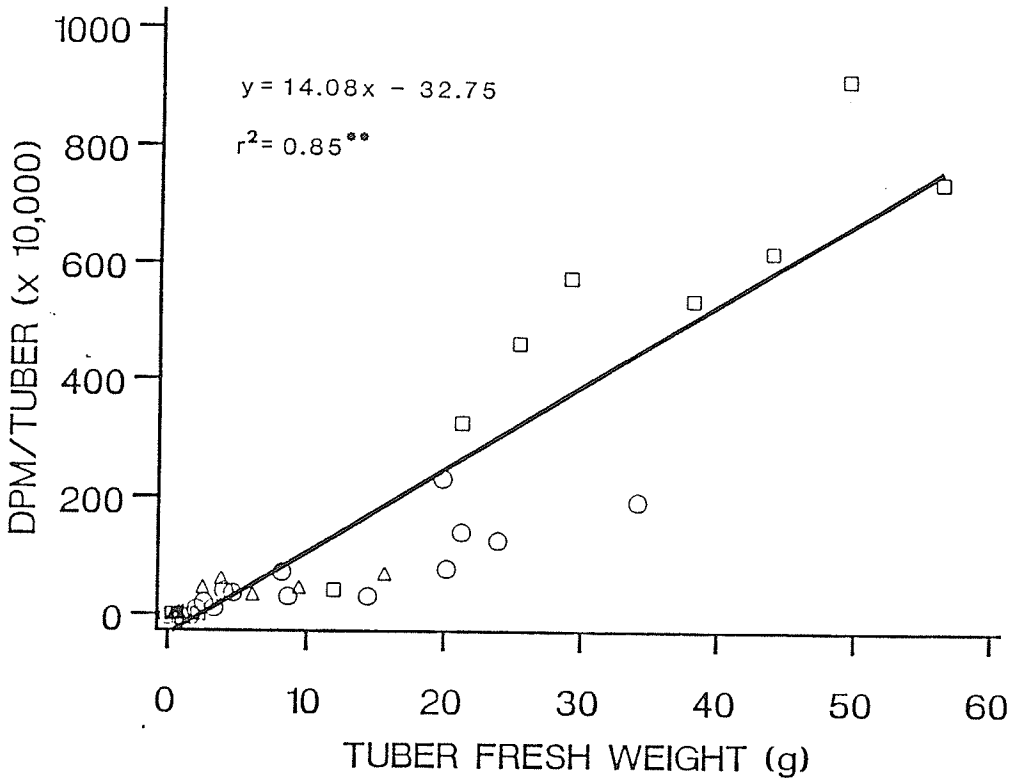
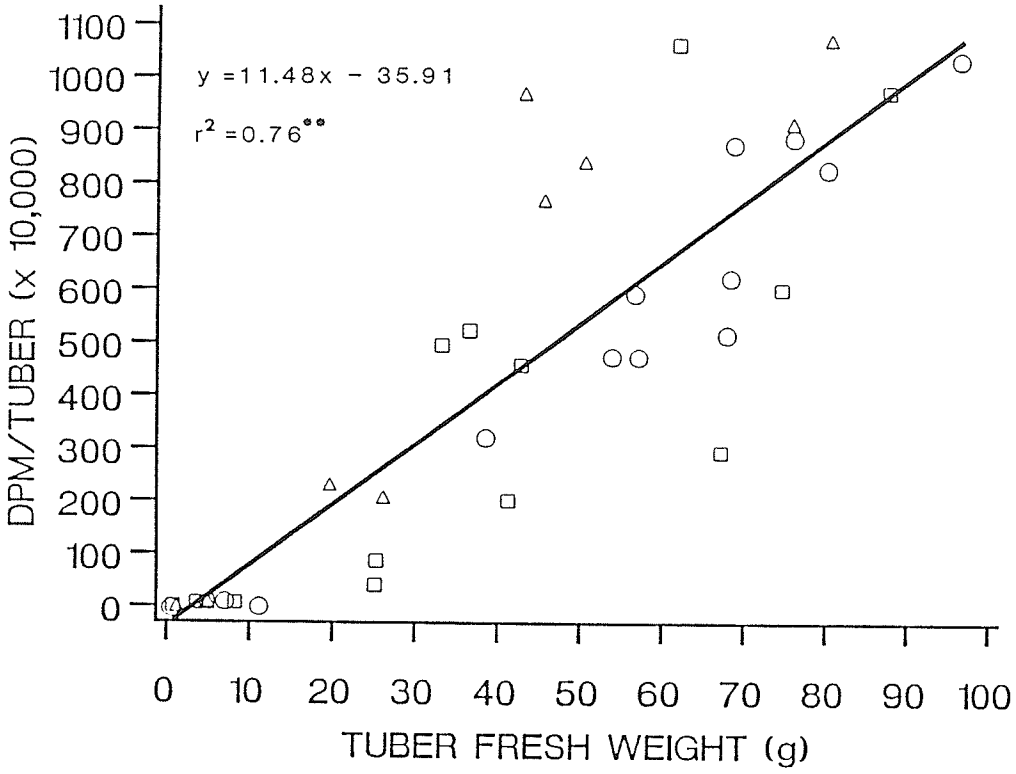


Fig. 2. Relationship between ^{14}C-content of tubers and tuber fresh weight for potato plants labelled with $^{14}CO_2$ thirty-five and forty-five days after tuber initiation (○ , □ , △ , = tubers from three individual plants).

THIRTY-FIVE DAYS AFTER TUBER INITIATION



FORTY-FIVE DAYS AFTER TUBER INITIATION

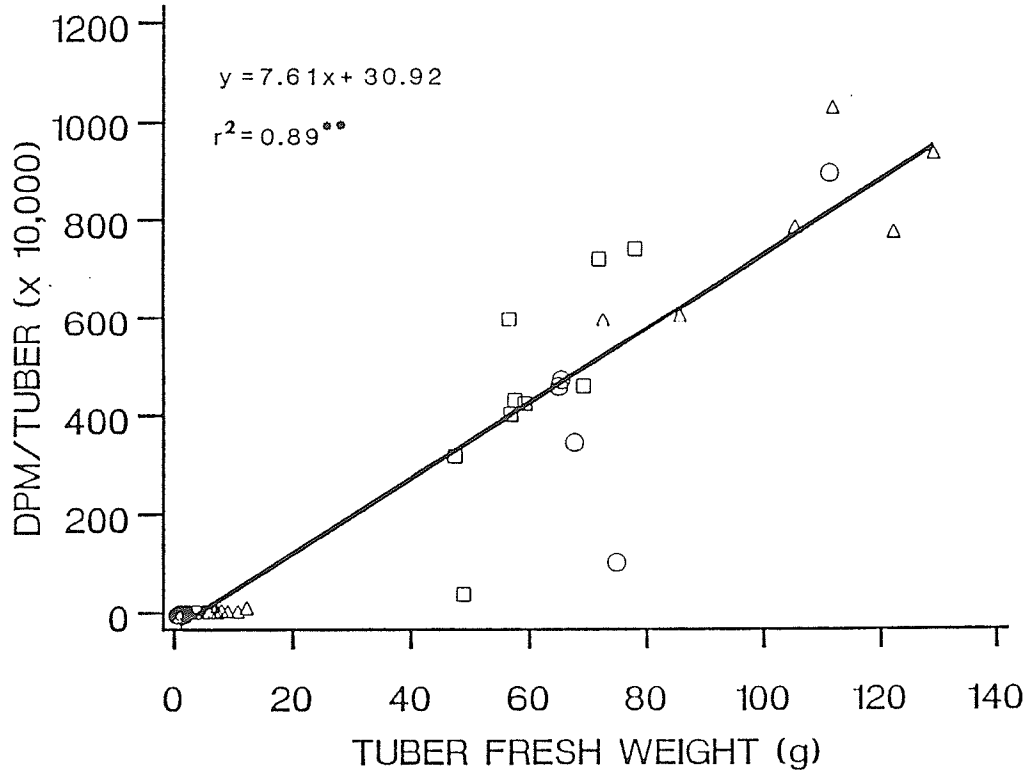
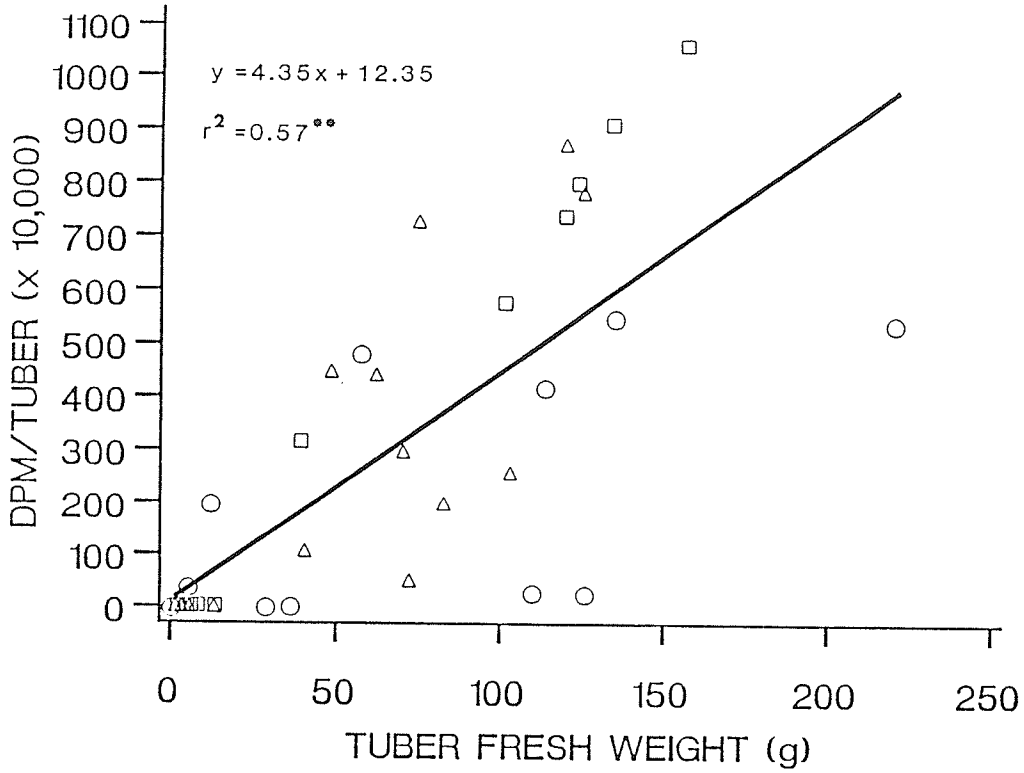
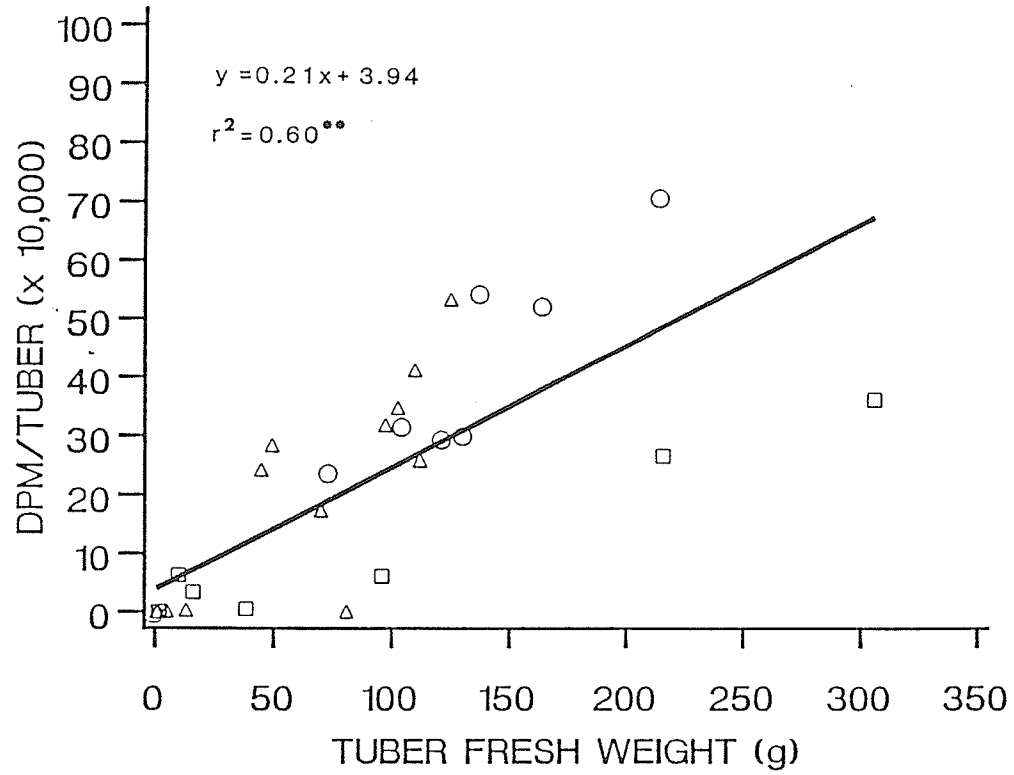


Fig. 3. Relationship between ^{14}C-content of tubers and tuber fresh weight for potato plants labelled with $^{14}CO_2$ fifty-five and sixty-five days after tuber initiation (○ , □ , △ , = tubers from three individual plants).

FIFTY-FIVE DAYS AFTER TUBER INITIATION



SIXTY-FIVE DAYS AFTER TUBER INITIATION



At the first labelling date there was a significant relationship (r^2) between tuber weight and ^{14}C-accumulation (Table 2), but it was not as strong as in the later stages of tuber development when tubers were larger.

Table 2. Coefficients of determination (r^2) and slopes of regression lines (b) over time for ^{14}C in tubers from potato plants labelled at various intervals after tuber initiation.

