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A comprehensive study of factors affecting postharvest disorder development in celery

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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 ºC) 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 ºC); and c) the effect of preharvest deficit irrigation on the quality of fresh-cut celery during shelf-life (20 ºC). 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

50 evidence indicates that pithiness can be induced by pre-harvest factors. For instance, infrequent
51 drip irrigation during summer periods has been shown to significantly increase pithiness
52 (Breschini and Hartz, 2002; Saltveit and Mangrich, 1996). Also, mechanical perturbation and
53 Ethephon application increased pithiness, especially at the basal part of the petioles (Pressman
54 et al., 1984).
55 Previous research has developed solutions to minimise postharvest browning in celery. For
56 example, heat shock treatments significantly reduced browning potential (Loaiza-Velarde et
57 al., 2003; Viña and Chaves, 2008). Gómez and Artés (2004) showed that celery stalks stored
58 in controlled atmosphere (CA) with high CO_2 concentration (> 7 kPa) maintained a greener
59 colour compared to control. Also, the application of ethylene inhibitors such as 1-
60 methylcyclopropene (1-MCP) together with refrigeration showed promising potential for
61 extending the shelf-life of fresh-cut self-blanching celery (Massolo et al., 2019). This shelf life
62 extension is possible because PAL is regulated by ethylene. When fresh produce are treated
63 with 1-MCP the expression of transcripts for PAL and ethylene receptors decrease (*Pc-PAL*
64 and *Pc-ERS1*, respectively), reducing PAL activity and therefore the formation of quinones
65 precursors (MacLean et al., 2007). It is well-reported that controlling respiration rate is key to
66 delaying senescence. Together with organic acids, sugars are the main substrate for respiration
67 (Falagán and Terry, 2018) and indicators of metabolic processes leading to postharvest
68 disorders. Despite previous research into the causes of browning in fresh-cut celery the
69 underlying physiological and biochemical mechanisms involved have not yet been fully
70 elucidated.
71 In addition, the influence of preharvest factors on the development of postharvest browning are
72 not well understood. Guerra et al. (2010) reported that a delay in celery harvest date increased
73 its browning potential and total quinones content. Research on other crops susceptible to
74 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 synthetized 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

100 Spanish spring season [(cv. 'Monterey'); between 10 March and 7 April], the second in the late
101 Spanish spring season [(cv. 'Monterey'); between 5 May and 2 June], and the third in the late
102 UK season [(cv. 'Victoria'); between 11 August and 8 September]. Details of growing
103 conditions, geographical coordinates and harvest frequency are included in **Table S1**).
104 In all three trials, the experimental field was divided into three blocks: top, middle and bottom
105 and samples were randomly harvested from each block. Harvest took place at different
106 horticultural maturity stages: a) two weeks prior to optimum harvest date [HM(-2)], b) one
107 week before optimum harvest date [HM(-1)], c) at optimum harvest date [HM], d) one week
108 after optimum harvest date [HM(+1)] and e) two weeks after optimum harvest date [HM(+2)].
109 Celery was hand-picked using a lightweight field knife. Optimum harvest dates were decided
110 by considering two parameters: stalk length (~ 55 cm) and the expected harvest date indicated
111 in reference schedule tables prepared by G's Fresh Ltd. every growing season. Plants were then
112 packed directly in the field. Thereafter, they were vacuum-cooled to 3 °C as per standard
113 commercial practice and dispatched (2 h transit) to the Plant Science Laboratory (PSL) at
114 Cranfield University (Beds., UK) via refrigerated freight (5 °C), within three days.
115 Upon arrival, celery plants were washed under running tap water to remove soil and dried with
116 a soft paper towel. Subsequently the celery samples were randomly divided into two batches
117 (for shelf-life and cold storage evaluation).
118
119 2.1.2. Shelf-life assessment
120 The celery plants selected for shelf-life assessment were placed into three different crates
121 (replicates) per horticultural maturity stage in a storage room at constant temperature of 20 °C
122 and 56 RH%. Storage temperature was set up at 20 °C to encourage browning, hence, to
123 represent a worst-case scenario in the supply chain. Thereafter, samples were subjected to
124 visual, physiological and biochemical analysis at regular time intervals. More precisely,

125 samples were analysed upon receipt (baseline), after 6 d and 12 d in storage. Three replicates
126 were taken from each crate for a total of 9 replicates for each sampling day.
127
128 **2.2. Experiment 2: Postharvest treatments under cold storage**
129 2.2.1. Plant material
130 The aim of this experiment (Exp. 2) was to study the effect of postharvest treatments on the
131 development of physiological disorders under cold storage conditions. A subsample of the
132 celery plants at different horticultural maturity stages ([HM(-2)], [HM], [HM(+2)]) harvested
133 for Exp. 1 was used for Exp. 2.
134
135 2.2.2. Ethylene and 1-MCP treatments
136 Celery selected for cold storage were divided into three batches and subjected to the following
137 treatments: a) continuous air (control), b) continuous exogenous ethylene (Et) and c) 1-MCP.
138 All samples were stored at 5 °C and 95% relative humidity (RH) for 10 d in total. For ethylene
139 treatment, samples were placed in water-sealed, 264 L polypropylene boxes covered with
140 polypropylene lids and flushed with continuous exogenous ethylene at 10 μL L^{-1} concentration.
141 The gas flow was controlled from a 50 L cylinder of 5000 μL L^{-1} certified standard
142 concentration ethylene in nitrogen (BOC, Surrey, UK) and was reduced to 10 μL L^{-1} by mixing
143 with pure flowing air following Amoah et al. (2017). Analysis was carried out as previously
144 described in Terry et al. (2007a).
145 1-MCP treatment was applied as reported by Downes et al. (2010) with slight modifications.
146 A sample of 1.47 g 1-MCP powder (SmartFresh®, Rohm and Haas, product code: AFxRD-
147 0014) was mixed with 16.3 mL of warm water (50 °C) and shaken to release 1 μL L^{-1}
148 concentration in water sealed 264 L polypropylene boxes.
149

150 **2.3. Experiment 3: Postharvest response to deficit irrigation**

151 2.3.1. Plant material

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

160

161 2.3.2. Experimental design and sampling

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

175 immediately transferred to 20 °C constant temperature. Visual and physiological attributes
176 were assessed immediately after harvest, after 3, 6 and 10 d of storage (baseline, sampling day
177 1, sampling day 2 and sampling day 3 respectively).
178
179 2.3.3. Physiological determinations
180 *2.3.3.1 Respiration rate*
181 Respiration rate (RR) of celery plants was measured at 20 °C as reported by Collings et al.
182 (2013) with slight modifications using a Sable Respirometry System (Model 1.3.8 Pro, Sable
183 Systems International, NV, USA). Samples were incubated in 16 L air-tight polypropylene
184 boxes (L&L NordicOÜ, Estonia) in continuous air flushed by an 80 HP pump (Hiblow, Techno
185 Takatsuki Ltd., Philippines). Boxes were connected through Nalgene PVC tubes of 3 mm
186 internal diameter (Thermo Scientific, Rochester, NY) to the CA-10 carbon dioxide (Firmware
187 version 1.05) and FC-10 oxygen detectors (Firmware version 3.0) of the Sable System to detect
188 O_2 consumption / CO_2 emission real time for 10 min over three cycles. In addition, a water
189 vapour pressure detector (RH-300) was used to measure relative humidity in the outflowing
190 air. Data were analysed with ExpeData software (Release 1.3.8, PRO Version) and reported as
191 nmol CO_2 kg^{-1} s^{-1}.
192
193 *2.3.3.2. Pithiness*
194 Samples were visually assessed for pithiness at both cut petiole and butt ends of celery. A visual
195 scale from 1 to 4, provided by G's Fresh Ltd., was used to assess pithiness with 1 corresponding
196 to 'no pithiness' and 4 corresponding to 'severe pithiness' (**Figure S1**). Photos of celery
197 samples were taken at both cut ends to be used as references. Prior to visual assessment,
198 samples were cut 5 mm from the apical cut petiole ends and 5 cm from the butt ends.
199

200 *2.3.3.3. Colour*

201 Samples were visually assessed for browning at both cut petiole and butt ends of celery. A
202 visual scale from 1 to 4, was used again in this case to assess browning with 1 corresponding
203 to 'no browning' and 4 corresponding to 'severe browning'. Photos of celery samples were
204 taken at both ends to be used as references (**Figure S2-S3**).
205 Objective colour was measured with a CR-400 Minolta colorimeter and DP-400 data processor
206 (Minolta Co. Ltd, Japan) at both cut petiole and butt ends of each celery head. Each individual
207 measurement was the mean of four measurements randomly taken on both cut surfaces. Data
208 were expressed as chroma (C*), hue angle (H°) and lightness (L*) which were automatically
209 calculated. Calibration of the instrument was done using a Minolta standard white tile CR-400.
210
211 2.3.4. Biochemical analysis
212 *2.3.4.1. Sample preparation for biochemical analysis*
213 Cut celery sticks were snap-frozen in liquid nitrogen and stored at -40 ºC prior to freeze-drying
214 (Coolsafe 55-9 Scanvac, Scanlaf A/S, Lynge, Denmark). Lyophilised samples were powdered
215 with a mortar grinder (RM 200, Retsch Ltd., Derby., UK) and stored at -40 °C until further
216 analysis.
217
218 *2.3.4.2. Analysis of individual phenolic compounds*
219 Lyophilised powder (50 mg) were extracted and subjected to HPLC analysis and analysed
220 according to Giné-Bordonaba and Terry (2008). Agilent ChemStation Rev. B.02.01 software
221 was used for data integration and quantification.
222
223 *2.3.4.3. Analysis of soluble sugars*

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

2.3.4.4. Analysis of ABA and ABA catabolites

Extraction and quantification of ABA and ABA catabolites was assessed according to the method by Ordaz-Ortiz et al. (2015) with modifications as described in Anastasiadi et al. (2020). Lyophilized celery tissue (100 mg) was mixed with 6 mL 75:20:5 methanol:water:formic acid solvent (v/v/v). Then, 30 μL of 400 ng mL^{-1} internal standard mixture solution (deuterated compounds) was added to the extraction mixture and vortexed for 2 min and shaken at 4 °C for 1 h, then centrifuged for 15 min at 4500 rpm. Supernatant was removed and evaporated in a ScanVac freeze-dried overnight at -110 °C. Samples were then reconstituted with 400 μL of 10:99.9:0.1 acetonitrile:water:formic acid solvent, vortexed for 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 Eclypse Plus C18 column (2.1 x 50 mm, 1.8 μm 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**).

