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Osmotic and elastic adjustment, and product quality in cold-stored carrot roots (*Daucus carota* L.)

Osmotische und elastische Anpassung und Produktqualität von kalt gelagerten Möhren (*Daucus carota* L.)

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Summary

Pressure-volume-analysis was used to investigate the variations in water relations of carrot, harvested either 130 d (refered to as 'young') or 190 d ('old') after drilling, at intervals during cool (5 °C) and humid (>98 % RF) storage. The aim was to characterise changes in root water status which denotes an important determinant of internal product quality. Water potential was measured with a scholander-type pressure bomb. Relative water deficit (RWD) of stored roots remained low (≈2 %) and their pressure potential high (Ψ_P>0.9 MPa) during an initial 40 d period. Both parameters then rapidly changed to new levels (RWD ≈4 %; Ψ_P ≈0.5 MPa), and remained more or less constant for additional *c.* 100 d. Water potential and osmotic potential transiently decreased during early storage. Because maximum water content at water saturation remained constant throughout the study, the changes were due to active osmotic adjustment, i.e. a net accumulation of osmotically active solutes, manifested by the temporary reduction of the osmotic potential at water saturation ($^{S}\Psi_{\pi}$) and at turgor loss point ($^{TLP}\Psi_{\pi}$). This was accompanied by a reversible decrease in tissue elasticity during the initial phase of storage. All these changes were more pronounced in older carrots. The relatively small changes in water deficit and turgor may indicate that carrot internal quality did not decline or even was improved during initial storage. However, with prolonged storage the content of osmotically active substances decreased, and tissue elasticity increased. Thus, the quality of carrots declined without serious water losses.

Zusammenfassung

Die Änderung des Gesamtwasserzustandes unterschiedlich alt (130 d (young) bzw. 190 d (old) nach der Aussaat) geernteter Möhren wurde während der Lagerung (T = 5 °C, RH >98 %) mittels Druck-Volumens-Analyse verfolgt, um dessen Einfluss auf die interne Produktqualität näher zu charakterisieren. Das Wasserpotential wurde dabei mit einer Druck-Bombe nach Scholander gemessen. Während der ersten 40 Tage der Lagerung blieb das relative Wasserdefizit (RWD) der Möhren gering (≈2 %) und ihr Druckpotential hoch (Ψ_P>0.9 MPa). Beide Größen änderten sich danach relativ rasch auf ein neues, für den weiteren Untersuchungsverlauf (ca. 100 d) nahezu konstantes Niveau (RWD ≈ 4 %; Ψ_P ≈ 0.5 MPa). Am Anfang der Lagerung nahmen sowohl das Wasserpotential als auch das osmotische Potential vorübergehend ab. Da der Sättigungswassergehalt während der gesamten Untersuchung konstant blieb, war dies auf eine Nettoakkumulation von osmotisch wirksamen Substanzen zurückzuführen. Dies lässt sich aus der reversiblen Abnahme des osmotischen Potentials bei Wassersättigung ($^{S}\Psi_{\pi}$) und am Turgorverlustpunkt ($^{TLP}\Psi_{\pi}$) erkennen. In dieser Periode nahm auch vorübergehend die Rigitität der Möhren zu. Alle Veränderungen zeigten eine deutliche Altersabhängigkeit und waren in den älteren Möhren wesentlich stärker ausgeprägt. Die relativ geringen Änderungen von RWD und Ψ_P zeigen, dass die Lager- und wohl auch die Gesamtproduktqualität der Möhren während der ersten 4 Wochen nicht ab, sondern eher zu nimmt. Allerdings nimmt mit zunehmender Lagerdauer sowohl der Gehalt an osmotisch wirksamen Substanzen und die Gewebesteifheit ab. Damit verringert sich die interne Qualität der Möhren, ohne dass sie ernsthaft Wasser verlieren.

