

A comprehensive study of factors affecting postharvest disorder development in celery

Maria Anastasiadi, Natalia Falagán, Simone Rossi, Leon A. Terry*

Plant Science Laboratory, Cranfield University, Bedfordshire MK43 0AL, UK

*Corresponding author: Prof Leon A Terry – l.a.terry@cranfield.ac.uk

Abstract

Fresh-cut celery is an economically important crop, susceptible to postharvest disorders such as browning at cut ends, which can compromise quality and affect freshness perception. The study herein represents the most comprehensive attempt to date to determine the factors which mediate celery postharvest disorders and uncover the physiological and biochemical mechanisms involved. Three main experiments were conducted over two years, covering the early and late Spanish season and the late UK season. The aim of the experiments was to study: a) the effect of seasonal variation and horticultural maturity on shelf-life (20 °C) of fresh-cut celery; b) the effect of postharvest application of 1-methylcyclopropene (1-MCP) and continuous ethylene supplementation on browning and pithiness development during cold storage (5 °C); and c) the effect of preharvest deficit irrigation on the quality of fresh-cut celery during shelf-life (20 °C). Lesser horticultural maturity increased browning and pithiness; browning severity positively correlated with chlorogenic acid concentrations in celery cut-ends. Ethylene supplementation accelerated the metabolic activity of celery, leading to early senescence. We found that 1-MCP suppressed respiration rate and delayed browning. Deficit irrigation promoted browning, which coincided with a rapid increase in abscisic acid and its main catabolite phaseic acid during storage. Light deficit irrigation promoted the increase of chlorogenic acid after 6d of storage, while severe deficit irrigation did not show this increase.

These findings will help growers and retailers standardise industry practices ensuring uniform quality and better shelf-life estimations.

Keywords *Apium graveolens*, physiological disorders, horticultural maturity, deficit irrigation, abscisic acid.

Introduction

Celery (*Apium graveolens* L.) is a popular crop valued by consumers for its low calorific content and organoleptic characteristics, such as freshness and crisp texture (Craig 1999; Viña and Chaves, 2003). Fresh-cut celery is often offered as minimally processed sticks or slices in response to consumer demand for healthy, ready-to-eat produce (Álvarez et al., 2015; Massolo et al., 2019). The first signs of quality loss are perceived by consumers by the incidence of browning and pithiness (Gómez and Artés, 2005). Postharvest browning is attributed to phenylpropanoid metabolism, by which phenylalanine ammonia lyase (PAL, EC 4.3.1.5) catalyses the synthesis of phenolic compounds. These phenols can be oxidised into *o*-quinones, the black/brown pigments responsible for the undesirable colour on cut surfaces of fresh products. This process is catalysed by polyphenol oxidase (PPO, EC 1.14.18.1) and peroxidase (POD, EC 1.11.1.7) in the presence of oxygen (McEvily et al., 1992; Landi et al., 2013; Zhan et al., 2013). The main phenol related to browning is chlorogenic acid, a colourless, non-volatile, hydroxycinnamic phenolic acid (Liang and Were, 2020). Chlorogenic acid quinone is the product of the oxidation of chlorogenic acid by PPO, a coloured and key compound in enzymatic browning (Murata et al., 2002).

With respect to pithiness, it is considered one of the major problems negatively affecting quality and shelf-life of celery (Saltveit and Mangrich, 1996). It manifests with parenchyma tissue becoming less dense, whitish and fibrous, resulting in formation of aerenchyma. Current

evidence indicates that pithiness can be induced by pre-harvest factors. For instance, infrequent drip irrigation during summer periods has been shown to significantly increase pithiness (Breschini and Hartz, 2002; Saltveit and Mangrich, 1996). Also, mechanical perturbation and Ethephon application increased pithiness, especially at the basal part of the petioles (Pressman et al., 1984).

Previous research has developed solutions to minimise postharvest browning in celery. For example, heat shock treatments significantly reduced browning potential (Loaiza-Velarde et al., 2003; Viña and Chaves, 2008). Gómez and Artés (2004) showed that celery stalks stored in controlled atmosphere (CA) with high CO₂ concentration (> 7 kPa) maintained a greener colour compared to control. Also, the application of ethylene inhibitors such as 1-methylcyclopropene (1-MCP) together with refrigeration showed promising potential for extending the shelf-life of fresh-cut self-blanching celery (Massolo et al., 2019). This shelf life extension is possible because PAL is regulated by ethylene. When fresh produce are treated with 1-MCP the expression of transcripts for PAL and ethylene receptors decrease (*Pc-PAL* and *Pc-ERSI*, respectively), reducing PAL activity and therefore the formation of quinones precursors (MacLean et al., 2007). It is well-reported that controlling respiration rate is key to delaying senescence. Together with organic acids, sugars are the main substrate for respiration (Falagán and Terry, 2018) and indicators of metabolic processes leading to postharvest disorders. Despite previous research into the causes of browning in fresh-cut celery the underlying physiological and biochemical mechanisms involved have not yet been fully elucidated.

In addition, the influence of preharvest factors on the development of postharvest browning are not well understood. Guerra et al. (2010) reported that a delay in celery harvest date increased its browning potential and total quinones content. Research on other crops susceptible to browning, such as lettuce, has indicated that deficit irrigation could reduce the development of

this disorder (Luna et al., 2013). Also, the role of phytohormones such as abscisic acid (ABA) and metabolites thereof in the development of celery postharvest disorders has not studied in depth to date. It is well known that ABA is synthesized by plant roots in response to decreases in soil water potential (Sharp, 2002; Steuer et al., 1988). Once produced, ABA is translocated to the leaves, where it stimulates stomatal closure by altering guard cell ion transport, which in turn attenuates transpiration rate, and hence, water loss (Finkelstein, 2013). Additionally, ABA has been shown to induce expression of genes involved in the de novo synthesis of osmoprotectant molecules (Fujita et al., 2011).

In this context, the aim of this study was to understand the influence of preharvest factors (maturity at harvest and irrigation regime) and the application of postharvest treatments on the development of postharvest discolouration in fresh-cut celery, taking as reference the cultivars ‘Monterey’, ‘Victoria’ and ‘Imperial’.

2. Material and Methods

Three experiments were conducted over two years, exploring the effects of horticultural maturity at harvest, postharvest ethylene treatments under cold storage and postharvest response to preharvest deficit irrigation strategies. These experiments simulated the challenges that industry faces with postharvest disorders in celery.

2.1. Experiment 1: Horticultural maturity stage at harvest

2.1.1. Plant material

The aim of this experiment (Exp. 1) was to examine the effect of celery maturity stage at harvest on the development of physiological disorders during shelf-life. Exp. 1 was conducted in collaboration with G’s Fresh Ltd. (Cambs., UK) who provided all the plant material and consisted of three separate field trials, two of which were conducted in Spain (Cartagena, Murcia) and one in the UK (Stretham, Cambs.). The first trial was conducted in the early

Spanish spring season [(cv. ‘Monterey’); between 10 March and 7 April], the second in the late Spanish spring season [(cv. ‘Monterey’); between 5 May and 2 June], and the third in the late UK season [(cv. ‘Victoria’); between 11 August and 8 September]. Details of growing conditions, geographical coordinates and harvest frequency are included in **Table S1**).

In all three trials, the experimental field was divided into three blocks: top, middle and bottom and samples were randomly harvested from each block. Harvest took place at different horticultural maturity stages: a) two weeks prior to optimum harvest date [HM(-2)], b) one week before optimum harvest date [HM(-1)], c) at optimum harvest date [HM], d) one week after optimum harvest date [HM(+1)] and e) two weeks after optimum harvest date [HM(+2)].

Celery was hand-picked using a lightweight field knife. Optimum harvest dates were decided by considering two parameters: stalk length (~ 55 cm) and the expected harvest date indicated in reference schedule tables prepared by G’s Fresh Ltd. every growing season. Plants were then packed directly in the field. Thereafter, they were vacuum-cooled to 3 °C as per standard commercial practice and dispatched (2 h transit) to the Plant Science Laboratory (PSL) at Cranfield University (Beds., UK) via refrigerated freight (5 °C), within three days.

Upon arrival, celery plants were washed under running tap water to remove soil and dried with a soft paper towel. Subsequently the celery samples were randomly divided into two batches (for shelf-life and cold storage evaluation).

2.1.2. Shelf-life assessment

The celery plants selected for shelf-life assessment were placed into three different crates (replicates) per horticultural maturity stage in a storage room at constant temperature of 20 °C and 56 RH%. Storage temperature was set up at 20 °C to encourage browning, hence, to represent a worst-case scenario in the supply chain. Thereafter, samples were subjected to visual, physiological and biochemical analysis at regular time intervals. More precisely,

samples were analysed upon receipt (baseline), after 6 d and 12 d in storage. Three replicates were taken from each crate for a total of 9 replicates for each sampling day.

2.2. Experiment 2: Postharvest treatments under cold storage

2.2.1. Plant material

The aim of this experiment (Exp. 2) was to study the effect of postharvest treatments on the development of physiological disorders under cold storage conditions. A subsample of the celery plants at different horticultural maturity stages ([HM(-2)], [HM], [HM(+2)]) harvested for Exp. 1 was used for Exp. 2.

2.2.2. Ethylene and 1-MCP treatments

Celery selected for cold storage were divided into three batches and subjected to the following treatments: a) continuous air (control), b) continuous exogenous ethylene (Et) and c) 1-MCP. All samples were stored at 5 °C and 95% relative humidity (RH) for 10 d in total. For ethylene treatment, samples were placed in water-sealed, 264 L polypropylene boxes covered with polypropylene lids and flushed with continuous exogenous ethylene at 10 $\mu\text{L L}^{-1}$ concentration. The gas flow was controlled from a 50 L cylinder of 5000 $\mu\text{L L}^{-1}$ certified standard concentration ethylene in nitrogen (BOC, Surrey, UK) and was reduced to 10 $\mu\text{L L}^{-1}$ by mixing with pure flowing air following Amoah et al. (2017). Analysis was carried out as previously described in Terry et al. (2007a).

1-MCP treatment was applied as reported by Downes et al. (2010) with slight modifications. A sample of 1.47 g 1-MCP powder (SmartFresh[®], Rohm and Haas, product code: AFxRD-0014) was mixed with 16.3 mL of warm water (50 °C) and shaken to release 1 $\mu\text{L L}^{-1}$ concentration in water sealed 264 L polypropylene boxes.

2.3. Experiment 3: Postharvest response to deficit irrigation

2.3.1. Plant material

A 5m-wide, 8 m-long and 2.5 m-high polythene polytunnel (Haygrove Ltd., Hereford, UK) was used to grow celery plants (cv. ‘Imperial’) from 7 July to 20 November. Celery seeds were initially sown in peat block (mixture of black, brown turf and fertilizer), covered with sand and transferred into germination rooms for 6 days at 18 °C. Then, they were moved to a greenhouse at a minimum temperature set up at 16 °C for 27 days. After this period, transplants were transported to Cranfield University and transplanted in the polytunnel. The plants were grown in 12 L capacity plastic pots filled with Fenland peat directly collected from Dimmocks Cote Farm (Stretham, Ely, Cambs., UK) fields (52°19’57.7” N; 0°15’58.3” E; **Table S2**).

2.3.2. Experimental design and sampling

Three different irrigation treatments were applied: 800 (full irrigation), 600 (light water stress) and 400 (heavy water stress) mL every 48 h. The full irrigation treatment was decided according to the standard celery growing practises adopted by G’s Fresh Ltd. and corresponded to the amount of water needed to reach soil field capacity (45% volumetric water content). The other two treatments were applied to induce two different levels of drought stress. Field capacity was derived by watering soil to full saturation, waiting until excess water drained away and measuring the soil moisture with a Thetaprobe meter (ThetaKit type ML2x, Delta-T Devices, Cambridge, UK). Plants were divided into three main blocks, with each arranged in three main plots for each irrigation treatment. Each main plot contained 15 plants [12 for postharvest analyses (3 replicates per treatment) and 3 additional as spare (1 per treatment)]. Plots were arranged in a completely randomised design. Harvest dates of 800, 600 and 400 mL per alternate day irrigated plants were 16 October, 3 November, and 20 November, respectively and were all at full maturity according to commercial practice. After harvest, samples were

immediately transferred to 20 °C constant temperature. Visual and physiological attributes were assessed immediately after harvest, after 3, 6 and 10 d of storage (baseline, sampling day 1, sampling day 2 and sampling day 3 respectively).

2.3.3. Physiological determinations

2.3.3.1 *Respiration rate*

Respiration rate (RR) of celery plants was measured at 20 °C as reported by Collings et al. (2013) with slight modifications using a Sable Respirometry System (Model 1.3.8 Pro, Sable Systems International, NV, USA). Samples were incubated in 16 L air-tight polypropylene boxes (L&L NordicOÜ, Estonia) in continuous air flushed by an 80 HP pump (Hiblow, Techno Takatsuki Ltd., Philippines). Boxes were connected through Nalgene PVC tubes of 3 mm internal diameter (Thermo Scientific, Rochester, NY) to the CA-10 carbon dioxide (Firmware version 1.05) and FC-10 oxygen detectors (Firmware version 3.0) of the Sable System to detect O₂ consumption / CO₂ emission real time for 10 min over three cycles. In addition, a water vapour pressure detector (RH-300) was used to measure relative humidity in the outflowing air. Data were analysed with ExpeData software (Release 1.3.8, PRO Version) and reported as nmol CO₂ kg⁻¹ s⁻¹.

2.3.3.2. *Pithiness*

Samples were visually assessed for pithiness at both cut petiole and butt ends of celery. A visual scale from 1 to 4, provided by G's Fresh Ltd., was used to assess pithiness with 1 corresponding to 'no pithiness' and 4 corresponding to 'severe pithiness' (**Figure S1**). Photos of celery samples were taken at both cut ends to be used as references. Prior to visual assessment, samples were cut 5 mm from the apical cut petiole ends and 5 cm from the butt ends.

2.3.3.3. *Colour*

Samples were visually assessed for browning at both cut petiole and butt ends of celery. A visual scale from 1 to 4, was used again in this case to assess browning with 1 corresponding to 'no browning' and 4 corresponding to 'severe browning'. Photos of celery samples were taken at both ends to be used as references (**Figure S2-S3**).

Objective colour was measured with a CR-400 Minolta colorimeter and DP-400 data processor (Minolta Co. Ltd, Japan) at both cut petiole and butt ends of each celery head. Each individual measurement was the mean of four measurements randomly taken on both cut surfaces. Data were expressed as chroma (C*), hue angle (H°) and lightness (L*) which were automatically calculated. Calibration of the instrument was done using a Minolta standard white tile CR-400.

2.3.4. Biochemical analysis

2.3.4.1. *Sample preparation for biochemical analysis*

Cut celery sticks were snap-frozen in liquid nitrogen and stored at -40 °C prior to freeze-drying (Coolsafe 55-9 Scanvac, Scanlaf A/S, Lynge, Denmark). Lyophilised samples were powdered with a mortar grinder (RM 200, Retsch Ltd., Derby., UK) and stored at -40 °C until further analysis.

2.3.4.2. *Analysis of individual phenolic compounds*

Lyophilised powder (50 mg) were extracted and subjected to HPLC analysis and analysed according to Giné-Bordonaba and Terry (2008). Agilent ChemStation Rev. B.02.01 software was used for data integration and quantification.

