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Pre- and postharvest development of carrot yield and quality

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ACADEMIC DISSERTATION

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Contents

Preface

The work described in this thesis was carried out at the Agricultural Research Centre of Finland (MTT) during 1995–1999. It has been a pleasure to work at MTT and to have the opportunity to utilise its excellent facilities and services. The study was started as a part of the research programme “Sustainable production of high-quality vegetables”. I wish to thank those participating in the programme for the inspiring atmosphere they provided during my first steps as a scientist. My warmest thanks are due to my closest colleague, Raili Pessala, for her help, guidance and friendly cooperation over the years.

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List of original publications

The thesis is based on the following articles, which will be referred to in the text by their Roman numerals.

I **Suojala, T.** 2000. Growth of and partitioning between shoot and storage root of carrot in a northern climate. Agricultural and Food Science in Finland 9: 49–59.

II **Suojala, T.** 1999. Cessation of storage root growth of carrot in autumn. Journal of Horticultural Science & Biotechnology 74: 475–483.

III **Suojala, T.** 1999. Effect of harvest time on the storage performance of carrot. Journal of Horticultural Science & Biotechnology 74: 484–492.

IV **Suojala, T.** 2000. Effect of harvest time, mechanical injuries and wound healing on infection by *Mycocentrospora acerina* in stored carrots *(manuscript)*.

V **Suojala, T.** 2000. Variation in sugar content and composition of carrot storage roots at harvest and during storage. Scientia Horticulturae *(in press)*.

VI **Suojala, T. & Tupasela, T.** 2000. Sensory quality of carrots: effect of harvest and storage time. Acta Agriculturae Scandinavica, Section B, Soil and Plant Science *(in press)*.

Abstract

Suojala, T. [1] 2000**.** Pre- and postharvest development of carrot yield and quality. University of Helsinki. Department of Plant Production. Section of Horticulture. Publication no. 37. Helsinki. 43 p. + appendices.

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Storage is a prerequisite for a year-round supply of domestic vegetables. The quality of vegetables after long-term storage is primarily determined during the growing season, and storage conditions can only help to maintain the quality as long as possible. Similarly, the quantity of the marketable yield is determined by conditions during the growing season, and loss during storage is affected by both pre- and postharvest factors.

This study aimed to show how the quality and quantity of carrot at harvest and after storage can be better controlled. The main emphasis was on the effects of harvest time on yield, storability and sensory quality, with the aim of optimising the timing of harvest. In addition, development of the carrot plant during the growing season was investigated to characterise the determinants of yield production. The sugar composition of carrot storage root was studied as a possible descriptor of the plant's stage of development. Field experiments were conducted at the Vegetable Experimental Site of the Agricultural Research Centre of Finland and on vegetable farms in 1995–1998. Two cultivars, 'Fontana' and 'Panther', were used, and there were 3–6 harvests in September–October.

Despite the large variation in average yield at different growing sites, the yield increase generally ceased in early October. On average, 10–36% of the total yield at the final harvest was produced after early September, when the weather was already less favourable for growth. This suggests that carrot still has considerable potential for yield production late in the growing season. The yield increase during the harvest period can be estimated on the basis of thermal time.

Delaying the harvest improved storability up to late September or early October; thereafter storability remained at the same level. Only a prolonged period of frost injured the plants so severely that their storability declined. The effect of harvest time was similar irrespective of cultivar, growing site, year and storage conditions. Weather conditions did not account for the improved storability. It is hypothesised that the concentration of antifungal substances increases at the end of the growing season, which makes the storage roots more resistant to storage pathogens. Healing at 10°C for 7 days was effective in decreasing the incidence of infections caused by *Mycocentrospora acerina*.

Changes in sugar content and composition during the harvest period were dependent on the year and growing site, and do not provide evidence for the existence of any developmental stage definable as maturity. Neither do changes during storage

seem to be related to storage potential. A new finding in carrot was the notable drop in the sucrose and total sugar content following frost injuries on farms in 1996. Unexpectedly, this did not have an adverse effect on the storability or sensory quality of carrots. Sensory quality improved slightly when harvest was delayed. The two cultivars analysed were not found to differ in sensory aspects, and the changes during storage were relatively small.

The results showed that the timing of harvest is an essential factor affecting the yield, quality and storability of carrot. It is concluded that, in southern Finland, the optimal harvest time for the carrot cultivars used in the study is early October, after which no major yield increase or improvement in quality or storability is to be expected; a later harvest only increases the risk of frost injuries. In large areas, harvesting must be started early enough to get the entire crop lifted before winter. The carrots intended for the longest storage should, however, be harvested late to minimise storage losses. The findings concerning optimal harvest time are likely to apply to other cultivars kept in storage, too.

Key words: *Daucus carota* L., development, growth, harvest time, maturity, sensory quality, storability, storage, sugars

1 Introduction

Carrot (*Daucus carota* L. ssp. *sativus* (Hoffm.) Schübl. & G.Martens) originates from the wild forms growing in Europe and southwestern Asia (Banga 1984). The western type of cultivated carrot is thought to derive from the anthocyanin-containing forms found in Afghanistan. Cultivation of carrot spread to Europe in the fourteenth century. The first cultivated carrot types were purple or violet; yellow and, later, orange types were derived from this anthocyanin type by selection. The orange-coloured form was selected in the Netherlands in the early seventeenth century.

In 1998, 18.5 million tonnes of carrots were produced worldwide in an area of 794 000 hectares (FAO 1999). On a global scale, carrot is only a minor crop, but in northern countries, it is one of the major field vegetables. In Finland in 1995–1998, the yearly production area of carrot ranged from 1650 to 1954 hectares, which makes carrot the most common field vegetable after garden pea (Information Centre of the Ministry of Agriculture and Forestry 1999). The harvested yield per year varied between 52 and 68 million kilograms in 1995–1998. Due to the short growing season, most of the yield has to be kept in cold storage for varying lengths of time to supply the domestic market.

Carrot has been a subject of active research throughout the 20th century. Most of the research has arisen out of practical problems, and lacks a sound theoretical background. Some areas, such as biomass partitioning (reviews by e.g. Hole 1996, Benjamin et al. 1997), have been studied in greater detail. Moreover, carrot has served as a model plant in plant physiology and more recently in biotechnology. In Finland, carrot has been studied in relation to storage diseases (Mukula 1957), plant nutrition (Evers 1989c, Salo 1999), the effects of soil physical properties (Pietola 1995) and the development of artificial seeds (Sorvari et al. 1997).

Despite the large amount of experimental work done on carrot, problems interfering with the production chain still exist. The background of this study was the variation in the storage performance of carrot. It is estimated that in Finland the average loss during storage can be as high as 30% (Lehtimäki 1995), which represents a considerable cost. Long storage can also impair the quality of carrot. Preharvest factors primarily determine the quality of the products at harvest and after storage; storage conditions can only help to maintain the quality as long as possible. By examining the effects of developmental stage and harvest time, this study aimed to show how the quality and quantity of carrot after storage could be better controlled. Development of the carrot plant during the growing season was investigated to characterise the determinants of yield production. Therefore, the whole chain – from biomass partitioning in the field to maintenance of quality at the end of storage – was covered.

1.1 Vegetative development and growth of carrot

1.1.1 Functions and initiation of storage root

The major ecological function of the carrot storage root is as a reserve of assimilates for the production of a flowering stem after appropriate stimuli (Hole 1996). It also forms the route for the translocation of photosynthates from shoot to fibrous roots and for the transport of water and nutrients from fibrous roots to the shoot (Benjamin et al. 1997). It may further act as a water reservoir, helping to maintain a constant supply of water to the leaves (Olymbios 1973, ref. Benjamin et al. 1997).

The storage organ derives mainly from root tissues but, in the mature state, the hypocotyl makes up about one inch of the upper

part of the storage organ (Esau 1940). The secondary growth resulting in the swollen taproot begins with the initiation of the secondary cambium between primary xylem and primary phloem. The cambium is formed simultaneously with the first leaves (Esau 1940). Hole et al. (1984) observed initiation of the cambium at 11 days after sowing and completion of the cambial ring at 20 days after sowing in a controlled environment. Under field conditions, initiation and completion of the cambium occurred ten days later (Hole et al. 1987b). Esau (1940) described the development of the secondary growth of carrot root. Cambial cells divide to form xylem on the inside and phloem on the outside. Most of the secondary tissues consist of parenchyma cells, which embed the vessels in xylem and sieve tubes and companion cells in phloem. As a consequence of enlargement of the circumference of the root, cells of the cortex and endodermis rupture. It is at this time that the orange colour appears in the root. Periderm, arising from meristematic activity in the pericycle, forms the new protective layer. Cell division continues throughout the development of the storage root in the field together with cell expansion (Hole et al. 1987c).

1.1.2 Partitioning of assimilates within a plant

Partitioning of the carbohydrates between plant parts is often described by the concepts “source” and “sink”. Source is a plant part that exports more carbon than it imports, while sink is a plant part that imports more than it exports (Ho et al. 1989). The ability of an organ to import assimilates, sink strength, is affected by the availability of assimilates and distance to the source and, in particular, by the genetically determined ability of the sink to compete for assimilates (Ho 1988). During vegetative growth, the storage root is considered as a sink, competing with fibrous roots and shoots for the assimilates produced by photosynthetic plant parts. The relationship between shoot and root can be simply described by estimating the ratio of their weights. However, the ratio is often related to plant size and age (Hole 1996). The effect on plant size can be overcome by using the ratio of logarithms of organ weights, the allometric ratio (Richards 1969).

Hole et al. (1983) found that late maturing carrot cultivars have a high shoot to root ratio. Among the cultivars used in their study, high root yields tended to be associated with large shoots, and the highest yielding cultivars invested in shoot growth during early development (Hole et al. 1987a). The differences between cultivars in partitioning arise very early, a subject which has been intensively studied. Timing of initiation of the storage root did not explain cultivar differences in dry matter distribution (Hole et al. 1987b). Hole et al. (1987a) found that the ratios of the growth rates of shoot to storage root before and after storage root initiation were positively correlated with the shoot to root ratio at final harvest 125 days after sowing. Fibrous roots may also play a role in the control of partitioning: a cultivar with a larger proportion of storage root at maturity was found to invest more carbohydrates in fibrous roots at the time of storage root initiation (Hole and Dearman 1990), and varietal differences in allocation between storage root and fibrous roots occurred soon after initiation (Hole and Dearman 1991).

Environmental conditions modify the partitioning between shoot and storage root. Light affects the shoot to root ratios, but mostly via the effect on plant size (Hole and Sutherland 1990, Hole and Dearman 1993), since the shoot to root ratio usually declines with time and as plant weight increases (Currah and Barnes 1979). Olymbios (1973, ref. Hole 1996) found an increase in shoot to root ratio at higher temperature, which may indicate a true change in partitioning, since the total weight also increased. The effect of density, like that of light, is attributed to the modification of photosynthesis and growth

(Barnes 1979, Hole and Dearman 1993), with a lower total weight and higher shoot to root ratio at high density or in low light.

1.1.3 Climatic factors affecting total plant and storage root growth

Storage root growth depends on the assimilate supply from the photosynthetic plant parts. Since partitioning to the storage root is more or less dependent on the genotype and total plant weight, storage root growth can be estimated from the total growth.

The main factors determining the potential crop yield are leaf area, net assimilation rate, length of growing period and utilisable fraction of the biomass (harvest index) (Forbes and Watson 1992). Leaf area index (LAI, ratio of the total area of the leaves of a crop to the ground area) determines the fraction of interception of light. Together with the net assimilation rate, which refers to the rate of dry matter production per unit leaf area, LAI determines the rate of dry matter production per area at a given time. The length of the growing period affects the yield by its effects on the duration of photosynthesis.

In addition, the growth pattern of a plant must fit the seasonal climatic cycle. Carrot has a slow growth rate in the early part of its vegetative development. Salo (1999) reported that the dry weight of the shoot increased rapidly from July up to the middle of August, whereas the rapid dry weight accumulation into storage roots did not start until the middle of July. Evers (1988) found that 40–68% of the final shoot weight but only 17–26% of the final root fresh weight was reached at 2–2.5 months after sowing, in August. Therefore, much of the early part of the growing season is used for constructing the growing potential for the later part of the season.