	Days after Tuber Initiation					
	14	24	35	45	55	65
r^2						
^{14}C/tuber	0.36**	0.85**	0.76**	0.89**	0.57**	0.60**
^{14}C/unit dry weight	0.05	0.19**	0.48**	0.69**	0.09	0.08
b						
^{14}C/tuber	8.95**	14.08**	11.48**	7.61**	4.35**	0.21**
^{14}C/unit dry weight	11.70	5.25**	2.87**	1.42**	0.41	0.01

** regression significant at P=0.01.

It is likely that the haulm of the plant was still acting as a sink for assimilates, which were being used to support haulm growth during this early stage of plant development. After tuber initiation haulm growth slows but develops parallel with tuber growth over some period (Moorby, 1968). The haulm of late maturing cultivars grows over a longer period when compared to early maturing cultivars (Kleinkopf et al., 1981). Therefore, less ^{14}C was transported to the tubers than to the leaves, which is related to the fact that Russet Burbank is a late maturing

cultivar. Engels and Marschner (1986) did find a good relationship between tuber weight and ^{14}C-accumulation soon after tuber initiation, and it may be that with the cultivar used in their experiments the haulm and the tubers were competing for assimilates at earlier stages of tuber growth than Russet Burbank. Therefore, the relationship between ^{14}C-accumulation and tuber weight may take longer to develop in Russet Burbank potatoes.

Based on the increase in ^{14}C-content over time the results of the present experiment indicated that the tubers became the major and dominant sink for assimilates as the plants aged. The relationship between tuber weight and ^{14}C-accumulation per tuber was stronger for the later labelling dates, 24, 35, and 45 days after tuber initiation (Table 2). This finding corresponds with the results of Gawronska and Dwelle (1989) who found that up until approximately 42 days after tuber initiation, the proportion of ^{14}C-assimilates exported from a labelled Russet Burbank leaf to the tubers generally increased with the age of the plant.

For field-grown plants Oparka (1985) found that the strongest relationship between the fresh weight of Maris Piper tubers and their ^{14}C-content occured 14 days after tuber initiation. On five subsequent labelling dates, done at 14 day intervals, the relationship in his experiments became weaker. The discrepancy between the field results in Oparka's (1985) study and the growth room results presented in this study may be the combined result of environmental and genotypic differences. However, the range in r^2-values in Oparka's (1985) field experiment was 0.90 to 0.64 over a 60 day period, indicating that there was probably no great difference between the sampling dates in terms of

the relationship of ^{14}C-accumulation and tuber weight. The use of an additional sampling date would have been useful to confirm the trend proposed by Oparka (1985). The results of the present experiment showed that the relationship between ^{14}C-accumulation and tuber weight was weak at first, increased for a period of 30 days and then began to decrease as the tubers matured.

At 55 and 65 days after tuber initiation, the relationship between tuber weight and ^{14}C-accumulation became weaker, and the ^{14}C-content of the tubers became slightly less dependant on tuber weight. Average tuber weight tended to increase on an average basis (Table 1) up to the last sampling date.

The slope of the regression line was greatest for the second labelling date, 24 days after tuber initiation (Fig. 1 to 3), and gradually flattened out up to 65 days after tuber initiation. All slopes for increasing tuber weight versus ^{14}C-accumulation per tuber over the total sampling time were highly significant. The slopes indicated the increase in concentration of label per unit change in tuber weight. The pattern illustrated by the slopes of the regression lines showed that accumulation of label per gram of tissue was low at first, increased in medium growing stages and then decreased again as tubers matured. This was a similar pattern to that shown by the r^2-values.

The present study was conducted over several stages of growth in the life cycle of the potato crop. The plants showed only slight signs of senescence and were still green at the time of the last labelling date. This would indicate that the timing of such studies as well as the cultivar involved is likely to influence the assimilate partitioning

observed. The regression lines change during growth and were different for each growth phase. If plants are grown in the field, the influence of the environment could change the pattern of assimilate partitioning. This may be most evident at the end of the season, when plants usually senesce naturally due to the effect of climatic conditions and/or disease. In growth rooms the tubers might be mature while the optimimum environmental conditions in the room allow the leaves of the plants to remain green. The research presented in this study supports findings of Oparka (1985) which showed that the larger tubers on a plant remain the dominant sinks for assimilates during tuber bulking and that there is a strong relationship between tuber size and carbon import. However, it was found that this relationship became weaker near the time of maturity.

4.1.2 Relationship between ^{14}C-accumulation per unit weight of tuber tissue and tuber dry weight

The relationship between the content of labelled assimilates per unit tuber weight for the early (14 days) and the late labelling dates (55 and 65 days) were non-significant (Fig. 4 to 6). Because there was a strong positive correlation between fresh and dry weight over all the sampling dates ($r = 0.98$ to 0.99) this relationship can be expressed in either fresh or dry weight. The results of the early stages of tuber development are supported by the work of Engels and Marschner (1986) who also found no relationship between the ^{14}C-content per unit fresh weight of tuber tissue (sink activity) and the tuber fresh weight (sink size) 14 days after tuber initiation. Engels (1983) concluded that the

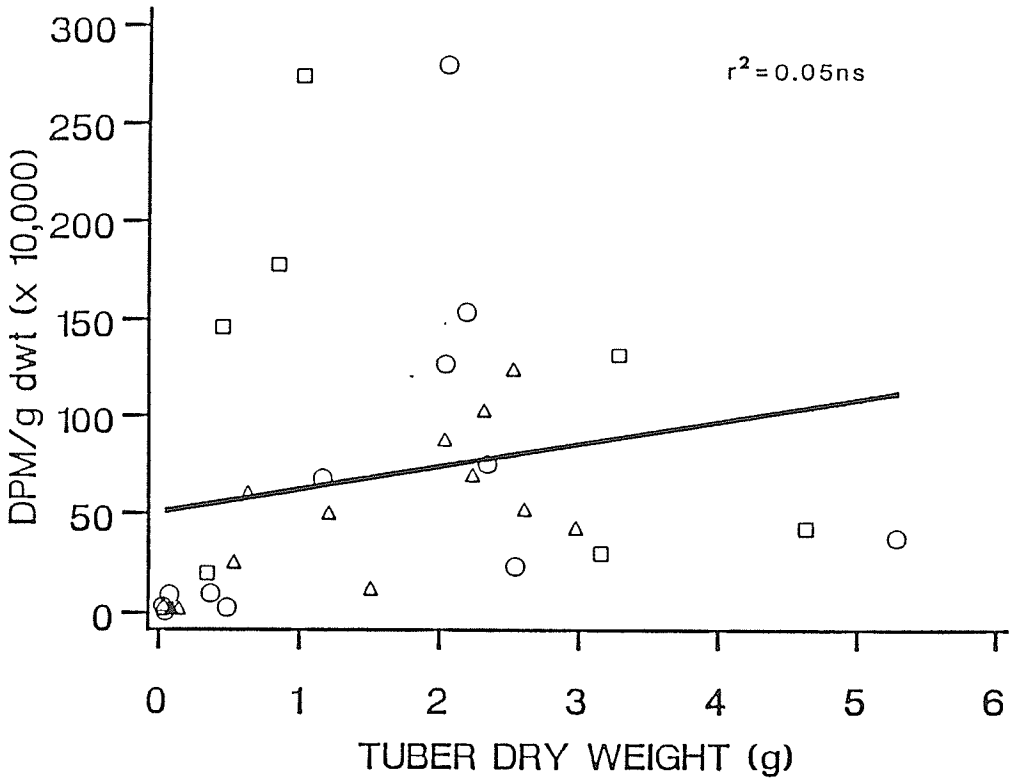
differences in tuber weight found within any one plant could not be accounted for by variation in the assimilate accumulation per unit weight at the early stage of tuber development. The difference was attributed to variation in sink size alone.

At the early or late stages of growth the larger tubers did not appear to be stronger sinks as a result of a greater sink activity. Starch concentration in potato tubers is correlated closely with the dry weight (Engels, 1983). Therefore, the strong correlation between fresh weight and dry weight found in this experiment, as described above, indicates that high tuber weight was not necessarily associated with a higher starch concentration in the tuber tissue per se. This is also indicated by the non-significant slope for 14, 55 and 65 days after tuber initiation (Fig. 4 and 6). The slope was almost horizontal for the last labelling date and tubers seemed to have slower overall growth and therefore these tubers did not have a high rate of ^{14}C-accumulation.

However, at intermediate growth stages sink activity may be related to tuber weight. This is illustrated by the significant slopes found for these growth stages (Fig. 4 to 5). For young, growing tubers, cell division and storage take place simultaneously (Plaisted, 1957). It would follow from this work that as tubers age starch storage in cells begins to predominate. In the present study a positive significant regression was found between ^{14}C-content per gram dry weight and tuber dry weight 24, 35 and 45 days after tuber initiation. This would indicate that the cell division in tubers of intermediate age had stopped, and only cell enlargement and starch storage were taking place.

Fig. 4. Relationship between ^{14}C-content per gram tuber dry weight and tuber dry weight for potato plants labelled with $^{14}CO_2$ 14 and 24 days after tuber initiation (○ , □ , △ , = tubers from three individual plants).

FOURTEEN DAYS AFTER TUBER INITIATION



TWENTY-FOUR DAYS AFTER TUBER INITIATION

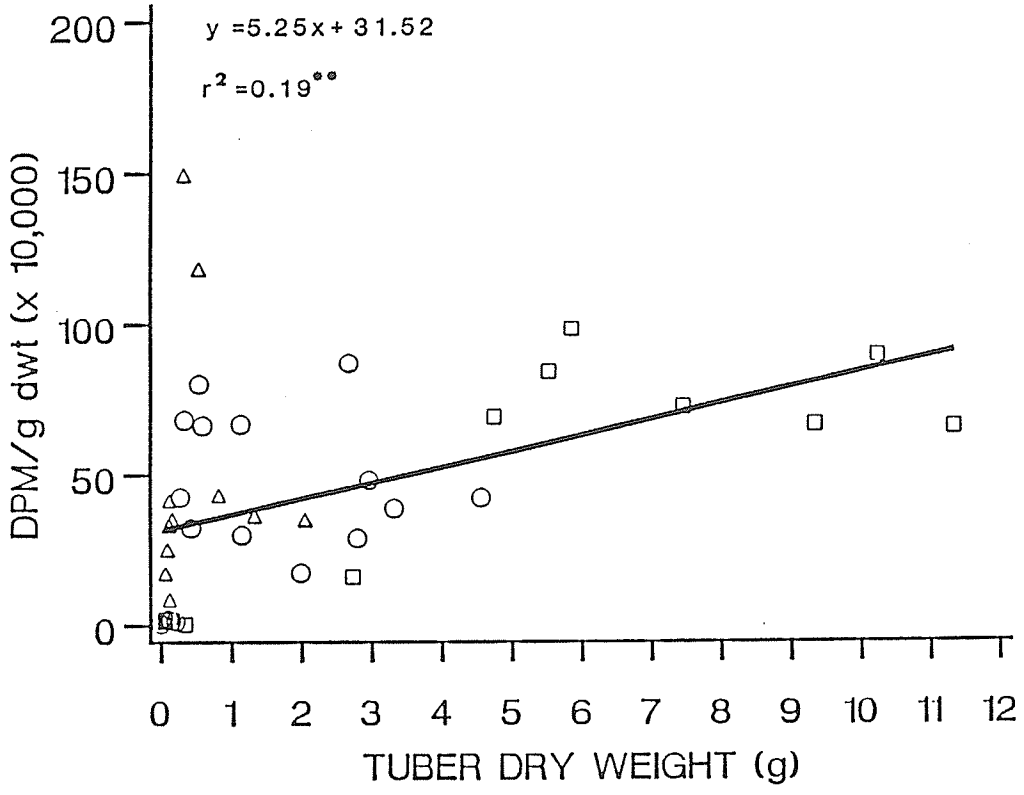
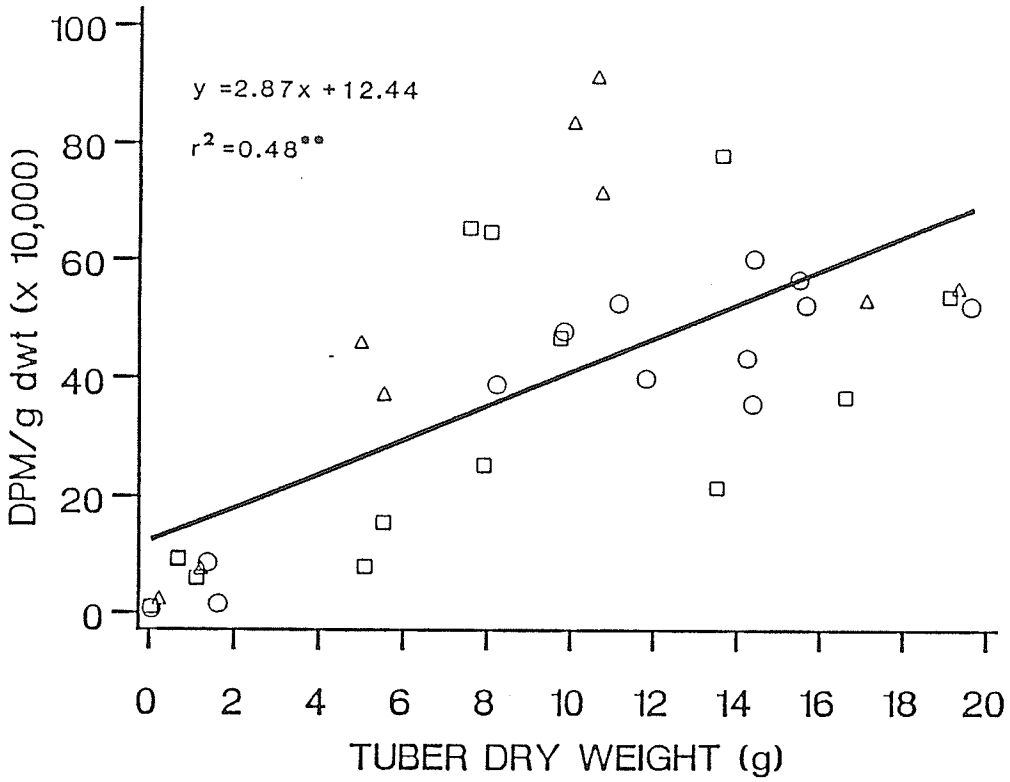


Fig. 5. Relationship between ^{14}C-content per gram tuber dry weight and tuber dry weight for potato plants labelled with $^{14}CO_2$ 35 and 45 days after tuber initiation (○ , □ , △ , = tubers from three individual plants).