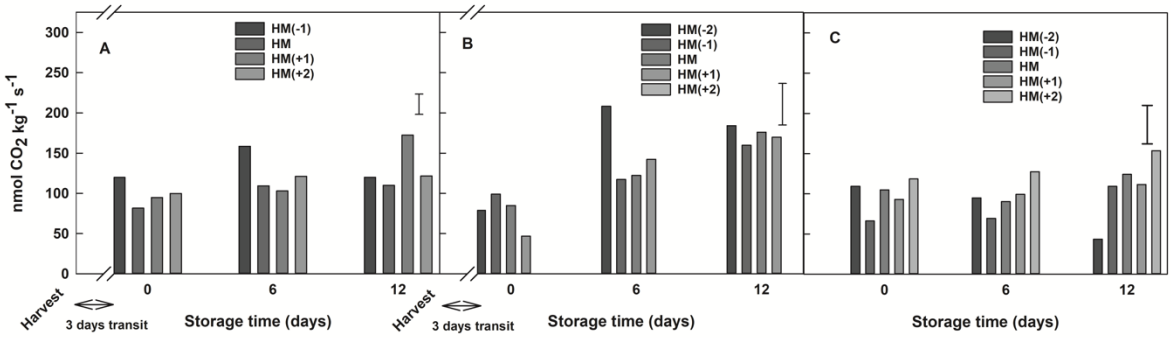
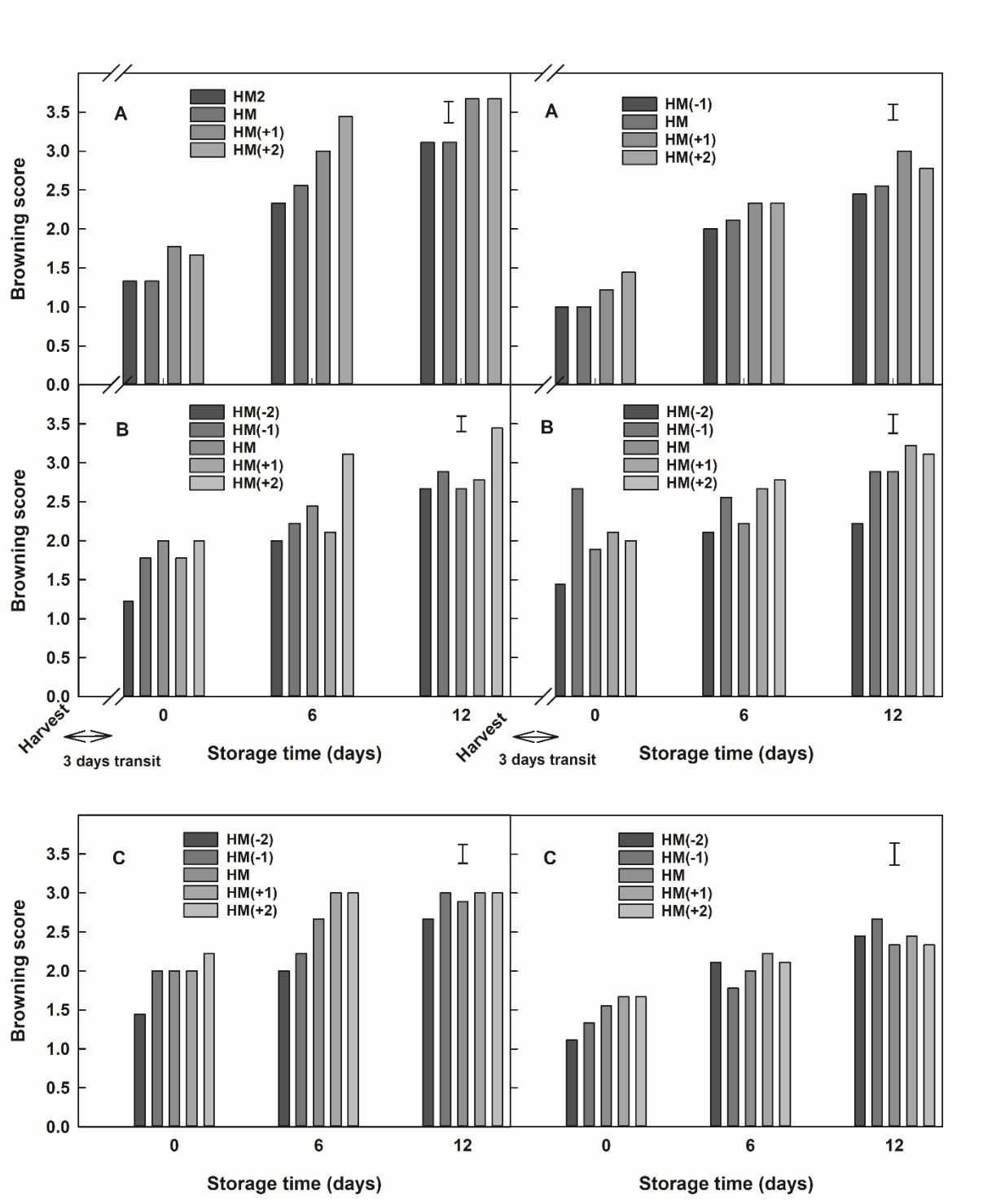


Figure 1. Respiration rate during shelf-life (20 ºC) of celery samples grown in three different seasons (A: early Spanish season; B: late Spanish season; C: late UK season) and belonging to five different harvest maturities [HM (-2): two weeks before optimum harvest date; HM (-1): one week before optimum 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 Hº which exhibited a systematic drop from harvest with values stabilising between 75-90 Hº by

the end of shelf life (**Figure S5**). This change in Hº 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 Hº values compared to samples harvested after the optimum harvest period, retaining a lighter yellow colour during shelf-life, especially in the butt ends.



299 **Figure 2.** Subjective colour score at 20 ºC of celery during shelf-life at cut petiole ends (on the
300 left) and butt ends (on the right), grown in three seasons (A: early Spanish season; B: late
301 Spanish season; C: late UK season) and belonging to five different harvest maturities [HM (-
302 2): two weeks before optimum harvest date; HM (-1): one week before optimum harvest date;
303 HM: optimum harvest date; HM (+1): one week after optimum harvest date; HM (+2): two
304 weeks after optimum harvest date]. Error bars represent least significant differences (LSD).
305
306 With respect to phenolic compounds, chlorogenic acid was mainly found in the butt ends and
307 cut petiole ends tissues of celery, rather than middle outer, apical inner and middle inner
308 petioles tissues (**Figure 3)**. In general, chlorogenic acid content was relatively low at harvest
309 (< 1.0 g kg^{-1} DW) irrespective of tissue, maturity level, season or cultivar and increased over
310 storage time at both butt and apical cut petiole ends. The highest concentrations were observed
311 after 12 d of shelf-life in the butt ends of optimum harvested celery plants [HM] grown in the
312 late Spanish season showing a more than 6-fold increase from harvest (**Figure 3B)**. A similar
313 pattern was observed in the early Spanish season. In contrast, samples from the UK season
314 deviated from this pattern, with chlorogenic acid in the butt ends remaining either stable or
315 exhibiting a moderate increase during shelf-life. The concentration of chlorogenic acid was
316 positively correlated with the subjective browning score of celery grown in all three seasons
317 with the highest correlation observed for butt ends in the Early Spanish season (R = 0.77).

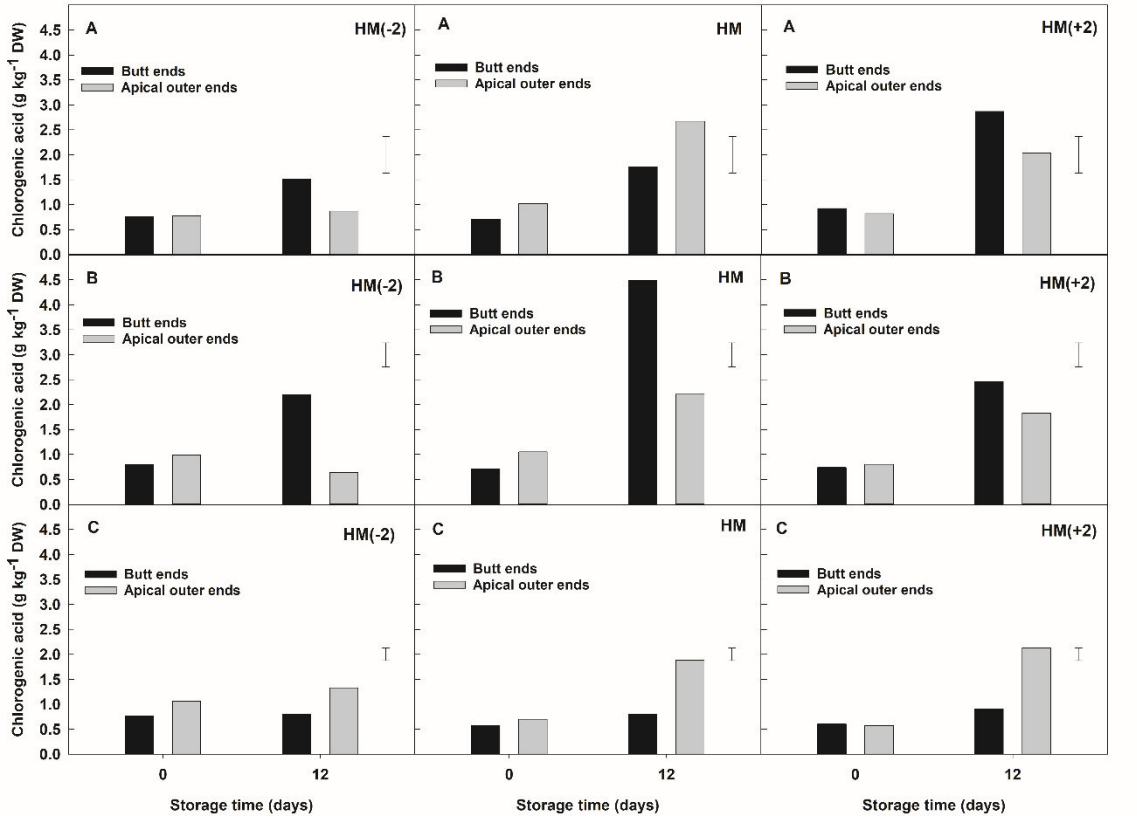


Figure 3. Effect of crop maturity stage on the chlorogenic acid content at butt ends and apical outer ends of celery (cv. 'Monterey') grown in the Early Spanish [A], (cv. 'Monterey') grown in the Late Spanish [B], and (cv. 'Victoria') grown in the Late UK season [C]; all stored in air at 20 °C. HM (-2): 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.