Introduction

Stored at low temperature and very high air humidity (APELAND and BAUGERØD 1971), the shelf life of carrots can be prolonged for many weeks (PHAN et al. 1973, FRITZ and WEICHMANN 1979, NILSSON 1987). Nevertheless, even under optimal storage conditions, changes in the chemical composition (LIST and ASKAR 1977, NILSSON 1987) and in the water content of carrots have been reported (NILSSON 1987). Tissue water status is an important determinant of the internal and the external quality of perishable horticultural products (SCHREINER et al. 1996). Hence, any reduction of the water status of a product may negatively influence its quality.

Tissue water status can be described in terms of water content or water potential (von WILLERT et al. 1995). Relative water losses, based on an initial fresh mass, are often used to determine changes in water content during storage (PHAN et al. 1973, SHIBAIRO et al. 1997). Water potential has been shown to sensitively reflect the influence of mechanical and climatic stresses during postharvest (HERPPICH et al. 1999). In addition, water potential is highly correlated with mechanical properties of carrot tissue (GOLACKI 1993, MCCARRY 1993).

Tissue water potential is determined by both osmotic and pressure relations. The interactive effects of the content of osmotically active substances, the actual water volume, and the cell wall elastic properties, and their respective changes may influence water potential in plants (TURNER and JONES 1980). When water is gradually lost during storage, maintenance of a positive pressure potential may be essential to guarantee physiological activity. This turgor adjustment may result from osmotic changes either by passively concentrating the cell sap due to water losses or by actively increasing the osmotic content (TURNER and JONES 1980). This reaction is linked to the chemical composition of the tissue (HERPPICH and PECKMANN 1998) and may thus influence the overall taste of the product.

It has also been shown that during desiccation either maximum tissue water volume may decrease (LEVITT 1986) or cell wall elasticity may either increase or decrease, depending on the drought adaptation strategy applied (SCHULTE 1992). The latter changes are closely related to the physical properties of the tissue. Both variations in pressure potential and in cell wall elasticity may thus affect tissue thoughness and crispness.

In contrast to the chemical composition of carrots, to our knowledge, there is no information available about changes in product water relations during long-term cold storage. A comprehensive investigation of all relevant water relations parameters provides deeper insight into metabolic responses to cold storage conditions which may reflect the natural winter situation of storage roots. Variations in water relations can be used to determine changes of product quality of carrots. Pressure-volume (PV) analysis with a scholander-type pressure bomb (cf. VON WILLERT et al. 1995) was used to characterise changes in root water status. This method allows the determination of osmotic potential at water saturation, and, thus maximum pressure potential, the water potential at the wilting point, as well as the bulk modulus of elasticity in a single procedure. The study was performed with carrot roots that had been harvested at different times after drilling because it has been shown that the ability to respond to storage condition may depend on the age of the tissue (NILSSON 1987).

Material and methods

Plant material and storage conditions: Carrots (F1-hybrids of the cultivar 'Nanthya') used for the experiments were grown on a commercial farm near Potsdam without additional irrigation. Carrots were carefully harvested by hand approximately 130 days (further referred to as 'young carrots') and 190 (further referred to as 'old carrots') after drilling, with the leaves cut off immediately in the field. Without previously washing, the roots were randomly placed in 6 plastic containers (40 x 60 x 40 cm ; approximately 25 kg roots per container), covered with plastic bags, and stored at 5 °C in a cooling chamber for up to 4 months. Air humidity during storage was always close to saturation within the bags.

Methods: At irregular intervals 18 roots (3 per container) were taken out of storage and washed gently. The water potential of all carrots was determined with a pressure bomb (Plant Water Status Console 3000, Soilmoisture Inc., Santa Barbara, CA, USA). For measurements a small part of the primary root tip was detached. The otherwise intact carrot was enclosed in the pressure vessel, with only *c.* 2 cm of the cut end protruded from the specimen holder through a silicone rubber seal. Pressure inside the vessel was slowly increased untill a drop of water emerged from the water conducting xylem tissue. The balance pressure obtained, closely reflects the average root water potential. As shown previously, this method of water potential measurement is sound and did not stress the roots (HERPPICH and MEMPEL 1999a).