Irradiation

Irradiation is the primary factor regulating photosynthesis. Hole and Sutherland (1990) studied the effects of different light regimes on the growth of carrot at 20°C and obtained higher plant weights with a longer day and higher photosynthetic photon flux density (PPFD). Comparison of light regimes with similar daily light integrals showed that a long photoperiod (16 h, 300 µmol $m^{-2}s^{-1}$) was more effective than a short photoperiod and high PPFD (8 h, 600 µmol $m^{-2}s^{-1}$). The importance of photoperiod was also emphasised by Rosenfeld et al. (1998c), who grew carrrots at constant temperatures under different light regimes during three periods of time in a controlled climate. In October–December, when day length was shortest and the total amount of photosynthetically active radiation (PAR) (natural + artificial light) was about one-third of that in the other two periods, the mean root size was 38 g. In April–June and July–September, the average day length and total level of PAR were the same, but the roots were heavier in the autumn period (130 g), when day length was decreasing towards harvest, than in the spring period (85 g), when day length increased. Therefore, long days and high radiation were particularly favourable during early growth stages.

Hole and Dearman (1993) found that carrot responded to decreasing PPFD in a different way from red beet and radish. Different light intensities at a constant photoperiod had no clear effect on shoot fresh weight or leaf area in carrot, but the dry weight of shoot and the fresh and dry weights of storage root and fibrous roots were reduced in low light. The reduction in storage root dry weight was much smaller in carrot than in red beet and radish. According to the authors, at decreasing PPFD, carrot maintains leaf area and shoot fresh weight, and its thus high photosynthetic capacity: storage root growth is not therefore severely limited. They concluded that the asymptotic response

of carrot yield to high plant density is comparable to the response to low light, and therefore light competition at high densities has little effect on the dry matter distribution in carrot.

Temperature

Temperature affects growth mainly by controlling the rates of chemical reactions, and thus the usage of photosynthetic products. Knowledge of the temperature requirements of carrot is still insufficient. Carrot is classified as a cool-season crop, the minimum temperature for growth being 5°C and the optimum temperature 18–25°C (Krug 1997). Barnes (1936) found that the optimum temperature for carrot growth is 16–21°C. In the study of Bremer (1931), in which soil temperatures ranged from 12 to 28°C, the highest growth rate was obtained at 16°C. Rosenfeld et al. (1998b) grew carrots at constant temperatures of 9, 12, 15, 18 and 21°C and observed the highest root weight at 12 and 15°C. However, light level had a more marked effect on root weight than had temperature in the temperature range investigated (Rosenfeld et al. 1998c).

Wheeler et al. (1994) studied the effects of temperature and CO_2 enrichment on carrot growth in polyethylene-covered tunnels along which a temperature gradient was imposed. A 1°C rise in mean soil temperature (in a range of 7.5 to 10.9°C) increased total weight by 37% and root weight by 34% at 134 days after sowing. At the stage of seven visible leaves, no effects of temperature on root or total weight were found. Hence the effect of temperature was caused by the advanced timing of growth and development.

Olymbios (1973, ref. Benjamin et al. 1997) found an increase in shoot weight with an increase in the temperature of shoot and/or root environment from 15 to 25°C. Root weight was also increased, but less so than shoot weight and it fell when root temperature was higher than shoot temperature. On the basis of this study and knowledge of other species, Hole (1996) suggested that the storage root has a lower temperature optimum than the shoot. The same phenomenon had already been noted by Bremer (1931), who reported that storage root weight did not increase when temperature rose above 20°C, whereas shoot weight was highest at the highest temperature (24–26°C).

CO_2

An increase in the concentration of carbon dioxide in air generally enhances photosynthesis and growth. Dry matter production of carrot has also been reported to be enhanced by an increased CO_2 concentration (Wheeler et al. 1994), especially at high temperatures (Idso and Kimball 1989). An increase in CO_2 concentration promoted dry matter partitioning to roots at an early growth stage (Wheeler et al. 1994) and raised the dry matter content of shoot and root (Mortensen 1994). Aware of the possibly smaller effects of a higher CO_2 concentration at low temperature, Mortensen (1994) studied the impact of an elevated CO_2 level on the yield of eight vegetable species under field conditions in Norway. A significant increase in dry weight was found only in lettuce, carrot and parsley.

Water

Water supply affects photosynthesis indirectly by inducing the stomata to close when there is a shortage of water. This results in a drop in the CO_2 concentration in the leaf, which inhibits photosynthesis (Forbes and Watson 1992).

Carrot is not very sensitive to drought as it has a deep and dense root system. Pietola (1995) reported that the root system of a carrot plant has a total length of 150–200 m at a depth of 0–50 cm. Soil compaction and irrigation increased the length of fibrous roots in the upper 30 cm of the soil profile.

Evers (1988) and Pietola (1995) found only slight effects of irrigation on final yield, regardless of the varying weather conditions in the experimental years. Evers (1988) even

found that irrigation decreased yield in the first year, when a crust formed on the soil surface due to heavy rain. Similarly, Dragland (1978) reported that a 3-week period of drought at an early stage, from the 2-true leaf stage onwards, increased the yield, but that drought in July–August or prior to harvest lowered the yield. Relying only on natural precipitation resulted in the poorest yield. Sørensen et al. (1997) found that drought stress during a 3-week period at any growth stage reduced the total yield, though always by less than 10%. Wind shelter may increase water use efficiency, since Taksdal (1992) reported yield increases and an improvement in quality due to the erection of artificial windbreaks especially in dry and sunny years.

However, larger yield losses due to drought have also been reported, particularly in a warmer climate (Sri Agung and Blair 1989, Prabhakar et al. 1991). Shortage of water also affects root shape, which is more pointed and conical under low moisture conditions (Barnes 1936, Sri Agung and Blair 1989).

To summarise, irradiation may be considered the main factor regulating carrot growth. Carrot is, however, able to maintain its photosynthetic capacity in low light better than some other vegetable species, and thus it is amenable to growth at high plant density. Temperature affects mainly the rate of development. Moderate temperatures are the most favourable for the growth of carrot, and the storage root seems to have a lower temperature optimum than the shoot. An increase in the CO_2 concentration promotes dry matter production, and hence carrot is likely to benefit from the greenhouse effect. Water stress interferes with photosynthesis, but due to the wide root system, irrigation has not always proved profitable in carrot production. Consisting mostly of very fine roots, the root system makes carrot relatively insensitive to nutrient availability, one of the basic requirements of growth in addition to climatic factors.

The deteriorating environmental conditions for growth at the end of the growing season in the north inhibit the yield production of carrot. However, little is known about the vegetative development patterns of carrot cultivars in relation to the seasonal cycle in a northern climate. The significance of the declining temperature, day length and irradiance in the latter part of the growing season is not clearly documented. Neither has the minimum temperature for growth and yield production been reported in the literature.

1.2 Changes in the quality of carrot during growing season

The optimal timing of harvest is influenced not only by yield quantity, but also by changes in quality. According to Mazza (1989), the most important quality attributes for carrot are size, shape, uniformity, colour, texture and internal aspects (sensory quality and nutritional value, especially vitamin A). The following looks at the development of these quality attributes during the growing season. In addition to the attributes mentioned, changes in sugar content and composition are discussed as possible descriptors of maturity.

1.2.1 Size, shape and uniformity

The size of the individual root increases with growing time and total plant weight and is affected by plant density. Root size depends on the purpose for which the carrots will be used, but uniformity of size is a common demand. Models for estimating the mean root size and size distribution at different spacings within and between rows were developed by Benjamin and Sutherland (1992) and further modified by Benjamin and Reader (1998).

Root shape is primarily determined by genotype but it changes during growth and can be modified by environmental conditions. Low temperature (10–15°C) and a low

soil moisture content increase the root length relative to width (Barnes 1936, Rosenfeld et al. 1998a). Rosenfeld (1998) found that cylindricity increased with growing time and was lower in carrots grown at low temperatures. Similarly, root tips were more rounded after a long growing time and at high temperature. Rounding of the root tips together with simultaneous thickening and colouring was defined as ripening (or maturation) of the fleshy root by Banga and de Bruyn (1968). Although Rosenfeld (1998) points out that the term maturity has little bearing on carrot root, he found that cylindricity showed the closest connection with chemical variables and might be used, together with root weight, as a criterion for fully developed roots.

1.2.2 Carbohydrates

Soluble sugars are the main form of storage compounds in carrot. They account for 34–70% of the dry weight of the storage root and are stored in the vacuoles of the parenchyma cells (Goris 1969a, Ricardo and Sovia 1974, Nilsson 1987a). Steingröver (1983) divided the development of carrot into three periods: period 1 (18–25 days after sowing at a constant temperature of 20°C), when no soluble sugars are stored; period 2 (25–32 days after sowing), when reducing sugars are stored; and period 3, when mainly sucrose is stored in the tap root. At 30–50 days after sowing, the concentration of sucrose starts to increase more rapidly than does that of hexoses (fructose, glucose), resulting in a higher sucrose to hexose ratio (Steingröver 1981, Hole and McKee 1988). Therefore, sucrose is the predominant transport and storage sugar at maturity (Daie 1984), but its proportion is affected by genotype and environment (Goris 1969a, Phan and Hsu 1973, Ricardo and Sovia 1974, Nilsson 1987a). Carrot cultivars differ three-fold in their ability to accumulate sugars, and cultivars with high net assimilation rates have a capacity for high sugar yield (Lester et al. 1982). The relationship between reducing and non-reducing sugars in a controlled environment also varies by cultivar (McKee et al. 1984).

The concentration of starch in carrot storage roots is low, ranging from 1% to 10% of dry matter (Goris 1969b, Steingröver 1981, Nilsson 1987a). Starch formation has not been extensively studied, but it has been suggested that it may reflect the assimilation rate and contribute to the regulation of sugar storage (Nilsson 1987a, Hole 1996).

Changes in the accumulation of reducing and non-reducing sugars have been related to the activities of enzymes, e.g. acid and alkaline invertases and sucrose synthetase (Ricardo and ap Rees 1970, McKee et al. 1984), although enzyme activities have not always shown a clear relationship with changes in carbohydrates (Hole and McKee 1988). Recently, Sturm et al. (1995) developed a detailed working model for the synthesis, transport, storage and usage of sucrose in carrot in which enzymes play a key role. Their model was supported by earlier results on the inverse relationship between the activity of acid invertase and sucrose accumulation (Ricardo and ap Rees 1970, Oldén and Nilsson 1992).

1.2.3 Carotenes and colour

Carotenes give carrot its characteristic orange colour. There is a positive correlation between carotene content and colour (Bradley and Dyck 1968, Rosenfeld et al. 1997b). Skrede et al. (1997) found that a high carotene content results in a more reddish and darker colour but a less intensive hue. Alfa and beta carotene account for more than 90% of all carotenoids in carrot (Simon and Wolff 1987). A high growing temperature is known to favour carotene production (Banga and de Bruyn 1968, Rosenfeld 1998). Nilsson (1987b) found a strong positive correlation between carotene content and accumulated day-degrees above 6°C. Carrots grown in more southerly locations contained a higher

level of carotenes than did carrots from northern growing sites (Balvoll et al. 1976, Skrede et al. 1997) and were a darker colour than those produced further north (Hårdh et al. 1977, Baardseth et al. 1996, Rosenfeld et al. 1997a,b).

Carotene content increases with the age and size of the root (Phan and Hsu 1973, Fritz and Weichmann 1979, Nilsson 1987a,b, Fleury et al. 1993, Rosenfeld 1998). Under field conditions, the general trend is for an increase in the carotene content during most of the growing season to be followed by a constant level of carotenes. In various studies, the maximum content was reached at 90–130 days after sowing (Phan and Hsu 1973, Fritz and Habben 1975, 1977, Lee 1986, Nilsson 1987a). The carotene level was clearly reduced when sowing was delayed up to July (Nilsson 1987a). In the greenhouse, carotenes continued to accumulate up to the last harvest (Fritz and Habben 1977). In a controlled climate (Rosenfeld 1998), the maximum carotene content had not been reached at 100 days after sowing, when the experiment was terminated.

1.2.4 Sensory quality

Sensory quality is an increasingly important quality aspect. The contribution of different components to the sensory quality of raw carrots has been studied but is still not fully understood. Alabran and Mabrouk (1973) suggested that the non-volatile chemical constituents (sugars and amino acids) are primarily responsible for the taste of fresh carrot and that the contribution of volatile components is small compared with that of non-volatile compounds. Simon et al. (1980) emphasised the importance of both sugars and volatile terpenes in determining raw carrot flavour. Their findings implied that sweetness and overall preference are enhanced by sugars and diminished by volatiles, whereas harsh, turpentine-like flavours are associated with the presence of volatiles and a reduction in sugars. Schaller et al. (1998) reported that intensity of taste was positively correlated with essential oils and sweetness with sugars in carrots cultivated at different levels of nitrogen fertilisation. Howard et al. (1995) found that high sugar to terpinolene ratios were associated with fresh carrot flavour, aroma, aftertaste and sweet taste. Heatherbell and Wrolstad (1971) noted that differences in volatiles were quantitative rather than qualitative. Habegger et al. (1996), however, emphasised that the volatile composition and amount of each compound were also important for carrot aroma.