2.3.4.3. *Analysis of soluble sugars*

224 Soluble sugars were extracted and analysed as previously described by Terry et al. (2007b).
225 Freeze-dried celery samples (50 mg) were mixed with 1 mL of extracting solution [62.5:37.5
226 HPLC-grade methanol:water (v/v)] and placed in a shaking water bath for 30 min at 55 °C; the
227 mixture was vortexed every 5 min for 20 s. Then, the extracts were then cooled at ambient
228 temperature and filtered with 2 µm PTFE filter (Jaytee Biosciences Ltd, Kent, UK), storing
229 them in 1.5 mL clear glass vials at -40 °C until biochemical analyses. Sugar content in the
230 extracts was analysed using a HPLC (Agilent Technologies 1260 series, Berkshire, UK) system
231 equipped with ELSD (Evaporative Light Scattering Detector). The stationary phase was
232 constituted by a Prevail carbohydrate Es (250 mm x 4.6 mm, 5 µm diameter particles). The
233 mobile phase was formed by HPLC-grade water (solvent A) and HPLC-grade acetonitrile
234 (solvent B). The program involved a linear increase/decrease of solvent B: 80-50%, 15 min;
235 50-80%, 5 min; 80%, 5 min at a flow rate of 1.0 mL min⁻¹ and column temperature of 30 °C.
236 Eluted compounds were identified and quantified by using commercial standards (fructose,
237 mannitol, glucose and sucrose).

238

239 2.3.4.4. Analysis of ABA and ABA catabolites

240 Extraction and quantification of ABA and ABA catabolites was assessed according to the
241 method by Ordaz-Ortiz et al. (2015) with modifications as described in Anastasiadi et al.
242 (2020). Lyophilized celery tissue (100 mg) was mixed with 6 mL 75:20:5
243 methanol:water:formic acid solvent (v/v/v). Then, 30 µL of 400 ng mL⁻¹ internal standard
244 mixture solution (deuterated compounds) was added to the extraction mixture and vortexed for
245 2 min and shaken at 4 °C for 1 h, then centrifuged for 15 min at 4500 rpm. Supernatant was
246 removed and evaporated in a ScanVac freeze-dried overnight at -110 °C. Samples were then
247 reconstituted with 400 µL of 10:99.9:0.1 acetonitrile:water:formic acid solvent, vortexed for
248 30 s, centrifuged for 10 min at 4500 rpm and filtered using 0.2 µm PTFE filters (Jaytee

Biosciences Ltd, Kent, UK). The filtrate was put into deactivated silanized amber vials. All operations were done in dark environment to prevent compound inactivation by light. Sample extracts were injected on an Agilent 1290 Infinity UHPLC system coupled with an Agilent 6540 Ultra High Definition Accurate Mass Q-TOF LC–MS System (Agilent Technologies). Stationery phase was constituted by a thermostated Zorbax Rapid Resolution High Definition Eclipse Plus C18 column (2.1 x 50 mm, 1.8 μ m particle size). The mobile phase was formed by two solutions: water + 0.1% formic acid (solution A) and acetonitrile + 0.1% formic acid (solution B). The program involved a linear increase/decrease of the following solutions: 0 min, 4% B; 1.5 min, 12.6% B; 7.0 min, 26% B; 10 min 40% B and hold for 0.5 min; 10.6 min 100% B and hold for 1 min. Lastly, the column was re-equilibrated for 1.35 min (4% B) for a total run time of 13 min. Samples concentration was compared with calibration standard curves prepared using seven calibrations solution levels (10, 25, 50, 75, 100, 150, 300 ng mL⁻¹) of each deuterated standard compound. Deuterated standards compounds used were: abscisic acid, phaseic acid, dihydrophaseic acid and trans-zeatin riboside.

2.4. Statistical analysis

Statistical analyses were carried out using Statistica for Windows version 13.2 (StatSoft, Inc. UK). Analysis of variance (ANOVA) was used to identify significant differences ($p < 0.05$) between treatments considering field block randomisation. The Fisher's Least Significant Difference (LSD) procedure was used for pairwise comparisons in order to calculate LSD at 95% confidence level.

3. Results

3.1. Experiment 1: Lesser horticultural maturity increases browning in celery

An increase in celery RR was observed during shelf-life for Exp. 1. The increase was most pronounced in samples harvested before the optimum maturity stage especially for the samples grown in the late Spanish season (**Figure 1A**).

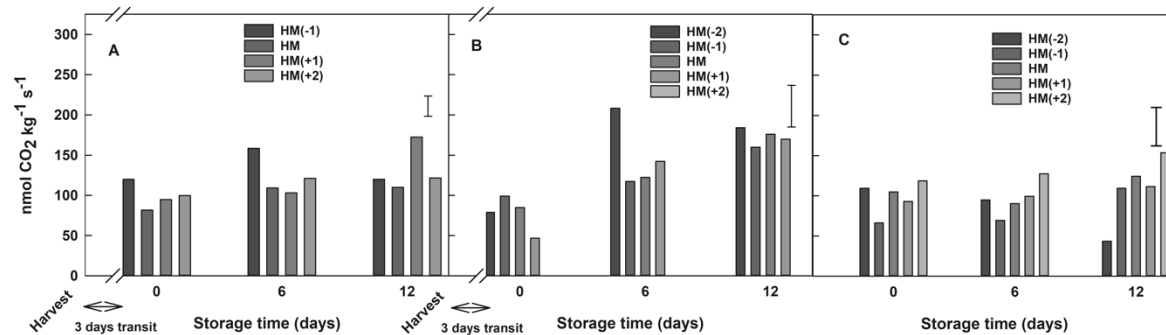


Figure 1. Respiration rate during shelf-life (20 °C) of celery samples grown in three different seasons (A: early Spanish season; B: late Spanish season; C: late UK season) and belonging to five different harvest maturities [HM (-2): two weeks before optimum harvest date; HM (-1): one week before optimum harvest date; HM: optimum harvest date; HM (+1): one week after optimum harvest date; HM (+2): two weeks after optimum harvest date]. Error bars represent least significant differences (LSD).

Late maturity stage samples showed a rapid increase in pithiness score even in the early stages of storage (**Figure S4**). UK grown celery showed a more moderate increase in pithiness scores, compared to Spanish grown celery, but the trend was the same.

Celery discolouration (browning development) was assessed using both subjective and objective methods. Visual scoring results revealed that browning intensified over storage at both butt and cut petiole ends of celery; with the increase being more pronounced during the first 6 d (**Figure 2A**). Petiole ends were generally more affected by browning development than butt ends. Changes in objective colour during shelf-life were mainly observed for H^o which exhibited a systematic drop from harvest with values stabilising between 75-90 H^o by

the end of shelf life (**Figure S5**). This change in H^0 values corresponds to a colour shift from light yellow to darker yellow/orange. Celery samples harvested prior to optimum maturity also tended to have higher H^0 values compared to samples harvested after the optimum harvest period, retaining a lighter yellow colour during shelf-life, especially in the butt ends.

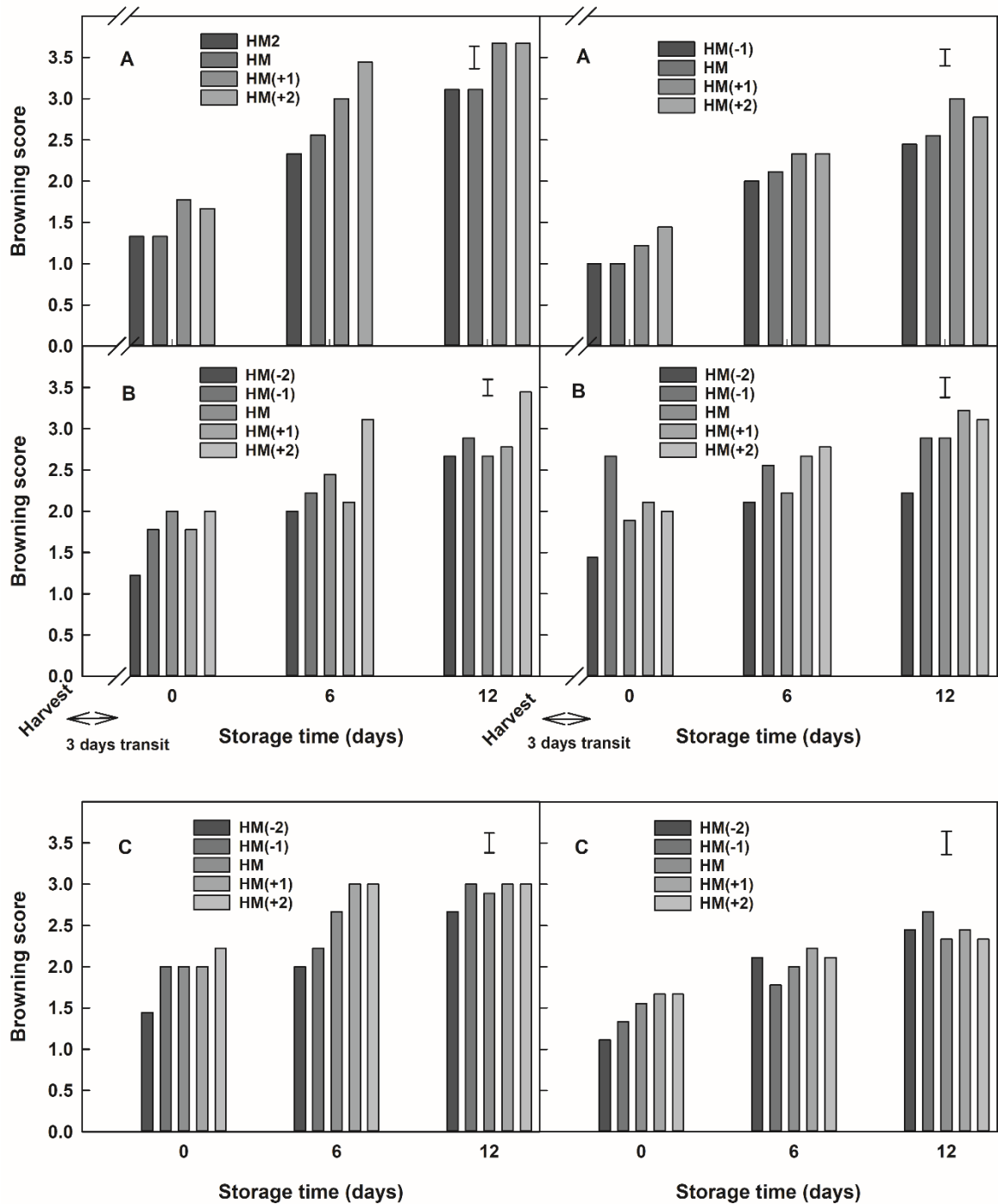


Figure 2. Subjective colour score at 20 °C of celery during shelf-life at cut petiole ends (on the left) and butt ends (on the right), grown in three seasons (A: early Spanish season; B: late Spanish season; C: late UK season) and belonging to five different harvest maturities [HM (-2): two weeks before optimum harvest date; HM (-1): one week before optimum harvest date; HM: optimum harvest date; HM (+1): one week after optimum harvest date; HM (+2): two weeks after optimum harvest date]. Error bars represent least significant differences (LSD).

With respect to phenolic compounds, chlorogenic acid was mainly found in the butt ends and cut petiole ends tissues of celery, rather than middle outer, apical inner and middle inner petioles tissues (**Figure 3**). In general, chlorogenic acid content was relatively low at harvest ($< 1.0 \text{ g kg}^{-1} \text{ DW}$) irrespective of tissue, maturity level, season or cultivar and increased over storage time at both butt and apical cut petiole ends. The highest concentrations were observed after 12 d of shelf-life in the butt ends of optimum harvested celery plants [HM] grown in the late Spanish season showing a more than 6-fold increase from harvest (**Figure 3B**). A similar pattern was observed in the early Spanish season. In contrast, samples from the UK season deviated from this pattern, with chlorogenic acid in the butt ends remaining either stable or exhibiting a moderate increase during shelf-life. The concentration of chlorogenic acid was positively correlated with the subjective browning score of celery grown in all three seasons with the highest correlation observed for butt ends in the Early Spanish season ($R = 0.77$).

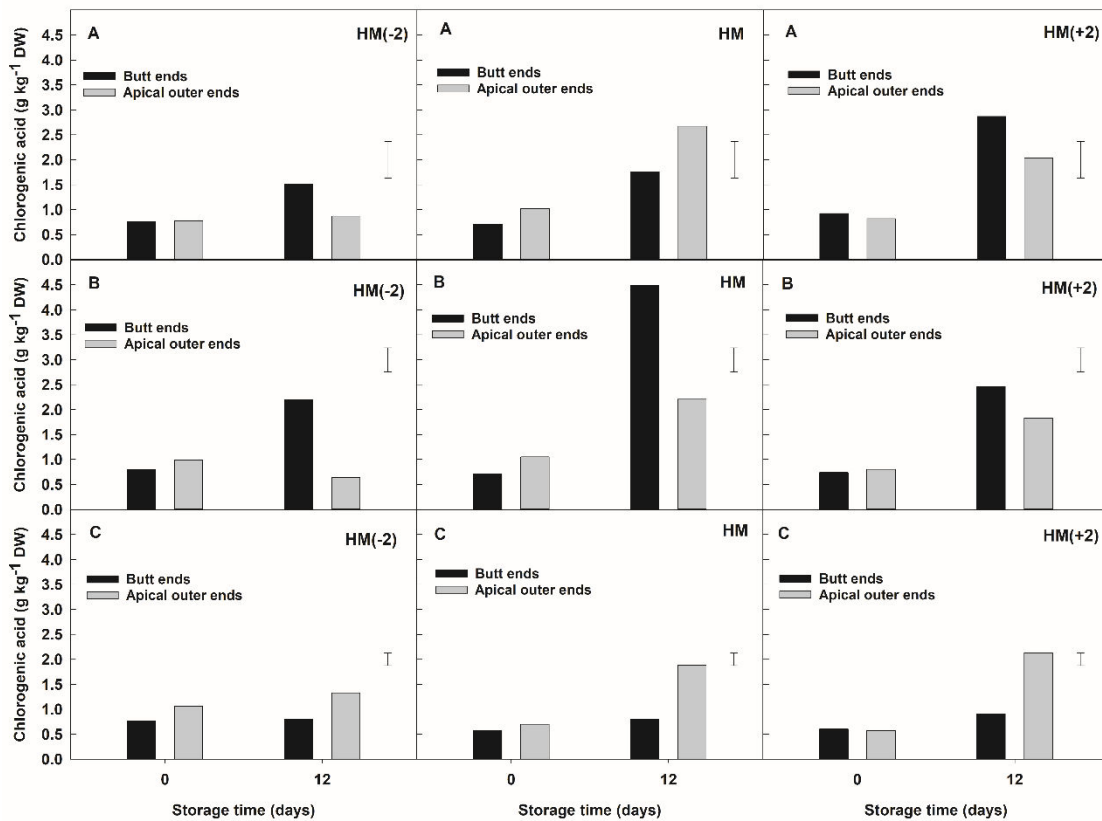


Figure 3. Effect of crop maturity stage on the chlorogenic acid content at butt ends and apical outer ends of celery (cv. ‘Monterey’) grown in the Early Spanish [A], (cv. ‘Monterey’) grown in the Late Spanish [B], and (cv. ‘Victoria’) grown in the Late UK season [C]; all stored in air at 20 °C. HM (-2): two weeks before optimum harvest date; HM: optimum harvest date; HM (+2): two weeks after optimum harvest date. Error bars represent least significant differences (LSD).