For PV-analysis 6 randomly selected carrots were hydrated at room temperature (*c.* 18 °C) in a water vapour saturated atmosphere, wrapped in paper tissue which was moistened with deionisised water, within a closed box for about 12 h. Pressure-volume curves were obtained on intact carrots using the "laboratory bench method" (cf. VON WILLERT et al. 1995). During controlled dehydration by free transpiration, changes in fresh mass (FM; electronic balance, BP 210 S, Satorius AG, Göttigen, Germany) and water potential were concomitantly assessed at intervals. When water potential fell below approximately –2.2 MPa the experiment was stopped and root dry mass (DM) was obtained by oven drying (48 h at 85 °C).

As outlined by HERPPICH and VON WILLERT (1995) saturation mass (SM) of roots was estimated by extrapolating experimental data to $\Psi = 0$ using an exponential model ($1/FM = A * e^{B*\Psi}$; A = y-axis intersect, B = slope). Relative water deficit (RWD) was calculated as 1- (FM-DM)/(SM-DM). PV curves were constructed by plotting the inverse water potential against RWD. They were analysed by combining the exponential fit and the standard linear approach, given by van't Hoff's law (cf. VON WILLERT et al. 1995).

The parameters derived were the osmotic potential at water saturation of the tissue ($^{S}\Psi_{\pi}$) and the osmotic potential ($^{TLP}\Psi_{\pi}$) at turgor loss point. The volumetric modulus of elasticity (ε) was calculated from changes in pressure potential ($\Delta\Psi_p$) and in fresh mass (ΔFM) during two subsequent measurements multiplied by the initial FM ($\varepsilon = \Delta\Psi_p / \Delta FM * FM_{initial}$). Furthermore, PV-curves were used to transform actual root water potential into its pressure and osmotic components (HERPPICH et al. 1994). Data were analysed by means of ANOVA and Tukey's test using the SAS package.

Results

Water deficits (Figs 1A, B) of stored carrot roots did not change during the first month of storage. This may indicate that transpirational water loss was negligible at the very high air humidity used. On the other hand, the water potential (Figs 1C, D) and the osmotic potential (Figs 1C, D) tended to decline during this time, most evidently in older roots (Fig. 1C, open symbols, significant at $p = 0.05$). As a result, pressure potential slightly (but not significantly) increased during this initial phase of storage. After approximately 40 d, however, it rapidly and substantially ($p = 0.05$) decreased (Figs 1C, D) when relative water deficit transiently increased in both experiments (Figs 1A, B). After about 3 months of storage, pressure potentials and water potentials