High sensory quality and sweetness have been reported to correlate with sugar content (Balvoll et al. 1976, Simon et al. 1982, Howard et al. 1995). However, sugar content did not predict sweet taste in the studies of Rosenfeld et al. (1997b, 1998b). Rosenfeld et al. (1998b) found that the sweetest carrots, which were grown at low temperatures, contained the highest amounts of glucose and fructose and lower amounts of sucrose and total sugars. The discrepancy between sugar content and sweetness was partly explained by the relative chemical sweetness, but other factors were also involved.

Results on the development of sensory quality before harvest time are few, but some information on the effects of environmental factors is available. Rosenfeld et al. (1998b) observed that a low growing temperature favoured sweet taste, acidic taste, crispness and juiciness of carrots, whereas high growing temperatures resulted in bitter taste and high firmness of roots grown in phytotrons. Similar results were obtained in carrot varieties grown in the field in southern and northern Norway, and it was suggested that the variation among geographical locations was determined by growing temperature (Rosenfeld et al. 1997a,b). Rosenfeld et al. (1998c) found that temperature had a more marked effect than light on sensory variables in carrots grown in climate chambers. Different day and night temperatures did not alter the sensory quality in comparison to a constant

temperature with the same mean temperature (Rosenfeld et al. 1999). In some experiments, growing season and site were more important in explaining the variation in sensory quality than was the cultivar (Martens et al. 1985, Rosenfeld et al. 1997a,b). These findings regarding the importance of environmental factors lead to the assumption that the timing of harvest might have a significant effect on sensory quality, as environmental conditions change continuously during the growing season.

Some information is available on the changes in volatile components during the growing season. Heatherbell and Wrolstad (1971) found that the total essential oil content remained relatively constant for the first 20 weeks of the growing season but that the concentrations of individual compounds changed. At the end of the growing season, the total content of essential oils increased. Likewise, concentrations of acetaldehyde and ethanol increased dramatically towards the end of the season, indicating anaerobic respiration. These changes may affect the flavour of carrot, but the subject was not analysed in depth in the study.

1.2.5 Compositional changes as indicators of maturity

According to Watada et al. (1984), physiological maturity, although not usually observed in organs like roots, foliage, stems and tubers, is the stage of development at which a plant or plant part will continue ontogeny, even if detached. They distinguish physiological maturity from “horticultural maturity”, the stage of development at which a plant or a plant part can be used for a particular purpose. In carrot, maturity in this sense would require a satisfactory outer, sensory and nutritional quality combined with an adequate potential for storage and shelf life.

Several scientists have attempted to find indicators for maturity to optimise the harvest time of carrot with regard to either nutritional values, yield or storage potential. Sugar content or composition has often been interpreted as a maturity index. Goris (1969b) and Phan and Hsu (1973) defined maturity as the time at which the concentration of soluble sugars attains a constant value but the root is still growing. Fritz and Weichmann (1979) suggested use of the sucrose to hexose ratio as the criterion of the appropriate harvest date from the standpoint of nutritional quality but not of storage ability. Later, Le Dily et al. (1993) monitored compositional changes in carrot overwintering in the field and defined maturity as the stage with the maximum sucrose to hexose ratio.

The use of sugar composition as an indicator of maturity has been questioned. In Sweden, Nilsson (1987a) found that sucrose accumulation continued up to the final harvest, a finding at variance with the presence of a real maturity stage. He concluded that “maturity” should only be considered as a reduction in metabolic activity in an environment no longer favourable for growth. However, he mentioned that since the carotene content seemed to be influenced by the accumulated day-degrees, the use of carotene as an indicator variable should be further studied. Rosenfeld (1998) noted that neither the ratio of sugars nor any other chemical variable indicated the presence of a definable stage of biological development that could be considered as maturity. He concluded that the computed term “cylindricity”, indicating root shape, might be used as a criterion for fully developed roots, together with root weight.

1.3 Postharvest development of carrot

The life of fruit and vegetables can be divided into three major physiological stages following germination: growth, maturation and senescence (Wills et al. 1998). Maturation usually starts before growth ceases and includes different activities, depending on the product. Senescence is defined as the period when catabolic (degradative) biochemical

processes overcome anabolic processes, leading to ageing and death of tissues. After harvest, the senescence gradually impairs the quality of the products and finally makes them unusable.

Postharvest life functions cannot be stopped, but they can be slowed down by controlling the storage environment. Biological processes affecting the quality of vegetables during storage are respiration, ethylene production, compositional changes, growth and development, transpiration, physiological breakdown, physical damage and pathological breakdown (Kader 1992). The relative importance of each factor varies largely from one species to another.

1.3.1 Factors causing storage loss

Carrot has good physiological storability. Provided that carrots are not infected by microbes causing storage diseases, they can be stored for 6–8 months without loss of quality under optimal storage conditions (temperature 0°C and relative humidity c. 98%) (Balvoll 1985). Carrot has low metabolic activity at low temperatures, as shown by the low respiration rate (Stoll and Weichmann 1987). A low storage temperature also prevents the onset of new growth. However, carrot is sensitive to wilting if not protected from water loss. In commercial refrigerated stores, storage diseases, mainly caused by pathogenic fungi, pose the greatest risk. Ethylene in the air may impair the sensory quality by inducing the synthesis of phenolic compounds, which give rise to a bitter taste (Sarkar and Phan 1979, Lafuente et al. 1989, 1996).

Transpiration

Transpiration is the mass transfer of water vapour from the surface of the plant organ to the surrounding air. The driving force is the gradient of water vapour pressure between the tissue and the surrounding air, which is affected by the relative humidity and temperature of the air and the product (Ben-Yehoshua 1987). The rate of water loss of carrot is affected by the surface area of the root, the water vapour pressure deficit and air velocity (Apeland and Baugerød 1971). The significance of the surface area is seen in the fact that large carrots lose less weight than small carrots and cylindrical carrots less than cone-shaped ones. Root tips, where the ratio of surface area to weight is high, are the most susceptible to water loss (Apeland and Baugerød 1971).

Water loss due to transpiration results in shrivelling, loss of bright colour and increased risk of post-harvest decay (van den Berg and Lentz 1973, Goodliffe and Heale 1977, Den Outer 1990). An 8% weight loss is reported to make carrots unsaleable (Robinson et al. 1975). Van den Berg and Lentz (1973) showed that the optimum relative humidity during storage is 98% to 100%, a level that efficiently reduced postharvest decay and moisture loss compared with storage at 90% to 95% RH. During storage, thin-walled cells, such as those in phellogen and oil ducts, die and form a fatty layer of dead crushed cells, which accounts for the loss of bright colour (Den Outer 1990). A new periderm is formed below to prevent further desiccation, but the process is slow at low temperatures and cannot prevent water loss.

Shibairo et al. (1997) observed some cultivar differences in moisture loss characteristics during short-term storage but they were mainly associated with the specific surface area of the root. Differences between cultivars were pronounced when carrots were harvested at a mature stage compared with those harvested early. Preharvest water stress increased postharvest weight loss and shortened the shelf-life of carrots (Shibairo et al. 1998a), which led the authors to recommend that carrots should not be harvested under water stress. They suggest that preharvest water stress lowers the integrity of the membranes in the root, which enhances moisture loss during storage. Increased potassium (K) application reduced the postharvest moisture

loss by increasing root weight and maintaining tissue integrity, but the K fertilisation is likely to be of benefit only in soils with a very low K content (Shibairo et al. 1998b).

Respiration

Storage compounds accumulating in the storage organ during growth and maturation are consumed in the course of metabolic activitites during storage. Respiration includes the oxidative breakdown of sugars, starch and organic acids into carbon dioxide and water, with the concurrent production of energy, heat and intermediary compounds to be used in biochemical reactions (Wills et al. 1998). At low temperatures, the respiration rate is low, and it comprises only a minor part of weight loss compared with transpiration (Apeland and Baugerød 1971). Apeland and Hoftun (1974) found that respiration first decreased after harvest and later increased with time in store, more at 2 and 5°C than at 0°C. Transfer to 5°C from a lower temperature initially increased the respiration rate above that at constant 5°C but the rate soon declined.

The respiration intensity of carrots decreases when they are harvested after a longer growing time (Fritz and Weichmann 1979, Mempel and Geyer 1999). According to Fritz and Weichmann (1979), in late maturing cultivars respiration increased again in the final two harvests in October. The differences between harvest dates persisted after storage but were smaller. Mempel and Geyer (1999) reported that the increase in respiration soon after harvest was larger in younger than in older carrots.

Mechanical loads increase the respiration rate, which may impair the quality of carrots (Mempel and Geyer 1999). Repeated drops from a lower height resulted in a larger increase in respiration than did fewer drops from a greater height. Respiration intensity also increased with each step of packing.

Lowering the oxygen concentration or increasing the carbon dioxide concentration in storage air reduces the respiration rate of carrot (Apeland and Hoftun 1971, Robinson et al. 1975), but the gas composition is critical. Carrot is very sensitive to CO_2 concentrations of 4% or higher or to oxygen concentrations of 8% or lower (Stoll and Weichmann 1987).

Fungal diseases

Storage diseases may cause considerable storage losses, since roots showing even minor damage must be discarded before marketing. Three pathogenic fungi, *Mycocentrospora acerina* (Hartig) Deighton, *Botrytis cinerea* Pers. and *Sclerotinia sclerotiorum* (Lib.) de Bary, have been considered the most harmful throughout the production area of carrot (Lewis and Garrod 1983) and they are also the most common storage pathogens in Finland. In the investigation of Mukula (1957), the most important pathogens during storage were *S. sclerotiorum*, *B. cinerea*, *Stemphylium radicum* and *Fusarium avenaceum*, with the first two fungi accounting for 77% of the total decay. *M. acerina* spread to Finland in the 1970s (Tahvonen 1985) and, as a soil-borne pathogen, is today viewed as the most serious storage disease of carrot. *M. acerina* has also been reported as one of the major storage diseases in other Nordic countries (Årsvoll 1969, Hermansen and Amundsen 1987, Rämert 1988) and other temperate areas (Derbyshire and Crisp 1971, Le Cam et al. 1993).

Mycocentrospora acerina (Hartig) Deighton

Carrot roots attacked by *Mycocentrospora acerina* are characterised by large, black and sunken lesions on their shoulders, sides and tips (Dixon 1981). In cross-section, the rotted area is mainly black but it has a diffuse water-soaked brown margin (Snowdon 1992). The fungus is able to grow at temperatures of -3 to 27°C; the optimum temperature is 17–21°C (Gündel 1976).

1°C (Gündel 1976).

The pathogen is soil-borne (Neergard and Newhall 1951), and it survives for long periods in the soil as dark thick-walled chlamydospores that germinate in the presence of a host plant (Snowdon 1992). Infected crop residues increase the pool of chlamydospores in the soil, and passive dispersal is possible by cultivation of the soil and by water running on the soil surface (Wall and Lewis 1980b); the role of air-dispersal from one field to another is insignificant (Hermansen 1992, Evenhuis et al. 1997).

Germination of the spores is stimulated by root exudates (Wall and Lewis 1980b). The main forms of the fungus on harvested carrots are chlamydospores and short lengths of the mycelia that remain on senescent petioles and in soil particles attached to the roots (Davies et al. 1981). Although the senescent foliage can maintain a supply of inoculum, foliar infection accounts for only a small proportion of the inoculum in the store (Wall and Lewis 1980a). Infection is brought about by germination of the chlamydospores through wounds (Davies and Lewis 1980, Davies et al. 1981).

M. acerina is predominantly a wound pathogen (Davies et al. 1981) as the root is usually infected via damaged lateral roots or abrasions in the periderm. An intact periderm is highly resistant to the pathogen, but the resistance diminishes gradually towards the inner tissues (Davies 1977, Davies and Lewis 1981b, Davies et al. 1981). The resistance of the periderm involves inhibition of spore germination and prevention of penetration (Davies and Lewis 1981b). Inhibition of spore germination at the root surface declines progressively during storage, but as the spores age simultaneously, inhibition remains high and penetration of an intact periderm is rare (Davies and Lewis 1981b). Resistance of the periderm is not likely to result from mechanical obstruction alone as the periderm is rarely completely intact (Davies and Lewis 1981b).