3.2. Experiment 2: 1-MCP suppresses respiration rate and delays postharvest browning

Two postharvest treatments (1-MCP and continuous ethylene) were further applied to samples from Exp. 1 in an attempt to decipher the mechanisms affecting postharvest browning development in celery by measuring physiological and biochemical responses.

3.2.1. Physiological responses and visual assessment

RR measurements during cold storage showed a similar range for samples grown in all three seasons, with results for the early Spanish growing season being the most stable and having the narrowest range. Overall, a clear pattern emerged, where within each crop maturity stage, ethylene-treated samples had the highest RR, whilst 1-MCP-treated had the lowest (**Figures S6-S8**).

The opposite trend was observed for pithiness, whereas it was significantly affected by stage of crop maturity, yet, it was not affected by postharvest treatments. Pithiness scores were particularly high in samples harvested 2 weeks past the optimum maturity stage (**Figure S9-S11**). In addition, pithiness scores increased with storage duration irrespective of maturity stage or postharvest treatment. Browning scores showed that browning development was closely related to maturity stage at harvest which agrees with the results presented in section 3.1. Browning was less severe in the most immature [HM (-2)] celery plants compared to the other two maturity stages (**Figure S12-S14**).

3.2.2. Individual sugar profile during cold storage

Individual sugar concentrations in different celery sections during cold storage are shown in **Figure 4**. The concentration of fructose and glucose at harvest was *ca.* 6-fold lower in the butt ends compared to the apical and middle petioles irrespective of treatment. Fructose concentrations in the butt ends remained stable throughout storage, while glucose content rapidly declined by 3-fold after 3 d of storage for control and Et treated sample. For 1-MCP samples glucose content was retained up to 3 d but subsequently concentrations dropped to the same levels as Et and control samples after 6 d in storage. Sucrose concentrations in different celery sections followed the opposite pattern to fructose and glucose, being present at *ca.* 65 g kg⁻¹ DW in the butt ends at harvest with concentrations more than doubling by the end of cold storage in all treatments. Apical and middle petiole sections on the other hand started at *ca.* 20

g kg⁻¹ DW sucrose at harvest with concentrations increasing to *ca.* 40 g kg⁻¹ DW towards the end of storage, with the exception of ethylene treated apical sections which after an initial increase declined to baseline concentrations towards the end of storage. Fructose concentrations in petiole sections exhibited an increase during storage in all treatments, with the middle inner and apical inner petioles showing the most significant increase. A similar pattern was observed for glucose with the concentrations in the middle inner and apical inner petioles increasing during storage in all treatments to levels similar to the other petiole sections.

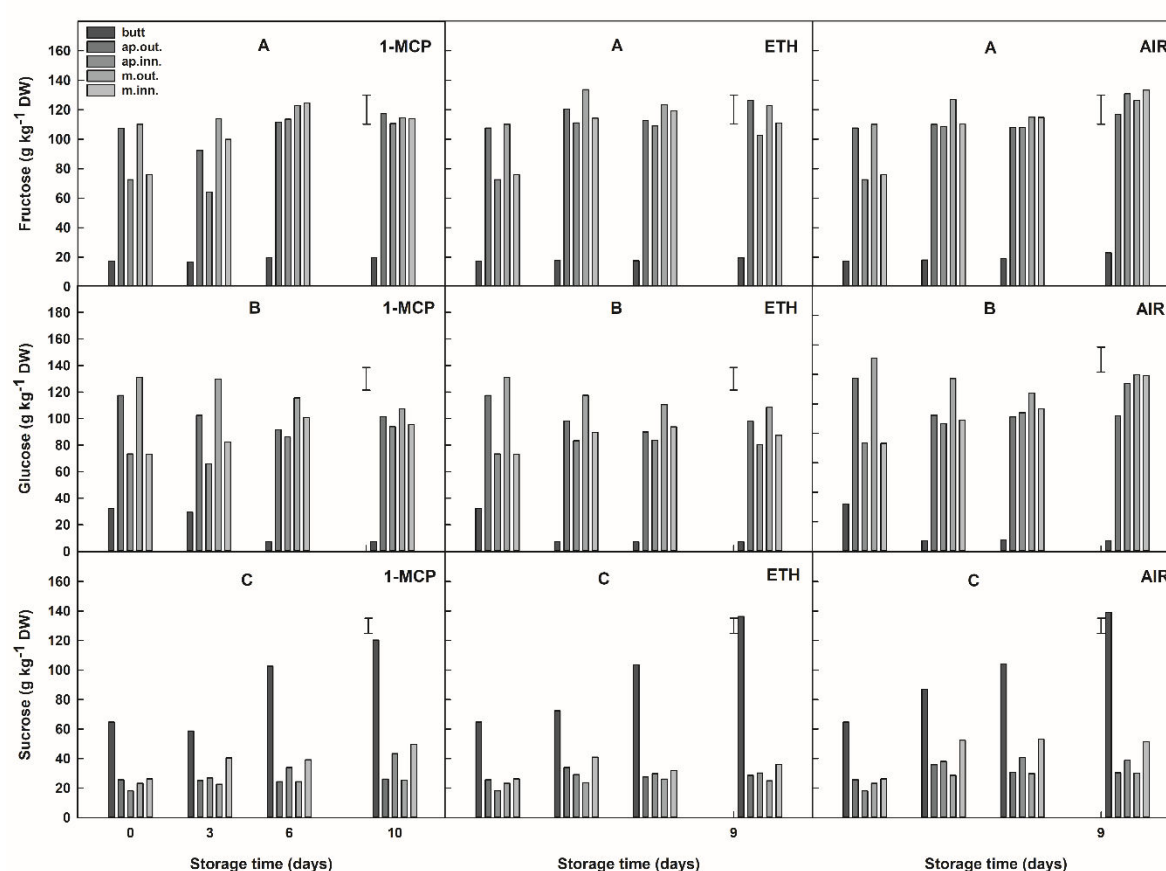


Figure 4. Concentration of fructose (A), glucose (B) and sucrose (C) at different celery sections harvested at optimum maturity in the late UK season and subjected to different postharvest treatments [1-MCP = continuous air after exposure to 1 µL L⁻¹ 1-MCP for 24 h at 20 °C, ETH = 10 µL L⁻¹ continuous ethylene, AIR = continuous air (control)]. Bars with different colours represent different portions (butt = butt ends, ap.out = apical outer petioles, ap.inn = apical

inner petioles, m.out = middle outer petioles, m.inn = middle inner petioles). Error bars represent least significant differences (LSD).

3.3. Severe water stress increases postharvest browning

In Exp. 3, RR increased in heavily stressed celery plants, which exhibited a 2-fold increase in respiration after 3 d of storage and consistently maintained higher RR throughout the storage period (**Figure S15**). Also, results indicated that increased water stress largely affected browning development in celery butt ends especially at the end of the storage period (**Figure S16**). In contrast, water stress or storage duration did not appear to significantly influence pithiness development in celery (**Figure S17**), in contrast with previous studies (Breschini and Hartz, 2002; Saltveit and Mangrich, 1996). This disparity can be related to genotype. Pithiness scores were comparable between water treatments especially in the butt ends, although deficit irrigation seemed to result in less incidents of the disorder, but the results were not statistically significant due to the large variability between biological replicates. It should also be noted that pithiness scores were relatively high for all samples even on harvest day, with scores ranging from 2.5 to 3.5 on day 0. This indicated that the disorder had already developed before optimum maturity was reached.

Irrigation regime did not affect chlorogenic content at harvest, but had a significant impact in the development of chlorogenic acid in the butt ends of cut celery during shelf-life. As shown in **Figure 5**, celery samples grown under no water stress (800 mL every after alternate day) and light water stress (600 mL every alternate day) exhibited a greater than 3-fold increase in chlorogenic acid after 6 d in storage (**Figure 5**). Samples grown under heavy water stress (400 mL every after alternate day) showed no differences. Chlorogenic acid content in the apical outer ends remained relatively stable during shelf-life irrespective of the irrigation regime applied.

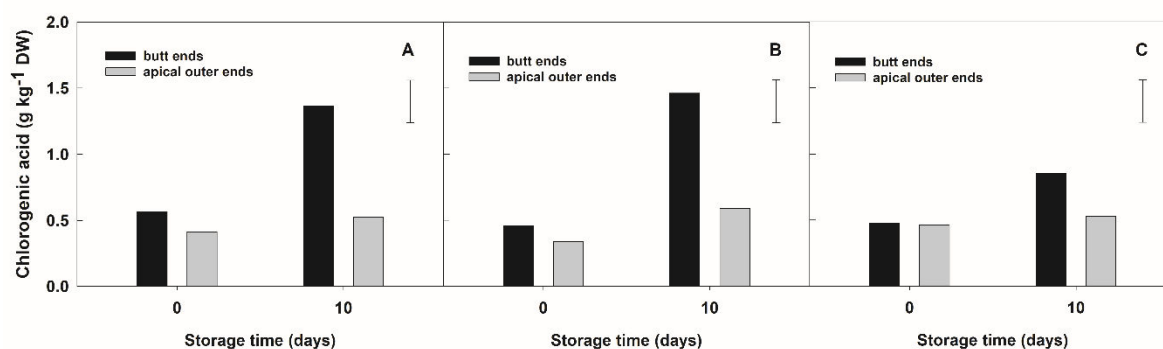


Figure 5. Chlorogenic acid content during shelf-life in the butt ends and apical outer ends of celery irrigated with 800 mL (A), 600 mL (B) and 400 mL (C) of water every alternate day. Samples were harvested at optimum maturity and stored in air at 20 °C for 10 d. Error bars represent least significant differences (LSD).

With respect to sugars, the irrigation regime decreased individual sugar content of celery petiole ends at harvest, proportionally to the level of water stress imposed (**Figure 6**). In contrast, only sucrose levels were marginally lower at harvest in the butt ends of celery subjected to light water stress.

Fructose, glucose and sucrose contents decreased during shelf-life, especially in the cut petiole ends of celery samples irrigated with 800 and 600 mL, while samples irrigated with 400 mL had the most stable sugar profile during storage. Glucose and fructose contents in the butt end region remained stable irrespective of irrigation regime, while sucrose decreased with water stress (**Figure 6**). The irrigation regime also significantly affected the sugar content in cut petiole ends with total sugar concentrations at harvest ranging between 280 and 60 g kg⁻¹ DW with concentrations sharply declining in samples subjected to light and heavy water stress.

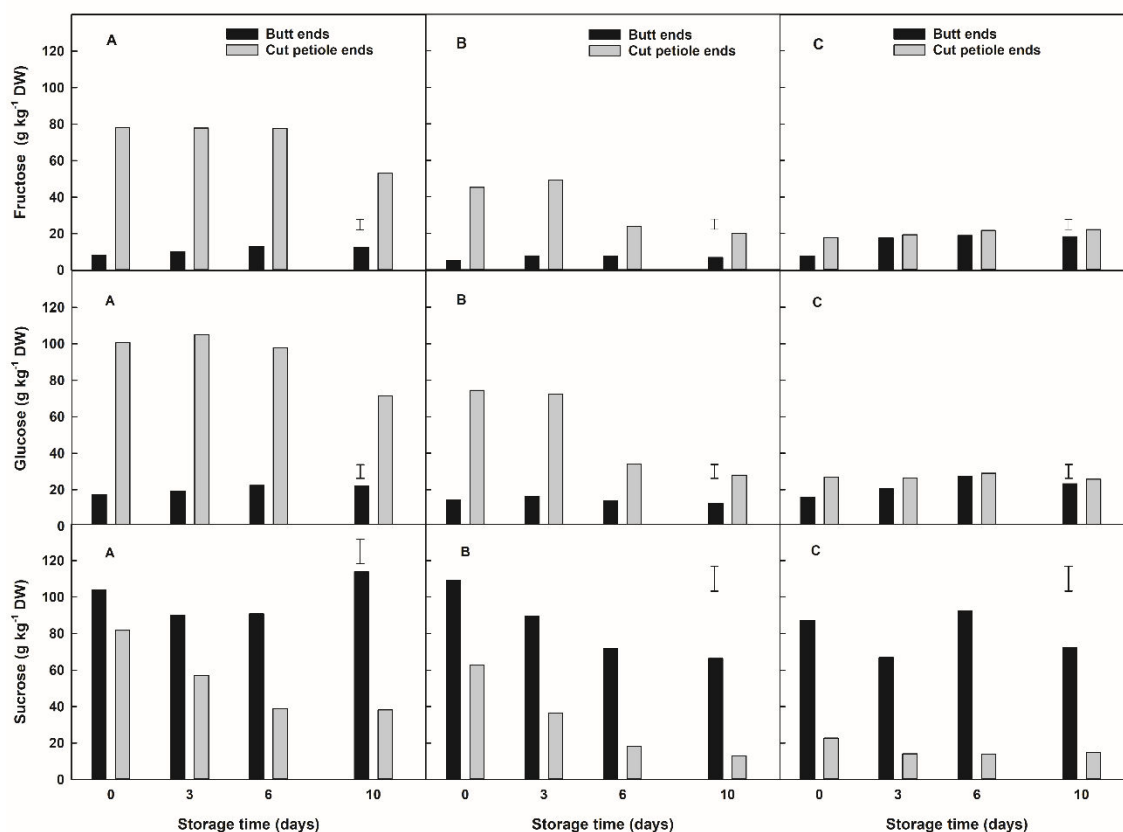


Figure 6. Effect of water treatments on the fructose, glucose, and sucrose concentration at cut petiole ends and butt ends of celery irrigated with 800 mL (A), 600 mL (B) and 400 mL (C) every alternate day. Error bars represent least significant differences (LSD).

Overall, the mean content of ABA and its catabolites was higher in water-stressed plants than in control-irrigated. ABA and its catabolites PA and DPA were identified and quantified in Exp. 3 and the results are shown in **Figure 7**. ABA content at harvest was $< 1.0 \text{ mg kg}^{-1} \text{ DW}$ in all tissues irrespective of irrigation regime with levels remaining stable in apical outer ends throughout shelf-life. In contrast, ABA concentrations in butt ends exhibited a rapid increase during shelf-life storage in all treatments with the increase being greater in the samples grown under light and heavy water stress. The same pattern was observed for PA, the main ABA catabolite which reached concentrations up to $18 \text{ mg kg}^{-1} \text{ DW}$ in the butt ends of lightly stressed

samples, and also in DPA with concentrations reaching up to 5 mg kg⁻¹ DW in the same samples.