THIRTY-FIVE DAYS AFTER TUBER INITIATION



FORTY-FIVE DAYS AFTER TUBER INITIATION

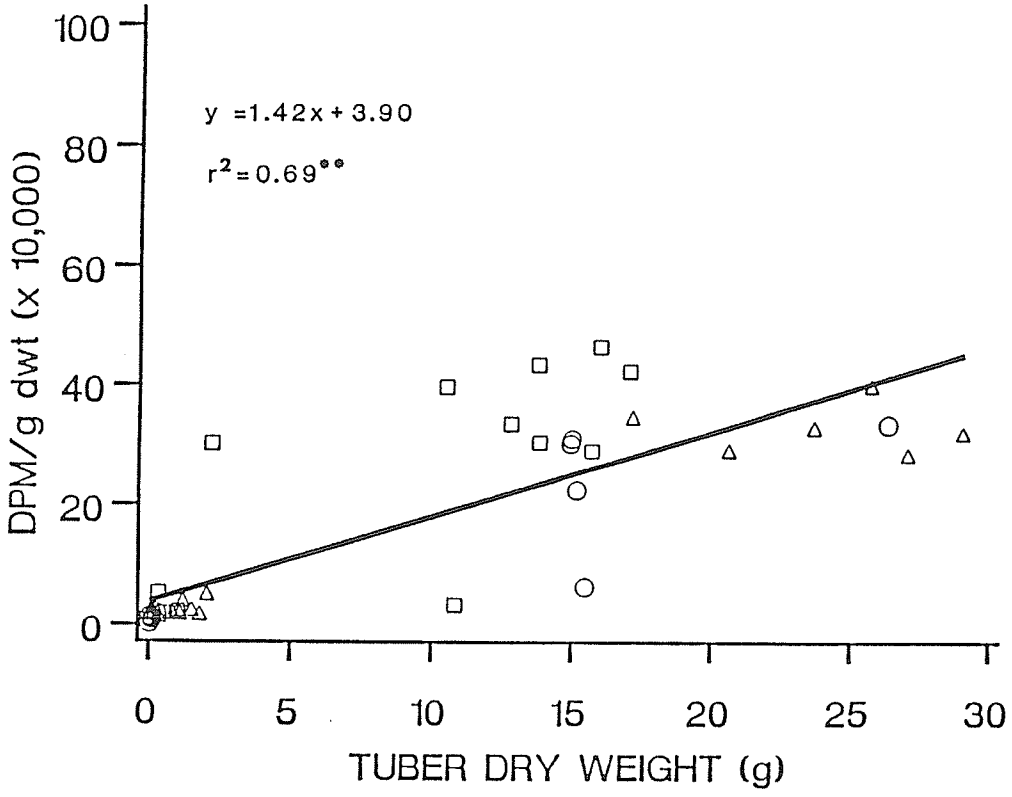
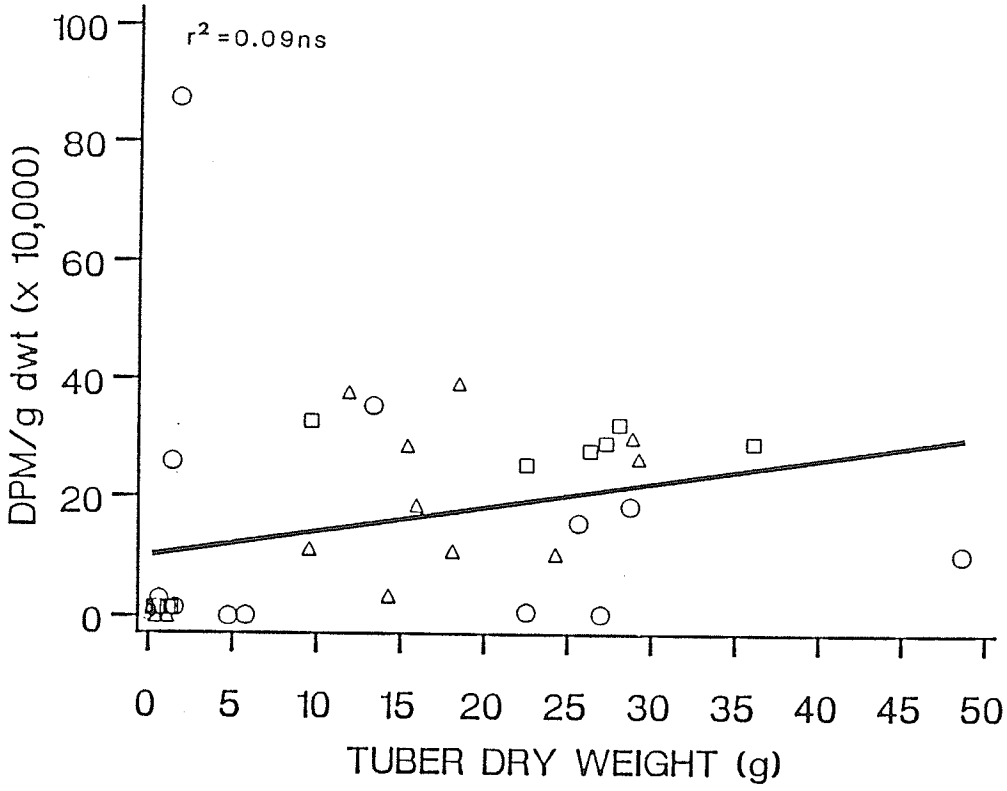
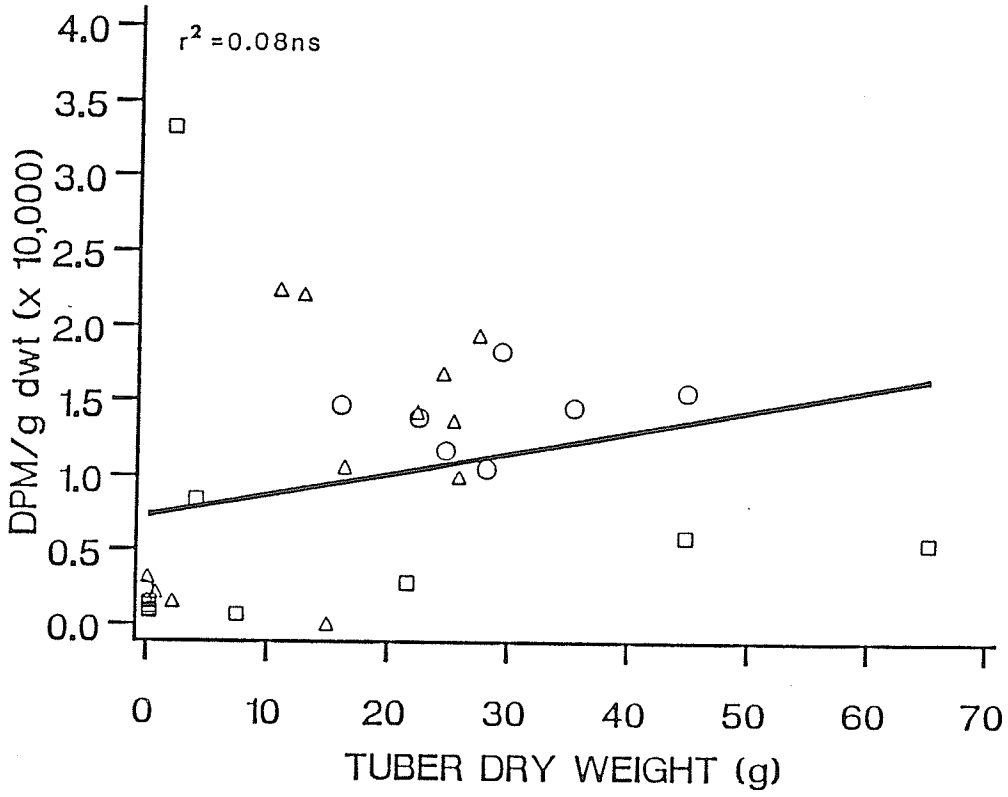


Fig. 6. Relationship between ^{14}C-content per gram tuber dry weight and tuber dry weight for potato plants labelled with $^{14}CO_2$ 55 and 65 days after tuber initiation (○ , □ , △ , = tubers from three individual plants).

FIFTY-FIVE DAYS AFTER TUBER INITIATION



SIXTY-FIVE DAYS AFTER TUBER INITIATION



4.2 Tuber Size in Relation to Sugar Content

4.2.1 1988

Average tuber weight at final harvest was low (85.8 g) (Table 3). The average weights of small and large tubers were 37 g and 110 g respectively. This illustrates the adverse conditions during the growing season which were characterized by very high temperatures and scarce rainfall (Table 3).

Table 3. Summary of growing degree days (GDD), tuber fresh weight (TFW), sampling date (DATE, days after tuber initiation), tuber growth rate (TGR), average temperature (AVT) and rainfall (PPT) during the sampling interval, for experiment I in 1988 and 1989.

DATE (days)	TFW (g)	GDD*	TGR (g/day)	AVT (°C)	PPT (mm)
			1988		
14	18.1	1146	1.3	20.2	16.5
28	34.6	1370	1.9	21.8	1.0
42	52.3	1586	1.3	21.0	2.0
56	78.3	1733	1.8	16.1	24.0
70	85.8	1813	0.5	11.6	24.0
			1989		
14	24.3	894	1.7	22.9	2.0
28	46.8	1111	1.6	21.0	10.2
42	67.4	1287	1.5	18.1	40.1
56	100.1	1441	2.3	16.5	11.8
70	135.6	1536	2.5	12.2	24.0

*5°C base

The analyses of variance showed there were no significant differences between smaller than average and larger than average tubers for glucose, fructose, or the total reducing sugars (Table 4). However, there was a significant difference between small and large tubers for sucrose content. The sucrose content was lower in the larger tubers compared to the smaller tubers. The effect of sampling date was highly significant in every case, and the size x date interaction was significant for sucrose only.

Table 4. Analysis of variance table for sucrose, glucose, fructose and total reducing sugar levels (mg/g fwt) of potato tubers from field experiments in 1988.

		Mean Square			
Source	df	Sucrose	Glucose	Fructose	Red.Sugars
Rep	3	0.081	0.128	0.344**	0.867**
Date (D)	16	21.713**	1.127**	0.861**	1.806**
Size (S)	1	1.226**	0.024	0.034	0.001
S * D	16	0.331**	0.144	0.032	0.143
Error	99	0.153	0.094	0.084	0.248
CV %		18.416	40.449	63.314	40.942

** significant at P=0.01

The interaction can be interpreted to mean that the differences in sugar content between small and large tubers were not expressed consistently across the 17 sampling dates.

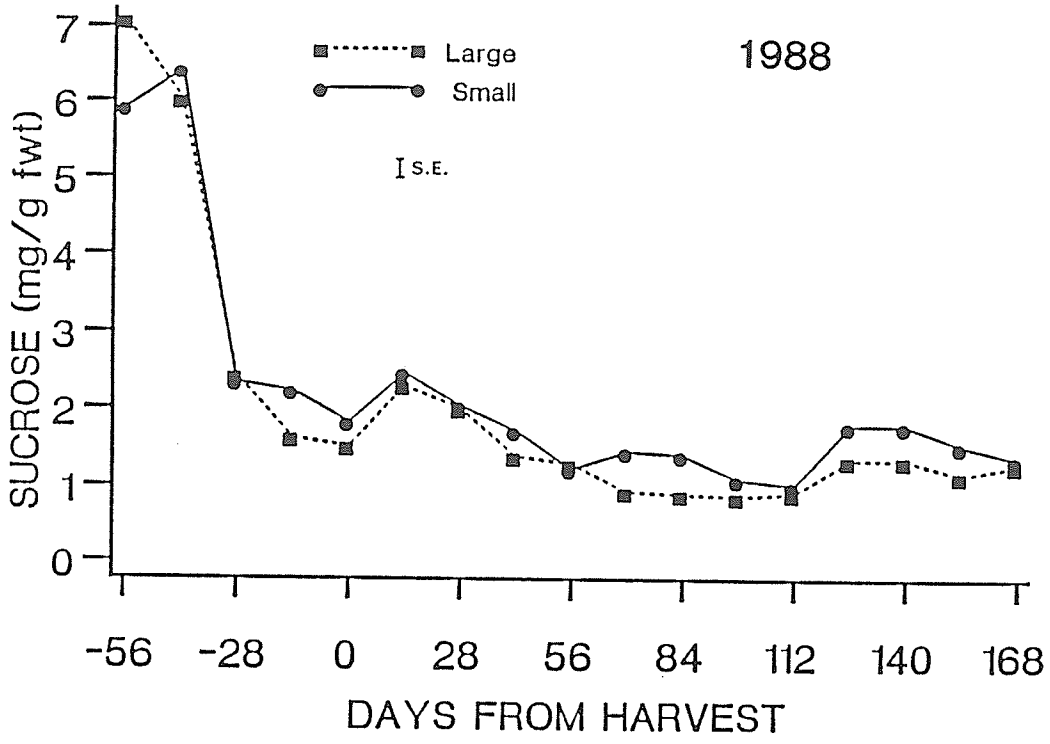
Sucrose was the predominant sugar and large tubers contained significantly less sucrose of a per gram basis than small tubers. However, this difference was too small to influence the content of reducing sugars during storage. Iritani et al. (1973) found no consistent trend between sucrose and reducing sugar content in Russet Burbank U.S. No.1 grade tubers in research done over a period of three years.

