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Carbohydrates and Yield Physiology of Asparagus – A Global Overview

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Abstract

The physiology of yield determination in asparagus (*Asparagus officinalis* L.) is complex. Above-ground growth of spears and ferns is the ultimate indicator of performance. However, growth is driven by soluble carbohydrate (CHO), which has a well-known pattern of gain and loss in the storage root system during the crop's annual cycle. Root CHO content is a better performance indicator, now that the relationship between above-ground growth and CHO changes is better understood. Recent research has improved the definition of the root CHO pattern, and of benchmark CHO contents at key times during the growth cycle. Detection of deviations from the 'ideal' pattern can help with early diagnosis of problems. The research has also led to a simple method for assessing the CHO content of roots and to an internet-based system for delivering interpretations of CHO content data. Together, these components constitute the *Aspire* decision support system. In this paper we review this research. In particular, we explore four topics that are crucial for the viability of the concept: (a) evaluate whether Brix% of root sap can be used as a surrogate for analytical root CHO content; (b) compare root CHO content patterns in different countries, with different climates and management systems; (c) analyse the significance of root system size; and (d) analyse the physiological capacity of crops to produce CHO during fern growth. We conclude that, provided the implications of these factors are recognised, the approach can deliver benefits to asparagus growers. The *Aspire* system is becoming available to increasing numbers of growers around the world. Already it is being used by growers in New Zealand and North America, supporting them in making management decisions to improve yields and the long-term sustainability of their crops.

INTRODUCTION

The physiology of yield determination in asparagus is complex because it is a perennial crop. Yield is the culmination of a sequence of physiological processes that are influenced by

environmental and management factors in both the current and previous seasons. This complexity can be described by incorporating knowledge about all the processes into models that simulate crop growth (Lampert et al., 1980; Wilson et al., 2002b). In most practical situations, however, growth of spears and ferns is usually the only readily available indicator of crop performance. Above-ground growth, and therefore yield, varies widely among crops, locations and years and, often, the causes of the variations cannot be identified. Variability can be reduced, and overall yield increased, by basing crop management decisions on sound information about the state of key crop factors that determine yield.

The level of stored soluble CHO in the root system is one of these key factors, because the root system is the ‘engine’ and CHO is the ‘fuel’ that drives crop performance. Root CHO fluctuates in a pattern that is associated with growth of spears and ferns. The pattern of gain and loss of CHO during the annual growth cycle reflects the effect of the physiological processes and all the influences on them. Thus, the level of CHO in the roots at any time is a very useful gauge of the condition of a crop.

The importance of root CHO has long been recognised but, until recently, it has not been easy to measure or interpret routinely. At the last International Asparagus Symposium we introduced *AspireNZ*, a decision support system for managing root CHO in asparagus crops (Wilson et al., 2002a). Since then there has been widespread interest in using root CHO as an indicator of the condition of crops, and many growers in New Zealand and North America have been using *AspireNZ* and *AspireUS*, an ‘Americanised’ version of the system. Many measurements of root CHO have been made in several countries, and revised or new versions of the *Aspire* system are being developed. This activity has improved the definition of the root CHO pattern and increased understanding of the relationship between CHO changes and above-ground growth of ferns and spears.

In this paper we review these international developments. First we briefly review the role of CHO in asparagus yield determination. Then we evaluate methods for measuring root CHO content and present results from different countries showing that CHO patterns are similar among diverse climates and production systems. Finally we analyse the effects on yield determination of root system size and the physiological capacity of crops to produce CHO during fern growth.

YIELD AND CHO

The potential yield of an asparagus crop depends on the availability of CHO in its storage root system. Enough CHO is needed to fuel spear growth during harvest and, also, to establish growth of a good fern canopy after the end of harvest. In general, potential spear yield is highest in crops with a complete population of plants that have large root systems with a high CHO content at the start of harvest. Usually, crops with these characteristics have higher spear production rates and can be harvested for longer than crops with low CHO availability. Whether or not the potential is achieved depends on factors such as management and weather conditions, especially temperature during harvest, and the available season length.

The amount of CHO per unit area (kg ha^{-1}) in a crop’s root system at any time is the product of three factors:

- plant population (plants ha^{-1}),
- mean biomass of the storage root system (kg plant^{-1}), and
- the mean CHO content of the roots (kg kg^{-1}).

Plant Population

Population differs widely among crops, locations and management systems, and usually decreases as crops age and plants die. However, the change is usually quite slow, so variation in population is not a common cause of CHO and yield variability in the short term. Nevertheless, minimising plant loss is important for the long-term viability of crops because yield potential declines in direct proportion to plant loss. One cause of plant death in some production systems is reduced vigour resulting from low root CHO content caused by harvesting for too long.

Root Biomass

The average size of the storage root system per plant differs among cultivars, depends on plant population, is very dependent on soil conditions, changes during each year and increases during the first few years as crops are establishing. Root dry weight can vary tenfold among crops. In New Zealand, for example, in established crops it ranges from about 0.12 to 1.2 kg plant⁻¹. Therefore, with a typical population of 20,000 plants ha⁻¹, root dry weight per unit area ranges from about 2,400 to 24,000 kg ha⁻¹. Corresponding values measured in Washington and California have ranged from about 4,000 to 20,000 kg ha⁻¹.

Root biomass cannot be measured readily. The most accurate method is to excavate, dry and weigh whole root systems. Even then, there is much variability in root system size among plants within each crop, so several samples are needed to estimate a crop's root biomass. Clearly, this is not practicable in commercial crops. A procedure to make the process easier by estimating root biomass from core samples was developed by Drost and Wilson (2003). However, while it is useful for research projects, this procedure also is not feasible for commercial crops.