At the beginning of carrot storage, infections are microscopic (Davies et al. 1981). The small light brown areas of collapsed cells remain localised, and cells around the lesions accumulate suberin and lignin. Lignification and suberisation are, however, not regarded as being the main barriers to the spreading of the lesions (Davies et al. 1981). Garrod et al. (1982) considered that structural barriers directly contribute only a very small proportion of the tissue resistance, but they may protect the cell protoplasts until they have accumulated high levels of antimicrobial substances. On the other hand, the onset of progressive lesions may coincide with a decline in levels of antifungal compounds, which can therefore be regarded as an aspect of senescence (Davies et al. 1981).

The main antifungal compounds produced by carrot roots, and which are active against *M. acerina*, are falcarindiol (heptadeca-1,9-diene-4,6-diyne-3,8-diole; Garrod et al. 1978) and 6-methoxymellein (6-methoxy-8-hydroxy-3,4-dihydroisocoumarin; Davies 1977). The concentration of falcarindiol decreases towards the inner tissues of the root, which corresponds to the gradient in the resistance (Garrod et al. 1978). Olsson and Svensson (1996) found a negative correlation between the concentration of falcarindiol and the susceptibility of a cultivar to *M. acerina* in 14 of 16 cultivars tested.

Garrod and Lewis (1979) showed that falcarindiol is present in the extracellular oil droplets found in periderm and pericyclic parenchyma in particular and, to a lesser extent, in phloem parenchyma. Falcarindiol is known to inhibit germination of the chlamydospores (Garrod et al. 1978) and also mycelial growth of *M. acerina* (Garrod and Lewis 1982). The antifungal effect is caused by disruption of the membranes not specific to fungi. The extracellular location of falcarindiol may prevent disruption of the membranes of the host plant (Garrod and Lewis 1979).

The formation of 6-methoxymellein is enhanced by inoculation or infection by fungi

(Davies and Lewis 1981a). It also accumulates in response to other exogenous agents, such as heat-killed conidia of *Botrytis cinerea*, surface freezing, ethylene or UV radiation (Harding and Heale 1981, Hoffman and Heale 1987, Hoffman et al. 1988, Mercier et al. 1993). The compound is also effective against *B. cinerea*. The potential to accumulate 6-methoxymellein falls with time in storage (Goodliffe and Heale 1978).

Botrytis cinerea Pers.

The tissue colonised by *Botrytis cinerea* becomes water-soaked, leathery and covered with grey mould and grey-brown spores (Snowdon 1992). Under cool humid conditions, the mould may remain white. The fungus survives in crop debris and in soil as sclerotia. Vigorous young plants are not attacked, but the senescent foliage can be infected by air-borne spores or through contact with soil or crop debris. Harvested roots carry the infection in leaf debris, in soil attached to the roots or on the root surface. The pathogen is usually present on stored carrots, e.g. in soil adhering to the root (van den Berg and Lentz 1968). During storage, the fungus can spread into adjacent roots by contact or over longer distances by air-borne spores (Goodliffe and Heale 1977). It is able to grow at temperatures of -0.3 to 35°C, with a maximum rate at 20°C (van den Berg and Lentz 1968).

Resistance to infection declines in the course of storage (Goodliffe and Heale 1977). The increased susceptibility has been associated with the decrease in the potential to accumulate 6-methoxymellein (Goodliffe and Heale 1978). Weight loss of roots increases the incidence of infections: water loss of more than 5% markedly reduces the ability of the phloem parenchyma to resist infection (Goodliffe and Heale 1977). Root tip, which has a high surface to weight ratio and is often damaged at harvest, is more easily infected than are other areas of the root. The ability of the roots to resist infection varies from year to year, due to differences in growing and storage conditions.

Periderm is an effective barrier to infection, but when carrots had lost water, a larger proportion of the surface inocula produced visible lesions (Goodliffe and Heale 1977). Goodliffe and Heale (1977) suggested that resistance to the pathogen might be due to the accumulation of the 6-methoxymellein found in resistant lesions. Accumulation of this substance is triggered by various stress factors (Hoffman et al. 1988), probably by the action of an endogenous elicitor possibly released after cell death. Hoffman et al. (1988) concluded that ethylene biosynthesis is required for resistance response to *B. cinerea* and for the accumulation of 6-methoxymellein, but other ethylene-induced compounds may also affect the resistance.

Sclerotinia sclerotiorum (Lib.) de Bary

Sclerotinia sclerotiorum is one of the most successful and widely-spread plant pathogens. According to information gathered by Boland and Hall (1994), 278 genera and 408 species are reported as host plants of the fungus. Carrot tissue infected by *S. sclerotiorum* is soft and watery but not discoloured (Snowdon 1992). Pure white mould appears on the surface. Primary lesions usually occur in the crown region, but during storage the mould may spread to adjacent roots by contact. The sclerotia form as irregularly shaped whitish bodies that, after exuding drops of liquid, dry out and turn to black resting bodies from 2 to 20 mm in size.

Sclerotia can persist in the soil for many years (Snowdon 1992). After wet weather or irrigation, the sclerotia germinate by producing apothecia and ascospores. The spores are injected into the air and foliage. Dense foliage, which can retain water, and dying foliage are susceptible to invasion. The primary infection is through leaf tissue very near to or in contact with sclerotia lying near the soil surface (Finlayson et al. 1989a). The myce-

lium invading to leaf tissue is able to grow down the petiole to the upper part of the root and so escape the mechanical barrier to penetration caused by root periderm. Symptoms of the disease are rarely present at the time of harvest, but roots have the incipient infection when taken to store. In storage, the fungus does not form spores but spreads only by direct contact of the mycelium (Snowdon 1992).

In the study of Le Cam et al. (1993), *S. sclerotiorum* was the most aggressive of the pathogens tested on carrot but only at temperatures above 5°C. Van den Berg and Lentz (1968) found that the fungus grows even at 0°C and that it has a maximum growth rate at 20°C. Rapid cooling after harvest is emphasised to control the spread of the fungus (Finlayson et al. 1989b, Pritchard et al. 1992).

1.3.2 Effect of harvest time on storage loss

Timing of harvest may affect storage losses via the effects of carrot age and developmental stage and weather conditions before and during harvest. Transpiration is affected indirectly by the size and shape of carrots (Apeland and Baugerød 1971, Shibairo et al. 1997) or directly by preharvest water stress (Shibairo et al. 1998a). The respiration rate of carrots during storage falls with the growing time (Fritz and Weichmann 1979, Mempel and Geyer 1999).

There is shortage of comprehensive studies on the effect of harvest time on storage diseases. According to Mukula (1957), the longer the growing period the lower were the amounts of *Sclerotinia sclerotiorum* and *Botrytis cinerea*. In one experiment, a slight increase in storage losses due to these pathogens was found again in the final harvest. The susceptibility of carrots to *Stemphylium radicinum* and *Fusarium* rots increased with an increase in growing period.

Davies and Lewis (1980) and Villeneuve et al. (1993) observed a higher rate of *Mycocentrospora acerina* in older carrots. In younger carrots, fewer inoculation sites became infected and fewer localised lesions developed into progressive infections (Davies and Lewis 1980). The age of the root affected mainly the rate of development of localised lesions and the development of progressive infection, not the final level of infection. The resistance of the periderm tissue was not affected by the age of the roots. Therefore, it was suggested that root age would influence either susceptibility to damage or the wound-healing potential, and that changes in the periderm structure would not have a direct effect on infection (Davies and Lewis 1980). The greater potential for wound-healing in younger roots was reported by Lewis et al. (1981), who found that the healing potential declined after 176 days.

The significance of weather conditions for the post-harvest life of carrots was emphasised by Fritz and Weichmann (1979), who found a positive correlation between storage loss and rainfall and high humidity before harvest. They concluded that weather conditions affect storage quality more than does the composition of the plant. Similarly, Villeneuve et al. (1993) suggested that high humidity and precipitation, which increase root turgor, would make carrots more susceptible to mechanical damage and thereby to infection by *M. acerina*.

1.3.3 Effect of mechanical injuries and healing on storage loss

Mechanical damage in harvest influences deterioration through weight loss and increased disease incidence. In addition, plant and soil debris among the roots increases the quantity of inoculum in the harvested yield (Derbyshire and Shipway 1978). Mechanical damage also raise the respiration rate and hence the consumption of reserve compounds of the roots (Mempel and Geyer 1999).

Infections by all the pathogens studied

are enhanced by wounding (Mukula 1957, Derbyshire and Crisp 1971), and infection by *M. acerina* is restricted mainly to wounds (Davies et al. 1981). Therefore, higher rates of diseases have been reported after mechanical harvesting than after hand-lifting (Apeland 1974, Tucker 1974b). Nevertheless, comparison between hand-lifted and machine-harvested yields in two seasons (Geeson et al. 1988) did not show any consistent differences in the incidence of rotting due to the major pathogens, *Botrytis cinerea* and *Rhizoctonia carotae*. Technical improvements to the lifting machinery in recent decades have probably reduced harvest damage, but injuries are still more likely to occur in mechanical harvesting than in manual harvesting.

Wound healing is an important factor in determining the storage potential of carrot. Davies and Lewis (1980) postulated that differences in the healing potential might also be related to the year-to-year variation in storage potential. Healing may be enhanced by prestorage treatments. Lewis et al. (1981) showed that healing of the wounds at 15 or 25°C before storage diminished the infection by *M. acerina*. On wounded phloem parenchyma tissue, maximum resistance was reached after 5 days' healing. In xylem parenchyma, a less resistant tissue, a healing period as short as 6–12 hours significantly reduced infections. Similarly, Le Cam et al. (1993) observed reduced infection by *M. acerina* when carrots were healed at 5–7°C for 12–36 hours before cold storage, and Hoftun (1993) found a positive effect of prestorage at 5°C for 2 or 3 weeks or at 10°C for 1 week.

Lewis et al. (1981) suggested that the beneficial effect of healing might be attributed to antifungal substances accumulating on wound surfaces. After a 40 h healing period, Garrod and Lewis (1980) detected a 20-fold increase in the concentration of falcarindiol in the surface layer of the wounded tissue, possibly due to breaking of the falcarindiol-containing oil ducts on the wound surface (Lewis et al. 1983). Lewis et al. (1983) concluded that the preformed inhibitor, falcarindiol, is probably the main barrier to infection during the first 16 h after wounding and healing, and that its effect is reinforced by the inducible compound, 6-methoxymellein.

Most studies on wound healing have been conducted on artificial wounds, which may not fully correspond to the damage caused by mechanical harvesting. However, in the Netherlands, it is recommended that carrots harvested under wet conditions should be given a prestorage treatment of 2–3 weeks at 5°C or 1 week at 10°C to enhance the healing process (Schoneveld and Versluis 1996). When harvested under dry conditions, carrots can be taken to the store immediately and forced cooling is not necessary at the beginning. The carrots should, however, be protected from transpiration.

1.3.4 Compositional changes during storage

The quality of vegetables deteriorates gradually during storage in response to endogenous factors and environmental conditions. Processes such as transpiration, respiration, activation of growth and attacks by pathogens lead not only to quantitative losses but quality losses, which can destroy the marketability of the product or remain invisible. Compositional changes are usually studied only in marketable carrots.

A common trend in sugar composition is for the hexose content to increase and the sucrose content to decrease, especially during the first months of storage (Phan et al. 1973, Nilsson 1987b, Oldén and Nilsson 1992, Le Dily et al. 1993). Most experiments record only minor changes in the total sugar content. Nilsson (1987b) found that compositional changes occurred irrespective of harvest date and that the differences were maintained throughout storage. In natural development of carrot root in the field in France (Le Dily et al. 1993), sucrose and total sugar contents

reached their maxima in December. The sucrose content started to decrease in mid-February and the fructose and glucose contents in March. In contrast to harvested and cold-stored carrots, there was no accumulation of hexoses. Therefore, the change in carrot composition in the post-harvest period differs from that in the natural environment.

Carotene content is little affected during storage (Fritz and Weichmann 1979, Le Dily et al. 1993). Phan et al. (1973) even found that the content increased slightly during storage, but when the roots started to form shoots and rootlets, the carotene content decreased in xylem but not in phloem. The nitrate content, which is not usually very high in carrots but may be noxious in children's food, decreases slightly during storage (Nilsson 1979, Kidmose and Henriksen 1994).

Changes in sensory quality during storage are not widely documented in the literature. Evers (1989b) found that taste and texture scores given after 4 or 6 months' storage were lower than after harvest. However, organically cultivated carrots received higher taste scores after storage.