Applied to the present research this would mean that sucrose was not consistently metabolised directly into reducing sugars. However, it has been shown that sucrose can serve as an intermediate in reducing sugar accumulation via the storage activated enzyme invertase (Pressey, 1969). Therefore, the greater amounts of sucrose in the smaller tubers could lead to higher reducing sugar development.

The amounts of all sugars on a per gram fresh weight basis decreased during tuber development until harvest (Fig. 8 to 11). This coincides with research by Wiese et al. (1975) and Burton (1978) who also found that sugar contents decreased with increasing maturity. Sucrose continued to decline in storage. Glucose reached the lowest levels at final harvest, increased after harvest slightly, and then declined again in storage. Fructose was only detected after the tubers had been in storage for two weeks.

On the whole sugar levels were acceptable at harvest and throughout storage for all of the three sugars and both tuber sizes. At no time did they exceed the permissible level for french frying, 4.0 to 5.0 mg per gram fresh weight for reducing sugars and 3.5 mg per gram fresh weight for sucrose (van Es and Hartmans, 1987; Sowokinos, 1977), despite the fact that the small tubers would not be acceptable for the

Fig. 7. Sucrose content of smaller than average and larger than average Russet Burbank tubers during growth in the field and in storage for 1988 and 1989 (0 days from harvest = Sept. 22, 1988 and Sept. 20, 1989).


1988
Large
Small
I S.E.
SUCROSE (mg/g fwt)
0
1
2
3
4
5
6
7
-56
-28
0
28
56
84
112
140
168
DAYS FROM HARVEST

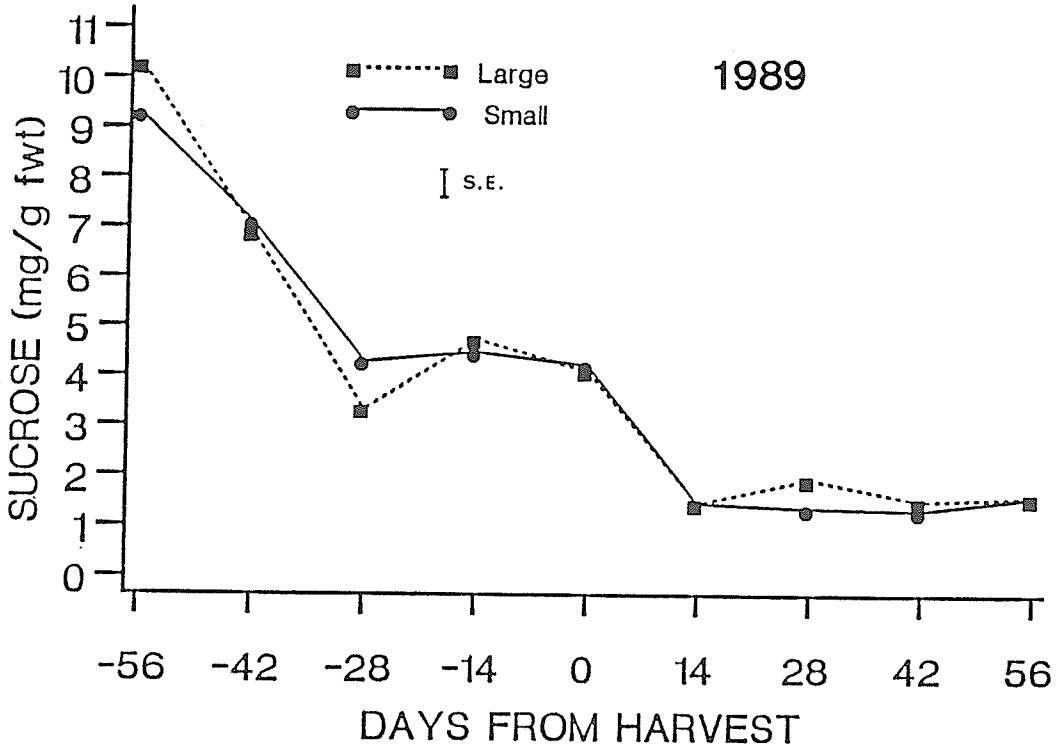
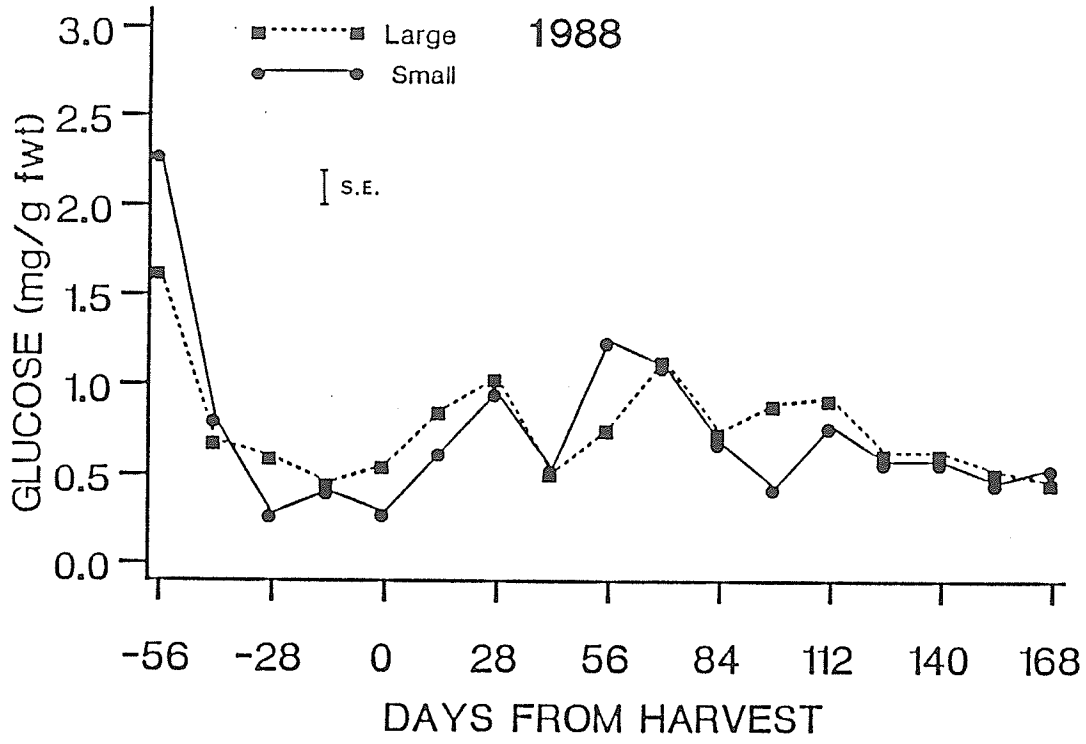

1989
Large
Small
I S.E.
SUCROSE (mg/g fwt)
0
1
2
3
4
5
6
7
8
9
10
11
-56
-42
-28
-14
0
14
28
42
56
DAYS FROM HARVEST

Fig. 8. Glucose content of smaller than average and larger than average Russet Burbank tubers during growth in the field and in storage for 1988 and 1989 (0 days from harvest = Sept. 22, 1988 and Sept. 20, 1989).


Large
Small
1988
S.E.
GLUCOSE (mg/g fwt)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-56
-28
0
28
56
84
112
140
168
DAYS FROM HARVEST

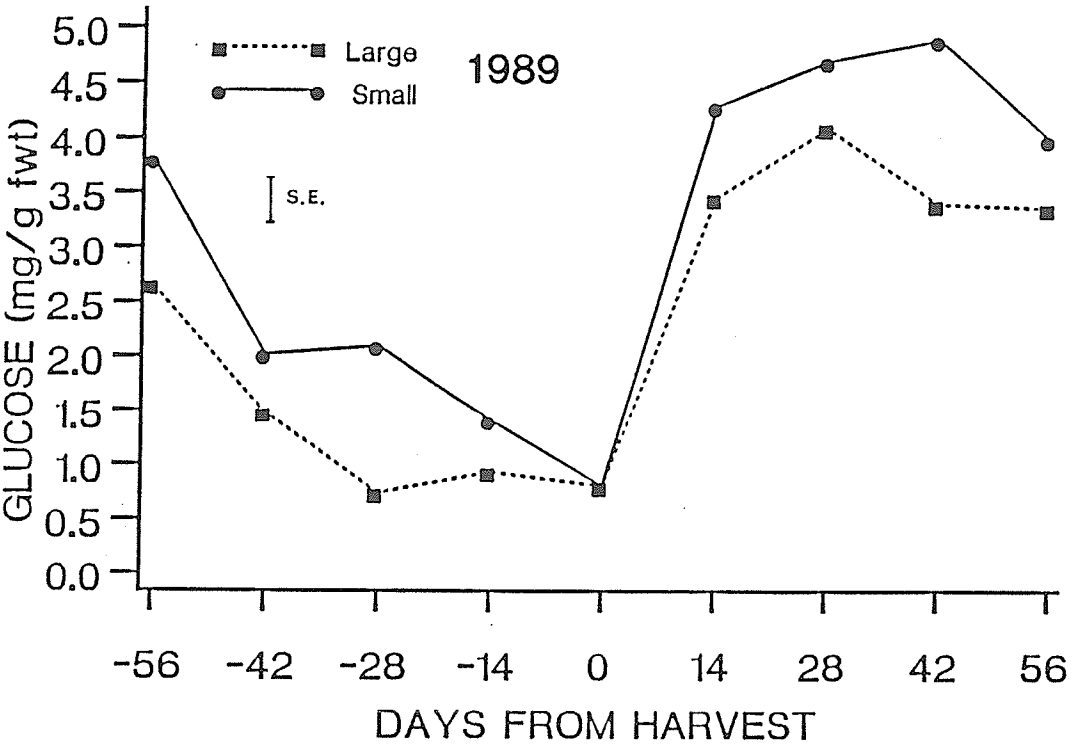
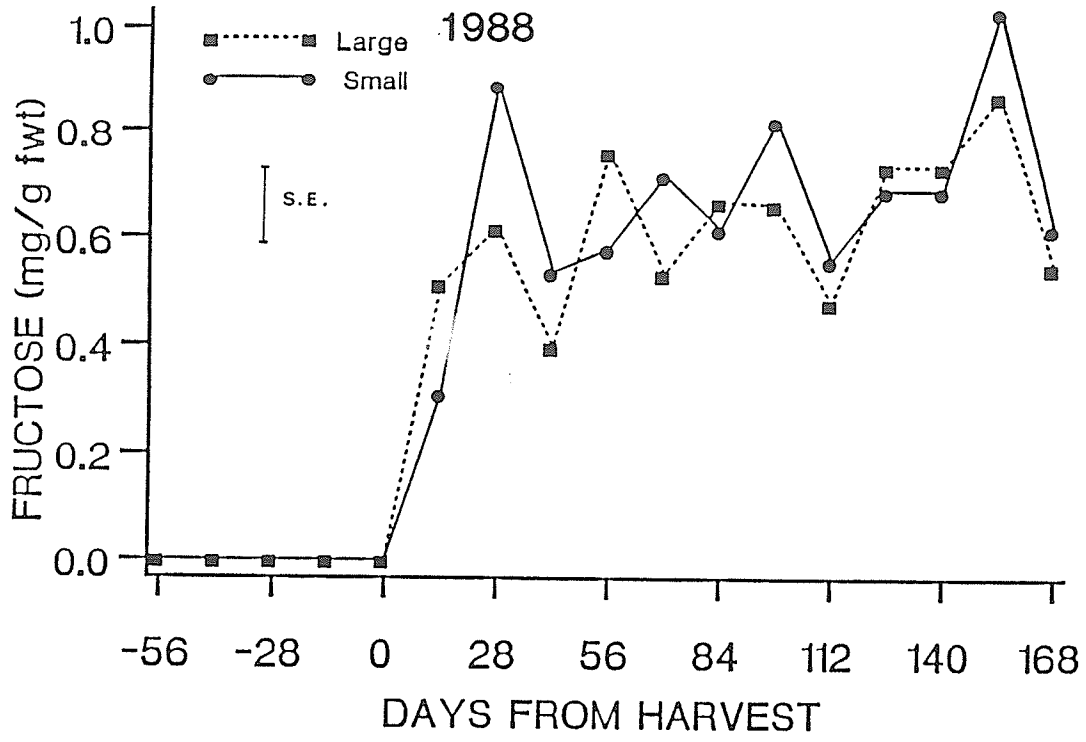

Large
Small
1989
S.E.
GLUCOSE (mg/g fwt)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-56
-42
-28
-14
0
14
28
42
56
DAYS FROM HARVEST

Fig. 9. Fructose content of smaller than average and larger than average Russet Burbank tubers during growth in the field and in storage for 1988 and 1989 (0 days from harvest = Sept. 22, 1988 and Sept. 20, 1989).