Storage root biomass consists of two components, structural material and soluble CHO, which behave differently. Structural biomass increases as the root system grows during crop establishment but subsequently it changes quite slowly. Therefore, in established crops, variation in structural biomass in the short term is not a major cause of yield variability. Some CHO is used continually in growth and respiration processes to maintain the structure because new roots grow and replace old ones which die.

Although yield may vary among years, the performance of crops in the longer term is an indirect indication of the size of root systems because it reflects their capacity to accumulate and store CHO. In general, high yielding crops have large root systems and low yielding crops have small root systems.

CHO Content

Root CHO content is easier to measure and much more dynamic than the other two factors. It varies considerably, and these fluctuations are the main cause of root and CHO biomass changes in established crops. Changes in CHO content can cause root biomass to vary by as much as 50% as stored CHO is depleted and replenished during each annual growth cycle. Therefore, against a background of slowly changing plant population and structural root biomass, values of CHO content can be interpreted to help make crop management decisions. This is the basis of the *Aspire* system.

DETERMINATION OF ROOT CHO CONTENT

The CHO physiology of asparagus was reviewed by Drost (1997). Most CHO in the root system consists of fructans. These storage CHOs are synthesized from simple sugars (sucrose, glucose and fructose) produced from photosynthesis in the ferns and translocated to the roots. They accumulate in the roots, and are hydrolyzed when they are required for spear growth, fern establishment or root and crown growth. Asparagus is very variable and, in particular, there is much variation of root CHO status among plants within crops. Therefore, obtaining a reliable assessment of a crop's CHO content requires consideration of the method of measurement and the root sampling strategy.

Methods

1. Analytical. The standard measure of root CHO status is the total content of water-soluble CHO (WSC), measured analytically and expressed on a dry weight basis (mg of CHO per g of dry weight). It is the most reliable indicator of the condition of a crop, and can be measured in several ways. The most common is the anthrone method (Quarmby and Allen, 1989). This has been used in tests in New Zealand (Wilson et al., 1999) and also in the USA. A different method was used in Germany, in which CHO extracted from root samples was hydrolysed with HCl for total-glucose and total-fructose detection, using two sodium hydroxide/sodium acetate gradients (Ernst and Krug,

1998). Total WSC was calculated as sum of the glucose and fructose fractions. Although it is the best measure, analytical root CHO content is suitable only for research purposes. It is not practicable for routine use on commercial crops because it is too slow and expensive.

2. Brix%. The refractive index of a solution, determined as Brix% with a refractometer, is often used as a measure of soluble sugar content in horticultural applications such as assessing the ripeness of fruits or vegetables. Brix% of sap extracted from asparagus roots that have been frozen and thawed was tested as a substitute measure of CHO content. It has the advantages that it is a simpler, faster and cheaper method and, therefore, it has potential to be used as a practical way to estimate root CHO content indirectly in growers' crops, provided it is related consistently to CHO content. Therefore, it is important to establish the reliability of the relationship between CHO content and Brix%.

3. Relationship between analytical CHO content and Brix%. Measurements of CHO content and Brix% on the same root samples from established crops have been completed at four locations (Table 1). There was much variation in the data, both within and among locations. After removing data points that were at the upper end of the refractometer range (i.e. Brix% = 32), we carried out three sets of statistical analyses to (a) estimate a separate linear regression equation between CHO content and Brix% for each location and check for significant differences in the equations among the locations, (b) determine whether curved equations gave better fits than straight lines, and (c) estimate a single linear equation for all the data sets. For each case, the validity of the regressions was checked by examining residuals in the standard way, and 95% confidence limits were obtained for new predictions using the equations. In summary, the analyses showed:

- A substantial part of the trend in the data was explained ($p < 0.001$) when a different linear regression was fitted for each location. Separate straight lines accounted for 73% of the total sums of squares. There was no evidence that CHO content was inherently more variable at one location than at another. The equations, with parameter standard errors in brackets, were:

$$\text{Washington: } \text{CHO} = 18.0 (0.8) \times \text{Brix\%} + 66.8 (12.2) \quad (1)$$

$$\text{California: } \text{CHO} = 21.3 (0.5) \times \text{Brix\%} + 16.8 (8.6) \quad (2)$$

$$\text{New Zealand: } \text{CHO} = 24.0 (0.7) \times \text{Brix\%} + 69.9 (11.6) \quad (3)$$

$$\text{Germany: } \text{CHO} = 24.2 (1.9) \times \text{Brix\%} + 39.0 (33.7) \quad (4)$$

- CHO content values predicted using the equations for New Zealand or Germany were higher throughout the range than those from the USA, with predicted values as much as 124 mg g^{-1} higher. For Washington, in particular, CHO values increased less with increasing Brix% than at the other locations. The reasons for the differences among locations are unclear. One possibility could be that the water content of the roots is consistently lower in warmer, drier climates, and that the correspondingly higher Brix% values alter the relationship between CHO content and Brix%.
- Allowing the relationships to be curved by adding a cubic smoothing spline (Verbyla et al., 1999) improved the fit to the data (75.6% of the total sums of squares). The fitted curve between Brix% and CHO content appeared to be almost linear between Brix% values of 3 and 18 but, for values above this, the relationship was less steep and noticeably curved.
- A substantial proportion of the variation in CHO content (67% of the total sums of squares) was accounted for by a single linear regression of CHO content on Brix% across all locations:

$$\text{All locations: } \text{CHO} = 21.1 (0.4) \times \text{Brix\%} + 42.9 (6.5) \quad (5)$$

However, this single line was a significantly worse fit to the data ($p < 0.001$) than were the separate lines for each location.

- Individual predictions of root CHO content with this equation have large uncertainty, as indicated by the large confidence limits (Fig. 1). However, equation (5) is adequate to use at all locations if (a) the predicted CHO content value is not too far from the corresponding value predicted from the spline model (so there is less accuracy at higher values) and (b) a large enough number of Brix% samples is taken to help account for the variability and, therefore, represent a crop accurately. Confidence limits for a predicted CHO content from the mean Brix% of several root samples will be substantially smaller in general.