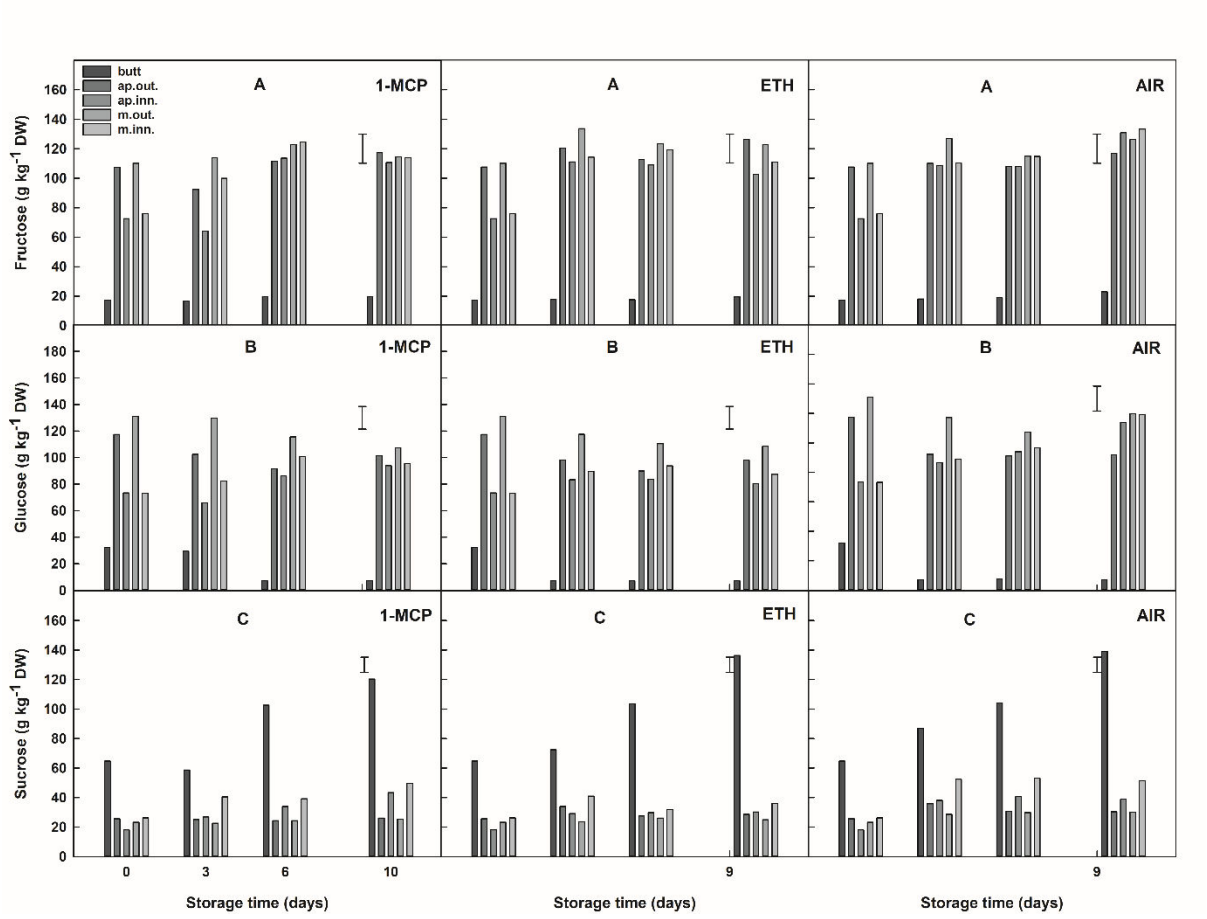


Figure 4. Concentration of fructose (A), glucose (B) and sucrose (C) at different celery sections harvested at optimum maturity in the late UK season and subjected to different postharvest treatments [1-MCP = continuous air after exposure to 1 µL L^{-1} 1-MCP for 24 h at 20 °C, ETH = 10 µL L^{-1} continuous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

370 inner petioles, m.out = middle outer petioles, m.inn = middle inner petioles). Error bars
371 represent least significant differences (LSD).
372
373 **3.3. Severe water stress increases postharvest browning**
374 In Exp. 3, RR increased in heavily stressed celery plants, which exhibited a 2-fold increase in
375 respiration after 3 d of storage and consistently maintained higher RR throughout the storage
376 period (**Figure S15**). Also, results indicated that increased water stress largely affected
377 browning development in celery butt ends especially at the end of the storage period (**Figure**
378 **S16**). In contrast, water stress or storage duration did not appear to significantly influence
379 pithiness development in celery (**Figure S17**), in contrast with previous studies (Breschini and
380 Hartz, 2002; Saltveit and Mangrich, 1996). This disparity can be related to genotype. Pithiness
381 scores were comparable between water treatments especially in the butt ends, although deficit
382 irrigation seemed to result in less incidents of the disorder, but the results were not statistically
383 significant due to the large variability between biological replicates. It should also be noted
384 that pithiness scores were relatively high for all samples even on harvest day, with scores
385 ranging from 2.5 to 3.5 on day 0. This indicated that the disorder had already developed before
386 optimum maturity was reached.
387 Irrigation regime did not affect chlorogenic content at harvest, but had a significant impact in
388 the development of chlorogenic acid in the butt ends of cut celery during shelf-life. As shown
389 in **Figure 5**, celery samples grown under no water stress (800 mL every after alternate day)
390 and light water stress (600 mL every alternate day) exhibited a greater than 3-fold increase in
391 chlorogenic acid after 6 d in storage (**Figure 5**). Samples grown under heavy water stress (400
392 mL every after alternate day) showed no differences. Chlorogenic acid content in the apical
393 outer ends remained relatively stable during shelf-life irrespective of the irrigation regime
394 applied.

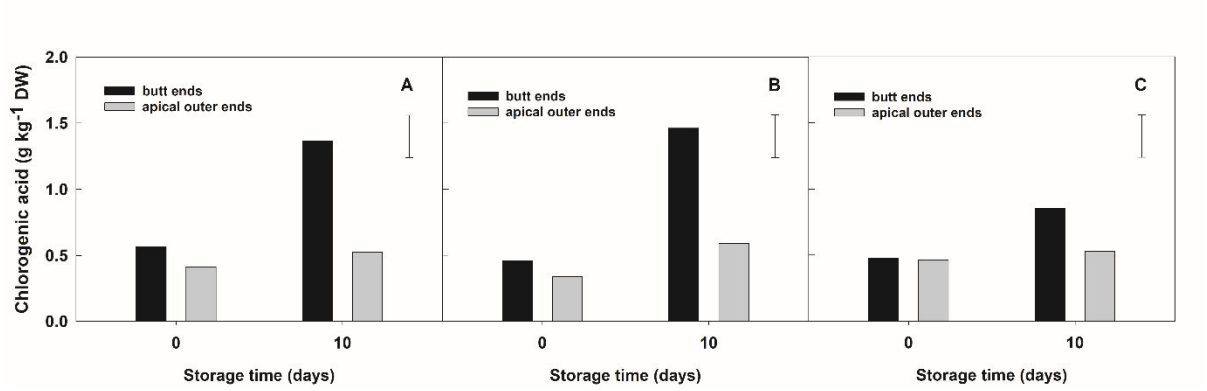
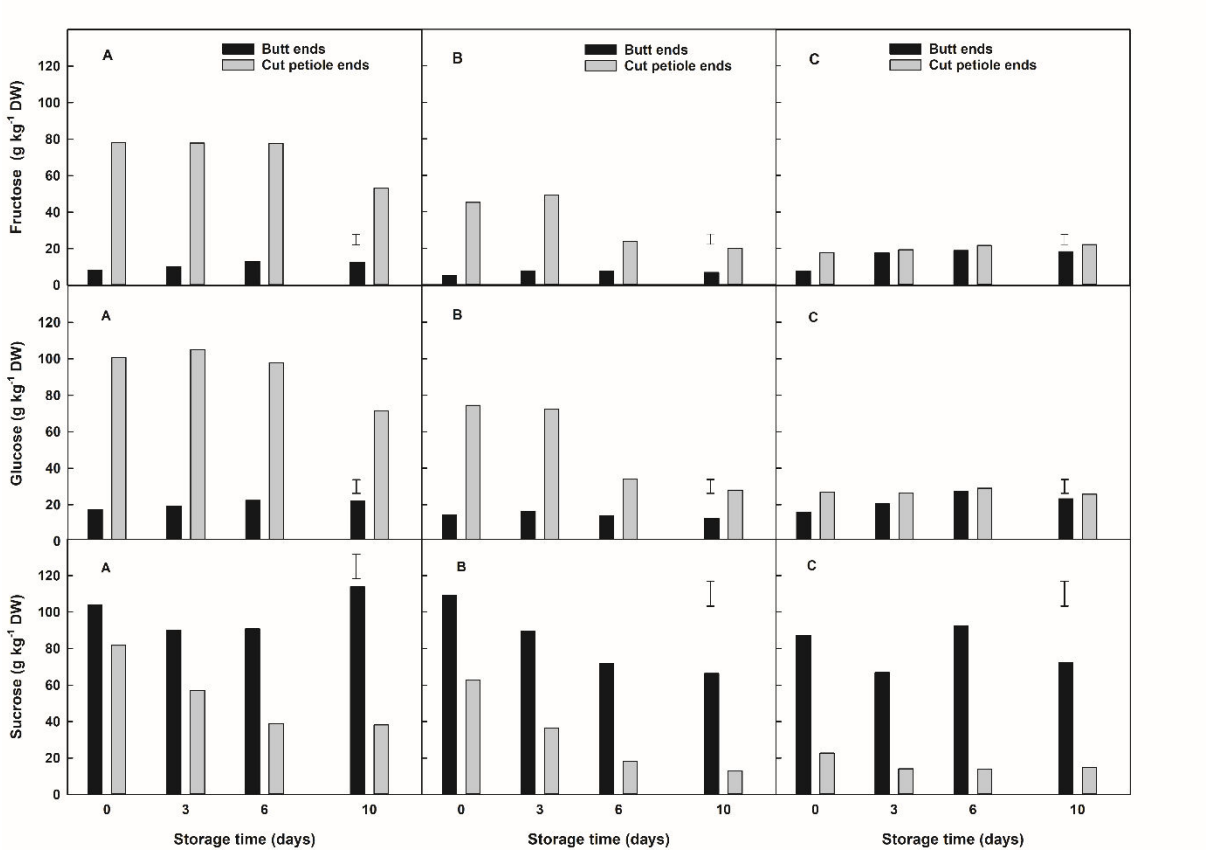


Figure 5. Chlorogenic acid content during shelf-life in the butt ends and apical outer ends of celery irrigated with 800 mL (A), 600 mL (B) and 400 mL (C) of water every alternate day. Samples were harvested at optimum maturity and stored in air at 20 °C for 10 d. Error bars represent least significant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