1988
Large
Small
S.E.
FRUCTOSE (mg/g fwt)
1.0
0.8
0.6
0.4
0.2
0.0
-56
-28
0
28
56
84
112
140
168
DAYS FROM HARVEST

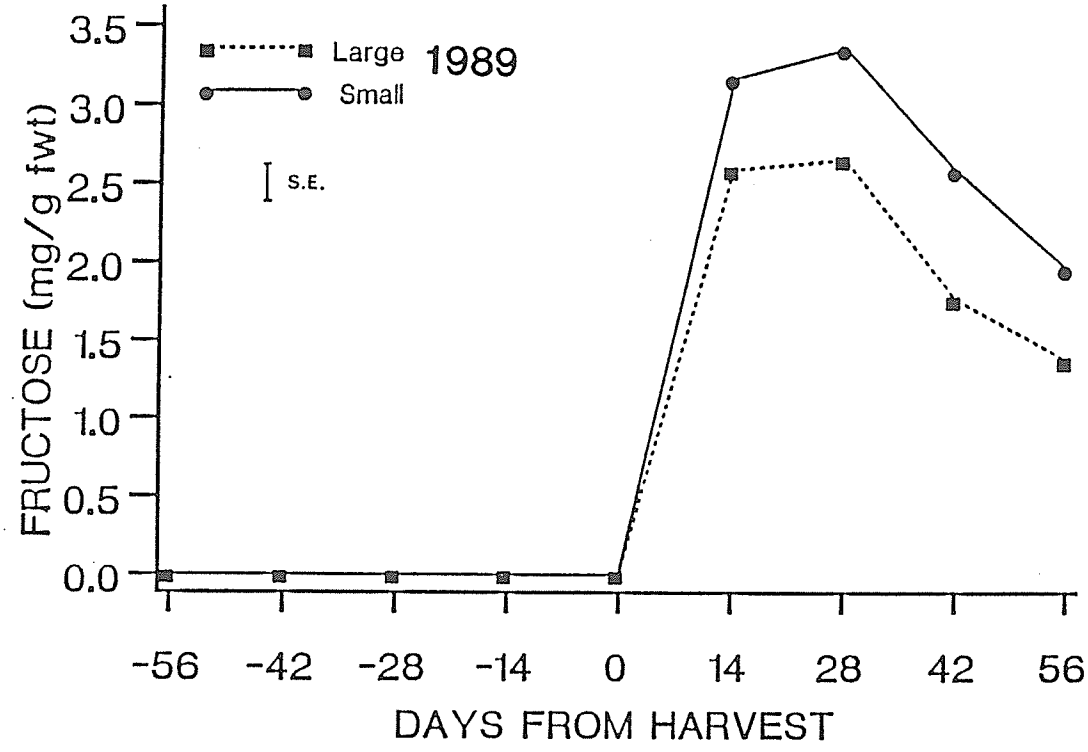
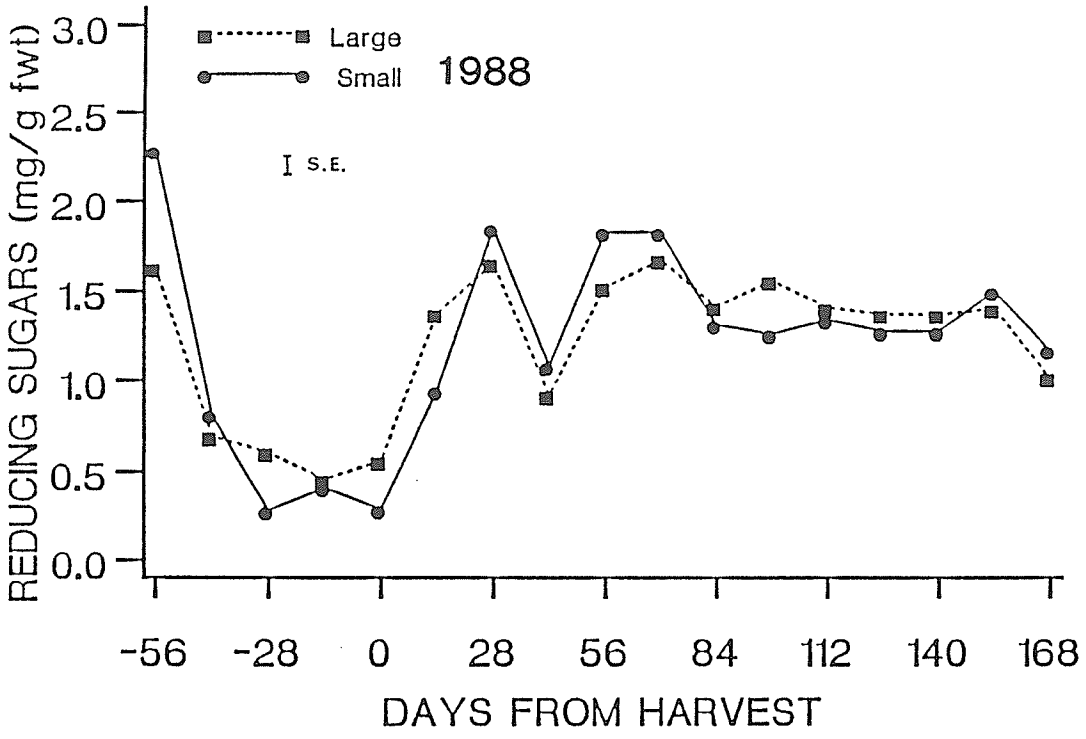
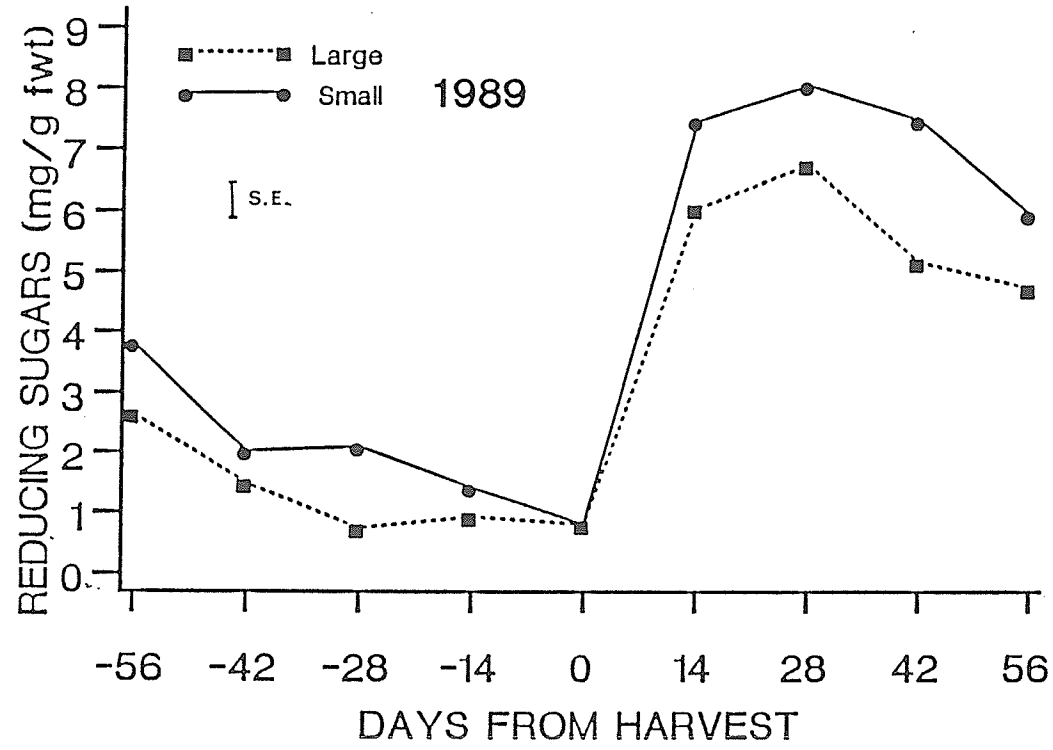

1989
Large
Small
S.E.
FRUCTOSE (mg/g fwt)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-56
-42
-28
-14
0
14
28
42
56
DAYS FROM HARVEST

Fig. 10. Total reducing sugars content of smaller than average and larger than average Russet Burbank tubers during growth in the field and in storage for 1988 and 1989 (0 days from harvest = Sept. 22, 1988 and Sept. 20, 1989).


Large
Small
1988
I S.E.
REDUCING SUGARS (mg/g fwt)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-56
-28
0
28
56
84
112
140
168
DAYS FROM HARVEST


Large
Small
1989
I S.E.
REDUCING SUGARS (mg/g fwt)
9
8
7
6
5
4
3
2
1
0
-56
-42
-28
-14
0
14
28
42
56
DAYS FROM HARVEST

processing industry because of the size. Tubers were mature at harvest; therefore, there was no difference in reducing sugar content between samller than average and larger than average tubers.

4.2.2 1989

The average weight of the small tubers at harvest was 91 g and for the large tubers 248 g, which was more than double the weight they reached in the previous season. Scarce rainfall in the middle of the growing season led to secondary tuber growth resulting in malformed or knobby tubers. Rainfall was adequate towards the end of the season and the plants and tubers were actively growing at harvest time (Table 3).

Sampling was continued during storage only up to the middle of November. Differences in maturity are reflected in storage within a short time after harvest. Analyses of variance showed no significant difference between small and large tubers for sucrose content (Table 5). Graphical analysis also showed no consistent trend for sucrose content in either of the tuber sizes over the nine sampling dates (Fig. 7). Again sucrose was the predominant sugar but only until harvest. Two weeks after harvest sucrose reached its lowest level and remained there during storage. There was a significant difference between large and small tubers in the content of the reducing sugars glucose and fructose (Table 5). Small tubers contained greater amounts of reducing sugars. While glucose reached its lowest level at harvest, it increased dramatically after two weeks in storage (Fig. 8). Fructose could again only be detected after the tubers had been stored for two weeks (Fig. 9).

Table 5. Analysis of variance table for sucrose, glucose, fructose and total reducing sugar levels (mg/g fwt) of potato tubers from field experiments in 1989.

		Mean Square			
Source	df	Sucrose	Glucose	Fructose	Red.Sugars
Rep	3	0.081	1.194	0.482*	2.673
Date (D)	8	66.700**	16.136**	14.384**	56.818**
Size (S)	1	0.117	11.202**	1.605**	21.288**
D * S	8	0.569	0.447	0.261	0.899
Error	51	0.892	0.695	0.171	1.360
CV %		23.955	30.632	38.132	30.666

*,**significant at P=0.05 and P=0.01 respectively.

The sucrose contents at time of final harvest would have been acceptable for the processing industry if processed right out of the field (Fig. 7). But with a sucrose content of about 4 mg per gram fresh weight at harvest, Russet Burbank potatoes would not process well within a short time in storage because the total reducing sugar content increased rapidly above 5.0 mg per gram fresh weight during storage (Fig. 10). For the large tubers the total reducing sugar content declined during storage and reached an acceptable level of 4.7 mg per gram fresh weight after 56 days.

Sucrose did not reach a low at harvest, indicating that tubers were physiologically immature at that time. Iritani and Weller (1977) found for Russet Burbank that the optimum time of harvest was reached

when the sucrose content of the tubers had reached its minimal physiological level.

In the present research tubers had the lowest sucrose content two weeks after harvest. At the same time reducing sugars went up, which meant that some of the sucrose must have been converted into reducing sugars after harvest. This is supported by Nelson and Sowokinos (1983) who found that reducing sugars accumulated rapidly in physiologically immature tubers during storage. This accumulation was probably the result of the conversion of sucrose to reducing sugars after harvest via the enzyme invertase. In the large tubers, reducing sugar content decreased later in storage which meant that in this case reducing sugars were probably converted into starch. Even though the small and large tubers had a similar sucrose content at harvest time, glucose and fructose increased to a higher level in the small tubers. This may suggest that the carbohydrate metabolism in small tubers is different than in large tubers. This difference in physiological maturity between the tuber sizes may mean that the conversion of sucrose to starch in small tubers was less efficient.

4.3 Influence of Chemical Topkill on Sugar Content of Tubers

4.3.1 1988

The influence of the chemical topkill on the development of sucrose and the reducing sugars glucose and fructose was investigated during the latter part of tuber bulking and beginning of storage. The analysis of variance showed that sampling date had a highly significant effect on sugar contents, but topkill had no effect on sugar contents

(Table 6).

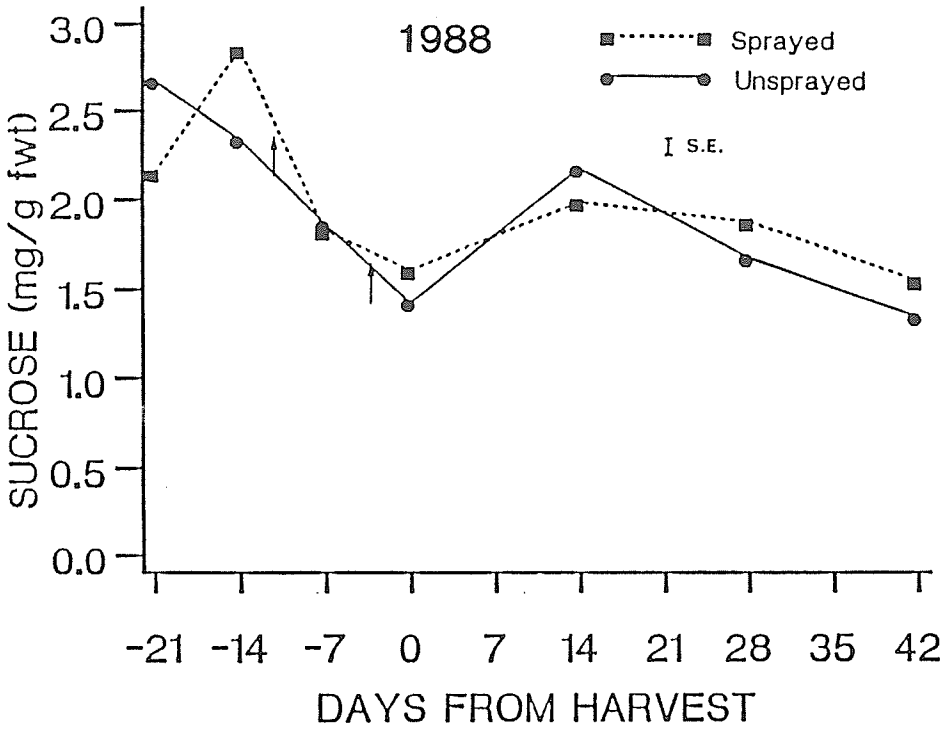
Table 6. Analysis of variance table for sucrose, glucose, fructose and total reducing sugar contents (mg/g fwt) of tubers from topkilled versus untreated potato plants in 1988.