- Brix% and root CHO content data from an experiment in Chile produced an equation that was very different. It was excluded from the composite analysis because the measurements were from a small number of one-year old plants grown in pots, and therefore they were not compatible with the data from the other locations.

Root Sampling

Whatever method is used to measure the CHO content of individual root samples, each with its associated uncertainty, it is necessary also to recognise the large variability that exists among plants within asparagus crops. Multiple samples are required to account for the variability and, therefore, obtain an accurate representation of a crop. We conducted statistical analyses on 87 sets of data, with different degrees of variability and a range of sample numbers, that were obtained from diverse asparagus crops in New Zealand. All samples were collected using a standard procedure. Roots were excavated to 30 cm depth between vertical cuts about 30 and 45 cm away from the centre of a typical plant at each sampling location. Ten 15 cm pieces of healthy root were collected for each sample. The coefficient of variation of the 87 data sets ranged from 10 to 36%.

Two methods were used to calculate the minimum number of samples needed to satisfy the criterion that a reliable Brix% estimate for a crop required that the 95% confidence limit must be less than 1% of the mean value. In the first analysis it was assumed that the data sets were normally distributed. In fact, several sets were not normally distributed or contained extreme outliers. These were accounted for in the second analysis with the boot-strap method (Efron and Tibshirani, 1986). The analyses showed that, although 10 samples were enough for the least variable cases, more than 18 samples were needed to obtain accurate representations of the most variable crops.

We conclude that the Brix% of sap solution extracted from roots can be used with confidence in place of analytical measurement of root CHO content, provided a mean value is obtained from Brix% measurements on at least 20 samples from a crop (Wilson et al., 2002a). However, the difference among locations is a problem that may require checks of the relationship between the two methods in different places. All root CHO content data in the following sections were calculated with equation (5).

GROWTH CYCLE AND PATTERNS OF ROOT CHO CONTENT

Much research has been done on changes of soluble CHO that occur in the storage root system of asparagus during the annual growth cycle. As a result, the pattern of CHO gain and loss associated with growth of spears and ferns is well-known (Shelton and Lacy, 1980; Robb, 1984; Haynes, 1987; Pressman et al., 1993; Drost, 1997; Wilson et al., 1999; Wilson et al., 2002a). Research in the last decade has improved the definition of this pattern and increased understanding of the relationship between CHO changes and above-ground growth of ferns and spears. Crops that follow the ideal pattern are the most likely to produce high yields. *AspireNZ* operates on the principle that knowledge of these patterns, and especially deviations from them, can be used to help make crop management decisions (Wilson et al., 2002a). Root CHO content values are evaluated taking into account the age of a crop and the stage of its annual cycle. Deviations from the ideal crop condition are identified by comparing the data with built-in performance benchmarks, and are used to help diagnose potential problems.

The original performance benchmarks and associated diagnoses applied only to conditions in New Zealand. The wider applicability of the system in different climates and crop management systems depends on the answers to several questions:

- Do all asparagus crops and cultivars have similar root CHO content patterns?
- Is the CHO content pattern similar for white and green asparagus production?
- Do all crops have similar benchmark values of root CHO content at key stages during the growth cycle?
- Do crops exhibit similar deviations from the ideal pattern in their responses to management and environmental influences?
- Do interpretations of deviations differ among climates and management systems?

In the rest of this paper, we will show that the answer to most of these questions is ‘Yes’, but with some qualifications. We will then show that, despite differences among climates and production systems, the approach pioneered in *AspireNZ* can be used elsewhere with appropriate modifications combined with an understanding of the significance of CHO fluctuations and, especially, deviations from normal.

Since the original work in New Zealand, measurements have been made of Brix% and/or root CHO content in several other countries during the last few years. In each case, the aim was to determine similarities and differences in the CHO pattern and benchmark values in different climates and production systems, and to determine causes of deviations. The measurements have been done in diverse conditions with different cultivars, management systems and crop age. Some have been in experiments and others in farmers’ crops. Some (e.g. in the USA, Netherlands, France, Germany and the UK) have been done through collaborations and, as far as possible, have followed standardised protocols. Others (e.g. Chile, Mexico) have been done independently. It is not possible to present all the results here. However, some examples are presented from each country as a basis for identifying and discussing similarities and points of difference.

New Zealand

Examples of root CHO content patterns in New Zealand were presented by Wilson et al. (1999, 2002a), and they are not repeated here. However, they consistently followed the expected annual pattern. When deviations from normal occurred, they were attributable to particular agronomic problems in crops.

USA

Root CHO content was measured five times per year in six commercial asparagus fields in California and in ten fields in Washington from 2002 to 2005. Examples from four fields, two each in Washington and California, are shown in Fig. 2a. Root CHO content followed the expected annual pattern in all cases, although values varied among crops and differed between the two states.

In California, both crops were young and their peak values at the start of harvest were over 600 mg g⁻¹. One recovered to a similar level at the end of the year while the other only recovered to about 450 mg g⁻¹, perhaps due to a factor such as foliar disease or water stress. Both had sharp CHO content declines during harvest and reached minimum values of about 250 and 350 mg g⁻¹ at the end of fern establishment. In Washington, where the harvest started later in the cooler climate, peak values were lower at the start of harvest (about 480 and 560 mg g⁻¹) and both recovered to about 600 mg g⁻¹ at the end of the season. Both declined less during harvest than in the Californian crops.

Root CHO content fluctuations were less in Washington where the crops were established Jersey Giant, which usually has a large root system, than in California where they were young UC157 crops, which usually has a relatively small root system.