412

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

416

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

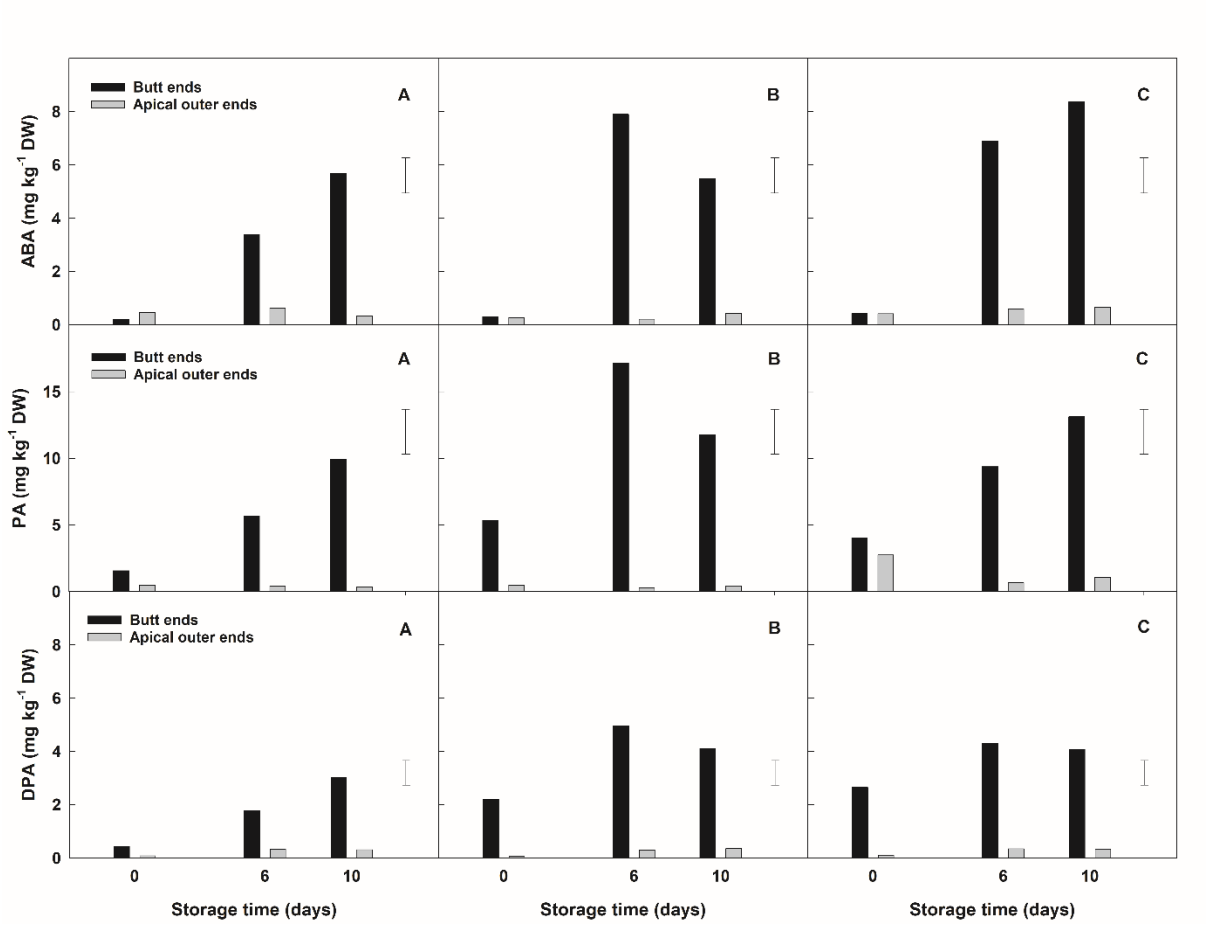


Figure 7. Content of ABA, PA and DPA at butt ends and apical outer ends of celery irrigated with 800 mL (A), 600 mL (B) and 400 mL (C) of water every alternate day. Error bars represent least significant differences (LSD).

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.

438 The development of browning and pithiness in celery was positively linked with storage time,
439 maturity stage and water stress. Browning development rose steeply during the first 6 d of
440 storage and was particularly evident in cut petiole ends. Spanish grown celery had higher
441 browning scores compared to UK grown celery, which could be attributed to the longer transit
442 time (3 d) and possibly genotypic variation.
443
444 *4.1.1 Maturity stage at harvest*
445 Physiological measurements showed that immature celery samples from the early and late
446 Spanish season had a steep increase in RR during the first 6 d in storage and generally
447 maintained higher RR throughout storage compared to samples harvested at optimum or post-
448 optimum maturity. This observation was directly linked to the developmental stage of celery
449 plants at the time of harvest with immature plants retaining higher metabolic activity
450 postharvest. High postharvest RR in immature plant tissues has been reported in other crops,
451 such as asparagus spears and broccoli heads, and has been linked to rapid quality deterioration
452 (Kader 1992; Page, Griffiths, & Buchanan-Wollaston, 2001). However, browning severity in
453 celery plants harvested at different maturity stages, was negatively correlated with RR and was
454 positively correlated with chlorogenic acid concentrations, which generally increased in
455 tandem during storage. The latter finding is in contrast with previous work by Viña and Chaves
456 (2006) who reported that chlorogenic acid content in celery sharply decreased at different
457 storage temperatures (0, 4 and 10 °C) over a period of 28 d. This contradiction could be
458 attributed to differences in cultivar (self-whitening 'Golden Boy' *vs* green celery cultivars
459 'Monterey' and 'Victoria' studied herein) and storage conditions.
460 The positive correlation of increased browning severity and maturity stage at harvest agrees
461 with Guerra et al., (2010) who also reported that the browning potential of leaf stalks of the
462 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

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

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

The severe browning incidence postharvest recorded for celery plants growing under heavy water stress coincided with significantly higher RR throughout storage indicating elevated metabolic activity which could have led to accelerated senescence. Furthermore, browning incidence in butt ends was most severe in the most water-stressed samples despite the fact that chlorogenic acid content was *ca.* 2-fold lower compared to the other two irrigation regimes. This observation could further support the assumption that water stressed plants were in a more advanced stage of senescence causing disruption of membrane integrity and browning development. In addition, ABA content exhibited a rapid increase in water-stressed samples during shelf-life, compared to control samples (800 mL water every alternate day), which also increased but at a reduced rate. A similar pattern was recorded for PA and DPA. The accumulation of ABA in plant tissues under water stress has also been observed in previous studies (Wang et al., 2019; Farcuh et al., 2020). The role of ABA in stomatal regulation as a response to salt/water stress has been well documented (reviewed in Finkelstein, 2013). ABA 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 ºC, 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.

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

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Supplementary Material

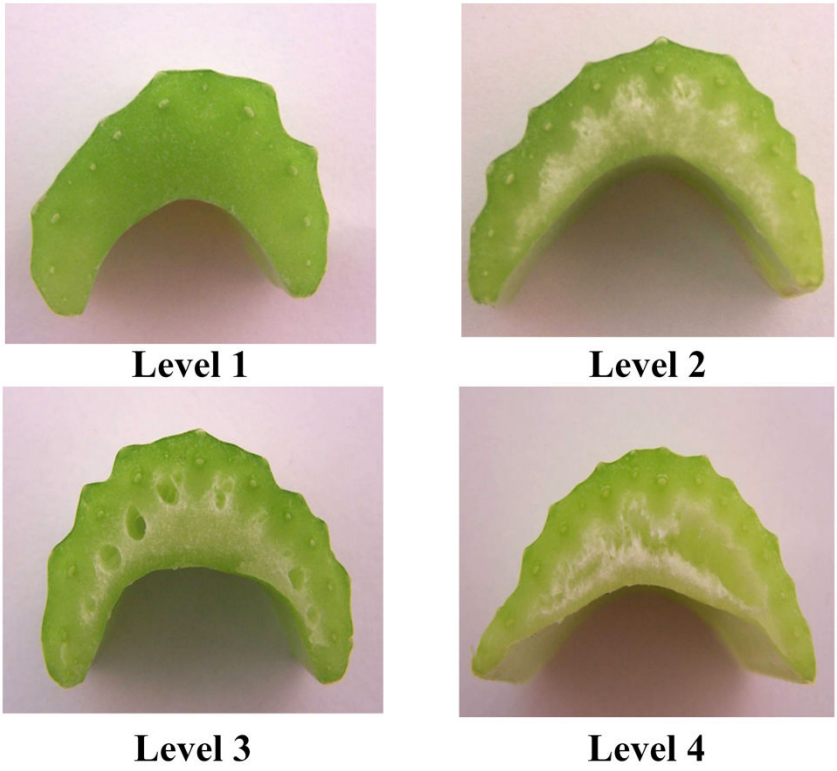

Figure S1. Visual scale used to assess pithiness disorder in celery, provided by G's Fresh Ltd. Level 1: 'no pithiness'; Level 2: 'slight pithiness'; Level 3: 'moderate pithiness'; Level 4: 'severe pithiness'.

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’.

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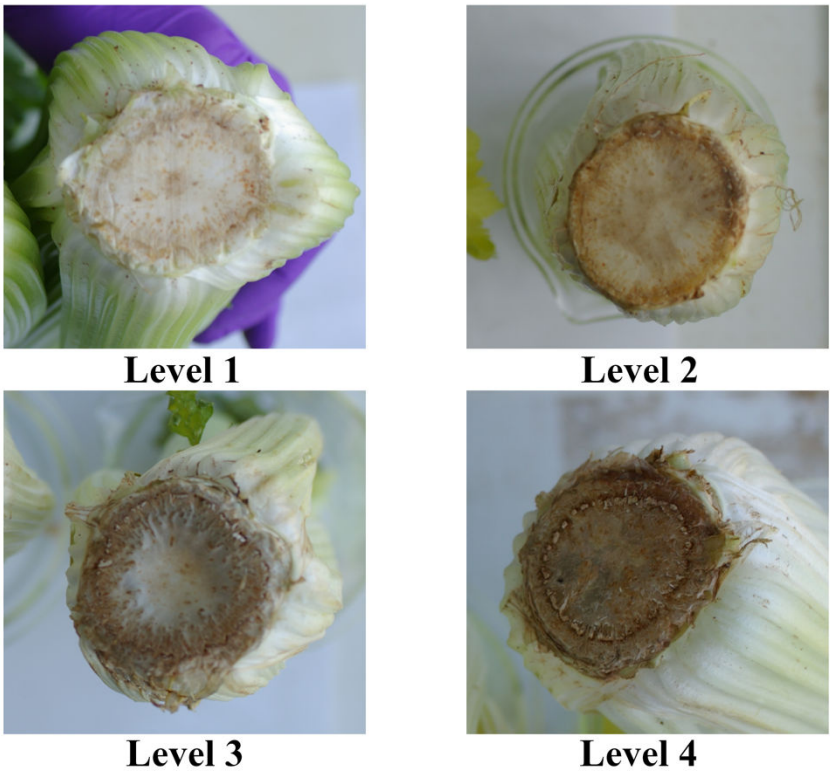

764

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'.