		Mean Square			
Source	df	Sucrose	Glucose	Fructose	Red.Sugars
Replicate	5	0.185	0.116	0.013	0.106
Treatment(T)	1	0.050	0.052	0.003	0.080
Error a	5	0.620	0.014	0.044	0.100
Date(D)	6	2.257**	0.264**	0.443**	1.344**
D * T	6	0.330	0.076	0.004	0.099
Error b	60	0.165	0.077	0.029	0.161
CV %		20.8	53.3	112.3	59.8

**significant at P=0.01

Graphical presentation of the results also showed no consistent trends for any of the sugars measured (Fig. 11 to 14). Again when looking at these results one has to consider the characteristics of the season at the location. Yields were low because of heat and inadequate moisture (Table 4). Furthermore, at the time of the topkill application the tops of the plants began to yellow and senesce. The tubers had reached physiological maturity, indicated by the low sucrose content, which is likely the reason the topkill application did not have an effect on sugar content.

Fig. 11. Sucrose content of Russet Burbank tubers from untreated plants and plants sprayed with diquat during 1988 and 1989 (↑ , indicates date of spray application; 0 days from harvest = Sept. 16, 1988 and Sept. 19, 1989).


1988
Sprayed
Unsprayed
I S.E.
SUCROSE (mg/g fwt)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

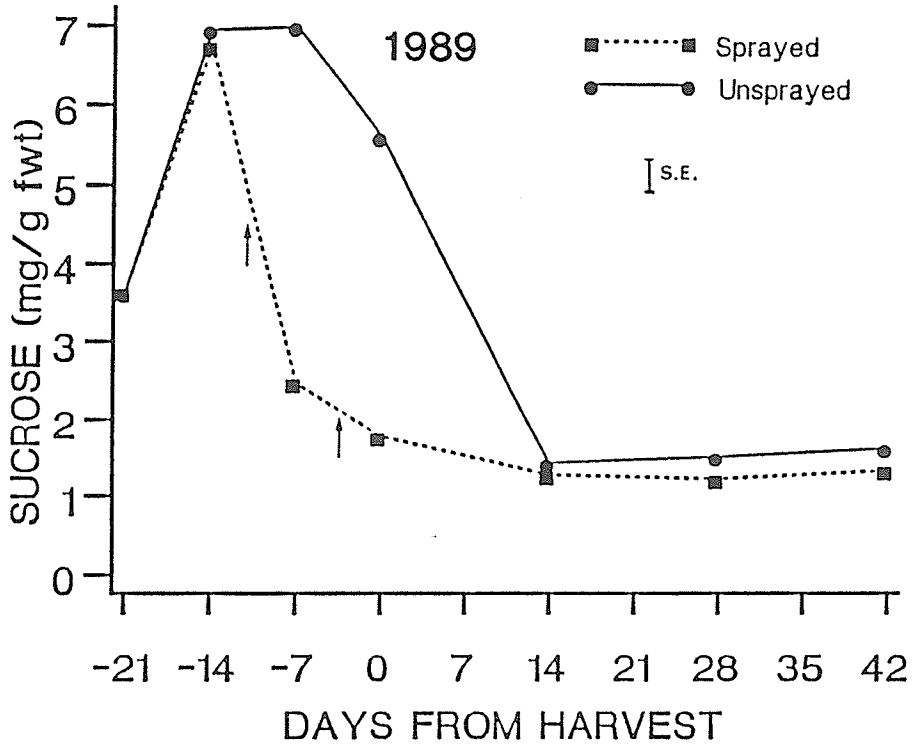
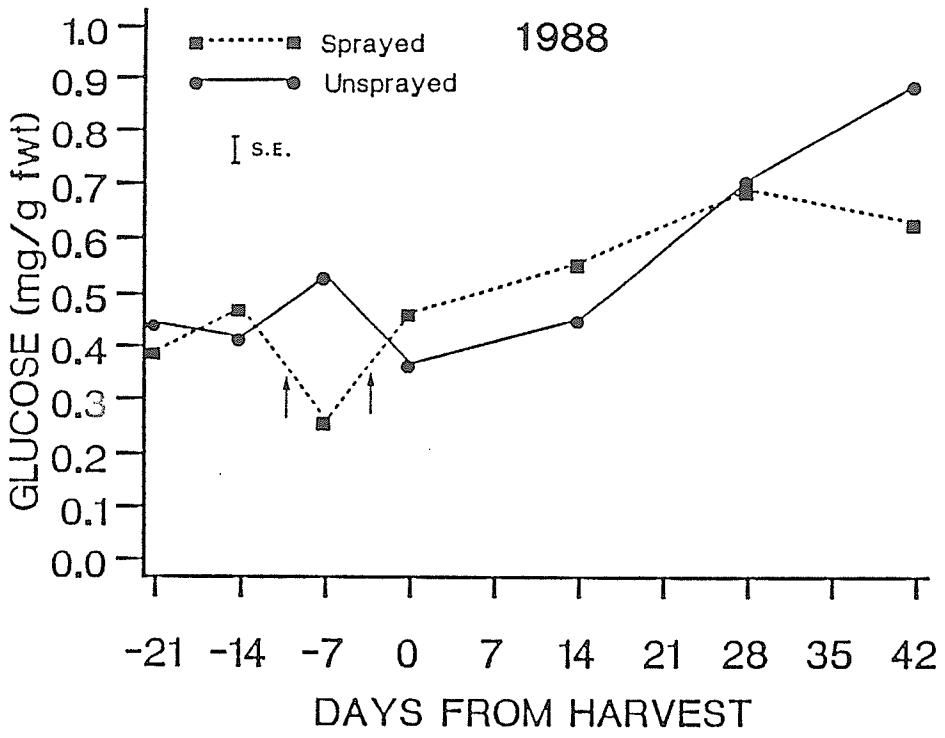

1989
Sprayed
Unsprayed
I S.E.
SUCROSE (mg/g fwt)
7
6
5
4
3
2
1
0
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

Fig. 12. Glucose content of Russet Burbank tubers from untreated plants and plants sprayed with diquat during 1988 and 1989 (↑ , indicates date of spray application; 0 days from harvest = Sept. 16, 1988 and Sept. 19, 1989).


1988
Sprayed
Unsprayed
S.E.
GLUCOSE (mg/g fwt)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

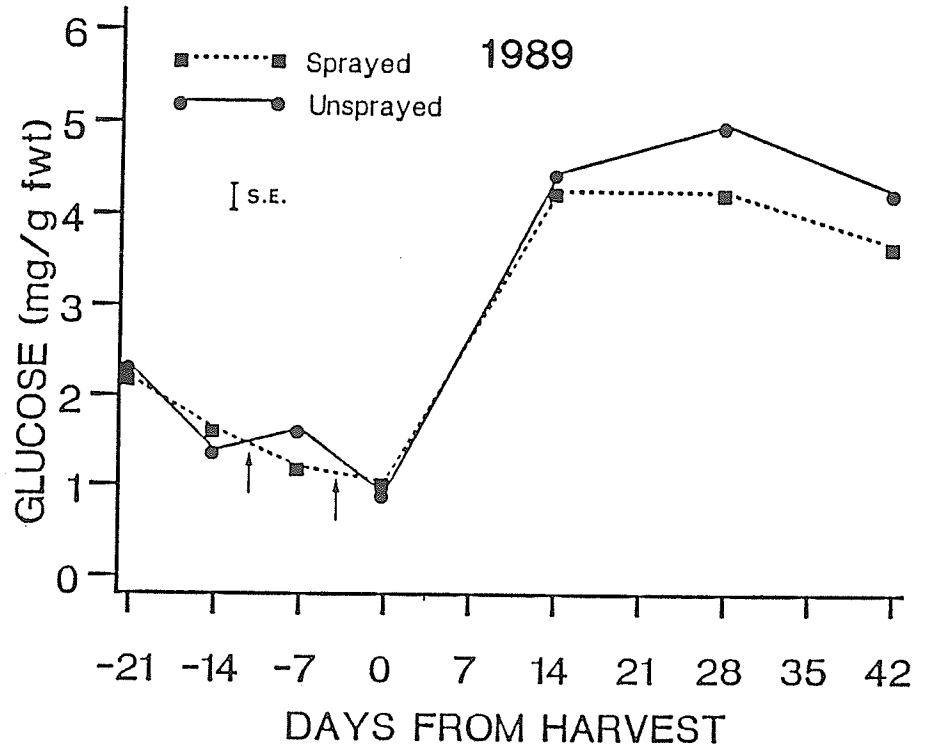
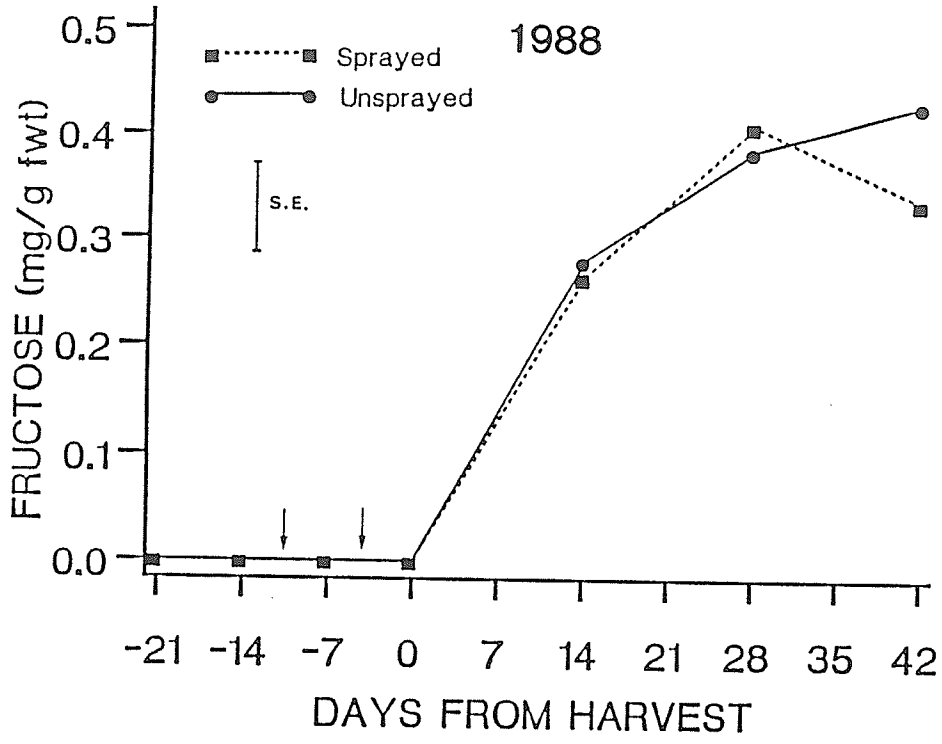

1989
Sprayed
Unsprayed
S.E.
GLUCOSE (mg/g fwt)
6
5
4
3
2
1
0
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

Fig. 13. Fructose content of Russet Burbank tubers from untreated plants and plants sprayed with diquat during 1988 and 1989 (↑ , indicates date of spray application; 0 days from harvest = Sept. 16, 1988 and Sept. 19, 1989).


1988
Sprayed
Unsprayed
S.E.
FRUCTOSE (mg/g fwt)
0.5
0.4
0.3
0.2
0.1
0.0
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