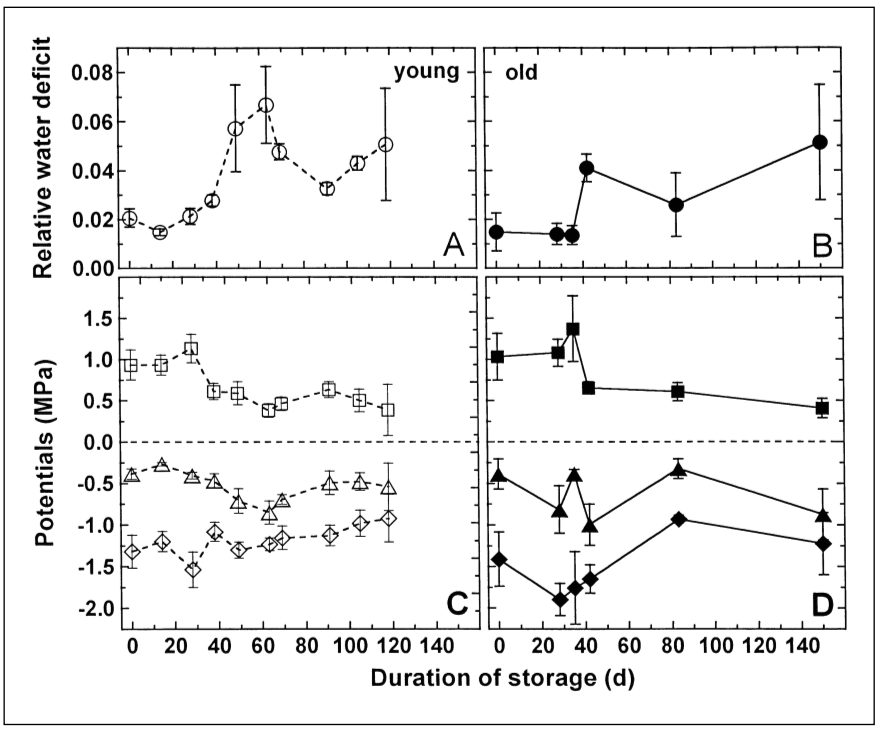


Fig. 1. (A, B) Relative water deficit, (C, D) actual pressure potential (squares), water potential (triangles) and osmotic potential (diamonds) of young (A, C) and old (B, D) carrots during storage. Given are means ± SD (n≥4).
(A, B) Relatives Wasserdefizit, (C, D) aktuelles Druckpotential (Vierecke), Wasserpotential (Dreiecke) und osmotisches Potential (Rauten) von jungen (A, C) bzw. alten (B, D) Möhren im Verlauf der Lagerung (Mittelwerte ± Standardabweichung; n≥4).