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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

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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

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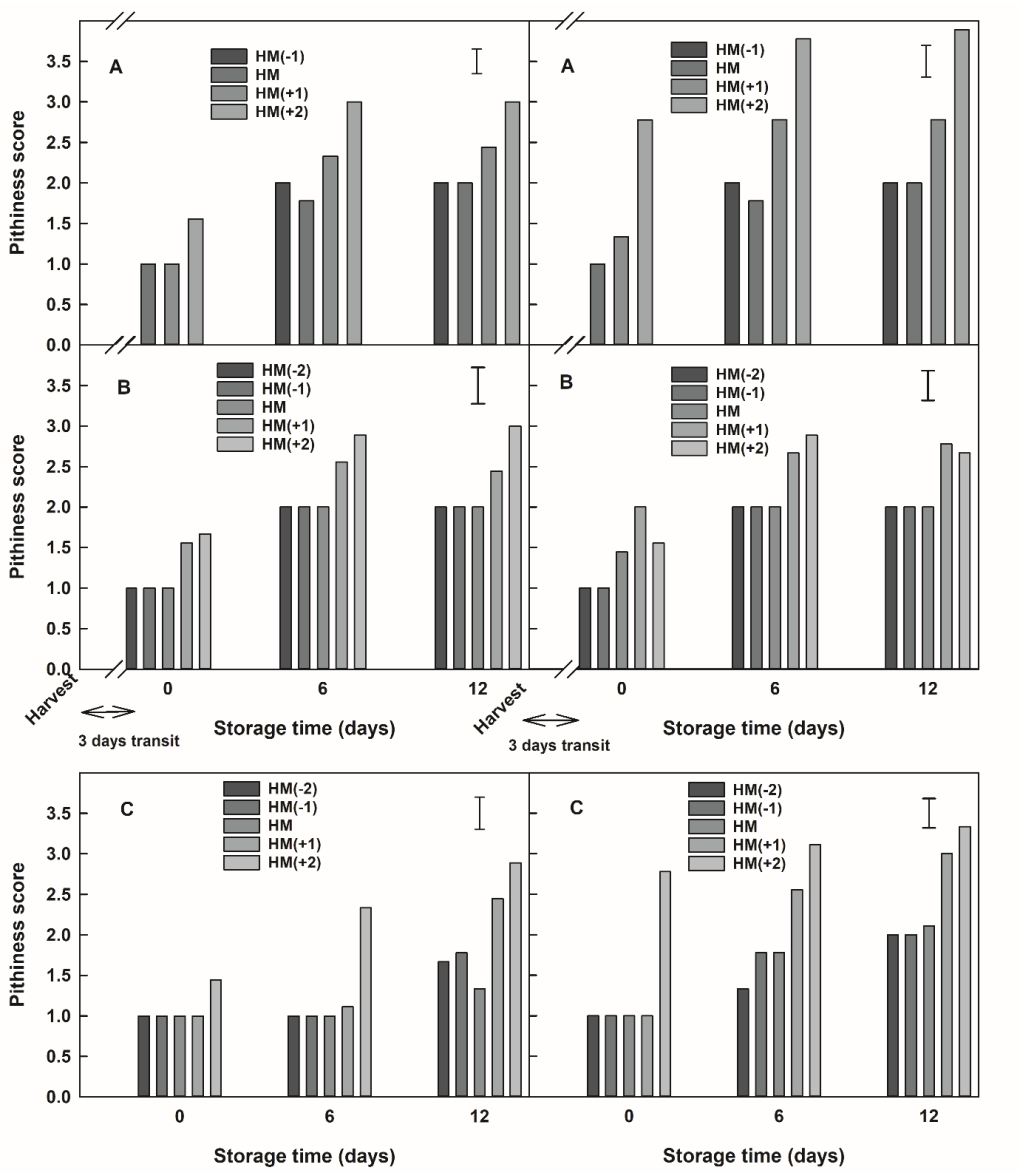

775

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

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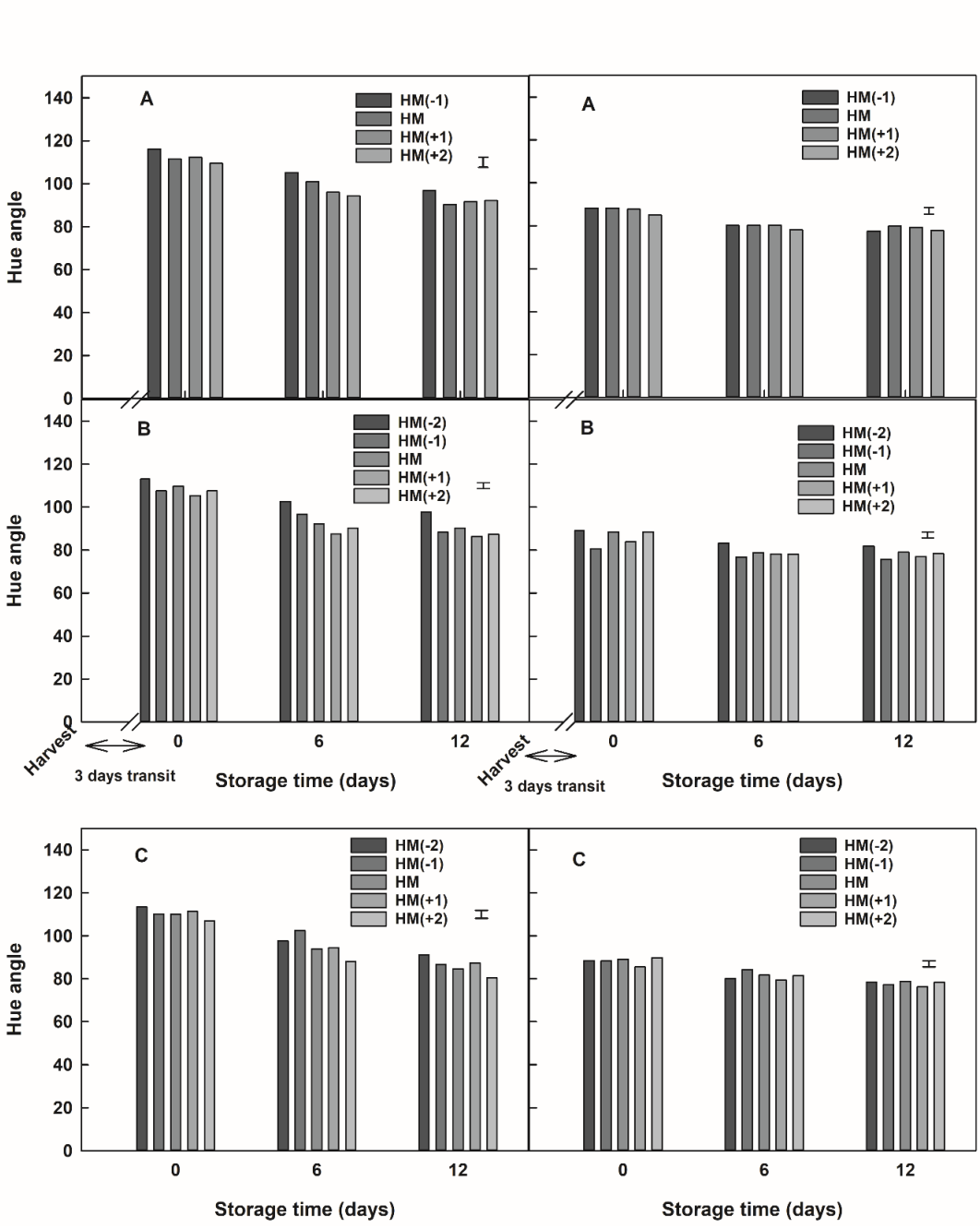

783

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

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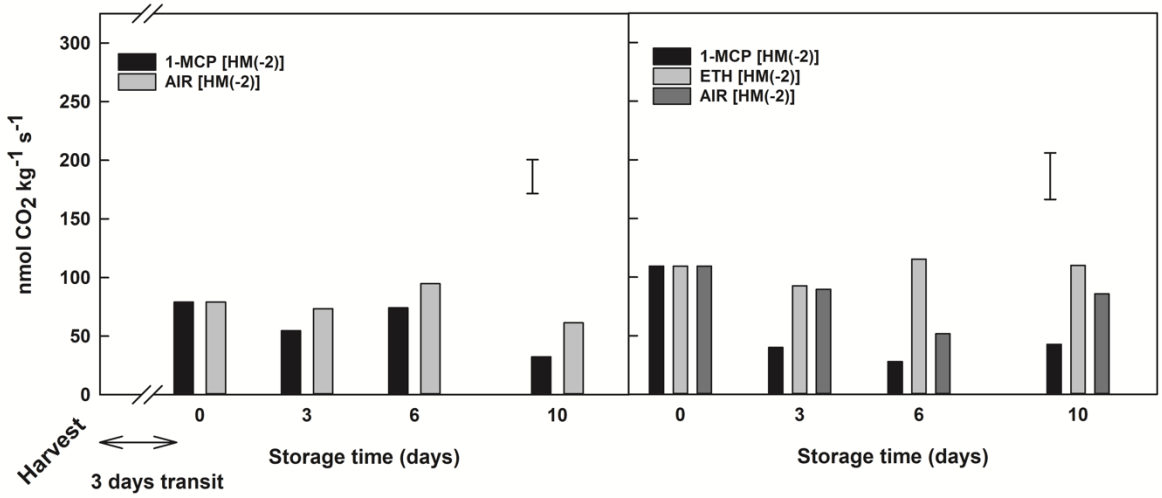


Figure S6. Respiration rate of celery grown in the Late Spanish season (left) and the Late UK season (right) and harvested two weeks prior to optimum maturity [HM(-2)]. Bar with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 µL L^{-1} 1-MCP for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

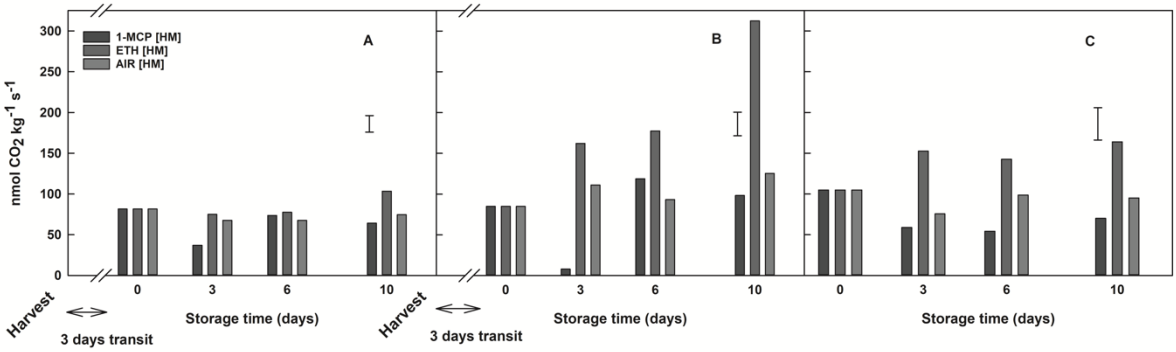


Figure S7. Respiration rate of celery grown in the Early Spanish season (A) Late Spanish season (B) and the Late UK season (C) and harvested at optimum maturity [HM]. Bar with different colours indicate different postharvest treatments [1-MCP = continuous air after exposure to 1 µL L^{-1} 1-MCP for 24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