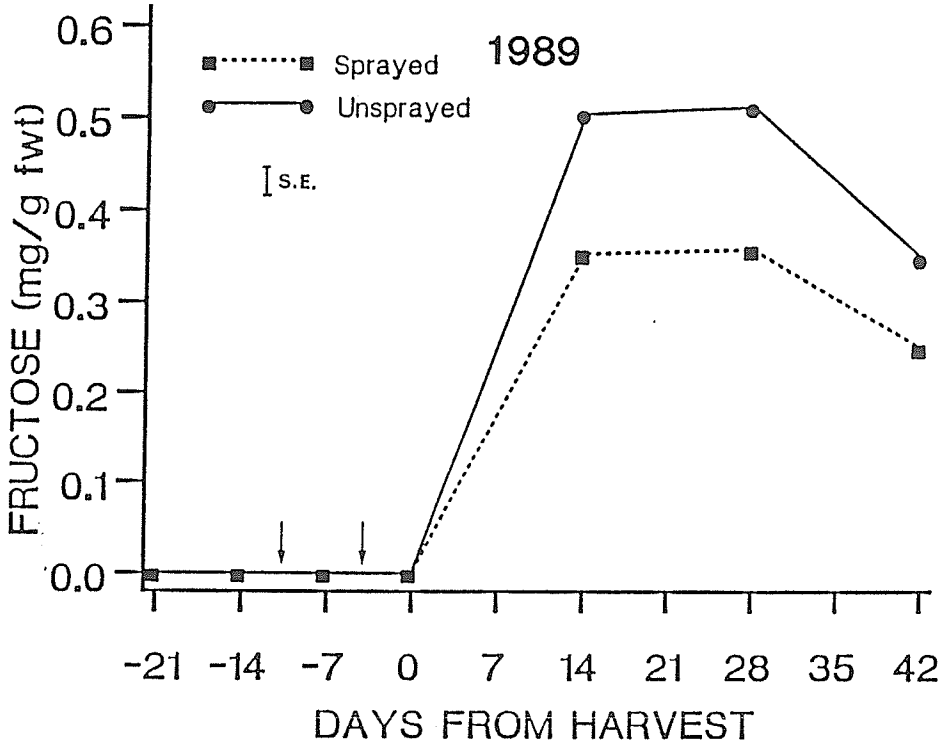
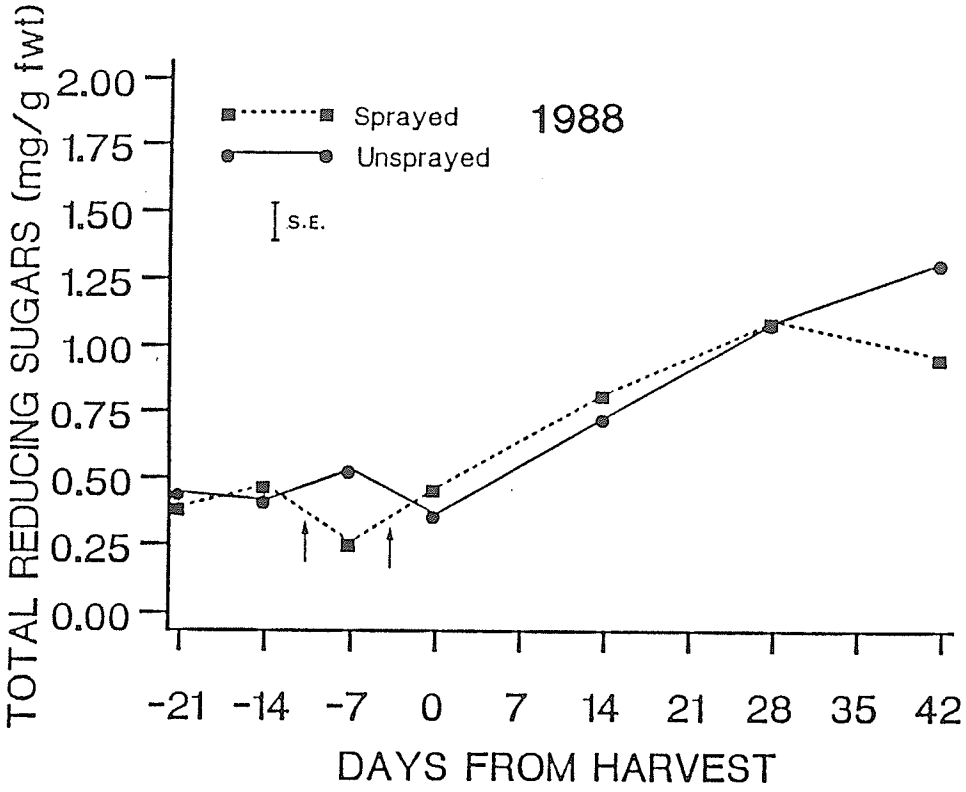
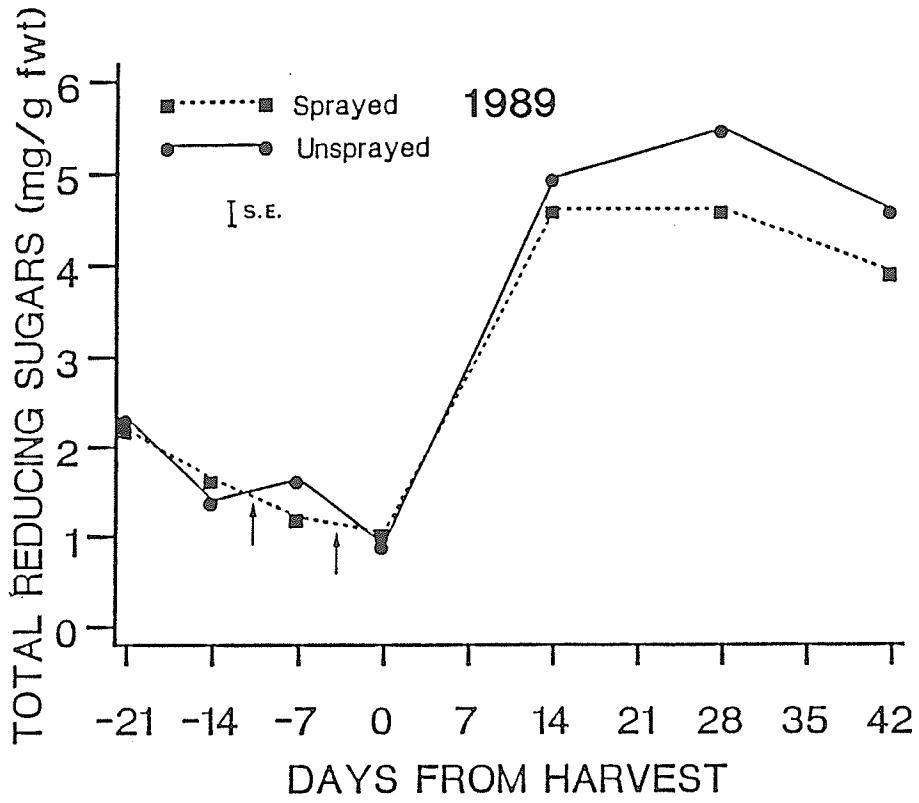

1989
Sprayed
Unsprayed
S.E.
FRUCTOSE (mg/g fwt)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

Fig. 14. Total reducing sugars content of Russet Burbank tubers from untreated plants and plants sprayed with diquat during 1988 and 1989 (↑ , indicates date of spray application; 0 days from harvest = Sept. 16, 1988 and Sept. 19, 1989).


TOTAL REDUCING SUGARS (mg/g fwt)
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
Sprayed
Unsprayed
1988
S.E.
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST


TOTAL REDUCING SUGARS (mg/g fwt)
6
5
4
3
2
1
0
Sprayed
Unsprayed
1989
S.E.
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

4.3.2 1989

There was a significant difference in sucrose content in tubers from topkilled plants compared to tubers from untreated plants in 1989 (Table 7). Six days after the first spray application the sucrose content of tubers from the treated plants fell to 2.5 mg per gram fresh weight, while the sucrose content of tubers from the untreated plants remained at around 7 mg per gram fresh weight and was therefore high at harvest (Fig. 11). Since the sucrose content was low by the time of the second topkill treatment, there was little additional decrease by the time of harvest. After the tubers were put into storage, the difference between treatments was only 0.3 mg per gram fresh weight, with sucrose content in the tubers from the topkilled plants remaining slightly lower than those from untreated plants.

There was however, no significant difference in glucose content between the treatments at harvest but tubers from topkilled plants had a lower glucose content after 28 days in storage (Fig. 12). Fructose was again only detected after the tubers had been put into storage and there was a significant difference between both treatments (Fig. 13). Tubers from untreated plants developed a higher fructose content during storage. Therefore, a significant difference for the total reducing sugars, glucose and fructose, was observed, resulting in a slightly lower content for tubers from the topkilled plants (Fig. 14). At harvest time, reducing sugar contents for both treatments were at their lowest and the tubers would have been acceptable for the processing industry. Two and four weeks after final harvest reducing sugar content for tubers of untreated plants increased to levels (> 5 mg/g)

Table 7. Analysis of variance table for sucrose, glucose, fructose and total reducing sugar levels (mg/g fwt) of tubers from topkilled versus untreated potato plants in 1989.

		Mean Square			
Source	df	Sucrose	Glucose	Fructose	Red.Sugars
Replicate(R)	5	0.444	0.750	0.006	0.774
Treatment(T)	1	36.789**	1.224	0.071**	1.884*
Error a	5	0.776	0.483	0.005	0.524
Date(D)	6	51.567**	28.643**	0.541**	36.775**
D * T	6	11.455**	0.385	0.017**	0.505
Error b	60	1.295	0.432	0.003	0.459
CV %		34.5	24.1	30.9	23.4

*,**significant at P=0.05 and P=0.01 respectively.

unacceptable for the processing industry. However, the reducing sugar levels for the topkill treatment were still acceptable (< 5 mg/g). At the same time sucrose content decreased during storage for both treatments. After 42 days in storage the reducing sugar content of tubers from untreated plants declined to a level (< 5 mg/g) which would be acceptable by the processing industry.

The results of these experiments show that the desiccant, sprayed to kill the tops of the plants, enhanced chemical maturity at harvest. Its effect was to decrease the accumulation of reducing sugars in storage and as a consequence would produce a superior processed product. The tubers from untreated plants were physiologically immature at the

time of final harvest and held high contents of sucrose and reducing sugars. Tubers from the topkilled plants had low sucrose contents at harvest and therefore, one would not have expected that the reducing sugars would increase to high levels (Fig. 11 and 14). Nonetheless, the tubers from the topkilled plants developed only slightly lower reducing sugar contents during storage than those from unsprayed plants. It may be possible that tubers from the unsprayed treatment were converting sucrose to reducing sugars while tubers from the sprayed treatment were converting starch to reducing sugars. Sowokinos (1977) had similar results and found that the higher the sucrose content was at the time of lifting, the faster reducing sugars were formed during storage .

Timely application of chemical topkill does not seem to have a negative impact either on the sugar content or on the direct aim of high yields. Therefore it could be beneficial in situations where tubers would be physiologically immature at harvest and sucrose contents are high. But if tubers have reached their lowest sugar contents and highest specific gravity at time of harvest, a chemical topkill to induce physiological maturity would not be recommended because tubers have reached this maturity already, and sugar contents will not increase in storage to unacceptable levels. In the case of plants which have physiologically mature tubers, a topkill would only serve to kill vines for easier harvest.

4.4 Influence of Chemical Topkill on Specific Gravity

4.4.1 1988

There was no effect on specific gravity when plants were topkilled

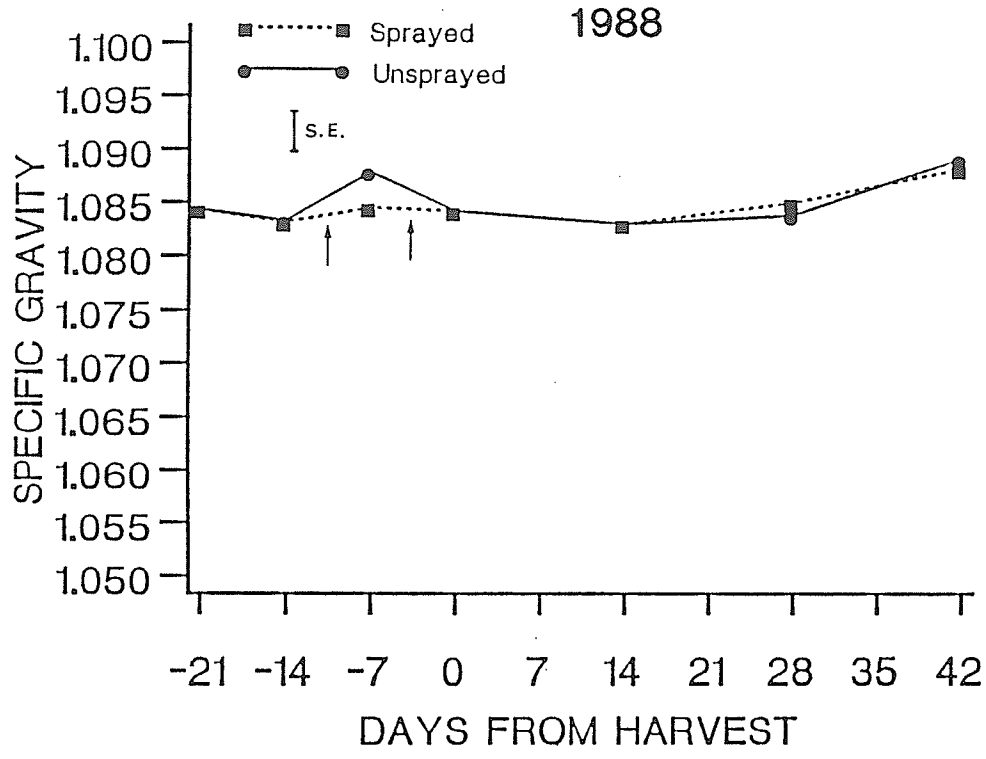
(Table 8) and specific gravity did not change during storage (Fig. 15). Average specific gravity for both treatments at harvest was high (1.085) and indicated that tubers were physiologically mature.

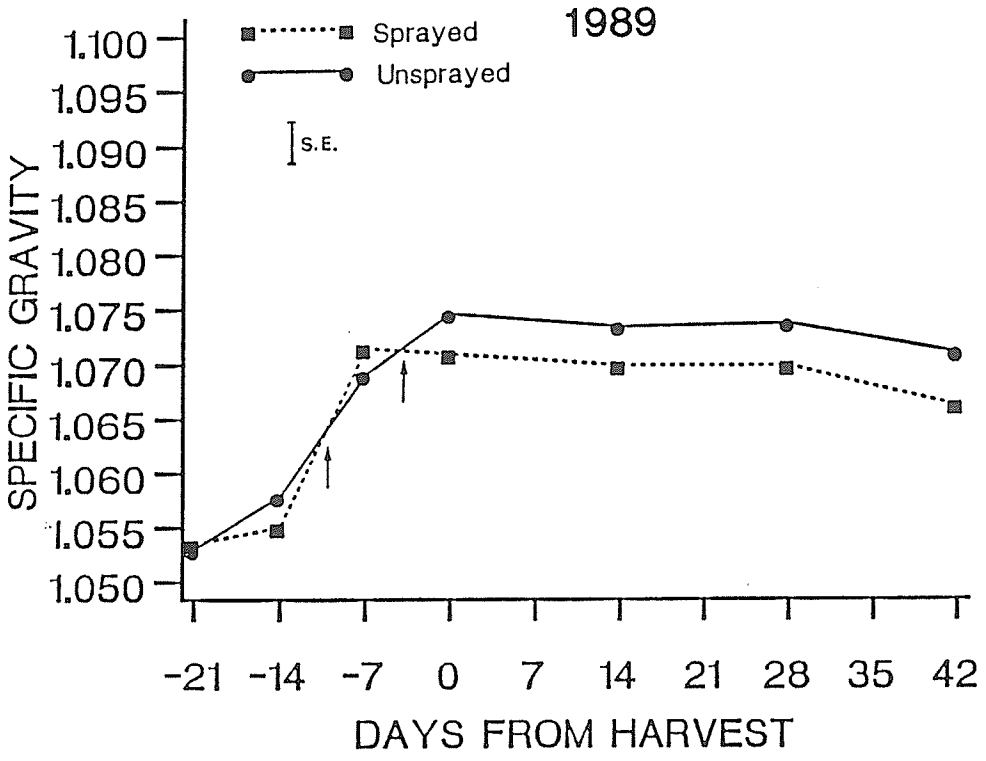
Table 8. Analysis of variance table for specific gravity of tubers from topkilled versus untreated potato plants in 1988.