1.4 Aims of the study

Storage is a prerequisite for a year-round supply of domestic vegetables. The quality of root vegetables after long-term storage is primarily determined during the growing season. Quality is at its highest at harvest, after which it can only be maintained at the same or a lower level. The natural senescence of products sets limits on the maximum period of storage. Conditions prevailing during storage control the rate of postharvest changes and affect the maximum storage time. Similarly, the quantity of marketable yield is determined by conditions during the growing season. The proportion of yield that is still marketable after storage is affected by both pre- and postharvest factors.

This study aimed to show how the quality and quantity of carrot after storage can be better controlled. The main emphasis was on the effects of harvest time, with the aim of optimising the timing of harvest. Criteria for the optimal harvest time were defined as 1) high total yield, 2) low storage loss, 3) high quality of yield at harvest and 4) maintenance of quality during storage. Development of the carrot plant during the growing season was investigated to characterise the determinants of yield production. Evaluation of quality concentrated on sensory quality, which, together with outer quality, is the most easily perceptible quality characteristic in fresh consumption. The sugar composition of carrot storage root was studied as a possible descriptor of the plant's stage of development.

More specific objectives were:

1. to investigate the patterns of shoot and storage root growth of carrot in a northern climate (I);
2. to establish when the growth of carrot storage root ceases in autumn and no further yield increase is gained (II);
3. to determine the optimal harvest time to minimise storage loss (III);
4. to characterise the factors accounting for changes in storability during the harvest period (IV);
5. to study changes in soluble sugar content and composition during the harvest period and storage as chemical energy reserves and possible descriptors of maturity (V); and
6. to establish the optimal harvest time for the best sensory quality at harvest and after storage (VI).

2 Material and methods

2.1 Field experiments in 1995–1997 (I–III, V–VI)

Field experiments were conducted at the Vegetable Experimental Site of the Agricul-

tural Research Centre of Finland at Kokemäki and on vegetable farms. Two cultivars were used: Panther F_1 (Sluis and Groot, the Netherlands), a fresh-market variety commonly used for storage in Finland, and Fontana F_1 (Bejo Zaden, the Netherlands), a late variety cultivated for the processing industry. At Kokemäki, a split-plot experiment with the two cultivars in whole plots and harvest time in subplots was conducted in 1996 and 1997. There were six harvest dates at approximately 10-day intervals in September and October (Table 1).

The experiments on farmers' fields were conducted:

1. to obtain a large volume of experimental data within three years;
2. to provide insight into the variation in yield level and average storage loss between farms; and
3. to estimate the uniformity of the effect of harvest time under varying growing conditions.

The farm experiments were started in 1995, when the yield of cv. Fontana was harvested from nine farms three times at 2-week intervals (Table 1). Most of the farms were located near Huittinen, two of them were near Pori and one was the Häme Research Station at Pälkäne, which is here considered as a farm. In 1996, the experiments were continued on six 'Fontana' farms in the Huittinen region. Nine farms (five in the Forssa and four in the Laitila region) with cv. Panther were included in the study in 1996 and 1997, and there were four harvest dates at approximately 2-week intervals in September and October.

Measurements and analyses

At the Vegetable Experimental Site, samples for growth analysis were taken at approximately 10-day intervals starting at 43 and 54 days after sowing in 1996 and 1997, respectively (I). The samples were analysed for the number of true leaves per plant (longer than 0.5 cm), the length of the longest leaf, the fresh and dry weights of the leaves, the maximum thickness and length of the storage root, and the fresh and dry weights of the storage root. In addition, leaf area was measured six times in 1996 and four times in 1997. Specific leaf area (SLA) and mean relative growth rate (RGR) were calculated according to the formula given by Hunt (1990).

At each harvest date in all experiments, the variables measured were:

* total fresh and dry yield per area (not on farms in 1995) (II)
* fresh weight of the shoot per plant (II)
* contents of soluble sugars (fructose, glucose, sucrose) at harvest (V)
* contents of soluble sugars after 2–3 durations of storage (only in 1995 and 1996) (V)

Table 1. *Harvest dates in experiments.*

Coding of harvest	Vegetable Experimental Site		Farm experiments			
	1996	1997	cv. Fontana 1995	cv. Fontana 1996	cv. Panther 1996	cv. Panther 1997
H1	5 Sept	8 Sept	12 Sept	11 Sept	10–11 Sept	9–11 Sept
H2	16 Sept	18 Sept	26 Sept	25 Sept	23–24 Sept	23–24 Sept
H3	26 Sept	29 Sept	10 Oct	8 Oct	7–9 Oct	7–8 Oct
H4	7 Oct	9 Oct		22 Oct	21–22 Oct	21–22 Oct
H5	16 Oct	20 Oct				
H6	28 Oct	30 Oct				
Growing time from sowing to H1 (d)						
	106	117	107–130	114–120	104–120	113–128

* storage losses (weight loss, proportion of diseased carrots, total loss) after 3 storage durations (III).

In addition, the sensory quality of carrots produced at the Vegetable Experimental Site and on 2–3 farms was analysed soon after harvest and after 2 storage durations in 1996 and 1997 (VI).

Soluble sugars were analysed at the Laboratory of Food Chemistry of the Agricultural Research Centre of Finland (V). Fructose, glucose and sucrose were assayed by gas-liquid chromatography (GLC) employing the method of Li and Schuhmann (1980) with modifications of Haila et al. (1992). Total soluble sugars were calculated as the sum of fructose, glucose and sucrose.

Sensory analyses were performed in cooperation with the unit for Food Chemistry and Technology of the Agricultural Research Centre of Finland (VI). The sensory panel had 12 members, both people trained in sensory analysis and untrained vegetable specialists. The attributes evaluated were juiciness, crispness, sweetness, bitterness and overall flavour. The first four attributes, together with fruity taste, are regarded as the most important variables describing the inner sensory quality of carrots by Fjeldsenden et al. (1981). Overall flavour was included to describe the overall sensory quality of carrots as a preference attribute. A 9-point scale was used. For overall flavour, each integer on a scale from 1 to 9 was used but for other attributes, only integers 1, 3, 5, 7 and 9 were used. Each point of the scale was given a verbal description.

Storage experiments (III)

Yield samples were stored in woven polypropylene bags (75 g m^{-2}) in batches of approximately 10 kg of carrots. Samples from different experimental sites were stored in the same store, which differed each year. Storage conditions were as follows: in 1995–1996, temperature 0±0.5°C, relative humidity 80–85%; in 1996–1997, temperature 0±1°C, relative humidity 85–95%; in 1997–1998, temperature 0.5±0.5°C, relative humidity 90–100%. In the first two years, the cooling system comprised a refrigeration coil installed in the ceiling of the store. In the last year, an indirect cooling system with a heat exchanger cooled by outside air or by mechanical refrigeration, which maintains the humidity in the store, was used. In the last two years, water vapour was added to the air to raise the air humidity. Storage losses were analysed three times during storage between January and April.

2.2 Experiment in 1998–1999 (IV)

In 1998, carrots of cv. Panther were grown at the Vegetable Experimental Site in a randomised complete block design with four replicate blocks. The yield was harvested three times (H1 = 16 September, H2 = 30 September, H3 = 14 October). At each harvest, the carrots were randomly divided into the following treatments:

1. no mechanical treatment, storage at 0.5°C
2. mechanical treatment, storage at 0.5°C
3. mechanical treatment + inoculation with *Mycocentrospora acerina*, storage at 0.5°C
4. no mechanical treatment, 7 days at 10°C before storage at 0.5°C
5. mechanical treatment, 7 days at 10°C before storage at 0.5°C
6. mechanical treatment + inoculation with *M. acerina*, 7 days at 10°C before storage at 0.5°C.

The mechanical treatment was performed by a shaking apparatus developed in the Netherlands for assessing the susceptibility of potatoes to black spot (Meijers 1981). In treatments 3 and 6, the carrots were inoculated during shaking by adding 200 ml of coarse sand inoculated with *M. acerina*. Half of the carrots (treatments 1–3) were taken straight to the cold store on the afternoon of the har-

vest date. Carrots from treatments 4–6 were kept for 7 days at 10°C to heal the wounds, after which they were taken to the cold store. The temperature during cold storage was 0.5°C±0.5°C and relative humidity 90–100%. Storage losses were analysed on 1 February and 7 April, 138 and 203 days after H1, respectively.

2.3 Statistical analysis

The results were analysed mainly by mixed models (Littell et al. 1996). In the farm experiments with cv. Panther, the growing area (Forssa or Laitila region) was a fixed factor, and each farm within the area was regarded as a "random" farm representing typical cultivation methods and conditions in that area, although the farms could not be randomly selected (II–III, V). Therefore, it was assumed that results could be generalised within the area, and separate farms were not of primary interest. In the experiments with cv. Fontana, all the farms represented the same growing area, which can be regarded as the most important production area of this cultivar for the processing industry. When the sensory quality data from the farms were analysed, each farm's data were treated separately, since only 2–3 farms were included (VI).

The models used are presented in greater detail in separate papers (I–IV, VI). The SAS MIXED procedure (Littell et al. 1996) was used to fit the mixed models by the restricted maximum likelihood (REML) estimation method. The effect of harvest time, which was the primary objective of the experiments, was further studied by estimating differences in each response variable between harvest and the mean of following harvests.

3 Results and discussion

3.1 Patterns and cessation of carrot growth

Analysis of growth patterns (I) during the growing season showed that shoot fresh and dry weights and leaf area reached their maxima 90–130 days after sowing and started to decrease thereafter. On the other hand, temperature and the daily sum of irradiance remained relatively high up to approximately 100 days after sowing, mid or late August, after which they decreased clearly. Therefore, most of the growing season was used for building up the photosynthetic capacity, and much of the storage root growth occurred under less favourable conditions: the storage root weight of cv. Fontana doubled and that of cv. Panther increased slightly less after late August. Earlier studies on the shoot and root growth of carrot in Finland have given similar results: Salo (1999) reported that the dry weight of shoot increased up to mid August, whereas the rapid growth of storage roots started in mid July. Evers (1988) found that only 17–26% of the final root fresh weight was reached in the middle of the growing season 2–2.5 months after sowing. A slow growth rate in the early part of vegetative growth therefore inhibits efficient utilisation of the short growing season.

Our findings on the relation between leaf and storage root growth of carrot are in agreement with those of Fritz and Habben (1977), who found that, in the field, the shoot weight of different cultivars declined before the maximum root weight was achieved. In the greenhouse (mean day temperature 15°C, night temperature 10°C), shoot weight started to decrease at 100 days after emergence and under field conditions at 130–170 days after emergence. However, Nilsson (1987a) reported that the cessation of root growth at the end of September in Sweden coincided with

Table 2. *Yield increase after different harvest dates (in comparison to final harvest). In farm experiments, figures are means of all farms.*

Vegetable Experimental Site, Kokemäki

	Yield increase, t ha^{-1} (% of yield at final harvest)			
	1996		1997	
Harvest date	Fontana	Panther	Fontana	Panther
H1 = 5–8 Sept	29.4 (36)	20.1 (29)	23.4 (22)	17.0 (18)
H2 = 16–18 Sept	18.8 (23)	9.8 (14)	11.2 (11)	8.9 (10)
H3 = 26–29 Sept	11.5 (14)	4.5 (6)	9.6 (9)	11.3 (12)
H4 = 7–9 Oct	8.4 (10)	-0.1 (0)	-4.6 (-4)	-0.2 (0)
H5 = 16 Oct	3.4 (5)	-1.1 (-2)		
Yield at final harvest	**81.6**	**70.2**	**105.0**	**93.6**

Farm experiments

	cv. Panther				cv. Fontana
	1996		1997		1996
Harvest date	Forssa	Laitila	Forssa	Laitila	Huittinen
H1 = 9–12 Sept	14.3 (22)	4.8 (10)	16.5 (20)	19.9 (27)	6.4 (14)
H2 = 23–26 Sept	5.4 (9)	1.8 (4)	5.1 (6)	6.3 (9)	4.4 (9)
H3 = 7–10 Sept	3.2 (5)	-1.1 (-2)	-1.6 (-2)	0.9 (1)	2.6 (6)
Yield at final harvest	**64.0**	**46.6**	**81.9**	**74.3**	**47.0**

a fall in shoot weight, irrespective of sowing date. Wheeler et al. (1994) and Habben (1972) found no decline in shoot weight up to the last harvest at 4–5 months after sowing. Differences in the senescence of leaves may be related to genotype and the plant's nutritional status, but obviously maintenance of the photosynthetic potential, even at the end of the growing season, would ensure maximum root growth.