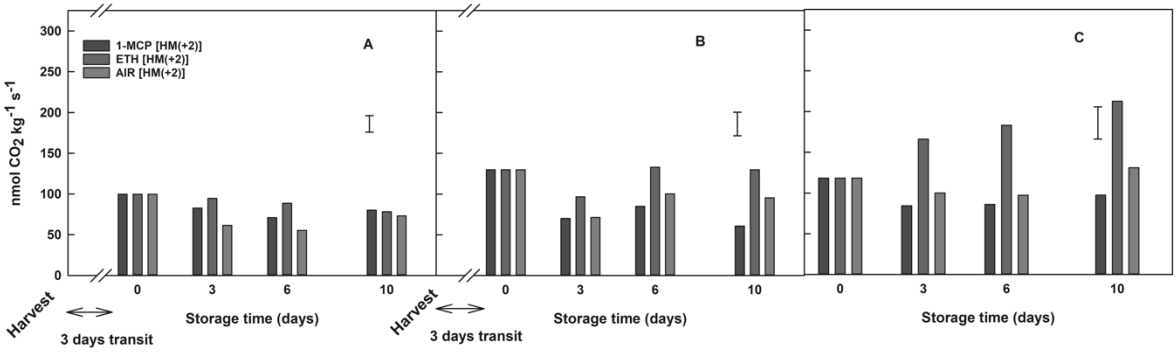


Figure S8. Respiration rate of celery grown in the Early Spanish season (A) Late Spanish season (B) and the Late UK season (C) and harvested two weeks after optimum maturity [HM(+2)]. Bar colour indicates different postharvest treatments [1-MCP = continuous air after exposure to 1 µL L^{-1} 1-MCP for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

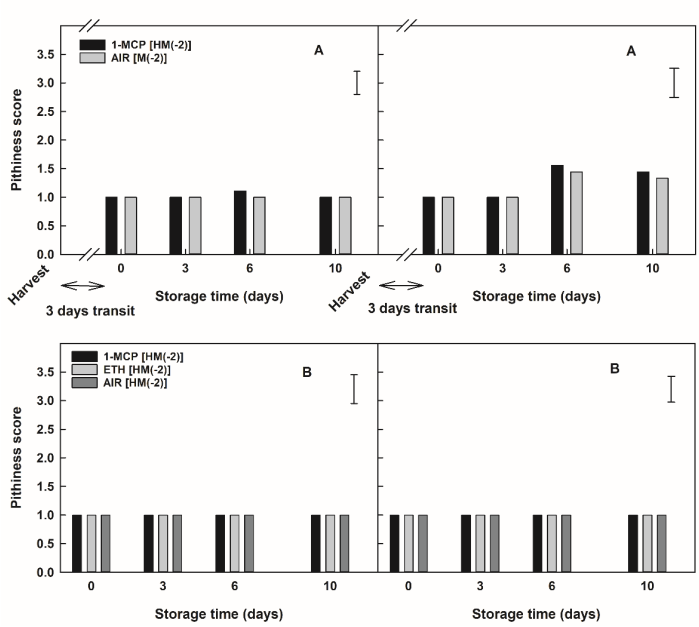


Figure S9. Pithiness score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Late Spanish season (A) and the Late UK season (B) and harvested two weeks prior to optimum maturity [HM(-2)]. Bars with different colours indicate different postharvest treatments [1-MCP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

= 10 µL L^{-1} continuous ethylene, AIR = continuous air (control)]. Error bars represent least significant differences (LSD).

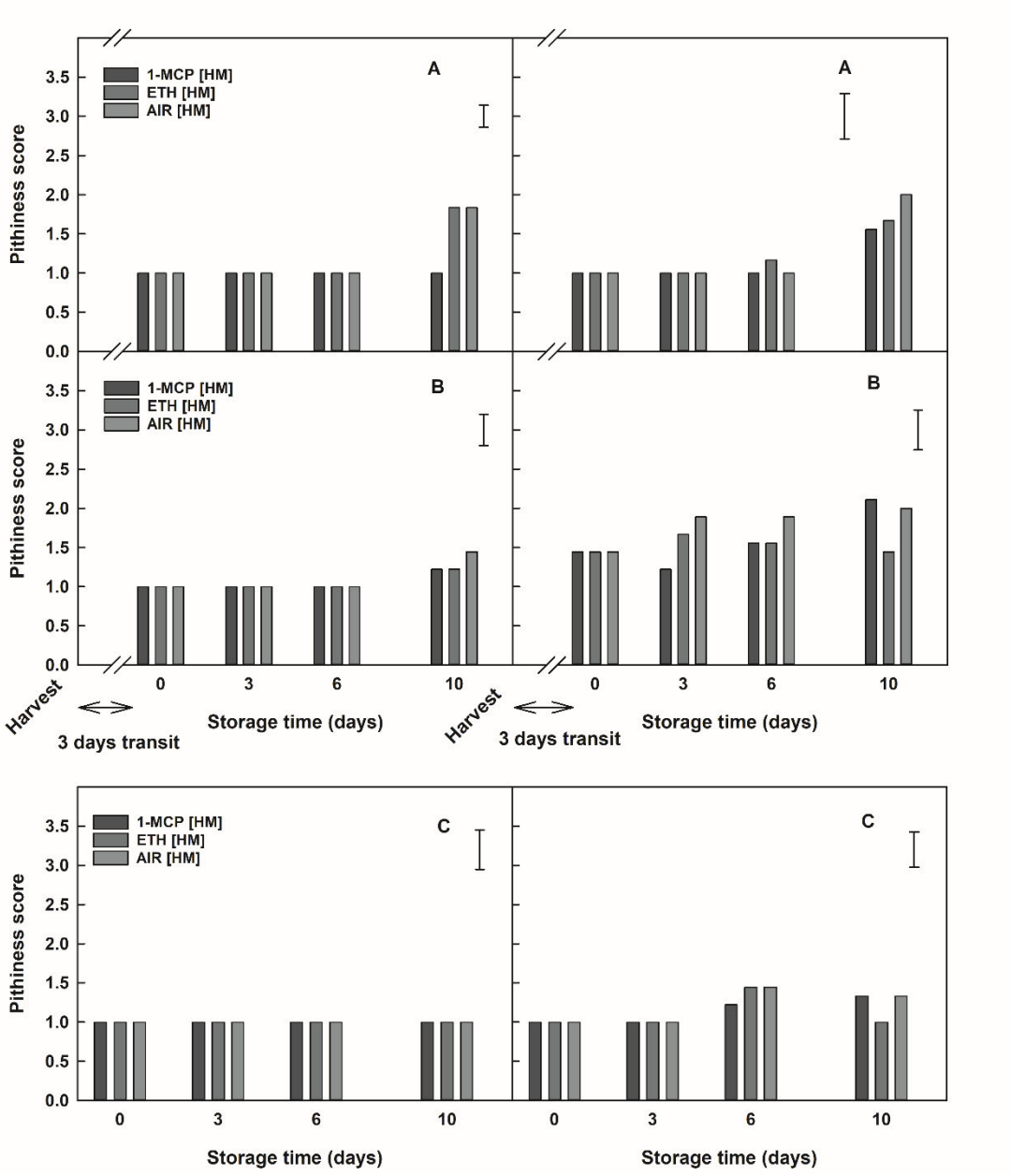


Figure S10. Pithiness score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Early Spanish Season (A), Late Spanish season (B) and the Late UK season (C) and harvested at optimum maturity [HM]. Bars with different colours indicate different postharvest treatments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