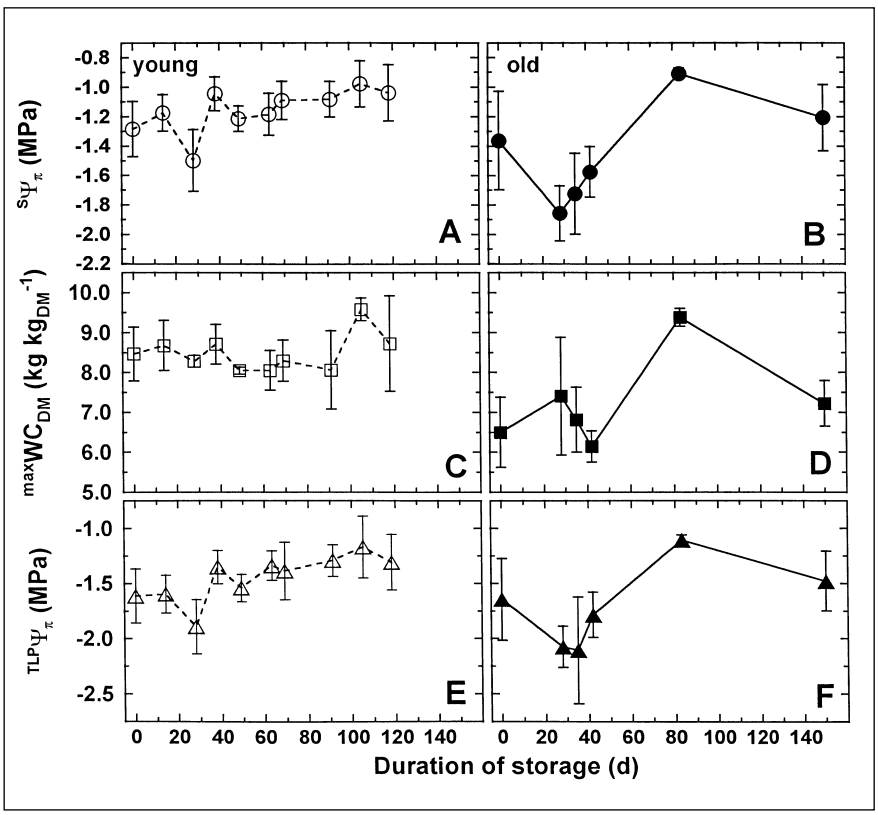


Fig. 2. (A, B) Osmotic potential at water saturation ($^{S}\Psi_{\pi}$), (C, D) root water content at water saturation ($^{max}WC_{DM}$) and (E, F) osmotic potential at wilting point ($^{TLP}\Psi_{\pi}$) of young (A, C, E) and old (B, D, F) carrots during storage. Given are means ± SD (n≥4).
(A, B) Osmotisches Potential bei Wassersättigung ($^{S}\Psi_{\pi}$), (C, D) Wassergehalt bei Wassersättigung ($^{max}WC_{DM}$) und (E, F) osmotisches Potential am Turgorverlustpunkt ($^{TLP}\Psi_{\pi}$) von jung (A, C, E) bzw. alt eingelagerten (B, D, F) Möhren (Mittelwerte ± Standardabweichung; n≥4).

slowly declined with increasing water deficits. During this period osmotic potentials increased to (Fig. 1 D) or above (Fig. 1 C) pre-storage values in old and young roots ($p = 0.05$).

The osmotic potential at tissue water saturation ($^{S}\Psi_{\pi}$) reflected the actual Ψ_{π}. It declined during early storage (Figs 2A, B), reaching a temporary minimum at about 1 month. Thereafter, it gradually increased again to values slightly higher than that found in freshly harvested carrots. Although changes were more distinct (and significant) in older carrots, the results indicated that changes in osmotic potential were always due to variations in the total amounts of osmotically active substances and did not result from a variation or reduction

in the water volume of the tissue. Indeed, maximum water content ($^{max}WC_{DM}$, Figs 2C, D) remained more or less constant throughout storage (except day 83 in old roots, Fig. 2B), which also supported this conclusion.

During the whole storage period variations of osmotic potential at turgor loss point ($^{TLP}\Psi_\pi$, Figs 2E, F) reflected that at water saturation. This means that during the initial storage carrot roots may obtain a lower water potential before they were wilted than in the later phase. Again, changes were more pronounced when carrots had been harvested at a later stage of development.

The relationship between pressure potential, i.e. the volume averaged turgor of the carrot tissue, and the relative water deficit is given in Fig. 3. Samples investigated during the early stage of storage (days 28 to 35) had a higher pressure potential over most of the range of relevant water content when compared to those measured after 5 months. Furthermore, pressure potential declined more rapidly with increasing water losses at the beginning of storage. Consequently, the bulk modulus of elasticity was higher during this period indicating that the tissue was stiffer (Fig. 4). During the initial phase (≈ 40 d) of cold storage ε even temporarily increased above pre-storage levels. Again, changes were considerably higher in older than in younger carrots. On the other hand, values of the bulk modulus of elasticity were similar in both groups of carrots during the later part of storage.

Changes in the bulk modulus of elasticity of a given tissue are related to variations in both water content and pressure potentials. Only at low water deficits a clear difference between tissue elastic properties during the different stages of storage could be observed (Fig. 5A). On the other hand, the linear relationship between ε and pressure potential remained unchanged during the whole storage period (Fig. 5B).

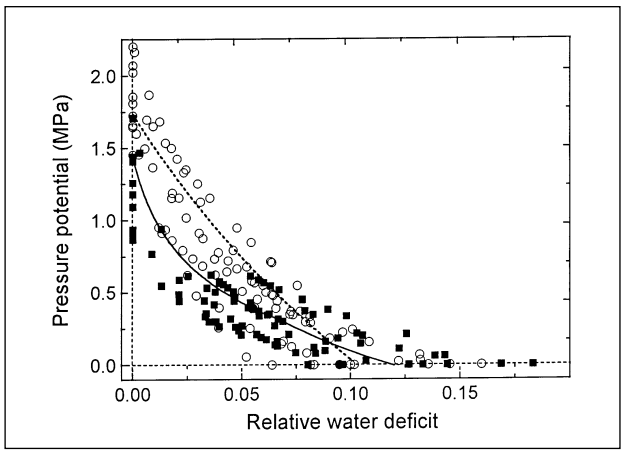


Fig. 3. Relationship between pressure potential and relative water deficit in carrot samples taken during the initial (days 28–35, open symbols) and the late phase (days 150–160, closed symbols) of storage. The data were by pressure-volume-analysis on individual roots (n = 12 per experiment).
Zusammenhang zwischen Wasserpotential und relativem Wasserdefizit von „alten" Möhren am Anfang (28.–35. Tag, offene Symbole) bzw. am Ende der Lagerung (150.–160. Tag, volle Symbole). Die Daten wurden mittel Druck-Volumen-Analyses an einzelnen Möhren gewonnen (n = 12 pro Messabschnitt).