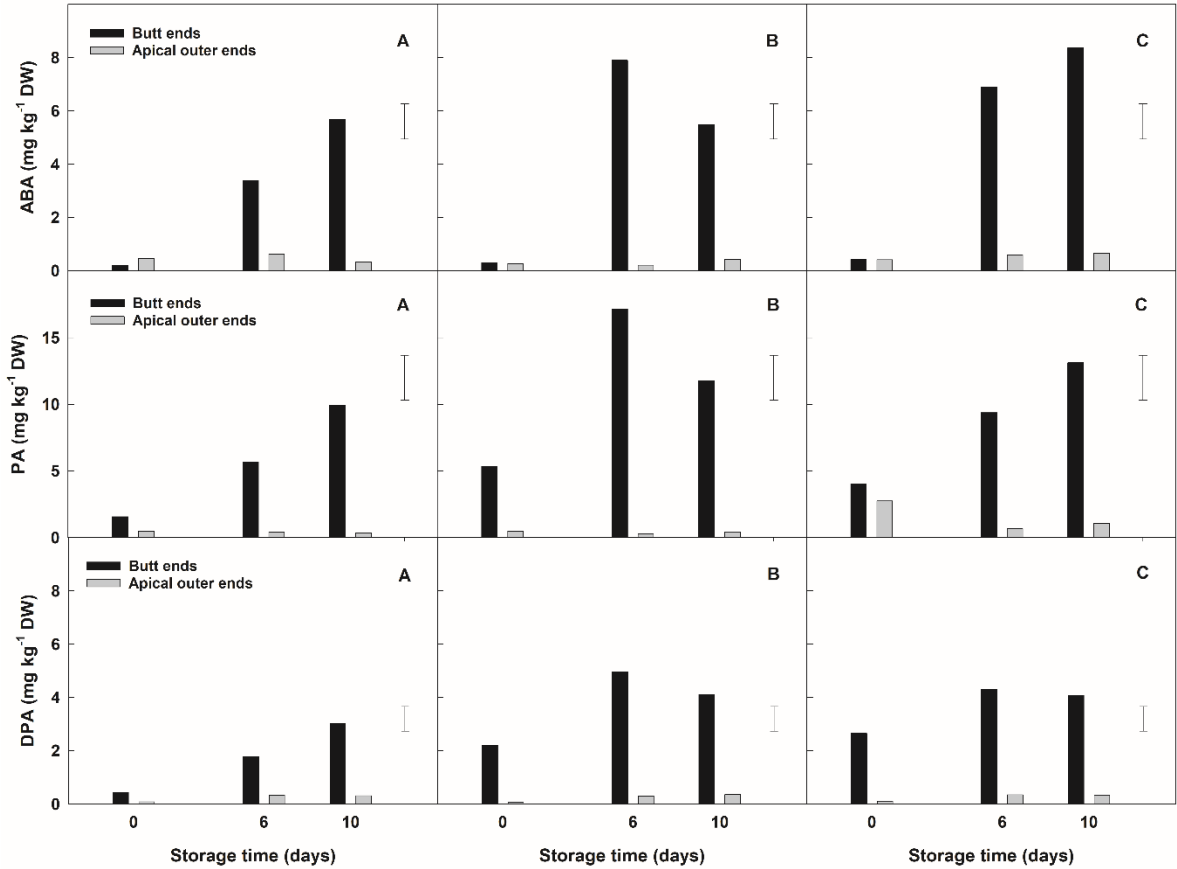


Figure 7. Content of ABA, PA and DPA at butt ends and apical outer ends of celery irrigated with 800 mL (A), 600 mL (B) and 400 mL (C) of water every alternate day. Error bars represent least significant differences (LSD).

Discussion

4.1 Development of postharvest browning and pithiness in celery is influenced by preharvest irrigation regime, maturity stage at harvest, and shelf-life duration

A series of experiments were conducted in an effort to determine the conditions affecting the development of postharvest physiological disorders in celery and the underlying mechanism involved, in three cultivars taken as a reference.

The development of browning and pithiness in celery was positively linked with storage time, maturity stage and water stress. Browning development rose steeply during the first 6 d of storage and was particularly evident in cut petiole ends. Spanish grown celery had higher browning scores compared to UK grown celery, which could be attributed to the longer transit time (3 d) and possibly genotypic variation.

4.1.1 Maturity stage at harvest

Physiological measurements showed that immature celery samples from the early and late Spanish season had a steep increase in RR during the first 6 d in storage and generally maintained higher RR throughout storage compared to samples harvested at optimum or post-optimum maturity. This observation was directly linked to the developmental stage of celery plants at the time of harvest with immature plants retaining higher metabolic activity postharvest. High postharvest RR in immature plant tissues has been reported in other crops, such as asparagus spears and broccoli heads, and has been linked to rapid quality deterioration (Kader 1992; Page, Griffiths, & Buchanan-Wollaston, 2001). However, browning severity in celery plants harvested at different maturity stages, was negatively correlated with RR and was positively correlated with chlorogenic acid concentrations, which generally increased in tandem during storage. The latter finding is in contrast with previous work by Viña and Chaves (2006) who reported that chlorogenic acid content in celery sharply decreased at different storage temperatures (0, 4 and 10 °C) over a period of 28 d. This contradiction could be attributed to differences in cultivar (self-whitening ‘Golden Boy’ vs green celery cultivars ‘Monterey’ and ‘Victoria’ studied herein) and storage conditions.

The positive correlation of increased browning severity and maturity stage at harvest agrees with Guerra et al., (2010) who also reported that the browning potential of leaf stalks of the self-whitening celery (cv. ‘Golden Clause’) was significantly higher in celery plants harvested

124 d after transplantation compared to those harvested 94 d after transplantation. Cut-end browning has not been extensively investigated in celery, yet it has been studied in other economically important crops like lettuce. A study conducted by Chutichudet et al. (2011), on the lettuce (cv. ‘Grand Rapids’) showed that, in leaves, browning appearances significantly increased with plant developmental stage which coincided with an increase in polyphenol oxidase (PPO) activity, reaching maximum levels at the later harvesting date (73 d after planting). Similar findings had been reported earlier by Kang et al. (2008) who also reported that browning of head lettuce (cv. ‘Capitata’) stored at 5 °C for 5 weeks was higher in over-mature plants. Zhan et al. (2013) applied light exposure treatment (2,000 lux) to fresh-cut celery, suppressing both PPO and POD activity and therefore, reducing the impact of browning in fresh-cut celery. Cut-end browning is related to the enzymatic activity of PPOs, which oxidase phenolic compounds to produce brown pigments (Queiroz et al., 2008). PPOs and phenolic compounds are normally compartmentalised in plant cells, hence, the browning reaction can only occur when plant tissues are broken or damaged (for instance, after harvest and during handling) or due to loss of cell membrane integrity as a result of advanced senescence. In our study, the increased browning score attributed to later maturity stage celery plants was likely a result of the observed increase in chlorogenic acid content over time, possibly accentuated by elevated PPO activity.

Pithiness development in celery has been found to be stimulated by several factors which can induce early senescence, such as irrigation regime (Pressman et al., 1984; Breschini and Hartz, 2002) and harvest delay (Guerra et al., 2010). Therefore, we hypothesised that plant developmental stage at harvest affects pithiness in a similar way to cut-end browning by inducing senescence and promoting enzymatic browning and pith breakdown.

4.1.2. Deficit irrigation

488 Changes in the biochemical profile of celery plants grown under different irrigation regimes
489 were investigated during shelf-life. These included sugars (fructose, glucose, and sucrose),
490 phenolic compounds (chlorogenic acid) and plant growth hormones (ABA and catabolites).
491 Although harvest dates for different irrigation regimes were approximately two weeks apart,
492 the statistical analysis considered all the samples simultaneously, as the plants were growing
493 under controlled conditions and shelf-life was conducted in the same rooms under the same
494 conditions.

495 Fructose and glucose were generally higher at cut petiole ends rather than butt ends. This trend
496 was opposite for sucrose, which minimum content was at cut petiole ends. These findings
497 correspond with Keller and Matile (1989) who reported that sucrose concentration was lower
498 in the parenchyma tissue of celery petioles compared to other sugars.

499 The severe browning incidence postharvest recorded for celery plants growing under heavy
500 water stress coincided with significantly higher RR throughout storage indicating elevated
501 metabolic activity which could have led to accelerated senescence. Furthermore, browning
502 incidence in butt ends was most severe in the most water-stressed samples despite the fact that
503 chlorogenic acid content was *ca.* 2-fold lower compared to the other two irrigation regimes.
504 This observation could further support the assumption that water stressed plants were in a more
505 advanced stage of senescence causing disruption of membrane integrity and browning
506 development. In addition, ABA content exhibited a rapid increase in water-stressed samples
507 during shelf-life, compared to control samples (800 mL water every alternate day), which also
508 increased but at a reduced rate. A similar pattern was recorded for PA and DPA. The
509 accumulation of ABA in plant tissues under water stress has also been observed in previous
510 studies (Wang et al., 2019; Farcuh et al., 2020). The role of ABA in stomatal regulation as a
511 response to salt/water stress has been well documented (reviewed in Finkelstein, 2013). ABA
512 levels at harvest were similar for all irrigation regimes, indicating that there was no significant

water stress during plant development. Also, dry matter content at harvest was almost identical for all three irrigation regimes (*ca.* 12%), but the samples receiving the least amount of water (400 mL every alternate day), exhibited a rapid increase in dry matter content during storage (**Figure S18**). Similar incidences of postharvest increase in dry matter in other species such as asparagus (Mastropasqua et al., 2016) have been attributed to increased transpiration due to longer opening time of stomatal aperture resulting in greater water loss and water stress. Another factor contributing to accelerated senescence rates in plants under deficit irrigation regime, could have been the decreased sugar content at harvest and during storage in the cut petiole ends, compared to the control. Reduced sugar content at harvest due to environmental factors and agricultural practices as well as loss of sugars postharvest, have been associated with reduced shelf-life in celery and other fresh cut products (Gómez and Artés, 2005; Anastasiadi et al. 2020). However, the inverse correlation between the amount of water applied and the sugar content at harvest, reported herein contradicts the majority of previous reports which have found that both dry matter and sugar content increase under water stress, in species such as iceberg lettuce, basil and strawberry (Luna et al., 2012; Bekhradi et al., 2015; Terry et al., 2007b). The main reason driving sugar accumulation in drought conditions is the important role of these molecules as osmotic solutes, attracting water and increasing cell turgor (Rodrigues et al., 1993).

4.1.3. Postharvest treatments did not have an effect on browning

The results observed for RR agreed with Massolo et al. (2019), who showed that ethylene treatment (in the form of ethephon) increased the respiration rate of apical celery slices stored at 4 °C, while 1-MCP treated celery slices maintained much lower respiratory rates during 20 d in storage, compared to control and ethylene treatment. The same authors also reported a respiratory burst after 13 d in storage in both control and ethylene treated samples which was

attributed to advanced senescence. Ethylene treatment of over-mature celery plants, could have accelerated senescence processes causing a similar ethylene burst.

In this study, postharvest treatments did not affect the development of browning and pithiness in celery. Statistical analysis of browning and pithiness scores, revealed that the deciding factor for the development of these disorders was maturity stage at harvest, with later-harvested plants [HM (+2)] being the most susceptible, together with irrigation regimes. This is probably an indication that the membrane integrity in over-mature celery plants is already compromised at harvest rendering postharvest treatments such as 1-MCP ineffective.

Conclusions

The present study represents the most comprehensive attempt to date to study the preharvest and postharvest factors affecting the development of physiological disorders in fresh-cut celery, taking as physiological models the cultivars ‘Monterey’, ‘Victoria’ and ‘Imperial’. Maturity stage at harvest and irrigation regime were confirmed to be the main factors affecting cut-end browning with browning severity increasing for late harvested plants and the water stress imposed. Postharvest treatment with 1-MCP showed a moderate success in suppressing RR and delaying browning only in celery plants harvested before and at optimum maturity, providing further evidence of the importance of maturity stage for minimising postharvest disorders in fresh-cut celery. These findings can be used by growers and retailers to standardise industry practices ensuring uniform quality and better shelf-life estimations.

Acknowledgments

The authors would like to acknowledge AHDB Horticulture for financial support and thank G’s Fresh Ltd. for supplying all plant material and for providing practical support to carry out the field experimental work. The underlying data can be accessed at:

<https://doi.org/10.17862/cranfield.rd.12496946>.

References

Álvarez, M.V., Ponce, A.G., Moreira, M.R., 2015. Combined effect of bioactive compounds and storage temperature on sensory quality and safety of minimally processed celery, leek and butternut squash. *Journal of Food Safety*, 35(4), 560-574. DOI: <https://doi.org/10.1111/jfs.12206>.

Amoah, R.S., Landahl, S., Terry, L.A., 2017. The timing of exogenous ethylene supplementation differentially affects stored sweet potato roots. *Postharvest Biology and Technology*, 120, 92-102. DOI: <https://doi.org/10.1016/j.postharvbio.2016.05.013>

Anastasiadi, M., Collings, E.R., Shivembe, A., Qian, B., Terry, L.A., 2020. Seasonal and temporal changes during storage affect quality attributes of green asparagus. *Postharvest Biology and Technology*, 159, 111017. DOI: <https://doi.org/10.1016/j.postharvbio.2019.111017>.

Bekhradi, F., Luna, M.C., Delshad, M., Jordan, M.J., Sotomayor, J.A., Martínez-Conesa, C., Gil, M.I. 2015. Effect of deficit irrigation on the postharvest quality of different genotypes of basil including purple and green Iranian cultivars and a Genovese variety. *Postharvest Biology and Technology*, 100, 127-135. DOI: <https://doi.org/10.1016/j.postharvbio.2014.09.017>.

Breschini, S.J., Hartz T.K., 2002. Drip irrigation management affects celery yield and quality. *HortScience*, 37(6), 894-897. DOI: <https://doi.org/10.21273/HORTSCI.37.6.894>

588 Chutichudet, B., Chutichudet, P. and Kaewsit, S. 2011. Influence of Developmental Stage on
 589 Activities of Polyphenol Oxidase, Internal Characteristics and Colour of Lettuce cv. Grand
 590 Rapids. *American Journal of Food Technology*, 6(3), 215-225. DOI:
 591 <https://doi.org/10.3923/ajft.2011.215.225>.

592

593 Collings E.R., García Cas, A.G., Ordaz Ortiz J.J. and Terry L.A. 2013. A new real-time
 594 automated method for measuring in-situ respiration rates of fresh produce. *Acta Horticulturae*,
 595 1012, 1151-1157. DOI: <https://doi.org/10.17660/ActaHortic.2013.1012.155>.

596

597 Craig, W.J. 1999. Health-promoting properties of common herbs. *The American Journal of*
 598 *Clinical Nutrition*, 70 (3), 491s–499s. DOI: <https://doi.org/10.1093/ajcn/70.3.491s>.

599

600 Downes K., Chope G. and Terry L.A. 2010. Postharvest application of ethylene and 1-
 601 methylcyclopropene either before and after curing affects onion (*Allium cepa* L.) bulb quality
 602 during long term cold storage. *Postharvest Biology and Technology*, 55, 36-44. DOI:
 603 <https://doi.org/10.1016/j.postharvbio.2009.08.003>.