The Netherlands

Root CHO content was measured in three contrasting crops (low, medium and high yields) during two years (Fig. 2b). Conditions were favourable during fern growth in the first year (warm and sunny with little disease) but they were less favourable in the second year (cooler and wetter with more *Stemphylium*).

Root CHO content followed the expected pattern during each year in all the crops, but there were different values and deviations among the three crops. The low yielding crop consistently had the lowest root CHO contents. It had the lowest value at the start of each harvest (April), reached very low minimum values at the end of fern establishment each year (July), and had poor recovery of root CHO content by the end of autumn each year (October). These results corresponded with the observation that the crop had low fern vigour in both years.

The medium crop followed the characteristic pattern and had the largest CHO content fluctuations, which implied that it had a relatively small root system. Lower recovery of root CHO

content by the end of autumn corresponded with the observation that the fern was infected by *Stemphylium* early in the second year.

Root CHO content fluctuations were intermediate in the high yielding crop, suggesting that it had a big root system with large CHO storage capacity. *Stemphylium* infection occurred later in this crop in the second year, and CHO recovery was high.

France

Root CHO content was measured in several crops during two years. Values followed the expected pattern in all cases, but there were differences among the crops.

Measurements were completed in seven farmers' crops in one year (Fig. 2c). Values at the start ranged from about 330 to 400 mg g⁻¹, declined to about 200 mg g⁻¹ at the end of fern establishment in most cases, and recovered to values over a wide range (from about 350 to 550 mg g⁻¹) at the end of the season.

Measurements in the other year compared crops that were irrigated, not irrigated, flooded, and affected by pests during fern growth (data not shown). Root CHO content began at a low post-harvest value of about 250 mg g⁻¹ in all cases, and recovery by the end of the season differed among the crops. The pests reduced CHO accumulation, apparently because of damage to the ferns, and it went no higher than about 350 mg g⁻¹. Recovery to about 450 mg g⁻¹ was similar in all the other treatments, although there was evidence of a decline caused by flooding late in the season.

Chile

Measurements were made in two established UC157 crops. They were in separate experiments, but measurements in the two crops overlapped during two years (Fig. 2d). Root CHO contents in a tilled, furrow-irrigated crop varied from 150 mg g⁻¹ at the end of fern establishment to about 360 mg g⁻¹ at the beginning and end of the season. The other crop, which was drip irrigated and not tilled, had values varying over a smaller range, from about 230 to 400 mg g⁻¹. The minimum values both followed harvests that produced large yields of 14 and 10 t ha⁻¹ in the two successive years. This and the relatively small range of CHO content suggest that the crop had a large storage root system.

Germany

Root CHO content patterns have been measured in many experimental and commercial crops. Examples from eight different crops that were measured during two years are shown in Fig. 2e. Values at the end of autumn in the first year varied from about 350 to 500 mg g⁻¹. In all crops there was a notable decline during winter, so that values at the start of harvest in the second year were between 300 and 380 mg g⁻¹. Minimum values at the end of fern establishment were as low as 200 mg g⁻¹ and, in the four crops where measurements continued, values at the end of autumn were from 350 to 450 mg g⁻¹.

United Kingdom

A new project started recently to measure root CHO patterns during two annual growth cycles in twelve established and establishing crops. The first measurements were completed in March 2005 and, as expected at pre-harvest, most values were high. Root CHO content values ranged from 341 to 515 mg g⁻¹. All except two root CHO contents were over 400 mg g⁻¹, and the mean was 440 mg g⁻¹. As well as continuing root CHO content measurements, yield and root biomass will be measured in all crops during the next two years in order to understand the reasons for the differences among the crops.

Mexico

Root CHO contents have been measured in many commercial crops, some for as long as three years. One grower is measuring CHO patterns regularly in 54 crops. Typical examples from three crops are shown in Fig. 2f. Root CHO content followed the usual annual pattern in all cases.

There were small differences among the crops and much larger differences among the seasons. Apparently, conditions were more favourable during the fern growth season in the middle year than in the first and third years, when peak values were about 600 and 450 mg g⁻¹ respectively. Minimum values also varied among the years from about 250 to 350 mg g⁻¹. Spear yield data are not available, but we infer that production was highest in the middle year. The cultivar grown in Mexico is UC157, and the large CHO content fluctuations reflect its relatively small root system.

SYNTHESIS

“Every crop is different, but every crop is the same”.

Despite the diversity of climates and production systems in different countries, in all cases changes of root CHO content were associated in a consistent and predictable manner with above-ground growth of spears and ferns during each annual cycle. CHO content was always high at the start of harvest, declined during harvest, declined further to a minimum level during fern establishment, and then recovered again during fern growth to reach a high value by the end of autumn. So, in this respect, *every crop was the same*. However, on the other hand, *every crop was also different*. Most crops deviated from the ‘ideal’ pattern in some way and there was much variation in the root CHO content values at various times during the cycle. There were many possible reasons for the variation that depended on the circumstances of each crop. However, the reasons can be separated into two categories:

- Differences associated with the size of the root system. Root biomass varies widely among crops. The size of the system determines the capacity of a crop to accumulate and store CHO and, therefore, it influences the extent of CHO content fluctuations during the annual cycle. In general, crops with small root systems (i.e. small CHO storage capacity) exhibit larger CHO content fluctuations than ones with big root systems, even though the quantity of stored CHO may be considerably greater in the latter. The impact of root system size is evaluated below.
- Differences attributable to particular agronomic conditions in individual crops. Many differences were caused by effects of management and environmental factors that can be identified readily. One example was reduced CHO accumulation caused by the effects of an unfavourable growing season, low fern vigour and infection of the fern by *Stemphylium* in The Netherlands. Another example was the effect of pest infestation of the fern in France. Wilson et al. (2002a) also cited an example showing how fern damage caused by *Stemphylium* reduced CHO accumulation.