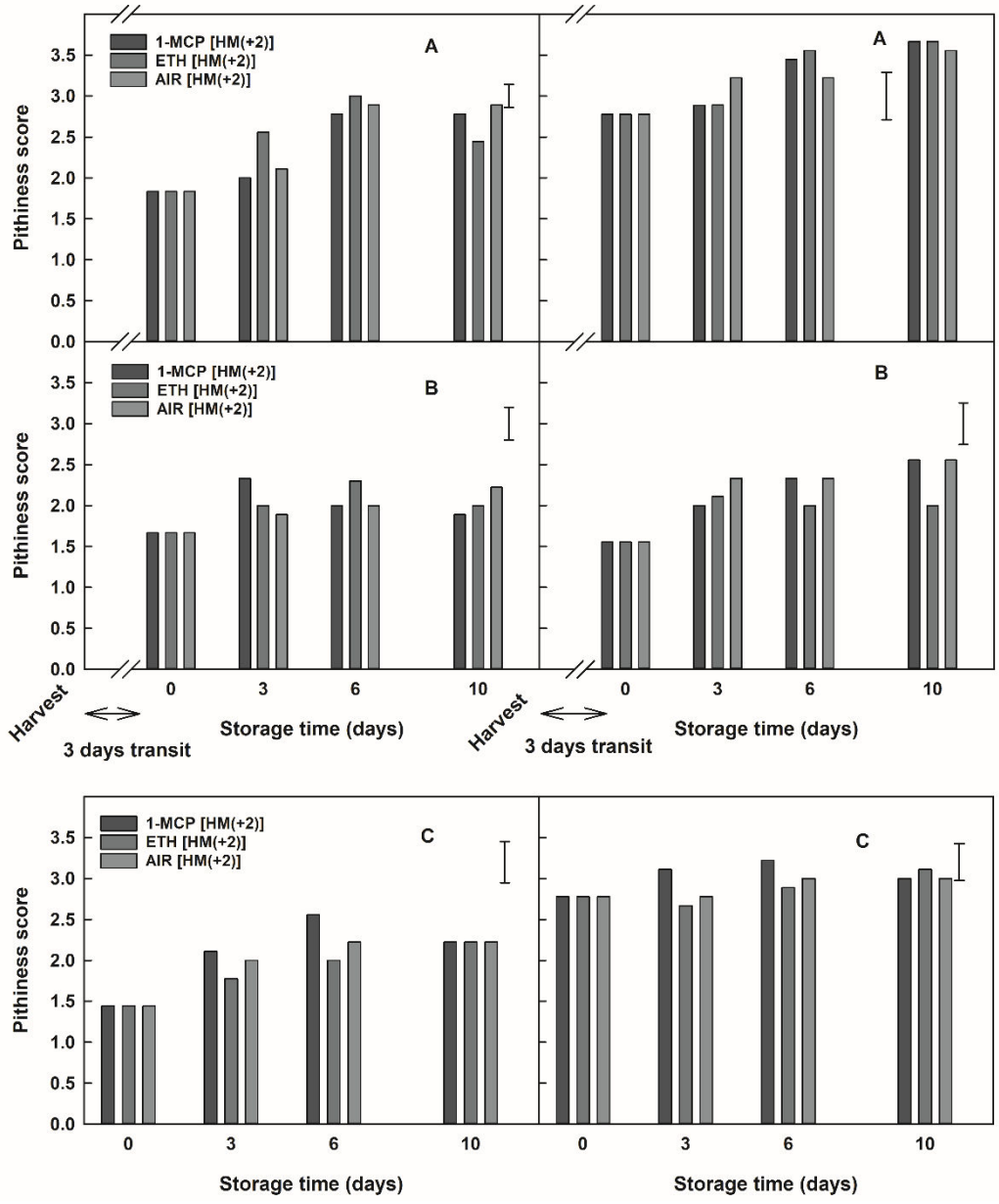
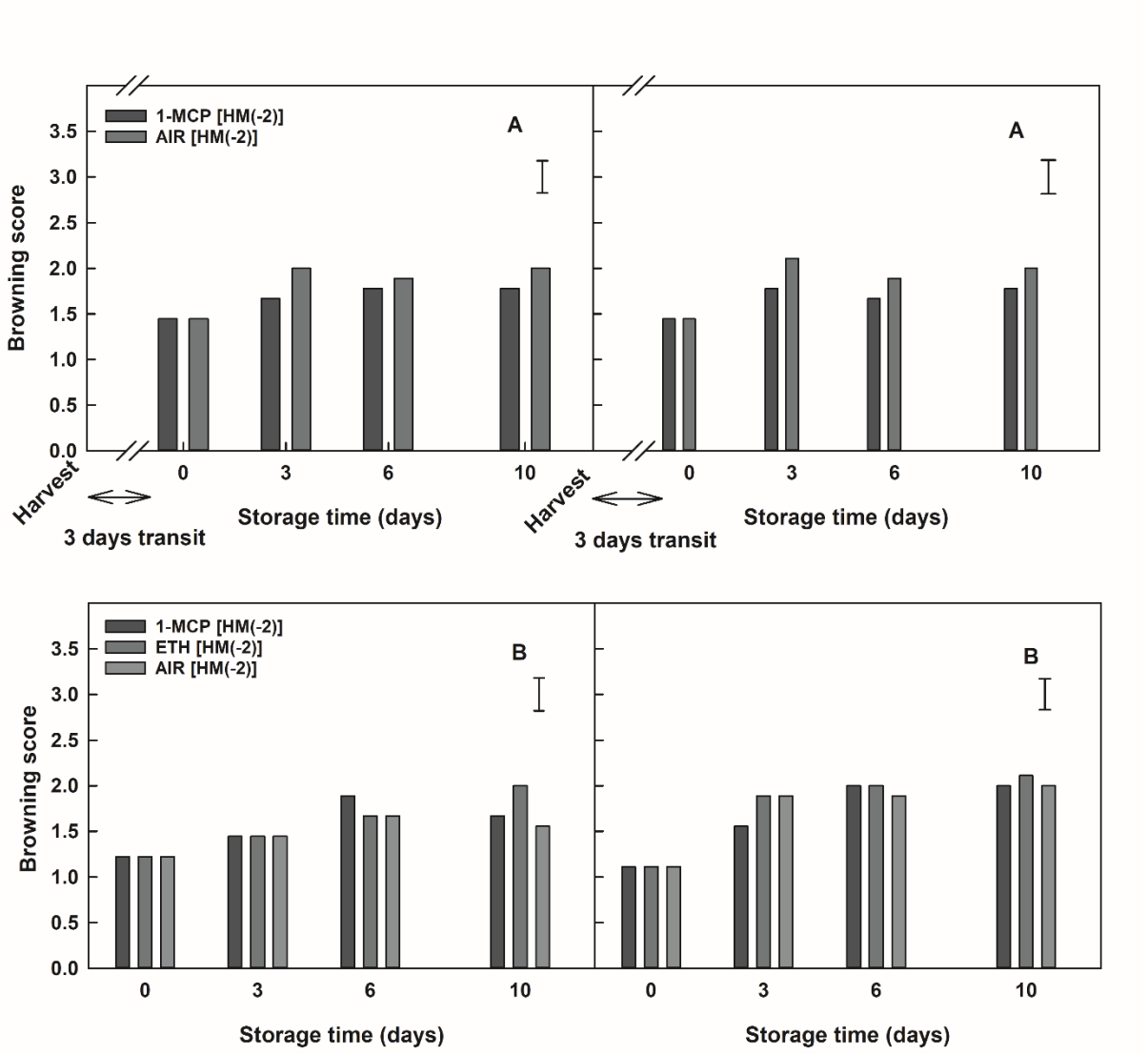


Figure S11. Pithiness score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Early Spanish season (A), the Late Spanish season (B) and the Late UK season (C) and harvested two weeks after optimum maturity [HM(+2)]. Bars with different colours indicate different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



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832 **Figure S12.** Browning score of celery at cut petiole ends (on the left) and butt ends (on the
833 right) and grown in the Late Spanish season (A) and the Late UK season (B) and harvested two
834 weeks prior to optimum maturity [HM(-2)]. Bars with different colours indicate different
835 postharvest treatments [1-MCP = continuous air after exposure to 1 μL L^{-1} 1-MCP for 24 h at
836 20 °C, ETH = 10 μL L^{-1} continuous ethylene, AIR = continuous air (control)]. Error bars
837 represent least significant differences (LSD).

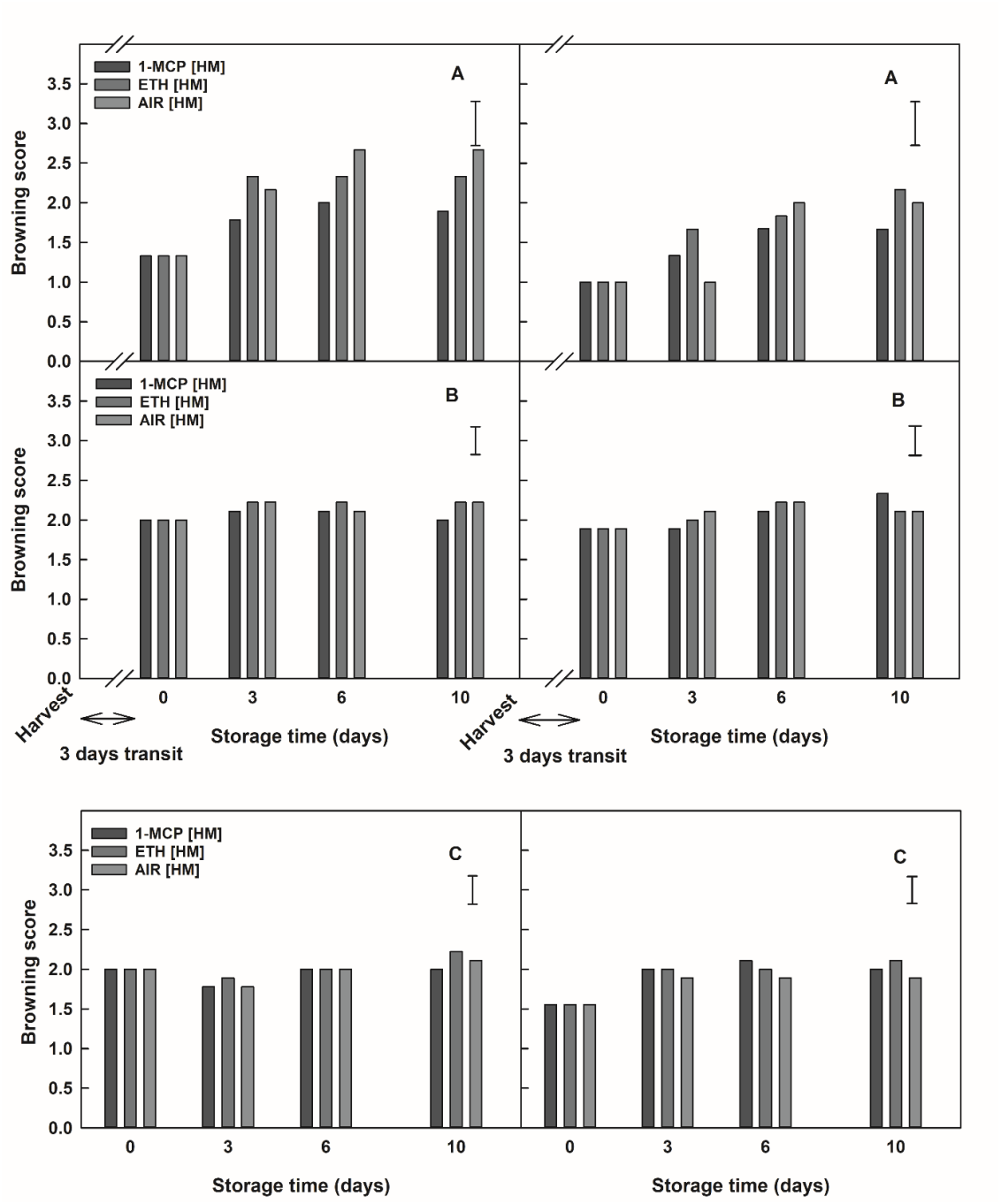
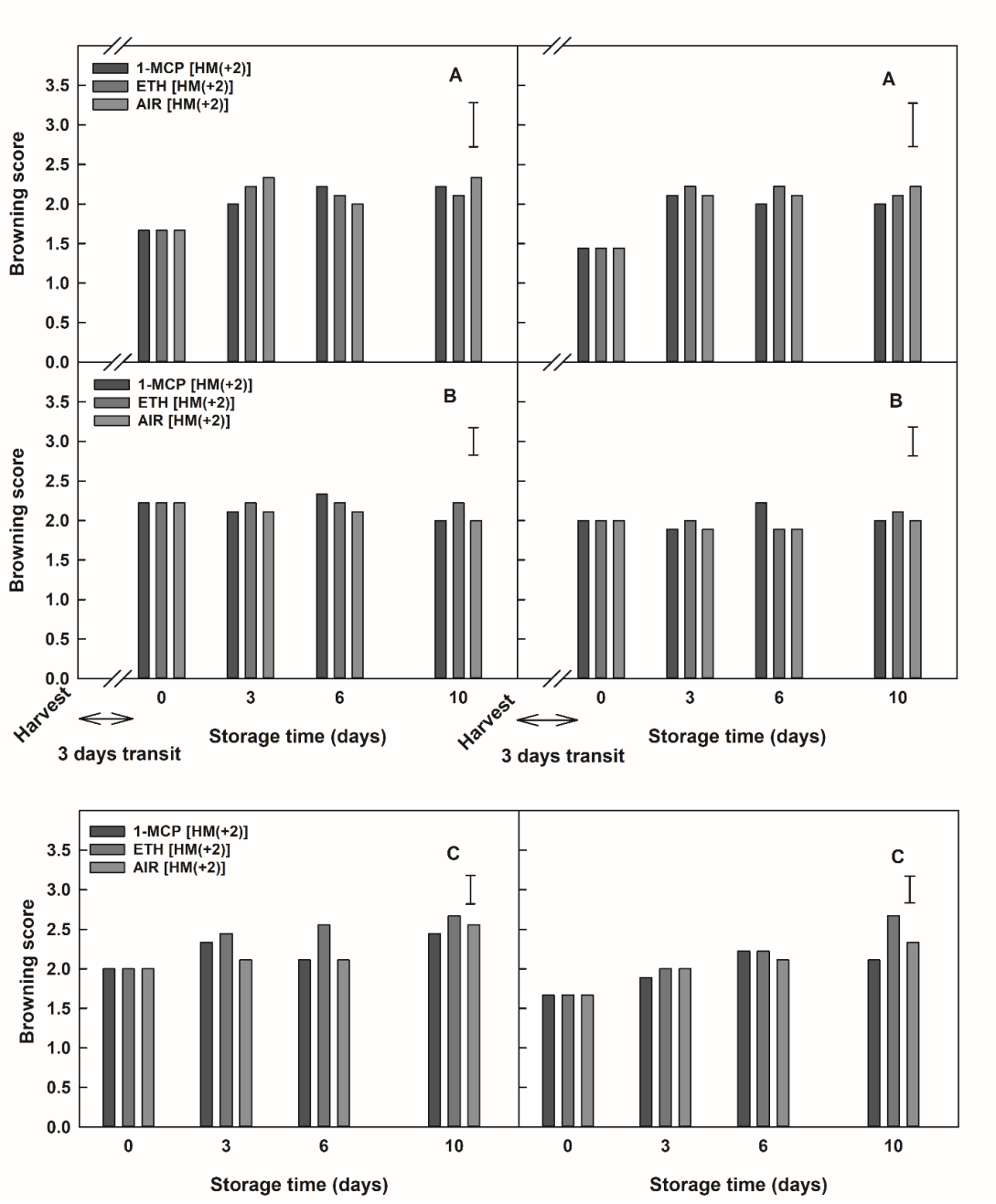