		Mean Square (x1000)
Source	df	Specific Gravity
Replicate	5	0.076**
Treatment(T)	1	0.005
Error a	5	0.001**
Date(D)	60	0.046**
D * T	6	0.006
Error b	60	0.011
CV %		0.3

**significant at P=0.01

Fig. 15. Specific gravity of Russet Burbank tubers from untreated plants and plants sprayed with diquat during 1988 and 1989 (↑ , indicates date of spray application; 0 days from harvest = Sept. 16, 1988 and Sept. 19, 1989).


1988
Sprayed
Unsprayed
S.E.
SPECIFIC GRAVITY
1.100
1.095
1.090
1.085
1.080
1.075
1.070
1.065
1.060
1.055
1.050
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST


1989
Sprayed
Unsprayed
S.E.
SPECIFIC GRAVITY
1.100
1.095
1.090
1.085
1.080
1.075
1.070
1.065
1.060
1.055
1.050
-21 -14 -7 0 7 14 21 28 35 42
DAYS FROM HARVEST

4.4.2 1989

There was a significant difference in specific gravity between tubers from topkilled plants and from untreated plants in 1989 (Table 9). At harvest specific gravity was higher in tubers from untreated plants and this did not change during storage (Fig. 15). Walsh (1988, personal communication) also found a significantly higher specific gravity in the tubers from untreated plants compared to tubers from topkilled plants. The values for specific gravity were low for 1989 over all the sampling dates, ranging from about 1.05 at the first sampling date to about 1.07 at time of harvest. These data show that tubers had not reached maximum starch content and tubers in both treatments were physiologically immature at harvest, indicated also by the high reducing sugar content (Fig. 14). As in 1988, specific gravity remained relatively consistent during storage.

The difference in specific gravity can be attributed to the fact that the untreated plants were still vigorously growing compared to the treated plants in which haulms were already dying. The tubers of the untreated plants had the chance to accumulate more assimilates which were transported into the tubers where they eventually added to the starch pool.

Table 9. Analysis of variance table for specific gravity of tubers from topkilled versus untreated potato plants in 1988.

Source	df	Mean Square (x1000) Specific Gravity
Replicate	5	0.050**
Treatment(T)	1	0.072*
Error a	5	0.081
Date(D)	6	0.774**
D * T	6	0.017
Error b	60	0.015
CV %		0.4

*,**significant at P=0.05 and P=0.01 respectively.

5.0 GENERAL DISCUSSION

The study of assimilate partitioning (21 h after addition of $^{14}CO_2$) into different sized tubers of single plants during different stages of growth showed that there was always a strong relationship between tuber fresh weight and ^{14}C-accumulation, meaning that the larger the tuber the greater the ^{14}C-accumulation. This result would imply that tubers initiated late in the growing season would not become strong sinks and would therefore remain small. This relationship became slightly less towards 65 days after tuber initiation, but was still highly significant. Consequently, the weight of the tuber determined how much carbon was transferred into a tuber. The slopes of the regression lines indicated that the accumulation of label per gram of tuber tissue was greatest during the period of rapid sizing. No relationship was found for the early and late tuber development for dry weight and incorporation of ^{14}C into the tuber tissue on a per gram basis. However, at 24, 35, and 45 days after tuber initiation this relationship became significant, indicating that at intermediate growth stages sink activity may be related to tuber weight. It would be of further interest to determine the distribution of ^{14}C in the various fractions of the tuber (e.g. starch, sucrose, reducing sugars) during field growth and storage.

The sugar contents of tubers remained relatively constant and no differences were observed between either small and large tubers or chemical topkill treatments for both field trials and during storage in the first year, in 1988. Tubers were physiologically mature at harvest,

indicated by dead vines, high specific gravity and low sugar contents in tubers at harvest time.

Differences in sugar contents were found however, during the second year, which illustrates the difficulties inherent in any generalization related to sugar content with even a single cultivar. In 1989 tubers were physiologically immature at harvest and differences in treatments were observed. The tops of the plants were green at harvest and reducing sugar levels increased drastically at the beginning of storage. The larger than average tubers contained less reducing sugars than the smaller than average tubers. During the storage period of 56 days the small tubers contained levels of reducing sugars unacceptable for the processing industry.

Tubers from chemically topkilled plants developed lower sucrose content in 1989 than tubers from untreated plants and therefore acceptable reducing sugar content during storage. Glucose content of tubers from topkilled plants increased during the beginning of storage to a level similar to tubers from untreated plants. This result was unexpected because sucrose content of tubers from topkilled plants was low at harvest, therefore, glucose must have been mobilized from starch reserves during storage. Specific gravity was higher for tubers from untreated plants than from topkilled plants. The untreated plants were able to collect assimilates for an additional 10 days resulting in greater dry matter accumulation in the tuber and higher specific gravity.

The implication of physiological maturity is of utmost importance in the determination of the necessity of topkill treatments. If tops appear to be senescing naturally late in the season application of

topkill will not be necessary; however, if tops remain green late in the season a topkill appplication will enhance chemical maturity of tubers at harvest. The negative effect of topkill application on specific gravity will have to be balanced against reducing sugar content when the decision to apply topkill is made. If the processing industry has information about the state of maturity of tubers at harvest time for a certain cultivar, it would be possible to customize storage conditions for these tubers in order to achieve the desired state of physiological maturity.

When tubers are handled and stored identically, the conditions to which those tubers were exposed while in the field coupled with their stage of physiological maturity at harvest will influence subsequent storage physiology. Further studies, using controlled environments, may be necessary to completely define conditions which lead to excessive reducing sugar contents. Field studies which sample a large number of environments are essential before a reliable predictive model related to tuber quality can be determined. Studies related to the source of reducing sugars in tubers from topkilled immature plants would also be of interest.

LIST OF REFERENCES

Burton, W.G. 1966. The potato. Veenman and Zonen, Wageningen, Holland.

Burton, W.G. 1977. Senescence in stored potato tubers. Ann. App. Biol. 85:433-436.

Burton, W.G. 1978. Post-harvest behaviour and storage of potatoes. p.122-156. *In* T.H. Coaker (ed.) Applied Biology, Vol. III. Academic Press, London, New York, San Francisco.

Dwelle, R.B. 1985. Photosynthesis and photoassimilate partitioning. p.35-52. *In* P. Li (ed.) Potato Physiology. Academic Press, Orlando, Florida, U.S..

Dwelle, R.B. and Stallknecht, G.F. 1978. Respiration and sugar content of potato tubers as influenced by storage temperature. Am. Potato J. 55:561-571.

Engels, C. 1983. Wachstumsrate der Knollen von Solanum tuberosum var. Ostara in Abhaengigkeit von exogenen und endogenen Faktoren - Konkurrenz zwischen Einzelknollen um Assimilate -. PhD Thesis. University of Hohenheim, West Germany. 220 p.

Engels, C. and Marschner H. 1986. Allocation of photosynthate to individual tubers of *Solanum tuberosum* L.. III. Relationship between growth rate of individual tubers, tuber weight and stolon growth prior to tuber initiation. J. of Experim. Bot. 37:1813-1822.

Engels, C. and Marschner H. 1987. Effects of reducing leaf area and tuber number on the growth rates of tubers on individual potato plants. Potato Res. 30:177-186.

Es, A. van and Hartmans, K.J. 1987. Starch and sugars during tuberization, storage and sprouting. p.79-113. *In* A. Rastovski et al. (ed.) The storage of potatoes. Pudoc, Wageningen, Netherlands.

Gawronska, H. and Dwelle, R.B. 1989. Partitioning of photoassimilates by potato plants (*Solanum tuberosum* L.) as influenced by irradiance. I. Partitioning patterns in cultivar Russet Burbank grown under high and low irradiance. Am. Potato J. 66:201-213.

Grassert, V. 1979. Einfluss des Reifegrades und der Krautabtoetung auf den Gehalt an reduzierenden Zuckern in Kartoffelknollen waehrend der Lagerung. Arch. Acker. Pflanzenbau Bodenkd. 23:609-615.

Gregory, L.E. 1965. Physiology of tuberization in plants (tubers and tuberous roots). Encyclopedia Plant Physiol. 15:1328-1354.

Halderson, J.L., Haderlie, L.C., and Skrobacki, A. 1988. Mechanical vine killing of potatoes. Am. Potato J. 65:415-423.

Iritani, W.M. 1981. Growth and preharvest stress and processing quality of potatoes. Am. Potato J. 58:71-80.

Iritani, W.M., Weller, L. and, Russel, T.S. 1973. Relative differences in sugar content of basal and apical portions of Russet Burbank potatoes. Am. Potato J. 50:24-31.

Iritani, W.M. and Weller, L. 1977. Changes in sucrose and reducing sugar contents of Kennebec and Russet Burbank tubers during growth and post harvest holding temperatures. Am. Potato J. 54:395-404.

Iritani, W.M. and Weller, L. 1978. Influence of low fertility and vine killing on sugar development in apical and basal portions of Russet Burbank potatoes. Am. Potato J. 55:239-246.

Kleinkopf, G.E., Westermann, D.T., and Dwelle, R.B. 1981. Dry matter production and nitrogen utilization by six potato cultivars. Agron. J. 73:799-802.

Krijthe, N. 1955. Observations on the formation and growth of tubers on the potato plant. Netherlands J. of Agric. Sci. 3:291-304.

Maillard, L.E. 1912. Formation of malanoidins in a methodical way. Acad. Sci. 154:66-88.

Manitoba Agriculture, 1986. Vegetable crop production guide. p. 42. Manitoba Agricuture, Manitoba, Canada, Agdex 250-32.

Mares, D.J. and Marschner H. 1980. Assimilate conversion in potato tubers in relation to starch deposition and cell growth. Ber. Deutsch. Bot. Ges. 93:299-313.

Moorby, J. 1968. The influence of carbohydrate and mineral nutrient supply on the growth of potato tubers. Ann. Bot. 32:57-68.

Moorby, J. 1970. The production, storage, and translocation of carbohydrates in developing potato plants. Ann. Bot. 34:297-308.

Moorby, J. and Milthorpe F.L. 1978. Potato. p.225-257. *In* L.T. Evans (ed.) Crop physiology - Some case histories. Cambridge University Press, Cambridge, U.K..

Morrel, S. and Rees, T.A. 1986. Sugar metabolism in developing tubers of *Solanum tuberosum*. Phytochemistry 25:1579-1585.

Murphy, H.J. 1968. Potato vine killing. Amer. Potato J. 45:472-478.

Nelson, D.C. and Sowokinos, J.R. 1983. Yield and relationships among tuber size, sucrose and chip color in six potato cultivars on various harvest dates. Am. Potato J. 60:949-958.

Oparka, K.J. 1985. Changes in partitioning of current assimilate during tuber bulking in potato (*Solanum tuberosum* L.) cv Maris Piper. Ann. Bot. 55:705-713.

Oparka, K.J., Davies H.V., and Prior, D.A.M 1988. Long-term metabolism of [^{14}C] sugars in stored potatoes. Ann. Bot. 61:185-191.

Peterson, R.L., Barker, W.G., and Howarth, M.J. 1985. Development and structure of tubers. p.123-152. *In* P. Li (ed.) Potato Physiology. Academic Press, Orlando, Florida, U.S..

Plaisted, P.H. 1957. Growth of the potato tuber. Plant Physiol. 32:445-453.

Pressey, R. 1969. Role of invertase in the accumulation of sugars in cold stored potatoes. Am. Potato J. 46:291-297.

Reeve, R.M., Timm, H., and Weaver, M.L. 1973. Parenchyma cell growth in potato tubers. II. Cell divisions vs. cell enlargement. Am. Potato J. 50:71-78.

Rowberry, R.G. and Johnston, G.R. 1966. A note on the effect of vine killing on specific gravity of Kennebec and Sebago tubers. Am. Potato J. 43:381-383.

SAS. 1985. SAS users guide: Statistics. SAS Institute. Cary, N.C. pp. 505

Schaupmeyer, C.A., Hanel, B., and Bergen, A. 1989. Effect of planting date, maturity, and speed of vine removal or desiccation on the incidence of stem end discoloration and yield of Russet Burbank and Norchip potatoes. p. 35-37. *In* C.A. Schaupmeyer et al. (ed.) Potato cultural trials, 1985-1988. Alta. Spec. Crops and Hort. Res. Cent., ASCHRC Pamphlet 89-8.

Smith, O. 1977. Potatoes: production, storing, processing. 2nd ed. The Avi Publishing Company, Inc., Westport, Connecticut, U.S..

Smith, O. 1987. Effect of cultural and environmental conditions on potatoes for processing. p.73-148. *In* W.F.Talburt and O.Smith (ed.) Potato processing. Van Nostrand Reinhold Company, New York, U.S..

Sowokinos, J.R. 1973. Maturation of Solanum tuberosum. I.Comparative sucrose and sucrose synthetase levels between several good and poor processing varieties. Am. Potato J. 50:234-247.

Talburt,W.F, Schwimmer, S., and Burr H.K. 1987. Structure and chemical composition of the potato tuber. p. 11-46. *In* W.F.Talburt and O.Smith (ed.) Potato processing. Van Nostrand Reinhold Company, New York, U.S..

Twiss, P.T.G. 1963. Quality as influenced by harvesting and storage. p.433-436. *In* J.D.Ivins and F.L.Milthorpe (ed.) The growth of the potato. Butterworths, London, U.K..

Vliet, W.F. van, and Schriemer, W.H. 1960. The sugar accumulation in potatoes kept at a low temperature, as studied in a small selection of samples of Dutch varieties. Eur. Potato J. 3:263-271.

Wiese, W., Bommer, D., and Patzold, C. 1975. Einfluss differenzierter Wasserversorgung auf Ertragsbildung und Knollenqualitaet der Kartoffelpflanze (Solanum tuberosum L.). Potato Res. 18:618-631.

Wilson, A.M., Work, T.M., Bushway, A.A., and Bushway, R.J., 1981. HPLC determination of fructose, glucose and sucrose in potatoes. J. of Food Sci. 46:300-301.

Wurr, D.C.E. 1977. Some observations of patterns of tuber formation and growth in the potato. Potato Res. 20:63-75.