Discussion

Accepting that the overall water status is an important determinant of the quality of perishable vegetables there are pronounced changes in the quality of the carrots during the initial 2 months of cold storage. During this period a temporary reduction in the osmotic potential of the carrot roots occurred. According to van't Hoff's law ($\Psi_\pi = -N / V_w$ * const.) relating the osmotic potential to the ratio of the sum of osmotically active substances (N) and the volume of water (V_w), the observed transitory decrease in osmotic potential may result from either an increase in N or a decrease in V_w. Results obtained in the present study indicate that the initial reduction in Ψ_π was nearly exclusively due to a net increase in N. This finding agreed well with the changes in the content of reducing and non-reducing sugars in cold stored carrot roots over time, previously reported by several authors (PHAN et al. 1973, LIST and ASKAR 1977, NILSSON 1987, HENTSCHEL 1997). The concentration of free, reducing sugars (glucose and fructose) was found to increase above pre-storage levels at the costs of sucrose during the initial 5 weeks (PHAN et al. 1973, LIST and ASKAR 1977, HENTSCHEL 1997). As these sugars are the most important osmotically active substances in carrots (HERRMANN 1994) any variation in their respective concentrations greatly affects osmotic relations. However, time of harvest and preharvest conditions are known to influence the extent of such changes (NILSSON 1987, FRITZ and WEICHMANN 1979, ROSENFELD 1998). NILSSON (1987) demonstrated that the ratio of sucrose to hexoses was lower and its decrease during storage smaller the younger the carrots were at harvest. This reduces the effect of the ratio of the concentration of these free sugars on total osmotic relations. The differences obtained between young and old carrots in the presented experiments clearly support these previous findings.

The final, slow increase in $^{S}\Psi_\pi$ observed in both studies inferred that the effective osmotic cell sap concentration was reduced again during prolonged storage while changes in maximum water content at full water saturation were negligible. Indeed, it has been found that the concentration of all three soluble sugars decreased again below the level determined after harvest (PHAN et al. 1973, NILSSON 1987). The minor increases in maximum water volume during late storage (Figs 2C, D) may well reflect a decrease in dry matter due to respiratory losses (FRITZ and WEICHMANN 1979) rather than a true variation in maximum attainable water volume.

On the other hand, it is known that maximum water volume may decline in response to water deficits (LEVITT 1986, FAN et al. 1994). This will allow a plant to maintain a positive turgor despite consecutive slow water losses (WEISZ et al. 1989). According to FAN et al. (1994), this "elastic adjustment" (LEVITT 1986) should result from an increase in cell wall elasticity as has been observed here during late storage. Turgor maintenance may aid stabilisation of physiological activity in the carrot roots in a natural over-winter situation, which is closely mimicked by cold storage in a water vapour saturated atmosphere.