A particular issue is that, in some crops in New Zealand and many crops in Germany, a substantial reduction has been observed between pre- and post-winter root CHO values. The reasons for the decline are uncertain, but there are several possibilities. They could result from utilisation of CHO in respiration processes to maintain the root system during winter. It could be that during winter CHO is transformed into insoluble storage forms that are not detected by Brix% assessments. This would change the relationship between Brix% and CHO and, therefore, lead to an underestimate of the total CHO content by Brix% assessments. A third possibility is that the reduction could be an artefact resulting from dilution of soluble CHO in the sap solution due to hydration over winter leading to increased root water content.

Root System Biomass

The *Aspire* system compares root CHO contents from growers’ crops with benchmark values. These values are the same for all crops. A better approach would be to base interpretations on the amount of CHO, rather than the content, in the root system. This would require measurements of root biomass in addition to CHO content. Growers in the USA have recognised this, and some are beginning to use the method developed by Drost and Wilson (2003) to measure on-farm root biomass. In Germany, a decision support system similar to *Aspire* (www.asparagus-info.org) is being developed that estimates the amount of CHO in root systems.

A major problem is that root biomass cannot be measured readily, and it is impracticable to assess it routinely in commercial crops. Furthermore, we suggest that regular assessments are

unnecessary because changes in structural biomass are slow once a crop is established, and variations are not a major cause of yield variability. Variations in CHO content are much more important.

We therefore propose that, instead of assessing root biomass, a much easier approach is simply to categorise crops as being 'small', 'medium' or 'large'. Each crop could be classified by a once-only measurement of root biomass or, more simply, by using its known performance as an indirect guide. In general, high yielding crops have large root systems and low yielding crops have small root systems. We also propose that different benchmark CHO content values are used for each root size category.

In the following sections we examine the implications of these proposals by analysing the growth and associated root CHO balances of hypothetical crops with 'small', 'medium' and 'large' root biomasses during the annual growth cycle. The yield physiology assumptions are based on information used in the model of asparagus growth described by Wilson et al. (2002b).

Harvest and Fern Establishment

First we analyse growth during harvest and fern establishment by following the sequence of calculations in Table 2, as follows:

1. Biomass ranges. The majority of established crops have root biomasses in the range from 6 to 20 t ha⁻¹. We begin the analysis by dividing the range into 'small', 'medium' and 'large' categories.

2. Target root CHO contents. We propose different benchmark CHO content values for each root size category at the start of harvest, but the same values at the end of harvest and the end of fern establishment. The values are based on deductions from results of many root CHO content measurements in diverse crops, including the ones presented above, and on the physiological capacity of crops to produce CHO during fern growth. The latter is analysed in the next section.

3. Root biomass at start of harvest. The total biomass is the mid-point value for each category. It is partitioned into structure and CHO components on the basis of its CHO content. The amount of CHO present at the start of harvest varies from 4.4 to 8.1 t ha⁻¹ for the 'small' and 'large' crops respectively.

4. Root biomass at end of harvest. Structure biomass is the same as at the start of harvest, but CHO and total biomasses are reduced on the basis of CHO content (300 mg g⁻¹ in all cases). The amount of CHO left at the end of harvest varies from 1.6 to 4.3 t ha⁻¹.

5. CHO used during harvest. The calculated reductions of CHO during harvest range from 2.8 to 3.8 t ha⁻¹. The CHO is assumed to be used in two ways. The first requirement is for respiration to grow and maintain the root system. Respiration depends on temperature but, to keep it simple, for this analysis we assume that it is proportional to the structural biomass (x 0.15). Therefore, the 'large' root system requires three times more CHO for maintenance (1.5 t ha⁻¹) than the 'small' system (0.5 t ha⁻¹). The remaining CHO is available for spear growth. It is similar for all three crops, although a little higher for the 'medium' crop than for the others.

6. Potential spear yield. The CHO available for spear growth is assumed to be converted to dry matter with 70% efficiency, and spears are assumed to have 10% dry matter content. Therefore, potential spear yields range from 16 to 19 t ha⁻¹.

7. Root biomass when fern established. Structure remains the same as before, but CHO and total biomasses are reduced on the basis of CHO content (200 mg g⁻¹ in all cases). The amount of CHO left at the end of fern establishment varies from 0.9 to 2.5 t ha⁻¹.

8. Fern establishment. The CHO used for fern growth is assumed to be converted to dry matter with 70% efficiency, so the amount of initial fern growth based on stored CHO varies from 0.5 to 1.3 t ha⁻¹. Therefore, fern establishment in crops with 'large' root systems is likely to be greater.

Fern Growth

There are physiological and environmental limits to the amounts of new growth and CHO that a fern canopy can produce. In this section we estimate these limits, and their implications for the capacity of crops to reach fully recharged root CHO content target values, by continuing the

analysis of three hypothetical crops during fern growth. These are potential values, with no limitations caused by agronomic factors such as water or nutrient deficiencies or pests and diseases.

The first part of the analysis considers the capacity of crops to store accumulated CHO by following the sequence of calculations in Table 3, as follows:

1. Target root CHO contents. The benchmark CHO content value at the start of fern growth (200 mg g⁻¹ for all root size categories) is the same as at the end of fern establishment (from Table 2) but we propose different values at the end of fern growth that are the same as they were at the start of harvest. Again, this is based on deductions from many root CHO content measurements in diverse crops and on the capacity of crops to produce CHO during fern growth.

2. Root biomass at start of fern growth. The starting values are the same as at the end of fern establishment (from Table 2).

3. Root biomass at end of fern growth. Structure, CHO and total biomasses are all back up to the same values as at the beginning.

4. CHO gained during fern growth. The calculated increases of CHO biomass during fern growth range from 3.5 to 5.6 t ha⁻¹.