Hole et al. (1987a) reported that cultivars with a high root yield tend to have high shoot weights. The same was seen in our study at the Vegetable Experimental Site, where cv. Fontana, having a high shoot weight and a large leaf area, also produced a higher root yield. Relative growth rates were similar in both cultivars in relation to time from sowing, which shows that the differences had arisen earlier. No clear differences in emergence rate of the cultivars were noticed. Therefore, the higher potential for yield formation in cv. Fontana seems to be determined soon after emergence. Partitioning to leaf production at an early stage, resulting in a higher shoot to root ratio, apparently ensures a potential for high biomass production and high root weight (Hole et al. 1987a). Hole et al. (1987a) concluded that the shoot to root ratio characteristic of a given cultivar was determined at 27–48 days from sowing.

Although the relative growth rates of the two cultivars were similar at a given time, they were lower in cv. Panther at a given plant weight. This is probably due to the fact that cv. Panther reached the same plant weight later as cv. Fontana in the growing season and therefore under less favourable growing conditions. The differences in root weight between cultivars increased markedly after late August, suggesting that the smaller leaf area of cv. Panther was not sufficient to fully utilise the diminishing growth factors. Early development of the photosynthetic potential is thus crucial for achieving a high yield in a northern climate, where the short growing season sets limits on growth.

Results concerning the development of yield at the Vegetable Experimental Site and on farms (II) showed that the statistically significant increase in total fresh yield generally ceased in early October, despite the large

variation in average yield level at different experimental sites. The only exceptions to this timing were the farms at Laitila in 1996, where no yield increase was gained after the second harvest at the end of September. The average yield gain after the first harvest was 4.8–29.4 t ha^{-1}, which corresponds to 10–36% of the total yield at the final harvest (Table 2). This means that up to one-third of the yield potential achieved was produced after the first harvest in early September. However, most of the yield increase was achieved before the end of September, and no statistically significant yield gain occurred when the harvest was delayed beyond the first week of October. Injuries due to night frosts on 21 September and low precipitation probably promoted leaf senescence and thereby reduced the growth potential on farms in 1996.

The timing of cessation of growth coincided with earlier results, although there is probably considerable variation between different cultivars. In Germany, Fritz and Habben (1977) found intervarietal differences in the cessation of growth in both the greenhouse and the field. In the field, root growth stopped between the end of September and the end of October. In southern Sweden, root yield increased significantly up to 23 September in the first year and up to 15 October in the following year (Nilsson 1987b). Fløthings (1973) reported that, in Norway, root growth was slight after the beginning of October. Earlier data on yield development in the late season are not available for Finland.

Yield increase resulted from continuing photosynthesis, as the dry matter yield usually increased up to the same harvest as the fresh yield. However, on farms in 1996, when severe night frosts injured the plant stands on 21 September, no further accumulation of dry matter was observed. Therefore, the increase in fresh yield in that year was due to solely the higher water content of storage roots. The possibility of dry matter being transported from senescing leaves to storage root has not been studied.

These findings suggest that, despite lowering temperature and irradiation, carrot still has substantial potential for yield production late in the growing season if the plants remain healthy and uninjured. The uniform timing of cessation of growth at different growing sites also suggests that the cultivars in the study do not reach an endogenous limit for yield production under conditions prevailing in Finland but that environmental factors determine the termination of growth. The same was noted by Rosenfeld (1998), who concluded that carrots can grow for long periods at temperatures above those required for vernalisation. Even after 3 months at a temperature as low as 9°C, carrots remained unvernalised and continued their growth.

Development of yield could be related to thermal time from sowing to harvest. Especially at Kokemäki, thermal time (T_B of 0°C) produced regression models with a good fit (II, Figure 6). The results from Kokemäki suggest that cv. Panther is able to produce, on average, 63 kg ha^{-1} (95% confidence interval (CI): 56, 70) of its root yield per one day-degree above 0°C, and cv. Fontana a yield increase of 83 kg ha^{-1} (95% CI: 75, 91) per one day-degree above 0°C at the end of the growing season. Farm experiments with cv. Panther gave similar slope values for yield increase in response to thermal time unless the carrot stands were injured by frosts (II, Table III). Hence, it is suggested that the models describe the cultivar-specific response to temperature under conditions suitable for growth. The higher response to thermal time in cv. Fontana may be due to the larger foliage of the cultivar. Even though senescence of the foliage started simultaneously in both cultivars, the mean fresh weight of foliage remained much higher in cv. Fontana throughout the harvest season.

Since the low T_B values proved successful in describing the yield response to temperature, carrot is able to utilise very low temperatures at the end of the growing season, too. Low base temperatures have previously been applied to early growth of carrot: Brewster and Sutherland (1993) obtained a

base temperature of 1.0°C for the seedling growth of carrot. In the growth model of Benjamin and Aikman (1995), a base temperature of 1.3°C was used for carrot and white cabbage. This was determined as the base temperature for seed germination (Wagenvoort and Bierhuizen 1977), and Benjamin and Aikman (1995) assumed that it also applied to subsequent growth. All in all, the minimum temperature for growth and development in carrot appears to remain near 0°C throughout the vegetative cycle.

Thermal time also explained the yearly differences in the average yield level: high yields were produced in 1997, a warm season (II). Analysis of growth showed that, in that year, plants invested more in leaf production by growing a lower number of thicker and longer leaves (I). The stronger partitioning to shoot was also seen in the linear equations between shoot and root weights, where the intercepts were higher in 1997. This supports the suggestion that high temperature is more favourable for shoot growth than for storage root growth (Hole 1996). Leaf area was, however, not much higher in 1997, a finding in accordance with the data of Hole and Dearman (1993), who showed that, at low photosynthetic photon flux density, carrot maintains its leaf area and leaf fresh weight, but that the dry weight of leaves is diminished. This limits storage root growth less than in red beet or radish. The maintenance of leaf area is also seen in our results for 1996, a year with less irradiance and lower temperature, when leaf fresh and dry weights were also reduced.

The large variation in yield level between growing sites is a striking feature of the farm experiments (II, Figure 4). The variation cannot be explained by a single factor but may be related to difference in sowing times, drought sensitivity of the soil and other edaphic factors. Although the levels of macronutrients in soil at the time of the first harvest and fertilisation practices were quite variable, no clear shortage of nutrients was observed (data not shown). The uniformity in yield development during the harvest period despite the variation in average yield suggests that the yield potential of a given cultivar in a given field is determined during the early part of the growing season, e.g. by the productivity of the soil and the cultivation technique used. In the latter part of the season, environmental conditions control the rate of growth, largely irrespective of the yield already produced.

3.2 Effect of harvest time on storage performance

The timing of harvest influenced markedly the total storage loss of carrot cvs Fontana and Panther (III). The earliest harvests were unfavourable for storability of the yield, and delaying harvest decreased the storage loss. In farm experiments, the point of time after which there was no further improvement in storability was H2 (25–26 September) in cv. Fontana in 1995 and 1996. In cv. Panther, the improvement in storability continued up to H3 (7–8 October) in 1996 and up to H2 (23–24 September) in 1997. At the Vegetable Experimental Site in 1996, storage loss of both cultivars did not decrease further after H4 on 7 October. In 1997, storage loss was much lower than the year before and it showed a decreasing trend up to H5 on 21 October, after which there was a sharp increase in diseases and total loss.

Even the unusually late harvest at the end of October did not increase storage loss, despite frost injuries and rainy weather during the last harvest in 1996. Only the yield from the very late harvest at Kokemäki on 30 October 1997 suffered great losses. This deterioration in quality is easy to understand, as the carrots were lifted from frozen soil and the daily minimum temperatures had ranged between -1.0 and -12.6°C during the previous 10 days.

The results from different locations show that, under northern conditions, delaying the harvest improves storability up to the end of

September or beginning of October. After this point in time, storability remains at a constant level. Only a prolonged period of very cold weather injures the plants so severely that their storability is impaired.

Similar effects of harvest time have been found by Weichmann and Käppel (1977), who noticed that late harvesting decreased weight loss and respiration intensity during storage. Only carrots from the latest harvest at the end of October had a higher weight loss and respiration intensity. Later, Fritz and Weichmann (1979) studied a larger volume of data and found no clear relation between harvest time and storage loss in late maturing cultivars. The occurrence of storage diseases was low, and losses consisted mainly of weight loss, which first decreased and then increased at the latest harvest dates. In the data of Nilsson (1987b), the incidence of storage diseases fluctuated and no relation to harvest date was found.

In the present study, the effect of harvest time was mainly due to the lower occurrence of storage diseases in the later harvests and the average level of diseases was higher than in earlier studies. This may have helped reveal the importance of harvest time. The largest differences between harvest dates were observed in the yield in which disease infections were common. Nevertheless, despite the differences in the level of diseased carrots in farm experiments, losses almost invariably diminished with a later harvest (III, Figure 3).

The large between-farm variation in average storage loss (III, Figure 3) cannot be satisfactorily explained. High rates of *Mycocentrospora acerina* were related to the frequent cultivation of carrot on the experimental fields (Suojala and Tahvonen 1999). The variation in the incidence of *Botrytis cinerea* may be partly associated with the variation in the mean size of the root: a negative correlation ($r = -0.73$, $P = 0.042$) was found between mean root size and *B. cinerea* infection on farms with cv. Panther in 1996, when the fungus was the major pathogen. The nutrient content of storage roots at different growing sites did not reveal any clear relationships with storage losses (data not shown). To improve the control of storability, more effort should be put into determining storage potential during the growing season, since the present results demonstrate that it is possible to produce carrots with very high storage potential.

The infection rates of both of the major storage pathogens, *M. acerina* and *B. cinerea*, decreased with a later harvest. Mukula (1957) found that the amount of *Sclerotinia sclerotiorum* and *B. cinerea* decreased with a longer growing period, a finding supported by the present results. However, the findings on *M. acerina* are in direct contrast to the results of Davies and Lewis (1980) and Villeneuve et al. (1993), who reported a higher level of *M. acerina* in older carrots. In the study of Davies and Lewis (1980), the youngest roots (127 days at harvest) were the most consistently resistant. The contradiction might be partly explained by the age of the carrots. Here, the age of carrots at harvest varied between 104 and 170 days in the different experiments and harvests and thus the plants were, on average, younger than those studied earlier.

Weight loss did not show any consistent trends in relation to harvest time, but it increased during storage. The direct effect of transpiration on total storage loss is usually very low compared with that of storage diseases, provided that water loss does not lead to wilting. Indirectly, weight loss increases storage loss by intensifying the susceptibility to pathogens, such as *B. cinerea* (Goodliffe and Heale 1977), and it may also impair the outer and sensory quality. Storage conditions (e.g. temperature, relative humidity, air circulation, method of cooling) affect weight loss markedly. In 1997–1998, when a store equipped with a heat-exchanger system was used, weight loss was much lower than in the previous years, which may have contributed to the low total loss in that year. On the other hand, the high incidence of *B. cinerea* in the

1996 yield may have partly resulted from the rather high weight loss during storage.

The general improvement in storability during the autumn was not explained by weather conditions, since the changes in precipitation and air temperature were very different in each year, whereas the changes in storability were uniform. This is in contrast to the observations of Fritz and Weichmann (1979), who emphasised the significance of weather conditions for the post-harvest life of carrots. Villeneuve et al. (1993) postulated that high humidity and precipitation, which increase root turgor, might make carrots more susceptible to mechanical damage and so to infection by *M. acerina*. This effect was not found in our experiments where carrots were harvested under conditions of varying humidity. The significance of environmental factors for storability cannot, however, be excluded. The decline in temperature of the soil and carrot roots during the autumn hastens the cooling of carrots when transferred to storage and so may enhance storability. Environmental conditions in late autumn may also be less favourable for the survival and spreading of pathogens. On the other hand, a low temperature during mechanical harvesting may increase the risk of harvest damage and hence provide a penetration route for the fungi to the root. All the material in the present study was hand harvested, which probably resulted in a slightly lower storage loss than in normal mechanical harvesting.