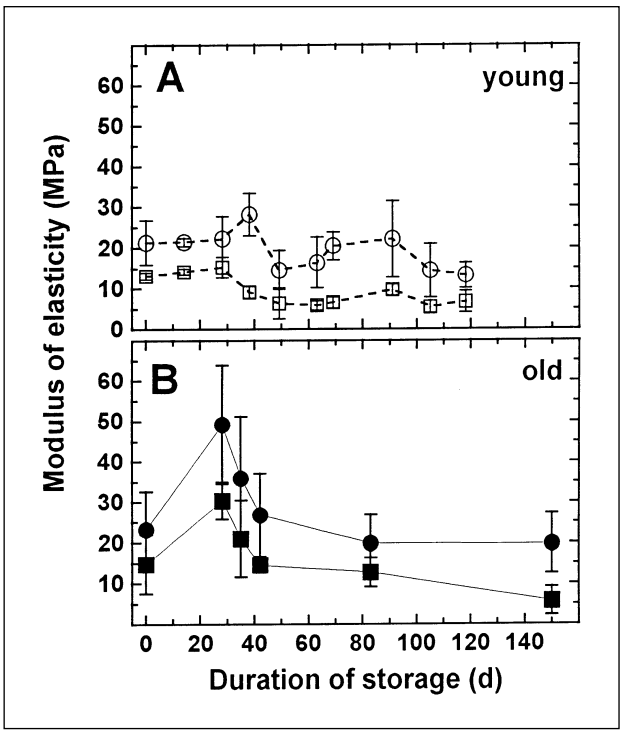


Fig. 4. Maximum bulk moduli of elasticity at water saturation (circles) and actual elastic moduli (squares) of young (A) and old (B) carrots during storage. Given are means ± SD (n = 6). *Maximale (Kreise) und aktuelle Elastizitätsmodule (Quadrate) von „jungen" (A) bzw. alten (B) Möhren während der gesamten Lagerung (Mittelwerte ± Standardabweichung; n ≥ 4).*

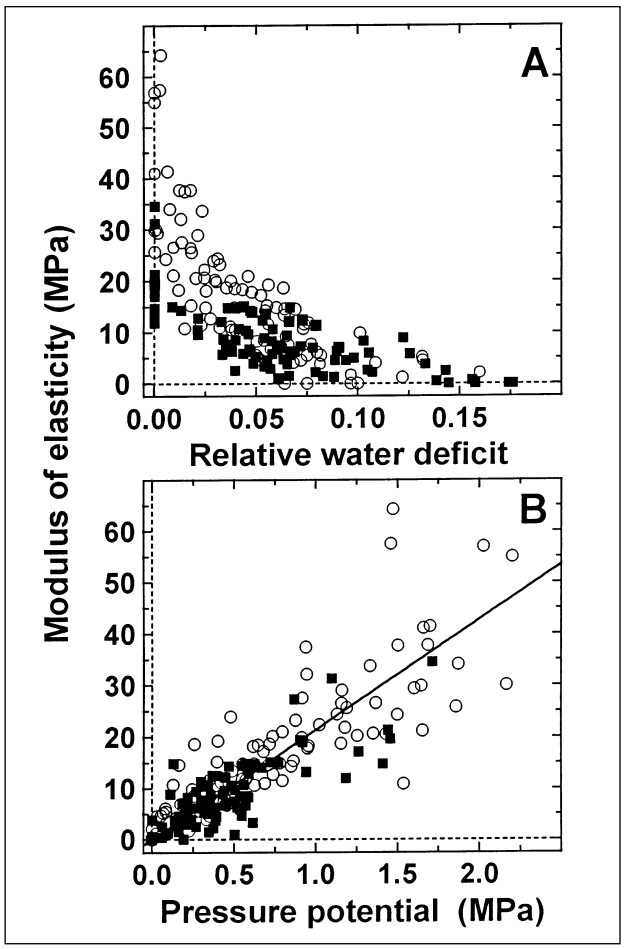


Fig. 5. Elastic moduli as a function of relative water deficit (A) and pressure potentials (B) of individual carrot samples (n = 12 per period) taken during the early (days 28–35, open symbols) and the late (days 150–160, closed symbols) storage period. *Zusammenhang zwischen Elastizitätsmodul und relativem Wasserdefizit (A) bzw. Druckpotential (B) von einzelnen „alten" Möhren (n = 12 pro Messabschnitt) am Anfang (28.–35. Tag, offene Symbole) bzw. am Ende der untersuchten Lagerdauer (150.–160. Tag, volle Symbole).*

However, mean mechanical properties of the carrots tissue mainly changed during the initial five weeks of storage during which the actual and the maximum bulk modulus of elasticity (i.e. at water saturation) reversibly increased, at least in old carrots. As a result, carrot tissue is less elastic during early storage. Under these condition carrots may, thus, be more susceptible to mechanical damage which has been shown to be positively related to root water status (KOKKORAS 1995). However, a direct correlation between the number of broken roots and their water potential could not be verified with freshly harvested carrots in practice experiments (MEMPEL and GEYER 1999).