5. Total CHO production. As well as accumulating CHO in the roots, crops also use CHO during this period to maintain the root system and grow new fern. Again, we assume that the first requirement is for respiration to grow and maintain the root system, and we use the values in Table 2. Following initial establishment based on stored CHO, fern growth depends on environmental and management factors. It varies among crops and has a major impact on the CHO balance. For this analysis we assume that all crops produce a fern canopy with a dry weight of 6 t ha⁻¹. Therefore, the new growth in addition to that produced from stored CHO during fern establishment is different for 'small', 'medium' and 'large' crops (5.5, 5.2 and 4.7 t ha⁻¹ respectively). This requires different amounts of CHO, which are converted to dry matter with 70% efficiency (1.4 g of CHO required to produce each g of dry weight). Thus, for these scenarios the total amounts of CHO that need to be produced during fern growth are 11.7, 13.2 and 13.7 t ha⁻¹ for 'small', 'medium' and 'large' crops respectively. Similar calculations could be done to assess the impacts of alternative scenarios with different amounts of fern growth.

The second part of the analysis considers whether crops have the physiological capacity to produce these amounts of CHO. We analyse this as follows:

1. Duration of fern growth. This varies among climates and production systems. For this example, we assume the situation in New Zealand where harvest typically ends on 24 December, fern establishment takes about 30 days until 23 January, and then fern growth lasts for about 60 days until late March.

2. Solar radiation. Production of CHO for storage, root maintenance and new growth depends on assimilation by the fern canopy, which is driven by solar radiation. Mean daily solar radiation is about 15 MJ m⁻² during February and March.

3. New growth. CHO is produced from solar radiation intercepted by the fern canopy with a conversion efficiency of 1.5 g MJ⁻¹. Therefore, the potential production over 60 days is 1.5 x 15 x 60 = 1350 g m⁻² = 13.5 t ha⁻¹. This is exactly the amount needed by the 'medium' and 'large' crops, and more than that needed by the 'small' crop.

Summary

The examples in these scenarios demonstrate the steps in our analysis and highlight the effects of root system size and physiological capacity during fern growth on yield determination in asparagus. They are based on assumed values, and alternative numbers can be substituted into the analysis to examine the implications of different values. Important results from the analysis are:

- Root system size has a smaller effect than anticipated on potential spear yield. This occurs because although large systems have a greater capacity to store CHO they also need more CHO for maintenance.
- Yield potential differences are associated much more strongly with fluctuations in the CHO content of roots in each size category than with differences among size classes.

- Large systems have more capacity to support growth during fern establishment, before ferns have developed the photosynthetic ability to grow and restore root CHO.
- The results of the analysis during fern growth support our proposal to set different ‘full point’ benchmark root CHO content values for each root size category. Furthermore, they suggest that the values set are about right for ‘medium’ and ‘large’ crops, but that the value for ‘small’ crops could be higher. These conclusions are based on the fact that the amounts of CHO produced during fern growth were very close to the amounts required by the hypothetical ‘medium’ and ‘large’ crops, i.e. there was a close balance between CHO supply and demand. Extra CHO was available for storage in the ‘small’ crop (i.e. supply exceeded demand) and, therefore, the target root CHO content could be higher.

CONCLUSIONS

The concept of monitoring root CHO to guide crop management decisions is gaining traction globally. The challenge is to make the technology available widely to asparagus growers in a readily usable form. This has started. The first system was *AspireNZ* (www.aspirenz.com), which is now being used on about 500 ha by growers in New Zealand. Subsequent research collaborations have extended the *Aspire* approach to several other countries. *AspireUS* (www.aspireus.com) was developed following testing programs in California and Washington, and it is being used on about 2000 ha by growers in the USA, Canada and Mexico. A new project was started recently with British asparagus growers to develop *AspireUK*. Some research has also been done in The Netherlands, France, Chile and Germany, but the *Aspire* system has yet to be adapted for use in those countries. An alternative system is being developed in Germany (www.asparagus-info.org).

The technology is being adopted readily because experience has shown that it helps growers make confident decisions about aspects of crop management such as when to stop harvesting and how best to manage crops during fern growth to enhance CHO accumulation in the storage roots. Overall, the approach provides a way of assuring that crops are healthy and in good condition.

In this paper we have identified three particular issues with the system that must be recognised by users:

- Uncertainty about the relationship between analytical root CHO content and Brix%. The relationship differed between some locations and there was considerable variability among individual measurements. We assessed this and concluded that the Brix% of sap solution can be used to estimate the mean root CHO content of a crop provided enough samples are taken to account for the variability and, therefore, represent the crop accurately. Because of this uncertainty, CHO content values are not precise and should be interpreted in broad bands. For practical purposes, changes with time and, especially, deviations from normal are more important than absolute values.
- A decline in root CHO content during the dormant period sometimes occurs. The causes are uncertain and more research is needed on this topic. It means that a pre-winter root CHO content assessment cannot always be used as a reliable indicator of crop performance in the next season. To be certain, a post-winter, pre-harvest measurement should also be taken.
- The effect of root system size on interpretations of CHO contents. Root biomass is an important determinant of the amount of CHO that a crop can accumulate. However, our analysis has shown that it is not crucial when two key factors are taken into account: (a) larger root systems need to use more CHO to maintain themselves, and (b) the ability of crops to produce CHO during fern growth can limit the amount that can accumulate, regardless of root system size. Our analysis provides a framework for assessing these factors in different climates and crop management systems.

Provided these issues are acknowledged, we conclude that understanding and applying knowledge about the role of CHO in the yield physiology of asparagus can lead to better crop performance.