604

605 Falagán, N., Terry, L.A., 2018. Recent advances in controlled and modified atmosphere of
 606 fresh produce: Postharvest technologies to reduce food waste and maintain fresh produce
 607 quality. *Johnson Matthey Technology Review*, 62(1), 107-117. DOI:
 608 <http://dx.doi.org/10.1595/205651318x696684>

609

610 Farcuh, M., Copes, B., Le-Navenec, G., MarroquinJ., Jaunet, t., Chi-Ham, C., Cantu, D.,
 611 Bradford, K.J. and Van Deynze, A. 2020. Texture diversity in melon (*Cucumis melo* L.):

612 Sensory and physical assessments. *Postharvest Biology and Technology*, 159, 111024. DOI:
613 <https://doi.org/10.1016/j.postharvbio.2019.111024>
614

615 Finkelstein, R., 2013. Absciscic Acid Synthesis and Response. *The Arabidopsis Book*. American
616 Society of Plant Biologists, 11, 1-36. DOI: <https://doi.org/10.1199/tab.0166>.
617

618 Fujita, Y., Fujita, M., Shinozaki, K., Yamaguchi-Shinozaki, K., 2011. ABA mediated
619 transcriptional regulation in response to osmotic stress in plants. *Journal of Plant Research*,
620 124, 509–525. DOI: : <https://doi.org/10.1007/s10265-011-0412-3>.
621

622 Giné-Bordonaba, J., Terry, L.A., 2008. Biochemical profiling and chemometric analysis of
623 seventeen UK-grown black currant cultivars. *Journal of Agriculture and Food Chemistry*, 56,
624 7422-7430. DOI: <https://doi.org/10.1021/jf8009377>.
625

626 Gómez, P.A. and Artés, F., 2004. Controlled atmospheres enhance postharvest green celery
627 quality. *Postharvest Biology and Technology*, 34(2), 203-209. DOI:
628 <https://doi.org/10.1016/j.postharvbio.2004.04.007>
629

630 Gómez, P.A., and Artés, F., 2005. Improved keeping quality of minimally fresh processed
631 celery sticks by modified atmosphere packaging. *LWT - Food Science and Technology*, 38(4),
632 323-329. DOI: <https://doi.org/10.1016/j.lwt.2004.06.014>.
633

634 Guerra, N., Carrozzi, L., Gõni, M. G., Roura, S., Yommi, A., 2010. Quality Characterization
635 of Celery (*Apium graveolens* L.) by plant zones and two harvest dates. *Journal of Food Science*,
636 75(6), S327-S332. DOI: <https://doi.org/10.1111/j.1750-3841.2010.01701.x>.

637

638 Kader A.A., 1992. Postharvest biology and technology: an overview. In Kader A.A. (ed)
639 Postharvest technology of horticultural crops. UC Publication No. 3311. University of
640 California, Division of Agriculture and Natural Resources, Oakland, pp. 15-20.

641

642 Kang, Y.J., Choi, J.H., Jeong, M.C., Kim, D.M., 2008. Effect of maturity at harvest on the
643 quality of head lettuce during storage. *Korean Journal of Horticultural Science and*
644 *Technology*, 26, 272–276.

645

646 Keller, F., Matile, P., 1989. Storage of sugars and mannitol in petioles of celery leaves. *New*
647 *Phytologist*, 113(3), 291-299. DOI: <https://doi.org/10.1111/j.1469-8137.1989.tb02406.x>.

648

649 Landi, M., Degl’Innocenti, E., Guglielminetti, L., Guidi, L., 2013. Role of ascorbic acid in the
650 inhibition of polyphenol oxidase and the prevention of browning in different browning-
651 sensitive *Lactuca sativa* var. *capitata* (L.) and *Eruca sativa* (Mill.) stored as fresh-cut produce.
652 *Journal of the Science of Food and Agriculture*, 93 (8), 1814-1819. DOI:
653 <https://doi.org/10.1002/jsfa.5969>.

654

655 Liang, Y., Were, L., 2020. Cysteine’s effects on chlorogenic acid quinone induced greening
656 and browning: Mechanism and effect on antioxidant reducing capacity. *Food Chemistry*, 309,
657 125697. DOI: <https://doi.org/10.1016/j.foodchem.2019.125697>

658

659 Loaiza-Velarde, J.G., Mangrich, M.E., Campos-Vargas, R., Saltveit, M., 2003. Heat shock
660 reduces browning of fresh-cut celery petioles. *Postharvest Biology and Technology*, 27(3),
661 305-311. DOI: [https://doi.org/10.1016/S0925-5214\(02\)00118-7](https://doi.org/10.1016/S0925-5214(02)00118-7).

662

663 Luna, M.C., Tudela, J.A., Martínez-Sánchez, A., Allende, A., Marín, A., Gil, M.I., 2012. Long-
664 term deficit and excess of irrigation influences quality and browning related enzymes and
665 phenolic metabolism of fresh-cut iceberg lettuce (*Lactuca sativa* L.). *Postharvest Biology and*
666 *Technology*, 73, 37-45. DOI: <https://doi.org/10.1016/j.postharvbio.2012.05.011>.

667

668 Luna, M.C., Tudela, J.A., Martínez-Sánchez, A., Allende, A., Gil, M.I., 2013. Optimizing
669 water management to control respiration rate and reduce browning and microbial load of fresh-
670 cut romaine lettuce. *Postharvest Biology and Technology*, 80, 9-17. DOI:
671 <https://doi.org/10.1016/j.postharvbio.2013.01.005>.

672

673 MacLean, D.D., Murr, D.P., DeEll, J.R., Mackay, A.B., Kupferman, E.M., 2007. Inhibition of
674 PAL, CHS, and ERS1 in 'Red d'Anjou' Pear (*Pyrus communis* L.) by 1-MCP. *Postharvest*
675 *Biology and Technology*, 45(1), 46-55. DOI:
676 <https://doi.org/10.1016/j.postharvbio.2007.01.007>

677

678 Massolo, J.F., González Forte, L., Concellón, A., Zulma-Viña, S., Vicente, A.R., 2019. Effects
679 of ethylene and 1-MCP on quality maintenance of fresh cut celery. *Postharvest Biology and*
680 *Technology*, 148, 176-183. DOI: <https://doi.org/10.1016/j.postharvbio.2018.11.007>.

681

682 Mastropasqua, L., Tanzarella, P., Paciolla, C., 2016. Effects of postharvest light spectra on
683 quality and health-related parameters in green *Asparagus officinalis* L. *Postharvest Biology*
684 *and Technology*, 112, 143-151. DOI: <https://doi.org/10.1016/j.postharvbio.2015.10.010>.

685

McEvily, A.J., Iyengar, R., Otwell, W.S., 1992. Inhibition of enzymatic browning in foods and beverages. *Critical Reviews in Food Science and Nutrition*, 32(3), 253-273. DOI: <http://dx.doi.org/10.1080/10408399209527599>.

Murata, M., Sugiura, M., Sonokawa, Y., Shimamura, T., Homma, S., 2002. Properties of chlorogenic acid quinone: relationship between browning and the formation of hydrogen peroxide from a quinone solution. *Bioscience, Biotechnology, And Biochemistry*, 66(12), 2525-2530, DOI: <http://dx.doi.org/10.1271/bbb.66.2525>

Ordaz-Ortiz, J.J., Foukaraki, S., Terry, L.A., 2015. Assessing temporal flux of plant hormones in stored processing potatoes using high definition accurate mass spectrometry. *Horticultural Research*, 2, 15002. DOI: <https://doi.org/10.1038/hortres.2015.2>.

Page, T., Griffiths, G., Buchanan-Wollaston, V., 2001. Molecular and Biochemical Characterization of Postharvest Senescence in Broccoli. *Plant Physiology*, 125, 718-727. DOI: <https://doi.org/10.1104/pp.125.2.718>.

Pressman, E., Huberman, M., Aloni, B., Jaffe, M.J., 1984. Pithiness in plants: I. The effect of mechanical perturbation and the involvement of ethylene in petiole pithiness in celery. *Plant Cell Physiology*, 25 (6), 891-897. DOI: <https://doi.org/10.1093/oxfordjournals.pcp.a076803>

Queiroz, C., Mendes-Lopes, M.L., Fialho, E., Valente-Mesquita, V.L., 2008. Polyphenol Oxidase: Characteristics and Mechanisms of Browning Control. *Food Reviews International*, 24(4), 361-375. DOI: <https://doi.org/10.1080/87559120802089332>.

711 Rodrigues, M.L., Chaves, M.M., Wendler, R., David, M.M., Quick, W.P., Leegood, R.C., Stitt
712 M., Pereira J.S., 1993. Osmotic adjustment in water stressed grapevine leaves in relation to
713 carbon assimilation. *Australian Journal of Plant Physiology*, 20(3), 309 – 321. DOI:
714 <https://doi.org/10.1071/pp9930309>.

715

716 Saltveit, M.E., Mangrich M.E., 1996. Using density measurement to study the effect of
717 excision, storage, abscisic acid, and ethylene on pithiness in celery petioles. *Journal of the*
718 *American Society of Horticultural Science*, 121, 137-141. DOI:
719 <https://doi.org/10.21273/JASHS.121.1.137>.

720

721 Sharp, R.E., 2002. Interaction with ethylene: changing views on the role of abscisic acid in root
722 and shoot growth responses to water stress. *Plant, Cell & Environment*, 25(2), 211-222. DOI:
723 <https://doi.org/10.1046/j.1365-3040.2002.00798.x>.

724

725 Steuer, B., Stuhlfauth, T., Heinrich, P.F., 1988. The efficiency of water use in water stressed
726 plants is increased due to ABA induced stomatal closure. *Photosynthesis Research* 18 (3), 327–
727 336.

728

729 Terry, L.A., Ilkenhans T., Poulston S., Rowsell L., Smith A.W.J., 2007a. Development of a
730 new palladium-promoted ethylene scavenger. *Postharvest Biology and Technology*, 45, 214-
731 220. DOI: <https://doi.org/10.1016/j.postharvbio.2006.11.020>.

732

733 Terry, L.A., Chope, G.A., Giné-Bordonaba, J., 2007b. Effect of water deficit irrigation and
734 inoculation with *Botrytis cinerea* on strawberry (*Fragaria x ananassa*) fruit quality. *Journal of*

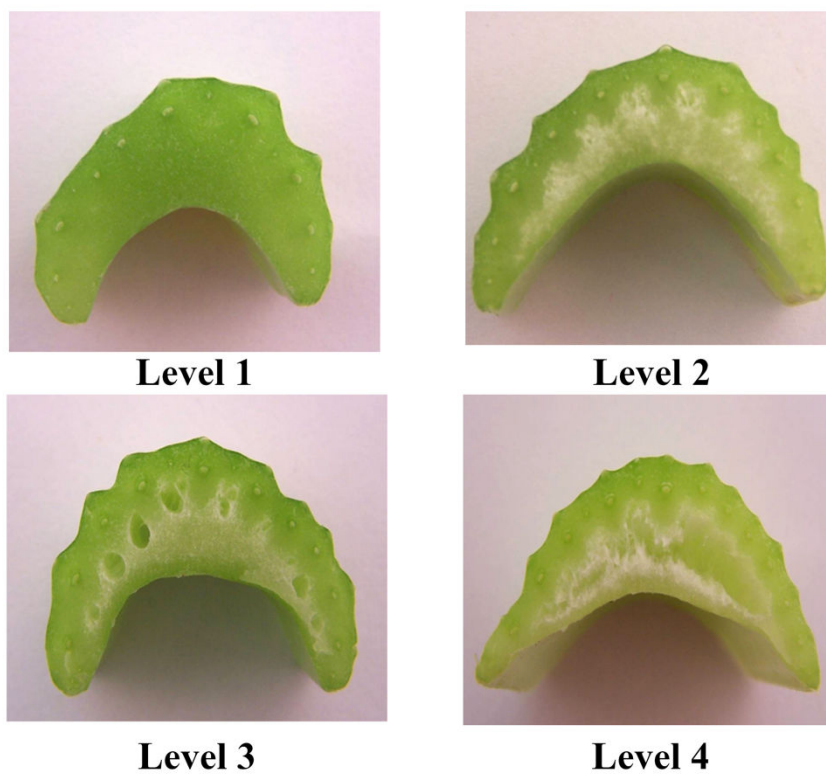
735 *Agricultural and Food Chemistry*, 55(26), 10812-10819. DOI:
 736 <https://doi.org/10.1021/jf072101n>.
 737

738 Vinã, S.Z., Chaves, A.R., 2003. Texture changes in fresh cut celery during refrigerated storage.
 739 *Journal of the Science of Food and Agriculture*, 83, 1308–1314. DOI:
 740 <https://doi.org/10.1002/jsfa.1540>.
 741

742 Viña, S.Z., Chaves, A.R., 2008. Effect of heat treatment and refrigerated storage on antioxidant
 743 properties of pre-cut celery (*Apium graveolens* L.). *International Journal of Food Science and*
 744 *Technology*, 43, 44-51. DOI: <https://doi.org/10.1111/j.1365-2621.2006.01380.x>.
 745

746 Wang, Y.T., Chen, Z.Y., Jiang, Y., Duan, B.B. and Xi, Z.M. 2019. Involvement of ABA and
 747 antioxidant system in brassinosteroid-induced water stress tolerance of grapevine (*Vitis*
 748 *vinifera* L.). *Scientia Horticulturae*, 256, 108596. DOI:
 749 <https://doi.org/10.1016/j.scienta.2019.108596>.
 750

751 Zhan, L., Hu, J., Lim, L.T., Pang, L., Li, Y., Shao, J., 2013. Light exposure inhibiting tissue
 752 browning and improving capacity of fresh-cut celery (*Apium graveolens* var. dulce). *Food*
 753 *Chemistry*, 141, 2473-2478. DOI: <https://doi.org/10.1016/j.foodchem.2013.05.035>.
 754



756

757 **Figure S1.** Visual scale used to assess pithiness disorder in celery, provided by G's Fresh Ltd.

758 Level 1: 'no pithiness'; Level 2: 'slight pithiness'; Level 3: 'moderate pithiness'; Level 4:

759 'severe pithiness'.



Level 1



Level 2



Level 3

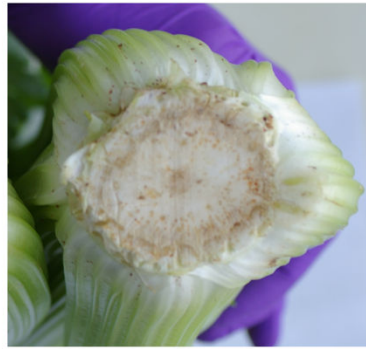


Level 4

760

761 **Figure S2.** Comparative visual scale for assessing browning at cut petiole ends of celery. Level
 762 1: ‘absent’; Level 2: ‘slight’, Level 3; ‘evident’; Level 4: ‘severe’.

763



Level 1



Level 2



Level 3



Level 4

764

765 **Figure S3.** Comparative visual scale for assessing browning at butt ends of celery. Level 1:

766 ‘absent’; Level 2: ‘slight’, Level 3; ‘evident’; Level 4: ‘severe’.

767

768

769

770 **Table S1.** Details of growing conditions, harvest frequency, year and location for Exp 1.