A transitory increase in the compressive Young's modulus, with some precautions comparable to the volume-related bulk modulus of elasticity obtained from pressure-volume-analysis (MARSHALL and DUMBROFF 1999), has also recently been reported for carrots during cold humid storage by NIELSEN et al. (1998). The degree of change in Young's modulus and the time course obtained by these authors closely fit the results presented here. NIELSEN et al. (1998) also reported that the compressive Young's modulus initially decreased in carrots slices rapidly dehydrate in dry air, but than increased again with further water losses. The latter response, however, could not be verified from our experiments. Instead, the general volume and pressure dependency of the bulk modulus of elasticity closely reflects that frequently found in other plant material (VON WILLERT et al. 1995). Furthermore, similar results on pressure potential, cell volume and bulk modulus of elasticity have been obtained for carrot tissue by direct measurements of cellular water relations using a cell pressure probe by PFEIFFENSCHNEIDER (1990). Although this author found significant differences between core and cortex tissue, the values of turgor and modulus of elasticity as well as their interrelationship fell within the range reported in the present study.

A decrease in tissue elasticity is assumed to maintain a higher water content even at the expense of lowering the water potentials (SCHULTE 1992). This type of elastic adjustment may help maintaining pressure potential (MARSHALL and DUMBROFF 1999). The results presented here support the conclusion of MARSHALL and DUMBROFF (1999) that elastic adjustment may increase pressure potentials if no or only low water losses occur.

Indeed, average pressure potential increased during the initial storage both in old and young carrots without any changes in water deficit. During early storage, water losses could be effectively prevented by very high air humidity, as also found by NIELSEN et al. (1998). However, water potential decreased slightly due to

changes in osmotic potential. Comparable results have been reported by SHIBAIRO et al. (1997) for several carrot cultivars during a short-term storage (21 d). The results presented by these authors also indicated a small increase in pressure potential. On the other hand, in that investigation, carrots packed in perforated plastic bags, lost considerable amounts of water in a less humid (80 % RH) atmosphere. In the present experiments as well as in many short-term storage experiments (HERPPICH and MEMPEL 1999a,b) any reduction in water content was accompanied by a considerable decline in pressure potential (c.f. Fig. 3) as expected from water relations theory (c.f. VON WILLERT et al. 1995).

The variations in actual modulus of elasticity during the later storage were only minor. Hence, changes in cell wall physical and chemical (NYMAN and NILSSON 1994) properties were important only during the early storage. No further large changes occured after approximately 50 d, when the very minor water losses resulted in a slow increase in tissue elasticity.

In summary, carrots stored at low temperatures and very high air humidity retained a high water content and a relatively high turgor over the whole storage period investigated. This was achieved by both osmotic and elastic adjustment occurring mainly during the initial phase of storage. The relative constancy of water relations should mean that carrot internal quality did not decrease. On the other hand, the increase in maximum osmotic potential (at water saturation) with prolonged storage clearly showed that the content of osmotically active substances, which are known to be mainly value adding sugars, decreased, thus possibly lowering the product quality. Furthermore, changes in elastic properties indicate that carrots became softer even without serious water losses, a second strategy of elastic adjustment to guarantee the maintenance of pressure potential (SCHULTE 1992). The presented results support the conclusion (WEISZ et al. 1989, SCHULTE 1992, FAN et al. 1994, MARSHALL and DUMBROFF 1999) that 'plants may actively govern the turgor-volume relationship … by induction of marked changes in the elastic properties of the cell walls' (MARSHALL and DUMBROFF 1999).

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