Literature Cited

- Drost, D.T. 1997. Asparagus. p.621-649. In: H.C. Wien (ed.), *The Physiology of Vegetable Crops*. CAB International, Wantage.
- Drost, D.T. and Wilson, D.R. 2003. Monitoring root length density and root biomass in asparagus (*Asparagus officinalis*) with soil cores. *NZ J. Crop Hort. Sci.* 31: 125-137.
- Efron, B. and Tibshirani, R. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Sci.* 1: 54-57.
- Ernst, M. and Krug, H. 1998. Seasonal growth and development of asparagus (*Asparagus officinalis* L.) III. The effect of temperature and water stress on carbohydrate content in storage roots and rhizome buds. *Gartenbauwissenschaft* 63: 202-208.
- Haynes, R.J. 1987. Accumulation of dry matter and changes in storage carbohydrate and amino acid content in the first two years of asparagus growth. *Scientia Hort.* 32:17-23.
- Lampert, E.P., Johnson, D.T., Tai, A.W., Kilpatrick, G., Antosiak, R.A. Crowley, P.H. and Goodman, E.D. 1980. A computer simulation to maximise asparagus yield. *J. Amer. Soc. Hort. Sci.* 105: 37-42.
- Pressman, E., Schaffer, A.A., Compton, D. and Zamski, E. 1993. Seasonal changes in the carbohydrate content in two cultivars of asparagus. *Scientia Hort.* 53: 149-155.
- Quarmby, C. and Allen, S.E. 1989. Organic constituents. p.164-166. In: S.E. Allen (ed.), *Chemical Analysis of Ecological Materials*. Blackwell, Oxford.
- Robb, A.R. 1984. Physiology of asparagus (*Asparagus officinalis*) as related to the production of the crop. *NZ J. Exp. Agri.* 12: 251-260.
- Shelton, D.R. and Lacy, M.L. 1980. Effect of harvest duration on yield and on depletion of storage carbohydrates in asparagus roots. *J. Amer. Soc. Hort. Sci.* 105: 332-335.
- Verbyla, A.P., Cullis, B.R., Kenward, M.G. and Welham, S.J. 1999. The analysis of designed experiments and longitudinal data using smoothing splines. *J. Royal Stat. Soc., Series C* 48: 269-311.
- Wilson, D.R., Sinton, S.M. and Wright, C.E. 1999. Influence of time of spear harvest on root system resources during the annual growth cycle of asparagus. *Acta Hort.* 479: 313-319.
- Wilson, D.R., Cloughley, C.G. and Sinton, S.M. 2002a. *AspireNZ*: a decision support system for managing root carbohydrate in asparagus. *Acta Hort.* 589: 51-58.
- Wilson, D.R., Cloughley, C.G., Jamieson, P.D. and Sinton, S.M. 2002b. A model of asparagus growth physiology. *Acta Hort.* 589: 297-301.

Tables

Table 1. Ranges of root CHO content and Brix% values measured at four locations, and the number of measurements at each location.

Location	Brix%		CHO content (mg g ⁻¹)		Number of measurements
	Minimum	Maximum	Minimum	Maximum	
Washington, USA	3.0	28.2	20	793	485
California, USA	4.2	32.0	27	855	587
New Zealand	3.2	31.0	51	789	317
Germany	6.3	30.5	93	731	36

Table 2. Root biomass, root CHO content and amount, growth and yield of three hypothetical asparagus crops with small, medium and large root systems during spear harvest and fern establishment.

	Small	Medium	Large
1. Typical root biomass range (t ha ⁻¹)	6.0 to 10.0	11.0 to 15.0	16.0 to 20.0
2. Target root CHO contents (mg g ⁻¹):			
When full at start of harvest	550	500	450
End of harvest	300	300	300
End of fern establishment	200	200	200
3. Mean root biomass at start of harvest (t ha ⁻¹):			
Total	8.0	13.0	18.0
Structure	3.6	6.5	9.9
CHO	4.4	6.5	8.1
4. Root biomass at end of harvest (t ha ⁻¹):			
Total	5.2	9.3	14.2
Structure	3.6	6.5	9.9
CHO	1.6	2.8	4.3
5. CHO used during harvest (t ha ⁻¹):			
Total	2.8	3.7	3.8
Maintain root structure (Biomass x 0.15)	0.5	1.0	1.5
Spear growth	2.3	2.7	2.3
6. Potential spear yield from CHO (t ha ⁻¹):			
Dry weight (CHO x 0.7)	1.6	1.9	1.6
Fresh weight (DW x 10)	16.0	19.0	16.0
7. Root biomass when fern established (t ha ⁻¹):			
Total	4.5	8.1	12.4
Structure	3.6	6.5	9.9
CHO	0.9	1.6	2.5
8. During fern establishment:			
CHO used (t ha ⁻¹)	0.7	1.2	1.8
Fern dry weight (CHO x 0.7; t ha ⁻¹)	0.5	0.8	1.3

Table 3. Root biomass, root CHO content and amount, growth and yield of three hypothetical asparagus crops with small, medium and large root systems during fern growth.

	Small	Medium	Large
1. Target root CHO contents (mg g ⁻¹):			
End of fern establishment	200	200	200
End of fern growth	550	500	450
2. Root biomass when fern established (t ha ⁻¹):			
Total	4.5	8.1	12.4
Structure	3.6	6.5	9.9
CHO	0.9	1.6	2.5
3. Root biomass at end of fern growth (t ha ⁻¹):			
Total	8.0	13.0	18.0
Structure	3.6	6.5	9.9
CHO	4.4	6.5	8.1
4. Gained during fern growth (t ha ⁻¹):			
CHO (and Total)	3.5	4.9	5.6
5. CHO used during fern growth (t ha ⁻¹):			
Maintain root structure (Biomass x 0.15)	0.5	1.0	1.5
CHO for new growth (DW x 1.4)	7.7	7.3	6.6
Total CHO	11.7	13.2	13.7