Season	Year	Location	Soil	Weather conditions	Harvest frequency
Early Spanish	March - April 2014	Puntal-Campo de Golf farm, Cartagena, Spain Coordinates: 37°36'42.55" N; 0°47'38.34" W	Soil type: fine texture clay-loam soil, Soil composition: clay: 33.8%, silt: 22.3%, sand: 43.9%, (EcoSur Laboratories, Murcia, Spain), Soil pH: 8.34 at 20 °C.	Avg Temp (°C): 12.5 ± 2.4 Avg Relative Humidity (%) : 60.3 ± 13.2 Total rainfall (mm): 41.8	weekly
Late Spanish	May – June 2015	Barranquillo farm, Cartagena, Spain Coordinates: 3 7°44'13.86" N; 0°58'39.08" W	Soil type: medium texture loam soil, Soil composition: clay: 29.4%, silt: 25.2%, sand: 45.4% (EcoSur Laboratories, Murcia, Spain), Soil pH: 8.5 at 20 °C.	Avg Temp (°C): 16.3 ± 3.0 Avg Relative Humidity (%) : 56.2 ± 11.0 Total rainfall (mm): 6.0	weekly
Late UK	August – Sept 2014	Dimmocks Cote farm, Cambridgeshire, UK Coordinates: 52°19'57.7" N, 0°15'58.3" E.	Soil type: Fenland peaty soil	Avg Temp (°C): 17.3 ± 2.8 Avg Relative Humidity (%) : 69.8 ± 10.8 Total rainfall (mm): 245.7	weekly

771

772

773 **Table S2.** Details of growing conditions, harvest frequency, year and location for Exp 3.

Year	Location	Soil	Treatments	Harvest
July – Nov 2015	Cranfield University, Bedfordshire, UK Coordinates: 52° 4' 9.1992" N; 0° 37' 52.9068";	Soil type: Fenland peaty soil from Dimmocks Cote Farm (Stretham, Ely, Cambridgeshire) fields (coordinates: 52°19'57.7" N; 0°15'58.3" E)	Fertiliser: NPK 10-10-30 + 3.3 MgO + trace elements water soluble fertilizer (Universol Violet, LBS Horticulture Ltd) Pesticides: Aphox® (2.5g in 5 L of water); Movento® (1 mL in 1 L of water)	At stalk length ~55 cm

774

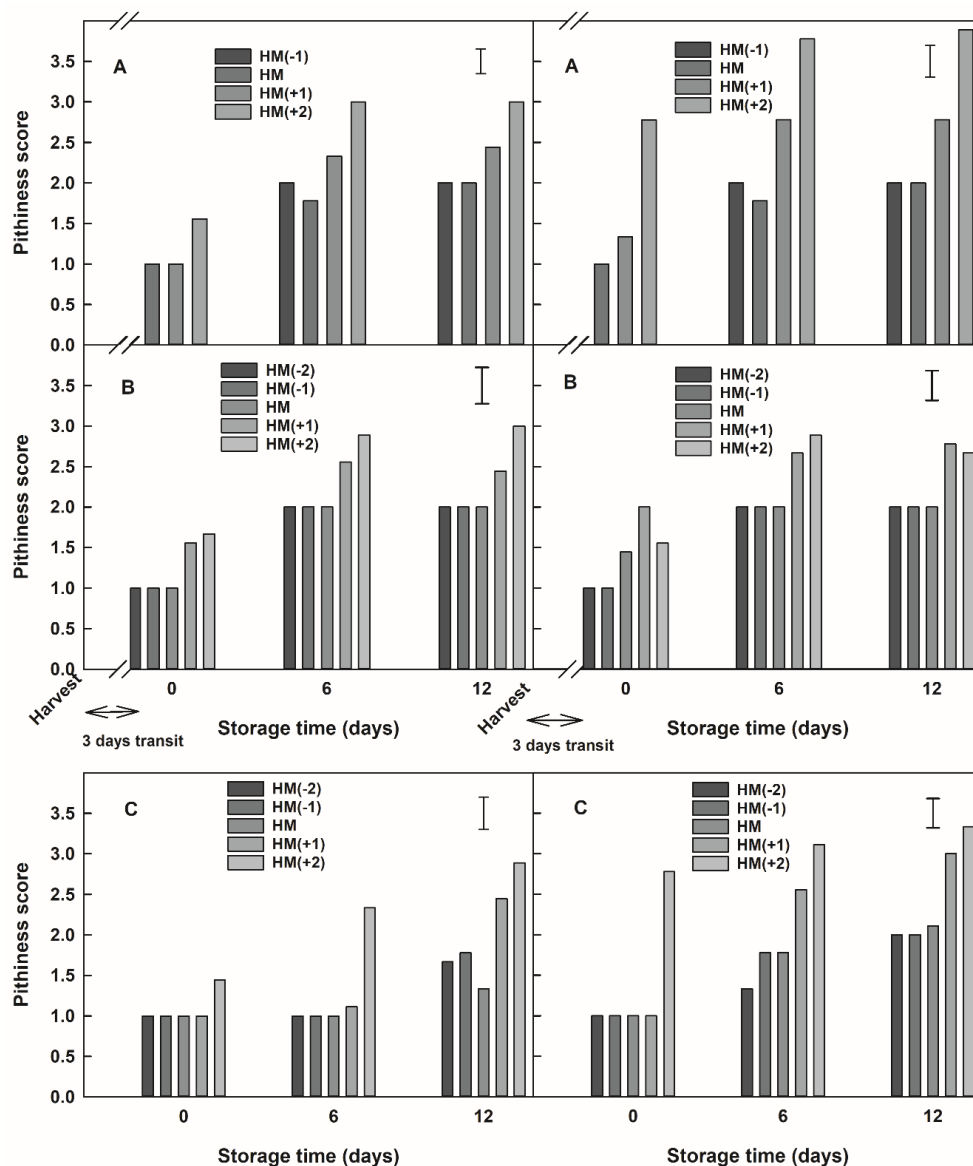


Figure S4 [A-C]. Pithiness score - during shelf-life (20 °C) - of celery samples at cut petiole ends (on the left) and butt ends (on the right), grown in three seasons (A: early Spanish season; B: late Spanish season; C: late UK season) and belonging to five different harvest maturities [HM (-2): two weeks before optimum harvest date; HM (-1): one week before optimum harvest date; HM: optimum harvest date; HM (+1): one week after optimum harvest date; HM (+2): two weeks after optimum harvest date]. Error bars represent least significant differences (LSD).

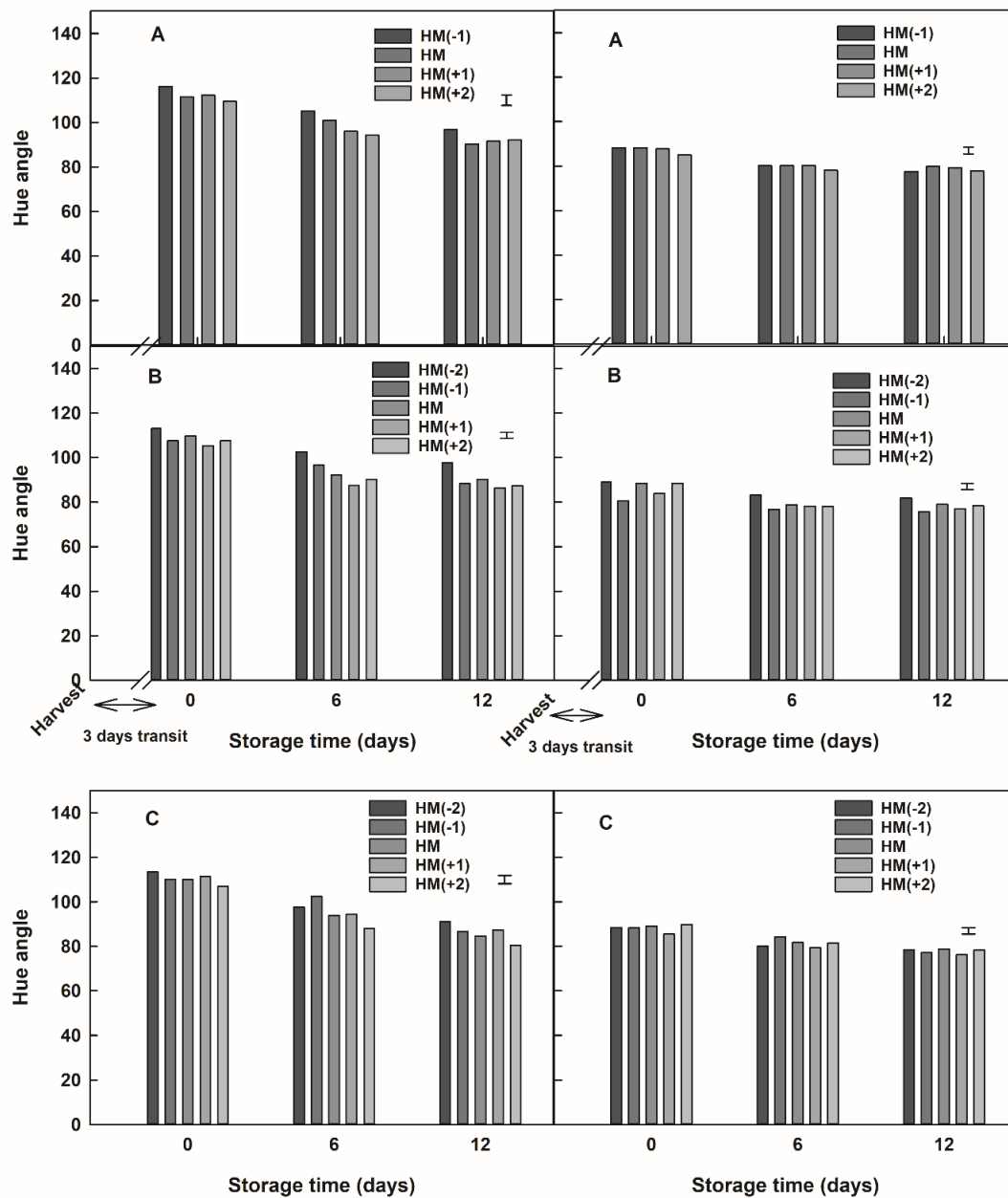


Figure S5. Objective colour of celery at cut petiole ends (on the left) and butt ends (on the right), grown in three seasons (A: early Spanish season; B: late Spanish season; C: late UK season) and belonging to five different harvest maturities [HM (-2): two weeks before optimum harvest date; HM (-1): one week before optimum harvest date; HM: optimum harvest date; HM (+1): one week after optimum harvest date; HM (+2): two weeks after optimum harvest date)]. Bars represent least significant differences (LSD).

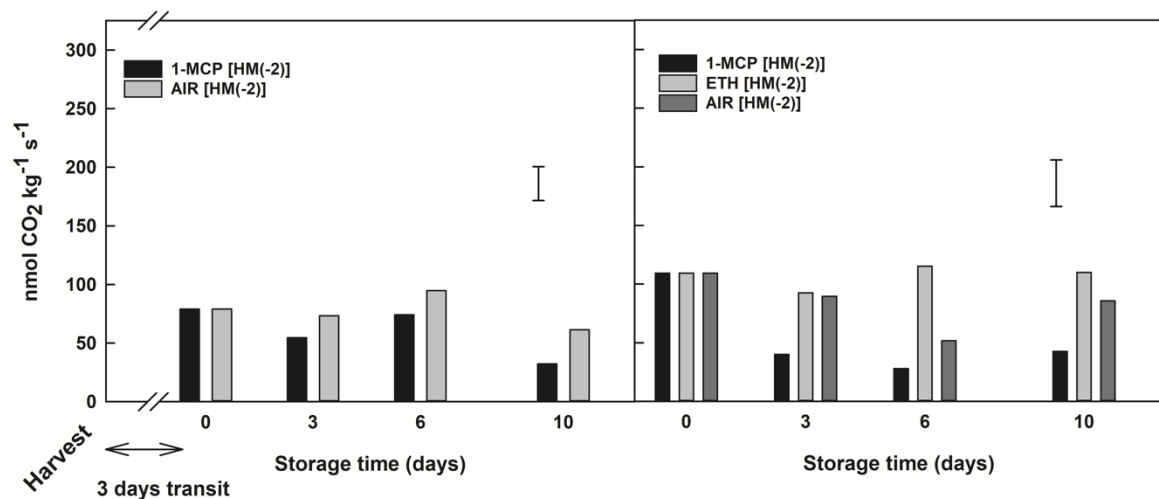


Figure S6. Respiration rate of celery grown in the Late Spanish season (left) and the Late UK season (right) and harvested two weeks prior to optimum maturity [HM(-2)]. Bar with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at 20 °C, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

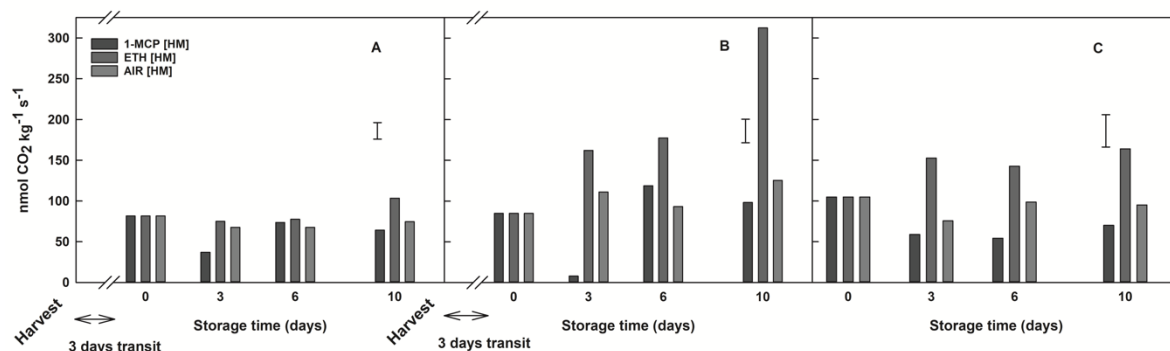


Figure S7. Respiration rate of celery grown in the Early Spanish season (A) Late Spanish season (B) and the Late UK season (C) and harvested at optimum maturity [HM]. Bar with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at 20 °C, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

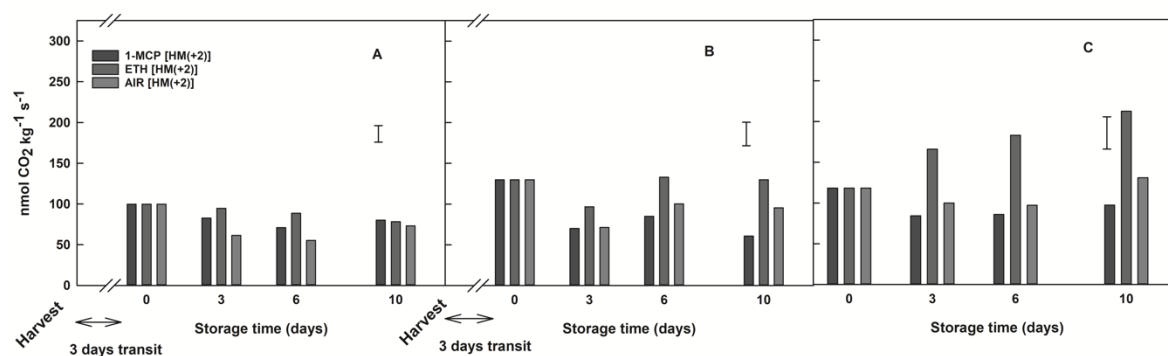


Figure S8. Respiration rate of celery grown in the Early Spanish season (A) Late Spanish season (B) and the Late UK season (C) and harvested two weeks after optimum maturity [HM(+2)]. Bar colour indicates different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at 20 °C, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