The results for 1996 and for the last harvest in 1997 showed that carrot roots can withstand very low temperatures without impairment of their storage quality. Although temperatures were not measured on experimental fields or in the soil, recordings made nearby at ground level suggest that the temperature of the upper part of the root must have fallen to -5 to -10°C. In carrots from farms in 1996, frost injuries were even seen as transversal cracks in the upper parts of the roots. These cracks must have been caused by ice formation in extracellular spaces, since the injuries did not result in disruption of the root tissues. Tucker (1974a) studied the freezing injuries of carrot roots by exposing overwintered carrots to -2.5°C for 24 hours. After thawing, these roots rotted quickly. Zhang and Willison (1992) observed that, following freezing at a cooling rate of 4.8°C h^{-1}, carrot root samples survived temperatures of -3 and -6°C but were partly injured at -9°C. LT_{50}, the temperature at which half of the cells were killed, was as low as -12°C. The duration of the freezing stress and different stage of cold acclimation may explain the differences in the observed frost tolerance of carrot. Our observations from the field also demonstrate that quite a low temperature for one night is not detrimental to the storability of the root but that a prolonged period of repeated frosts, as observed between H5 and H6 at Kokemäki in 1997, does impair the storability. A long period of frost probably leads to some intracellular freezing and cell death, which provides the route for the pathogens to the root.

Comparison of storage results for the different years is hindered by the use of different stores. The storage temperature was near optimum each year, but the variation in relative humidity may have affected the results. The polypropylene bags used in storage mitigated the effect of air humidity, but still the level of weight loss varied between years and stores. Nevertheless, preharvest conditions have an effect on overall storability and on the incidence of various pathogens. Preharvest water stress is reported to increase postharvest weight loss (Shibairo et al. 1998a), which in turn increases the susceptibility to *B. cinerea* (Goodliffe and Heale 1977). Hence the low precipitation at the end of the 1996 season may partly account for the high occurrence of *B. cinerea*.

On the other hand, it has been suggested that high humidity and precipitation might make carrots more susceptible to infection by *M. acerina* (Villeneuve et al. 1993). Similarly, the infection of leaves by *S. sclerotiorum*, which did not cause substantial losses in the present study, is enhanced by

high humidity in the canopy (Finlayson et al. 1989a, Snowdon 1992). However, changes in experimental fields and stores between years do not allow in-depth analysis of the causes for year-to year variation in average loss; more important, the harvest time effect was constant, irrespective of growing site, year and storage conditions.

The uniform results on the improvement in storability towards the late autumn prompted interest in the mechanisms of a reduced level of infections, especially by *M. acerina*. Davies and Lewis (1980) suggested that root age influenced infections by *M. acerina* by affecting the susceptibility to damage or wound healing potential. McGarry (1995) showed that the tissue toughness of carrot storage roots increases towards the end of crop growth, making roots less susceptible to mechanical damage and hence to storage pathogens. The contribution of mechanical damage and wound healing to the decrease in the incidence of infections was studied in 1998–1999 (IV).

The most important finding was that artificial inoculation with *M. acerina* resulted in fewer infections in later harvests, implying that the resistance of storage roots improved in the field (IV). The mechanism of the improved resistance was not the lower susceptibility to damage, since mechanical treatment alone did not affect the disease rate. This may have been caused by the low level of natural infection. Moreover, the method of causing mechanical damage by shaking may not have been effective enough. Neither could the better resistance to *M. acerina* in later harvested carrots be attributed to the better wound healing potential, since the relative effect of healing was greatest in early harvested carrots, that is, in those with the highest level of infections. Healing at 10°C was effective in reducing the rate of infection by *M. acerina* in inoculated carrots, although the effect was not clearly seen at the first date of analysis.

Combined with earlier research (Davies et al. 1981, Garrod et al. 1982), the results led to the hypothesis that the concentration of antifungal substances increases towards the end of the growing season, which makes the carrots more resistant to *M. acerina* and possibly to other storage diseases, too. The early harvested carrots would thus have a lower level of antifungal substances, and the healing period would raise their concentration, bringing it close to the level of later harvested carrots, in which better resistance cannot be achieved. There seems to be a common limit for resistance, probably irrespective of the type of tissue: Lewis et al. (1981) reported that healing tended to bring infections down to a similar level in all tissues despite the initial gradient in susceptibility. This hypothesis concerning the contribution of antifungal compounds needs to be assessed in future studies.

Our results suggest that infections due to *M. acerina* can be minimised by late harvesting, possibly combined with a prestorage healing treatment. Healing is especially beneficial for early harvested yield, which has poor resistance to storage fungi. Preharvest healing at 5 or 10°C, as recommended in the Netherlands for carrots harvested under wet conditions (Schoneveld and Versluis 1996), may, however, increase the risk of other diseases such as those caused by *S. sclerotiorum*, which benefit from a higher temperature. In practice, temperature control during transport and the early phase of storage is dependent on many factors, such as air and soil temperature, mass of harvested yield per day, method of storage and cooling capacity. Therefore, temperature does not usually drop to the recommended level very fast, which may promote healing of the wounds but, on the other hand, may enhance the spread of *S. sclerotiorum*. Methods for forecasting the quantity and species of storage diseases in the harvested yield, which have been tested by Hoftun (1985) and Hermansen and Amundsen (1995), would aid in optimising the handling of products.

As quite a short period of wound healing has proved useful in curbing *M. acerina*, an

optimal procedure for improving the resistance of carrot to storage fungi could be developed, possibly by combining temperature control with other methods of inducing resistance. The possible adverse effects of chemical resistance agents on sensory quality should be kept in mind, as it is known that some of them, especially 6-methoxymellein (Sarkar and Phan 1979, Lafuente et al. 1989, 1996) and possibly polyacetylenes (Lund 1992), may import off-flavours to carrot. Proper crop rotation remains the foundation of the prevention of severe storage diseases.

3.3 Changes in soluble sugar content and composition during harvest period and storage

Changes in sugar content and composition during the harvest period were dependent on the year and location (V). On farms in 1995 and 1997 and at the Vegetable Experimental Site in 1996 and 1997, the trend in sugar composition followed the general patterns reported in earlier studies (Goris 1969a, Phan and Hsu 1973, Ricardo and Sovia 1974, Nilsson 1987a), with an increase in the sucrose content and sucrose to hexose ratio. Fructose and glucose concentrations changed little during the harvest period, and any trends found were towards lower values. In farm experiments, the statistically significant accumulation of sucrose continued up to H2 in 1995 and up to H3 in 1997. At Kokemäki, sucrose concentrations increased statistically significantly up to H4 in 1996 and up to H5 in 1997.

In 1996, however, when severe frosts injured the plants on farms on 21 September, the accumulated storage carbohydrates were probably used in the production of new leaves a few weeks later. Sucrose and total sugar contents declined dramatically in both cultivars after H2. Changes in the fructose and glucose concentrations were small. By destroying part of the foliage, frost caused the storage root to become a “source” of assimilates. A similar effect has been noted in defoliated tap roots in which sucrose stored in vacuoles is used in the formation of new leaves (Sturm et al. 1995). Frost-injured carrots from H6 at Kokemäki in 1997 did not start new growth and showed no decline in sugar content.

The range of total sugar content in different harvests and years, 4.5–7.5% of fresh weight, was similar to the values obtained in earlier studies conducted at northern latitudes (Balvoll et al. 1976, Evers 1989a, Hogstad et al. 1997) and at more southerly locations (Lester et al. 1982, Le Dily et al. 1993). However, higher total sugar contents and sucrose to hexose ratios have been measured at high temperatures in a controlled climate (Rosenfeld 1998b,c) and under field conditions, especially after a long growing period (Weichmann and Käppel 1977, Fritz and Weichmann 1979, Le Dily et al. 1993). In the light of of the present results and other studies conducted in northern Europe (Balvoll et al. 1976, Evers 1989a, Hogstad et al. 1997), it seems likely that the relatively short and cool growing season reduces the accumulation of sucrose under northern conditions.

Of interest is that in farm experiments, the total sugar content and the sucrose to hexose ratio were, on average, lower in the warm growing seasons, 1995 and 1997, than in the cooler year, 1996, when comparing the results for the first harvest. A high sugar content has previously been associated with lower temperatures (Evers 1989a, Rosenfeld et al. 1998a). Other studies, however, report high sugar concentrations at higher temperatures (Nilsson 1987b, Hogstad et al. 1997, Rosenfeld et al. 1998b), and temperature was found to have a stronger influence on chemical composition than light (Rosenfeld et al. 1998c). These results seem to be in direct contrast to the findings of this study, at least in terms of temperature. Note, however, that August 1996 was quite warm and dry, although most of the growing season in that year was cool. The high sugar content in early harvests in 1996 may be partly ex-

plained by the low precipitation in August and September, as drought has been reported to increase the sucrose content of carrot (Barnes 1936, Dragland 1978).

As well as between years, the sugar content varied between farms. Differences in the total sugar content at H1 could be more than 2% units. The variation between farms was not related to the thermal time from sowing to harvest. The large variation in total sugar content and composition may be due to many environmental factors, such as microclimate, soil type (Habben 1972), susceptibility of the soil to drought and differences in fertilisation and other cultivation practices (Hogstad et al. 1997).

Differences between cultivars were less distinct than differences between growing sites and years. At the Vegetable Experimental Site, cv. Fontana, which is regarded as a late cultivar in Finland, had a lower sucrose to hexose ratio than had cv. Panther, the earlier cultivar. Moreover, the changes during harvest period were slightly different in the two cultivars. In the farm experiments, however, the sugar composition varied more between 1995 and 1996 in cv. Fontana than between the two cultivars in 1996.

During storage, the compositional changes usually followed the common trend, with an increasing hexose content and a decreasing sucrose content (Phan et al. 1973, Nilsson 1987b, Oldén and Nilsson 1992, Le Dily et al. 1993). In the 1995 yield, however, the sucrose content increased once again at the end of storage. Likewise in 1996, completely opposite results were obtained for the carrots from the last two harvests in farm experiments. In cv. Panther in particular, the fructose and glucose concentrations decreased and sucrose concentrations increased during storage.

The unusual trends observed in the late harvests in 1996 are probably due to preharvest frosts which reduced the sucrose content at harvest. The total sugar content of the injured carrots changed very little during storage, and hence most of the sucrose accumulation during storage was due to the recombination of hexoses to sucrose. Accumulation of sucrose might be related to the ageing of carrot roots, which was promoted by the frost injuries. Rutherford (1981) mentions that some recombination of reducing sugars to sucrose occurred after prolonged periods of storage, which was also observed in the 1995 yield at the end of storage. Similarly, Svanberg et al. (1997) noticed that in early cultivars, which were more mature at the time of harvest, sucrose increased in relation to hexoses during storage.

The significance of the post-harvest changes in sugar composition remains unknown. Nilsson (1987b) suggested that the accumulation of hexoses during storage was related to vernalisation and that removal of foliage and lateral roots at harvest might stimulate the onset of hexose accumulation. This assumption was not supported by our results, in which the hexose accumulation occurred after different times in storage, if at all. Compositional changes might indicate the storage quality by affecting the behaviour of carrots after they have been taken from storage, an issue that has not been extensively studied. Changes during storage do not appear to contribute to the storage potential, since the total amount of sugars, that is the source of energy for maintaining the metabolism of the plant, does not decrease much during cold storage and storage losses usually increase linearly with time (III).

Despite the large variation in sugar composition observed in the experimental data, changes during the harvest period do not provide evidence for the existence of either physiological or horticultural maturity, as already noted by Rosenfeld (1998). As the roots were still growing, when the contents of total sugar and sucrose decreased in 1996, the results do not show a clear relation between root growth and sucrose accumulation. Even under “normal” growing conditions, neither the changes in the sucrose or total sugar content nor those in the sucrose to hexose ratio coincided with the cessation of

growth (V, Table 3). Similarly, compositional changes do not seem to be related to storability, as each year the later was the harvest the better was the storability, with the exception of the very late harvest, H6, at Kokemäki in 1997 (III). Therefore, the compositional changes cannot be used to predict the storage root growth or storage perfomance of the yield.

3.4 Changes in sensory quality during harvest period and storage

The sensory quality of carrot was slightly affected when harvest was delayed (VI). At Kokemäki, the effect of harvest time was statistically significant in all sensory attributes in 1996 and in sweetness in 1997 which received higher scores for intensity in the later harvests. Similarly, the preference attribute overall flavour achieved higher scores in later harvests. No differences were found in the sensory quality of the two cultivars, and the harvest time effect was not dependent on cultivar in either of the years. On farms, the effect of harvest time was not so clear: in 1996, changes in sensory quality were statistically significant only on one of the three farms, where juiciness was higher in the later harvests. On the same farm in 1997, scores for all attributes except bitterness increased after H1 and H2. On the other farm, no clear effects of harvest time were found in that year either.

The attributes most affected were juiciness, crispness and sweetness. Harvest time influenced bitterness only at Kokemäki in 1996. The scores for the preference attribute overall flavour increased with increasing juiciness, crispness and sweetness and with decreasing bitterness. Therefore, the carrots from the later harvests seemed to have a higher sensory quality.