Figures

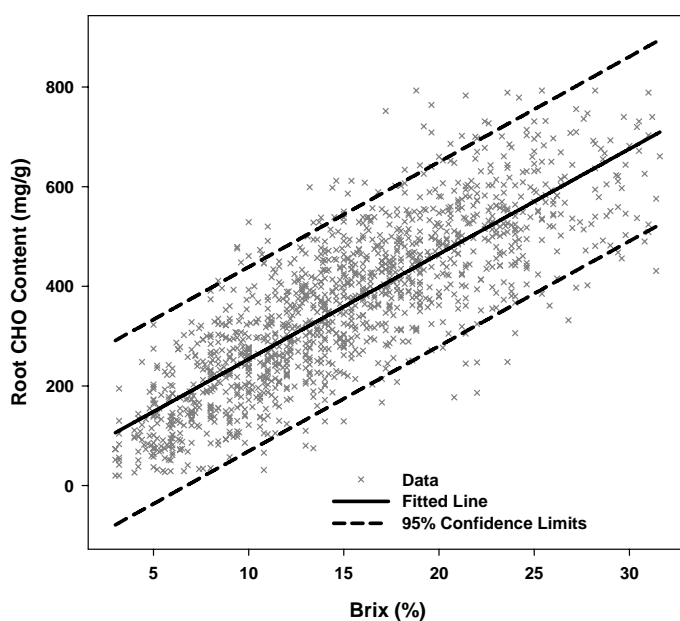


Fig. 1. Relationship between CHO content and Brix% for root samples, with data combined from USA (Washington and California), New Zealand and Germany. The regression equation is $\text{CHO} = (21.1 \times \text{Brix}\%) + 42.9$, with 95% confidence limits for predicting root CHO content from new Brix% values shown.

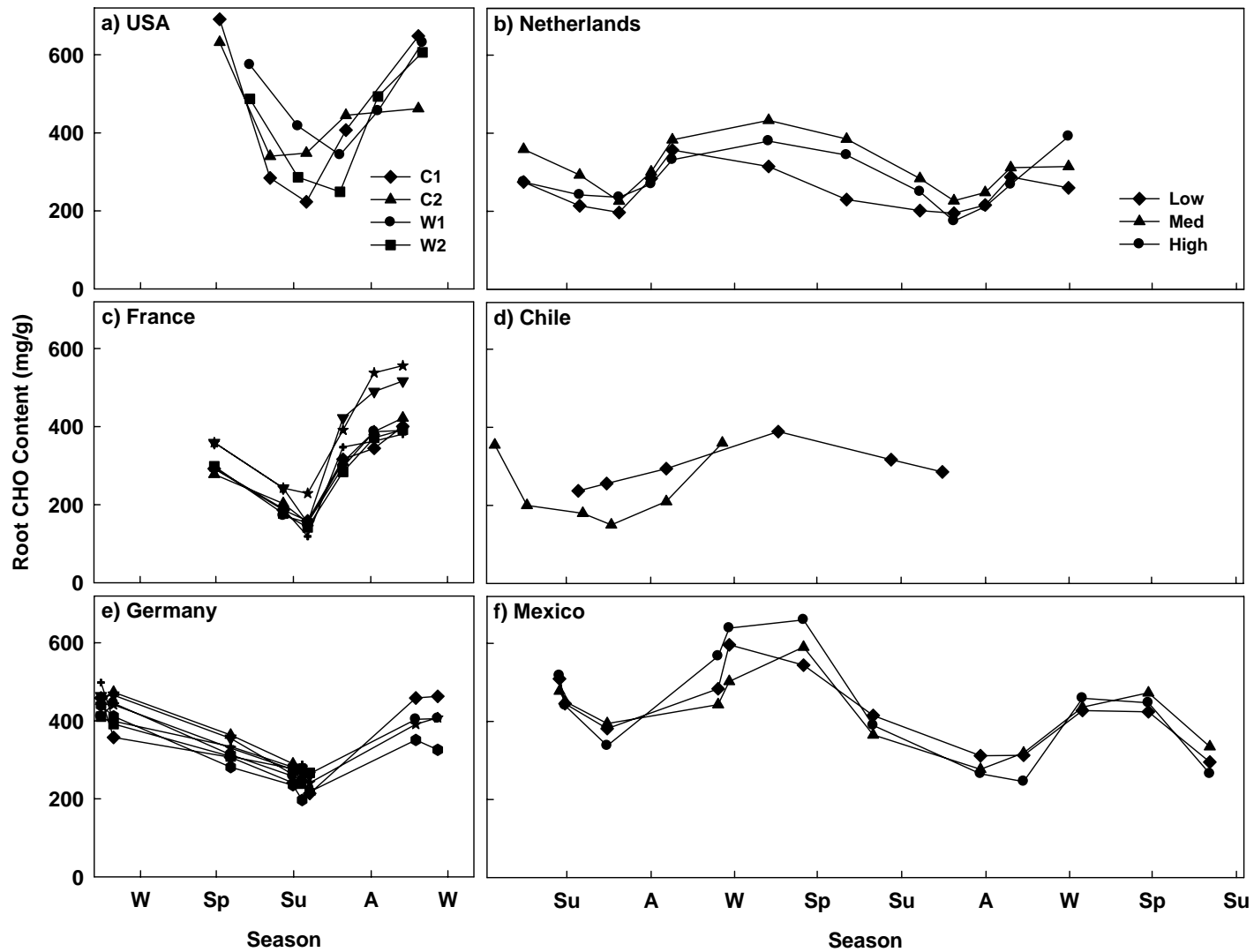


Fig. 2. Examples of root CHO content patterns from six different countries. See text for explanations. In (a), C1 and C2 are California, W1 and W2 are Washington. Seasons are: A = autumn, W = winter, Sp = spring, Su = summer.