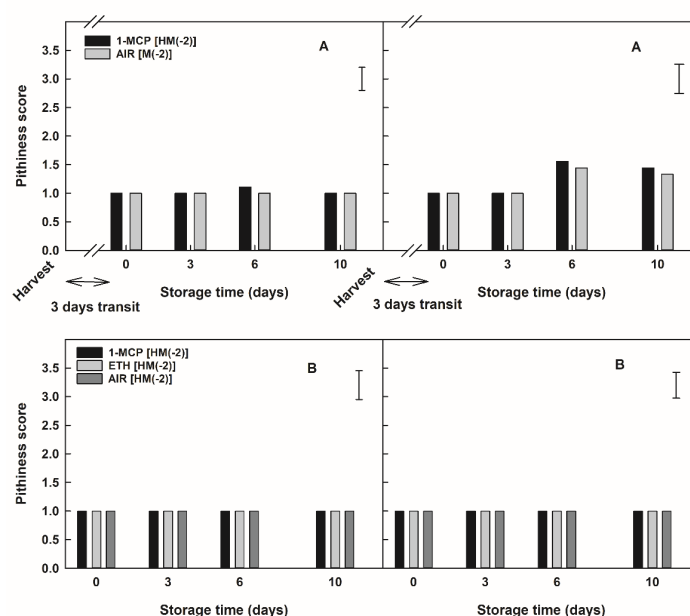
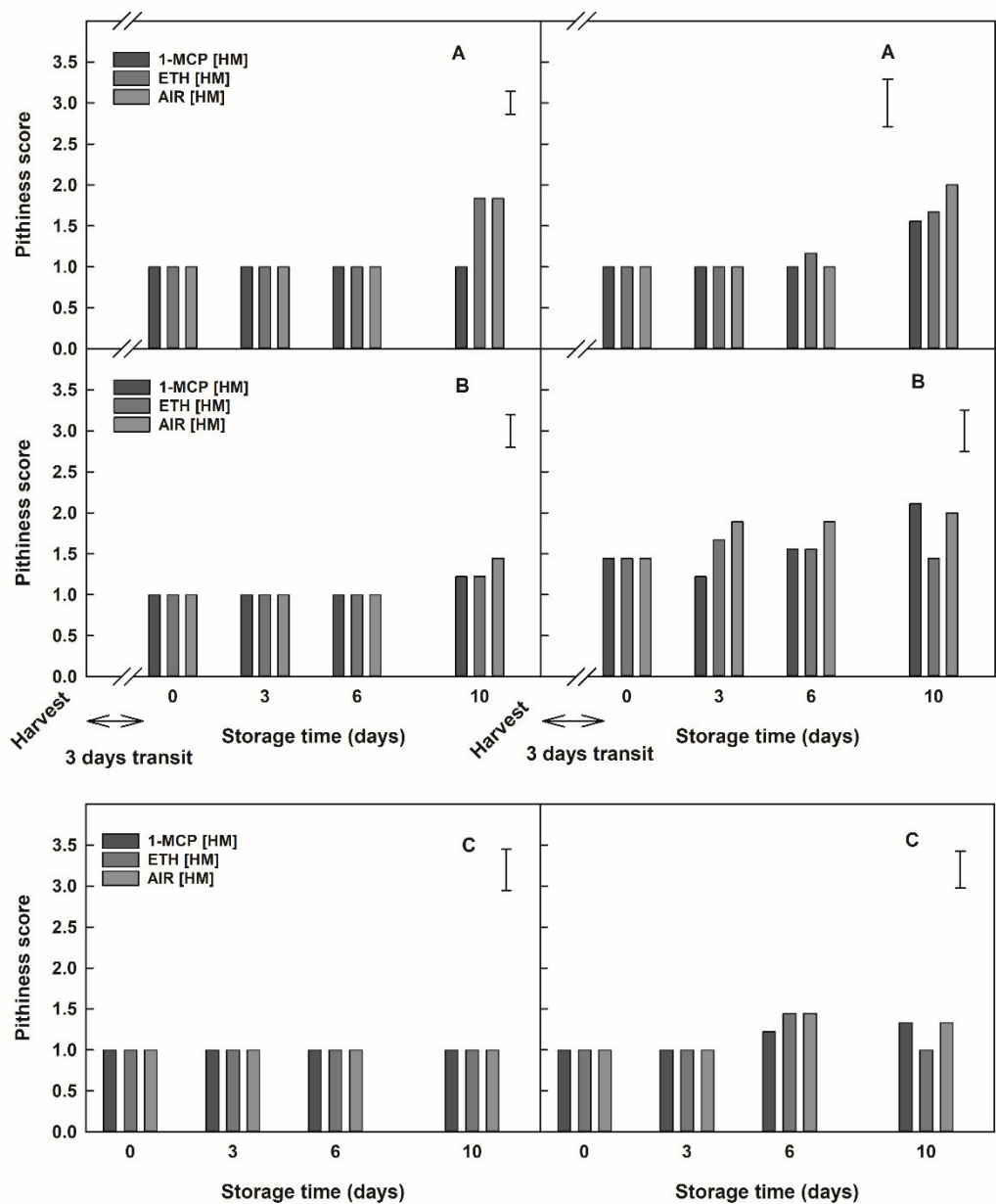
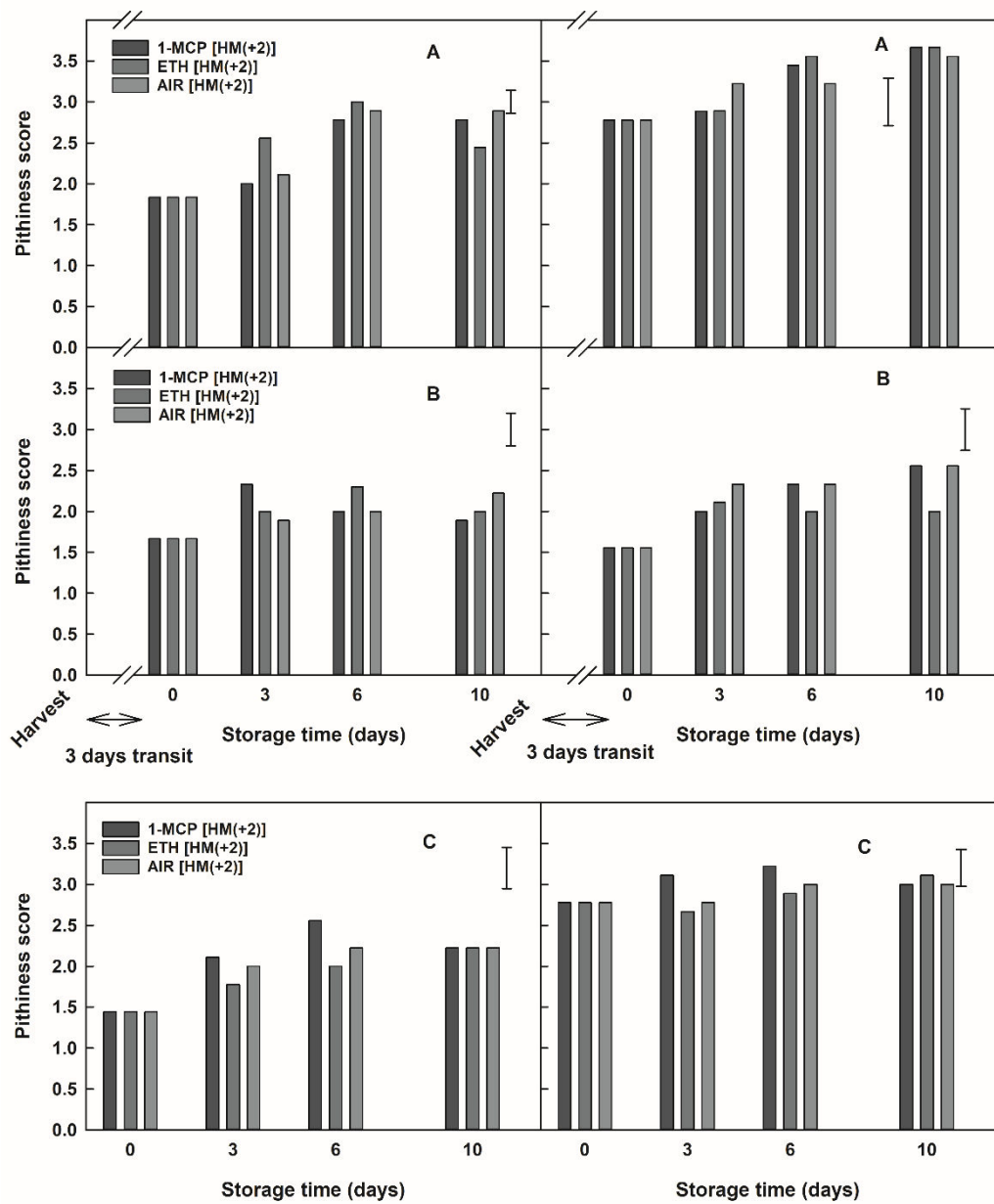


Figure S9. Pithiness score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Late Spanish season (A) and the Late UK season (B) and harvested two weeks prior to optimum maturity [HM(-2)]. Bars with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at 20 °C, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

814 = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least
 815 significant differences (LSD).



816
 817 **Figure S10.** Pithiness score of celery at cut petiole ends (on the left) and butt ends (on the right)
 818 and grown in the Early Spanish Season (A), Late Spanish season (B) and the Late UK season
 819 (C) and harvested at optimum maturity [HM]. Bars with different colours indicate different
 820 postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at
 821 20 °C, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars
 822 represent least significant differences (LSD).



824

825 **Figure S11.** Pithiness score of celery at cut petiole ends (on the left) and butt ends (on the right)
826 and grown in the Early Spanish season (A), the Late Spanish season (B) and the Late UK season
827 (C) and harvested two weeks after optimum maturity [HM(+2)]. Bars with different colours
828 indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-
829 MCP for 24 h at 20 $^{\circ}\text{C}$, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)].
830 Error bars represent least significant differences (LSD).

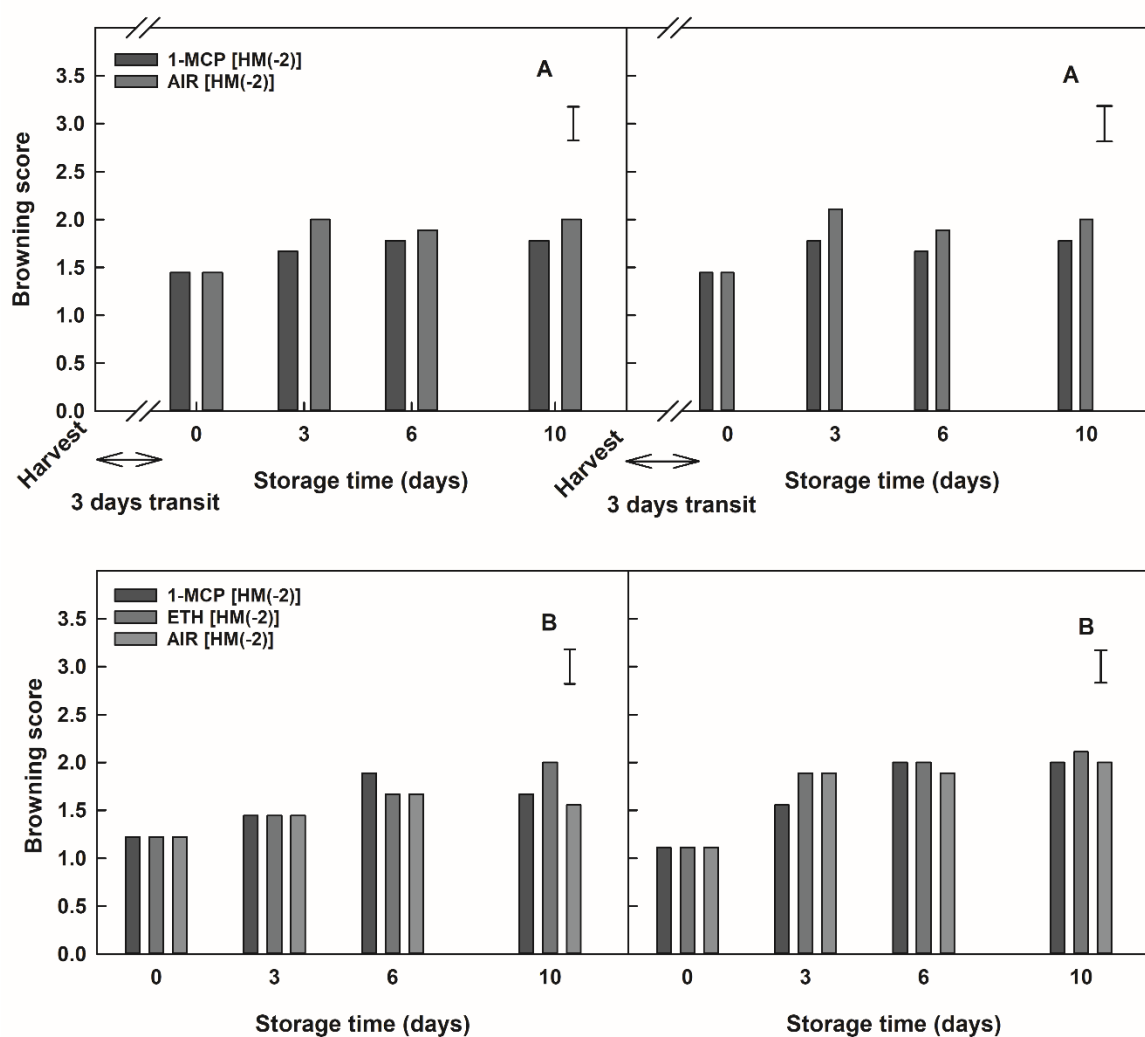


Figure S12. Browning score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Late Spanish season (A) and the Late UK season (B) and harvested two weeks prior to optimum maturity [HM(-2)]. Bars with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at 20 $^{\circ}\text{C}$, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