The changes in sensory quality continued up to different time points in 1996 and 1997. The risk of obtaining low sensory scores was particularly marked when the harvest was too early, as were H1 and H2 at Kokemäki and H1 on farm 2. On the two other farms, no clear effect of harvest time was found. The dependence of the harvest time effect on location may be partly related to the age of the carrots, since the growing time from sowing to harvest was shorter on farm 2 and at Kokemäki than on the other farms. Therefore, the more advanced developmental stage of carrots from farms 1 and 3 in 1996 and from farm 3 in 1997 might explain the similarity in the sensory quality of carrots harvested on different dates.

Of interest is that the sensory scores given for carrots from the latest harvests were at least as high as those given for earlier harvested carrots. Thus even the severe frosts that caused visible frost injuries to carrots on farms in September 1996 and at Kokemäki in late October 1997 (II) did not affect the quality. Neither did the notable decline in total sugar content, which was on average 5.9% of fresh weight in H1, 6.2% in H2 and 4.8% in H3 and H4 in the yield used for sensory analyses in 1996 (V, Fig. 4), interfere with the sensory quality. Other factors must have exceeded the contribution of sugar content to carrot flavour. This finding is in contrast to many earlier studies reporting a positive correlation between sensory quality and sugar content (Balvoll et al. 1976, Simon et al. 1982, Schaller et al. 1998). However, Rosenfeld et al. (1997b, 1998a) showed that sugar content did not predict sweet taste. The sweetest carrots, which were grown at low temperatures, contained the highest amounts of glucose and fructose and a lower amount of sucrose and total sugars (Rosenfeld et al. 1998a).

Changes in the sensory quality of marketable carrots during storage were relatively small and therefore the sensory quality remained high. Only the attributes related to texture showed some decline: at Kokemäki, scores given for crispness decreased during storage in 1996 and those for juiciness in 1997. On farm 2 in 1996, crispness decreased during storage. Other effects of storage time

were not statistically significant at the 5% level. The effect of storage is, however, difficult to determine, as the evaluations were performed at intervals of a few months and the panelists' usage of the evaluation scale may have changed with time. The harvest time effect did not usually depend on the time of evaluation. On farm 2 in 1997, the differences between harvest times were found only after storage, not in autumn. In some cases, the ranking of harvest times changed during storage (bitterness on farm 1 in 1996 and juiciness on farm 3 in 1997). On the whole, the differences found shortly after harvest still existed at the end of storage.

The improvement in sensory quality with a later harvest may be related to low temperatures at the end of the growing season, since Rosenfeld et al. (1998a) observed that a low growing temperature favoured positive sensory attributes in carrots, whereas high growing temperatures resulted in a bitter taste and high firmness of roots grown in phytotrons. The variation in sensory quality between geographical locations was tentatively attributed to growing temperature (Rosenfeld et al. 1997a,b). At the end of the growing season, day length and the daily light integral decrease together with temperature, but Rosenfeld et al. (1998b) found that temperature was more important than light in explaining the variation in sensory variables in carrots grown in climate chambers.

The two cultivars used at Kokemäki were not found to differ in sensory aspects. This is a somewhat surprising finding, since the cultivars are used for different purposes, cv. Fontana for processing and cv. Panther mainly for fresh consumption. However, Martens et al. (1985) and Rosenfeld et al. (1997a,b) showed that the variation in sensory quality was largely related to the growing season and growing site, only a smaller part being explained by the cultivar. Therefore, if we assume that the effect of harvest time, like that of growing site, arises from the lowering temperature, we should expect the effect of harvest time to exceed that of cultivar. Since only two cultivars were used in the study and since both were cultivated in the same experiment only at Kokemäki, firm conclusions cannot be drawn about the factors determining sensory quality.

3.5 Optimisation of harvest time

Data on the development of marketable yield and the average storage losses at different harvest dates show that a later harvest tends to produce a higher marketable yield and a lower storage loss. This results in a higher quantity of marketable yield per cultivated area after storage and reduces the average cost of storage per marketed kg of carrots. Timing the harvest to the very end of the season, which turned out also to be favourable for yield quality and its maintenance, is therefore recommended. Too early a harvest was particularly unfavourable for the quality aspects evaluated, that is sugar content and composition and sensory quality. A statistically significant yield increase or improvement in storability usually continued up to late September or early October.

In terms of total yield, quality and storage performance, harvesting in early October is therefore more advantageous than an earlier harvest in the cultivars used in the study. Delaying harvest until after mid October increases the risk of frost injuries, which may interfere with mechanical harvesting, even though yield storability and quality may not suffer. Moreover, in large areas, harvesting has to be started early enough to be sure that the entire yield is harvested before winter. Root size requirements may also necessitate an earlier harvest. However, the yield intended for the longest storage should be harvested late to minimise storage losses. Observations on some other cultivars let us assume that the present findings are likely to be valid for other cultivars used for storage, too. This optimal time of harvest applies to southern Finland, where most of the carrot cultivation is located.

4 Conclusions

The yield potential of carrot is determined during early stages of growth. A large leaf area and high shoot weight developing early enough are the basic factors determining the potential for high root yield, especially in a northern climate where a slow growth rate cannot be compensated for by a longer growing period. Maintenance of high shoot weight permits the better utilisation of diminishing growth factors at the end of the growing season, when decreasing temperature and irradiation control the cessation of growth, irrespective of plant size and yield level.

In the present data, 10–36%, on average, of the total yield at the final harvest was produced after early September, when the weather conditions were already less favourable for growth. The statistically significant increase in yield generally ceased in early October. Thus carrot still has substantial potential for yield production late in the growing season as long as plants remain healthy and uninjured. The yield increase during the harvest period can be estimated on the basis of thermal time.

Delaying the harvest improves storability up to the end of September or beginning of October under northern conditions, whether the risk for storage diseases is high or not. After this point in time, storability remains at the same level. Only a prolonged period of frost injures the plants so severely that their storability is impaired. The effect of harvest time was similar irrespective of cultivar, growing site, year and storage conditions. Weather conditions did not account for the improved storability. The better resistance to *Mycocentrospora acerina* could be attributed neither to the lower susceptibility to damage nor to the better potential for wound healing. It is hypothesised that the concentration of antifungal substances increases at the end of the growing season, which improve the resistance of storage roots to storage pathogens. Healing at 10°C was effective in mitigating infections by *M. acerina*, which may also be due to the accumulation of antifungal substances.

Changes in sugar content and composition were dependent on the year and growing site; they do not provide evidence for the existence of physiological or horticultural maturity. Neither do changes during storage seem to be related to storage potential. A new finding, not earlier reported in carrot, was the notable drop in the sucrose and total sugar content following frost injuries. Unexpectedly, this did not have an adverse effect on the storability or sensory quality of carrots.

Sensory quality improved slightly when harvest was delayed. It is concluded that avoiding too early a harvest ensures the best sensory quality of carrot. The two cultivars analysed were not found to differ in sensory aspects, and the changes during storage were relatively small. Therefore, high sensory quality could be maintained up to the end of storage.

Combining the results on the trends in yield level, quality and storability, it is concluded that the optimal harvest time for the carrot cultivated in southern Finland is early October, after which no major yield increase or improvement in quality or storability is reached. A later harvest increases the risk of frost injuries, which may interfere with mechanical harvesting and, after long duration, may be detrimental to storability and quality. However, over large areas, harvesting has to be started early enough to be sure that the entire yield is harvested before winter, but carrots intended for the longest storage should be harvested late to minimise storage losses. The results are likely to be valid for other cultivars used for storage, too.

The objective of this study was to achieve a better control of the quality and quantity of carrot after storage. It was shown that the timing of harvest is an essential factor affecting the yield, quality and storability of carrot yield, both at an experimental site and on commercial farms. Conducting a substantial part of the research on farms proved

successful in that a large volume of experimental data was obtained from a variety of experimental conditions and in verifying the applicability of the results. The large variation between growing sites in the average storage quality of carrots stresses the need for further studies on the determination of storage potential during the growing season and for the development of methods to forecast storability and improve the resistance to storage diseases.

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Selostus

Porkkanasadon määrän ja laadun muuttuminen kasvukaudella ja varastoinnin aikana

Kotimaisten vihannesten ympärivuotinen tarjonta edellyttää varastointia. Vihannesten laatu varastoinnin jälkeen määräytyy suurelta osin jo kasvukauden aikana, ja varasto-oloilla voidaan vain pyrkiä säilyttämään laatu mahdollisimman pitkään. Kasvukauden aikaiset tekijät ratkaisevat myös sadon määrän. Varastoinnin aikaiseen määrälliseen hävikkiin vaikuttavat sekä kasvukauden että varastoinnin aikaiset tekijät.

Tämän tutkimuksen tavoitteena oli parantaa porkkanan varastoinnin jälkeistä laatua ja pienentää varastohävikkiä. Tutkimuskohteena oli erityisesti sadonkorjuun ajoittumisen vaikutus sadon määrään, varastokestävyyteen ja aistittavaan laatuun, tavoitteena korjuuajan optimointi. Lisäksi tutkittiin kasvin kehitystä kasvukaudella ja kasvumuuttujien yhteyttä sadontuottoon. Porkkanan varastojuuren sokerikoostumusta tutkittiin mahdollisena kehitysvaiheen kuvaajana. Kenttäkokeet tehtiin MTT:n vihanneskoepaikalla Kokemäellä ja vihannestiloilla vuosina 1995–1998. Kokeissa käytettiin lajikkeita ‘Fontana’ ja ‘Panther’, ja satoa korjattiin 3–6 kertaa syys–lokakuussa

Sadon määrä kasvoi yleensä lokakuun alkupuolelle asti huolimatta keskisadon suuresta vaihtelusta koepaikkojen välillä. Keskimäärin 10–36 % viimeiseen korjuukertaan mennessä tuotetusta sadosta syntyi syyskuun alun jälkeen, jolloin sääolot olivat jo vähemmän otolliset kasvulle. Tämä osoittaa, että porkkanalla on huomattava sadontuottokyky vielä kasvukauden lopulla. Sadonlisäys korjuukaudella voidaan arvioida lämpösumman perusteella.

Sadonkorjuun siirtäminen syyskuun loppuun tai lokakuun alkuun paransi varastokestävuuttä. Tätä myöhäisempikään korjuu ei heikentänyt säilyvyyttä. Vasta pitkään jatkunut pakkasjakso vaurioitti porkkanoita niin, että niiden säilyvyys heikkeni. Sadonkorjuuajan vaikutus oli samanlainen lajikkeesta, kasvupaikasta, vuodesta ja varasto-oloista riippumatta. Sääolot eivät selittäneet säilyvyyden muutoksia. Varastotautien kestävyyden lisääntymisen arvellaan johtuvan antifungaalisten aineiden kertymisestä porkkanan juureen. Sadonkorjuuta seurannut viikon mittainen esijäähdytys 10 °C:n lämpötilassa vähensi porkkananmustamädän aiheuttamia varastotappioita verrattuna suoraan kylmävarastointiin.

Varastojuuren sokeripitoisuuden ja -koostumuksen muutokset sadonkorjuukaudella vaihtelivat vuosien ja kasvupaikkojen välillä, joten ne eivät näytä soveltuvan kehitysvaiheen kuvaajaksi. Myöskään varastoinnin aikaiset muutokset sokereiden määrissä tai suhteissa eivät näytä liittyvän varastokestävyyteen. Porkkanoiden aistittava laatu parani hieman, kun sadonkorjuuta siirrettiin myöhempään. Kahden tutkitun lajikkeen välillä ei havaittu eroja aistittavassa laadussa. Aistittava laatu ei myöskään muuttunut selvästi varastoinnin aikana.

Tulosten mukaan sadonkorjuun ajoittuminen vaikuttaa oleellisesti porkkanasadon määrään, laatuun ja varastokestävyyteen. Tutkittujen lajikkeiden optimaalinen korjuuaika Etelä-Suomessa on lokakuun alkupuoli, jonka jälkeen ei ole odotettavissa merkittävää sadonlisäystä tai varastokestävyyden ja aistittavan laadun paranemista. Myöhäinen korjuu lisää pakkasvaurioiden riskiä. Suurilla viljelyaloilla sadonkorjuu on aloitettava ajoissa ennen talven tuloa, mutta pitkään varastoitavat erät olisi syytä korjata myöhään varastotappioiden minimoimiseksi. Korjuuajan vaikutus lienee samanlainen myös muilla varastointiin soveltuvilla lajikkeilla.

Avainsanat: aistittava laatu, *Daucus carota* L., kasvu, kehitys, sadonkorjuuaika, sokerit, varastointi, varastokestävyys