Figure S13. Browning score of celery at cut petiole ends (on the left) and butt ends (on the right) and grown in the Early Spanish Season (A), Late Spanish season (B) and the Late UK season (C) and harvested at optimum maturity [HM]. Bars with different colours indicate different postharvest treatments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



845

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

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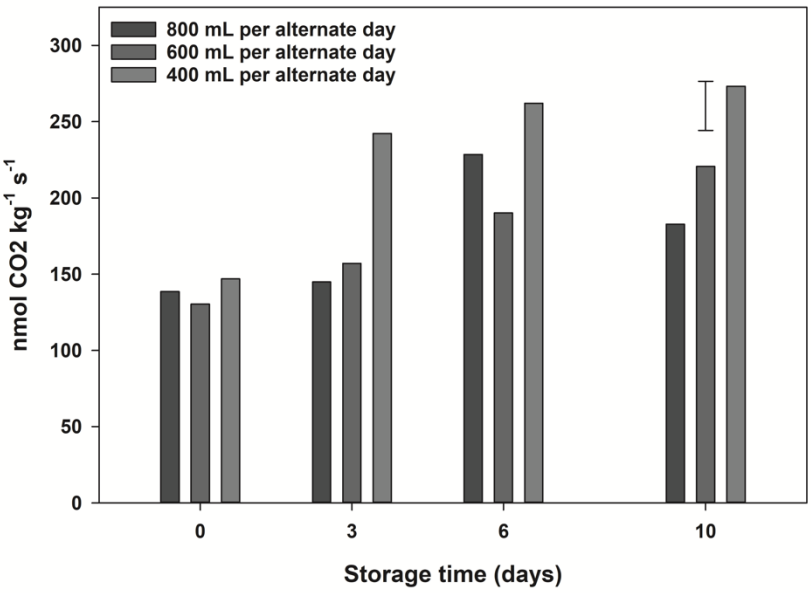
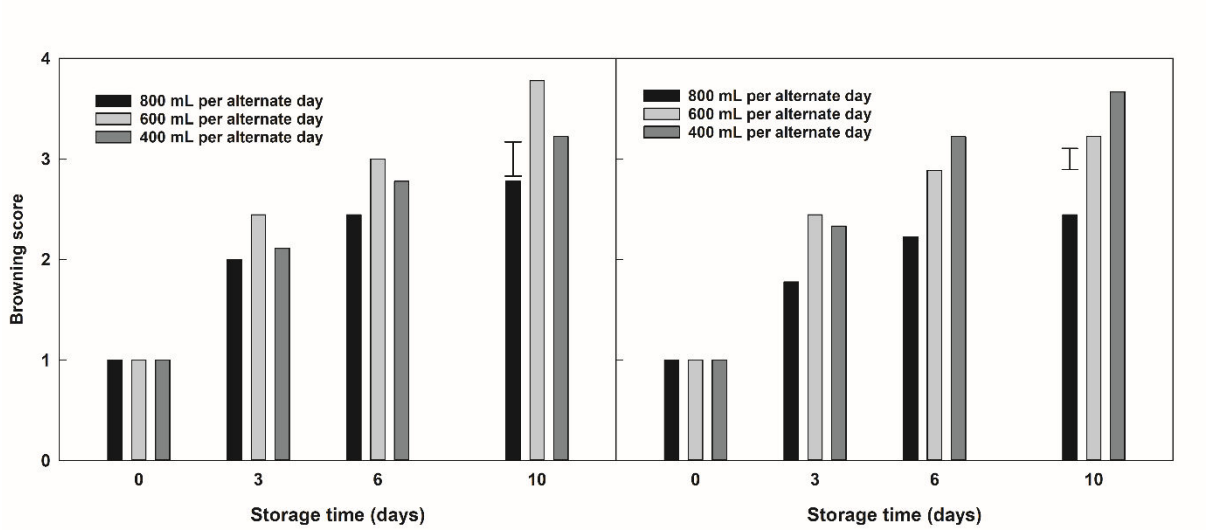


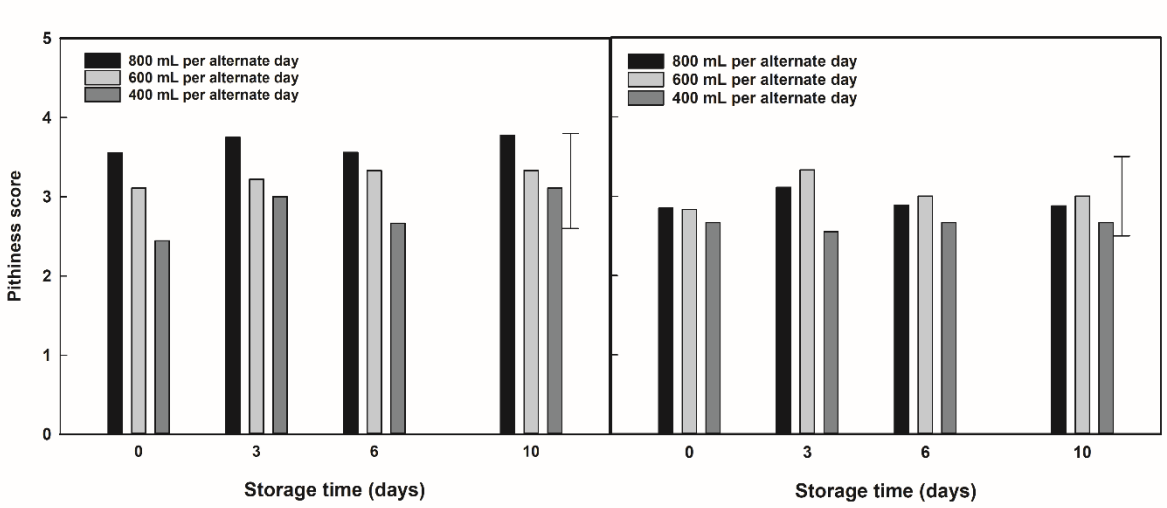
853

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



857

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



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

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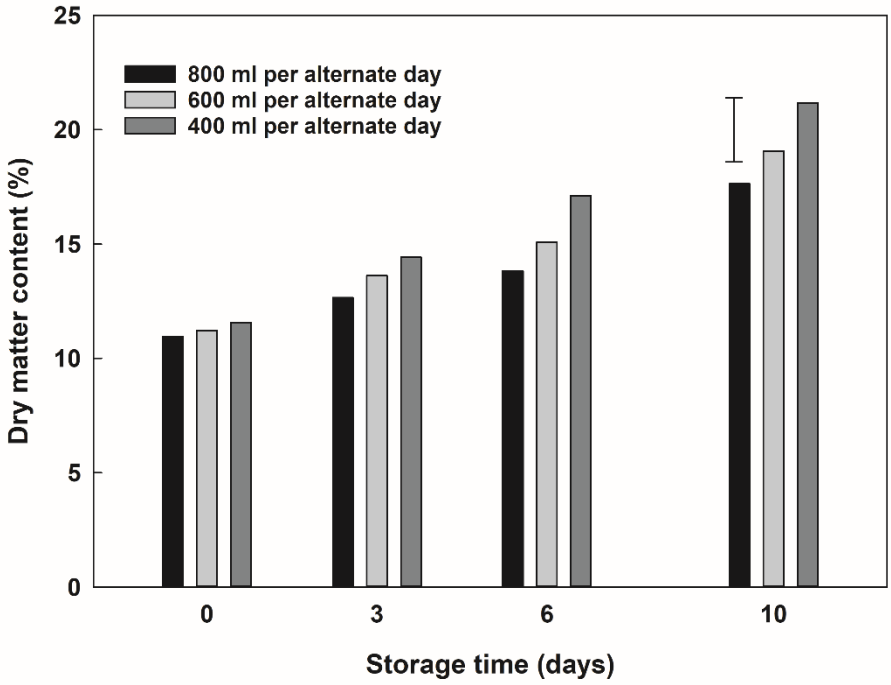

865 **Figure S18.** Effect of water treatments on the dry matter content of celery. Bars with different
866 colours indicate different water treatments: 800 mL every alternate day, 600 mL every alternate
867 day and 400 mL every alternate day. Error bars represent least significant differences (LSD).

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