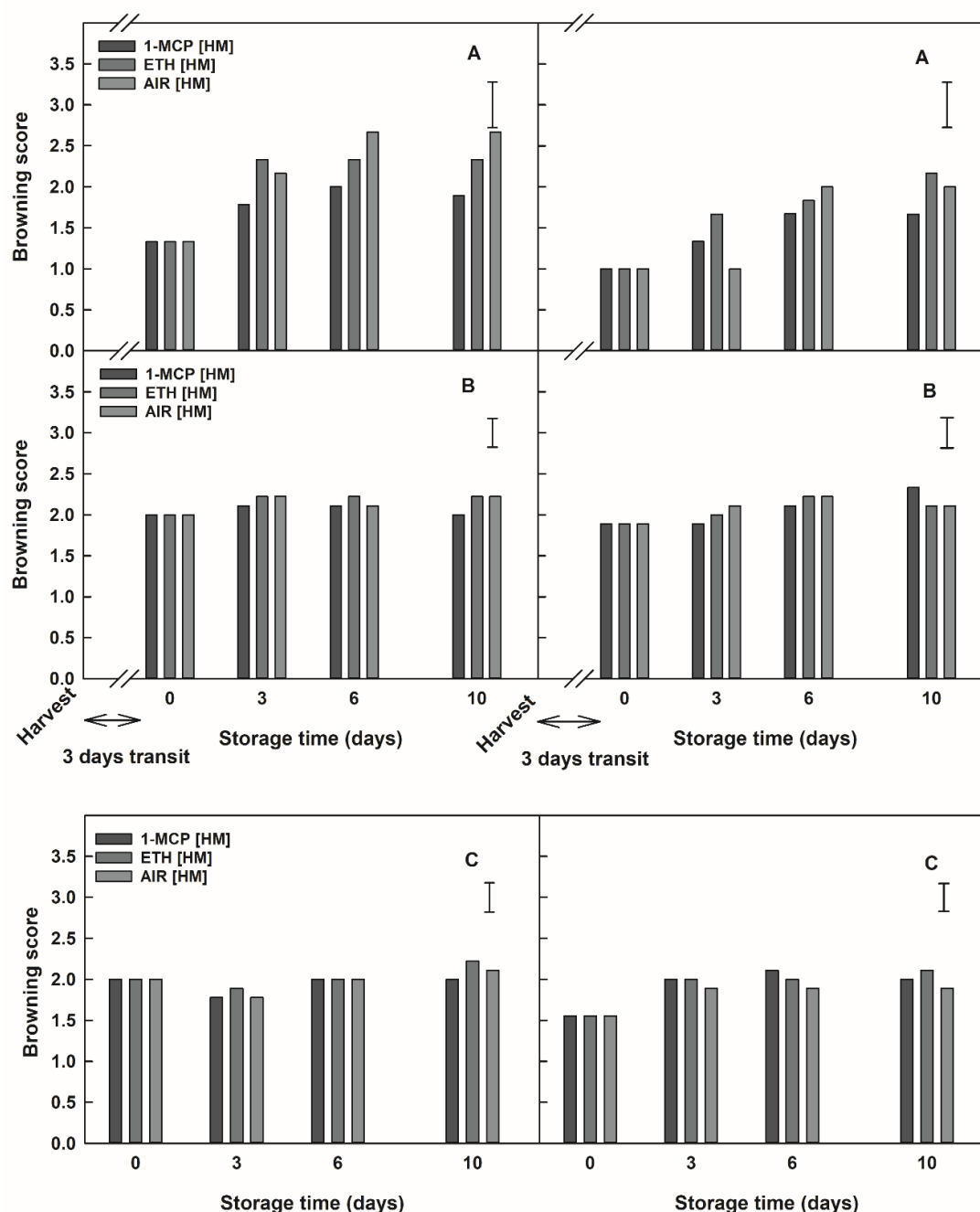


Figure S13. Browning score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Early Spanish Season (A), Late Spanish season (B) and the Late UK season (C) and harvested at optimum maturity [HM]. Bars with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to $1 \mu\text{L L}^{-1}$ 1-MCP for 24 h at 20°C , ETH = $10 \mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

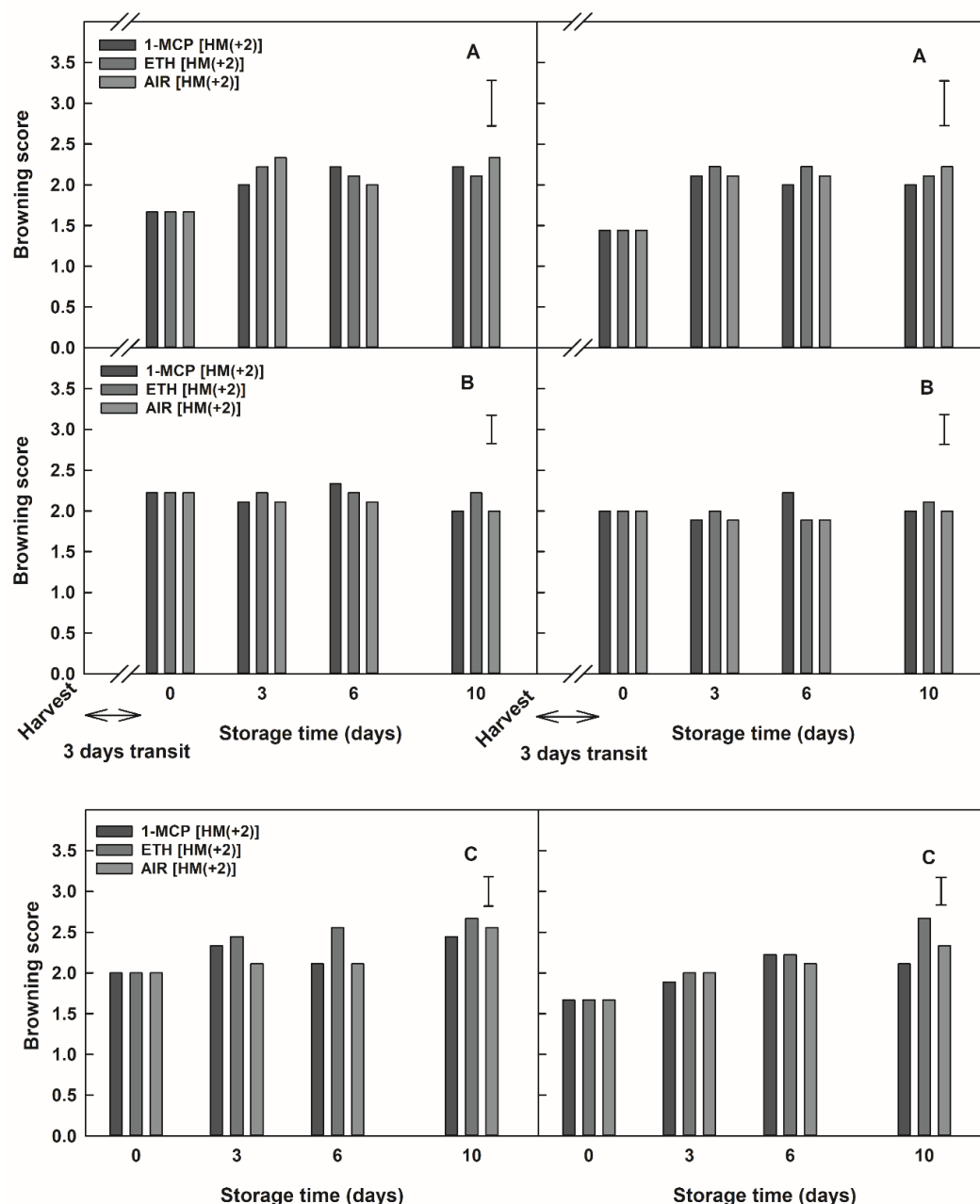


Figure S14. Browning score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Early Spanish season (A), Late Spanish season (B) and the Late UK season (C) and harvested two weeks after optimum maturity [HM(+2)]. Bars with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 $\mu\text{L L}^{-1}$ 1-MCP for 24 h at 20 °C, ETH = 10 $\mu\text{L L}^{-1}$ continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

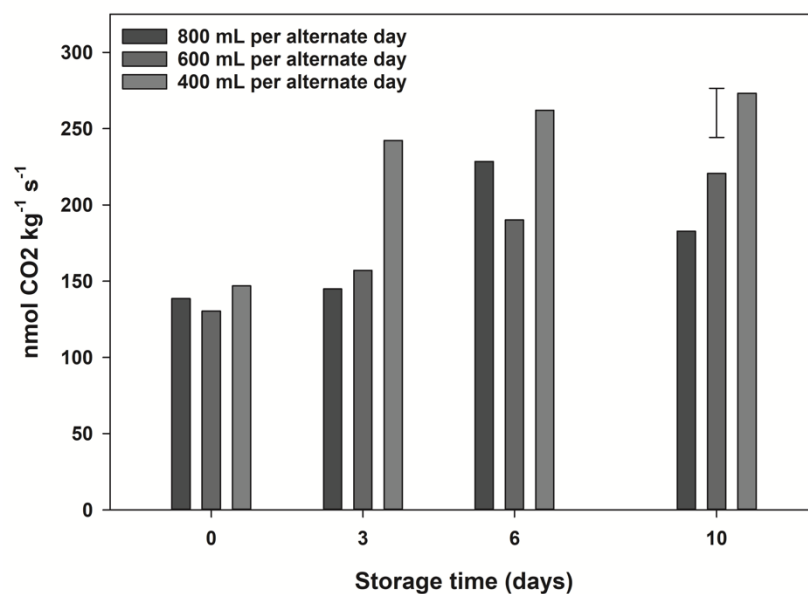


Figure S15. Effect of water treatments on the respiration rate of celery during shelf-life. Bars with different colours indicate different water treatments: Error bars represent least significant differences (LSD).

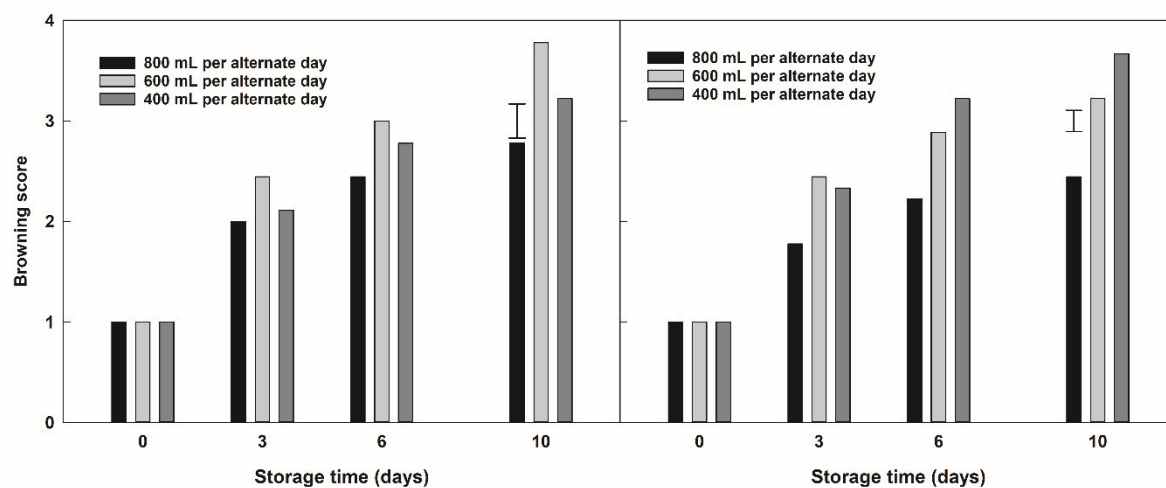


Figure S16. Effect of water treatments on browning development in celery during shelf-life, at cut petiole ends (on the left) and butt ends (on the right). Bars with different colours indicate different water treatments: Error bars represent least significant differences (LSD).

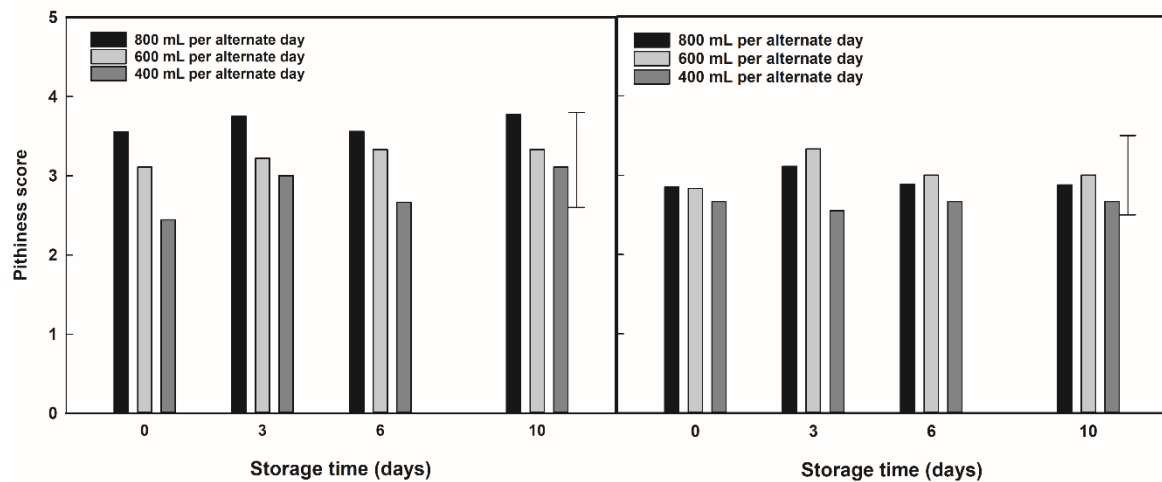


Figure S17. Effect of water treatments on pithiness development at cut petiole ends (on the left) and butt ends (on the right) of celery. Bars with different colours indicate different water treatments: Error bars represent least significant differences (LSD).

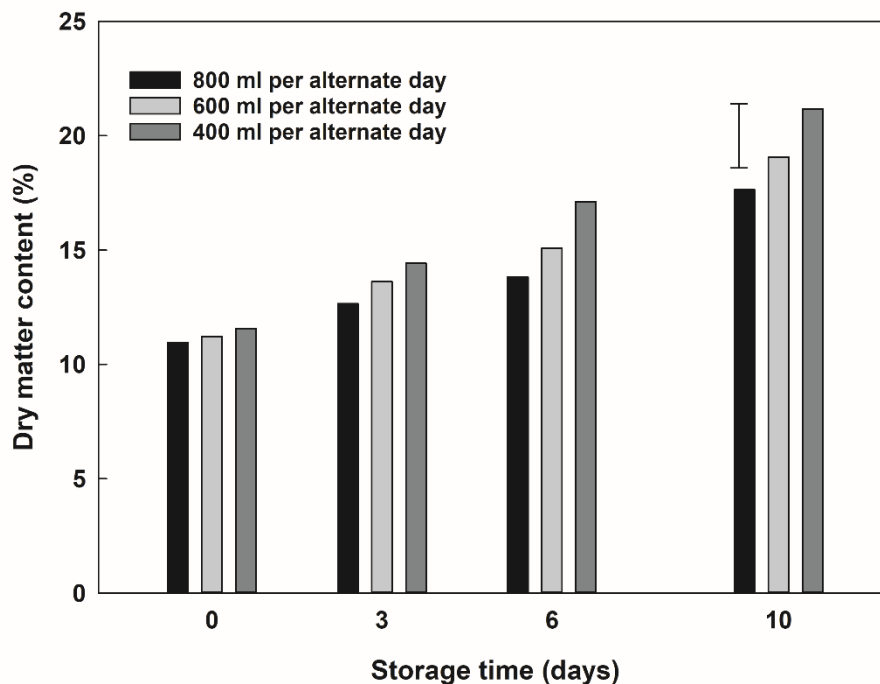


Figure S18. Effect of water treatments on the dry matter content of celery. Bars with different colours indicate different water treatments: 800 mL every alternate day, 600 mL every alternate day and 400 mL every alternate day. Error bars represent least significant differences (LSD).



DSPACE

<https://dspace.org/>

A comprehensive study of factors affecting postharvest disorder development in celery

Anastasiadi, Maria; Falagán, Natalia; Rossi, Simone; Terry, Leon A.

2020-11-05

Elsevier

<https://doi.org/10.1016/j.postharvbio.2020.111384>

Anastasiadi M, Falagán N, Rossi S, Terry LA. (2021) A comprehensive study of factors affecting postharvest disorder development in celery. *Postharvest Biology and Technology*, Volume 172, February 2021, Article number 111384