THE JOURNAL OF HORTICULTURAL SCIENCE AND BIOTECHNOLOGY
https://doi.org/10.1080/14620316.2024.2449032

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Postharvest stress manipulation in Tenderstem® broccoli – examining the potential for stress-adaptative responses to promote sustainable quality retention

Ewan Gage, Leon A. Terry and Natalia Falagán

Plant Science Laboratory, Cranfield University, Bedfordshire, UK

ABSTRACT

Low temperature postharvest management is used to reduce quality and nutritive losses in broccoli after harvest, although this increases postharvest energy demand and the environmental impacts of food supply chain. Hydrogen peroxide (H_2O_2) and methyl jasmonate (MeJA) have been shown to reduce postharvest yellowing in broccoli by enhancing oxidative stress resistance and were examined as treatments for Tenderstem® broccoli florets to offset the effects of warmer storage temperatures. H_2O_2 elicitation was perceived on a regulatory level through activation of the jasmonate pathway, but did not reduce postharvest yellowing. MeJA treatment was detrimental to quality, even at concentrations shown to be beneficial for conventional broccoli varieties. Carotenoid accumulation was shown to be a leading factor in Tenderstem® yellowing during early storage, while photopigment degradation contributed to late stage quality loss. The physiological basis for floret yellowing in Tenderstem® was also shown to be due to carotenoid accumulation rather than chlorophyll loss. These results highlight the impact of genotypic and developmental effects on stress perception and response, which hinder optimisation of hormesis-based approaches for postharvest management.

ARTICLE HISTORY
Received 20 June 2024
Accepted 23 December 2024

KEYWORDS
Hydrogen peroxide; methyl jasmonate; temperature; OPR3; pheophytinase

Introduction

Broccoli (*Brassica oleracea* var. *italica*) is a major vegetable crop worldwide because of its health benefits derived from its high antioxidant and chemoprotective potential (Latté et al., 2011). However, quality degradation can result in losses of up to 40% in the supply chain (Gage et al., 2024). Broccoli quality loss is perceived by the consumer through colour change arising from pigment modification and chloroplast degradation resulting in head yellowing (Page et al., 2001), alongside changes in flavour and nutritive content (Nishikawa et al., 2003). Reactive oxygen species (ROS) are key contributors to the senescence process through oxidative degradation of chloroplastic membranes and pigment bleaching (Hodges et al., 2004). Low-temperature storage reduces ROS production through respiratory suppression, conserving antioxidant and pigment content to maintain head colour (Balouchi et al., 2011). These processes are usually controlled through low temperature cold-chain handling, especially for Tenderstem® broccoli (*B. oleracea* var. *alboglabra* × *italica*) as it is particularly susceptible to postharvest decline. Tenderstem® or Bimi® broccoli is harvested close to anthesis as extended peduncles bearing large flower buds, compared with conventional broccoli varieties harvested earlier in development as dense heads with immature flower buds. Hybrid varieties such as Tenderstem® typically demonstrate increased metabolic activity (Martínez-Hernández et al., 2011) with greater sensitivity to sepal yellowing due to large buds compared with conventional broccoli varieties, showing ca. 90% reduction in postharvest storage life as a result. However, such handling is energy-intensive, contributing to significant environmental and economic costs, and so it is desirable to develop alternative postharvest strategies which enable warmer storage temperatures whilst maintaining quality and safety of broccoli.

Besides temperature management, the impact of postharvest oxidative stress can be mitigated through priming of innate biological tolerance mechanisms, such as through oxidative hormesis (Duarte-Sierra et al., 2020). Oxidative hormesis has been efficacious in reducing yellowing of broccoli stored at 20°C (Aiamla-Or et al., 2012; Martínez-Hernández et al., 2011), and therefore we propose that this approach can be exploited to enable warmer storage of broccoli and therefore facilitate reductions in postharvest energy demand. However, poor understanding of the underlying physiological processes and interactions with wider environmental conditions (e.g. temperature) hinders optimisation of this approach (Agathokleous & Calabrese, 2019).

CONTACT Ewan Gage ewan.gage@cranfield.ac.uk Postharvest Research Group, Faculty of Engineering and Applied Sciences, Cranfield University, Cranfield, Bedfordshire, MK43 0AL, UK

Supplemental data for this article can be accessed online at https://doi.org/10.1080/14620316.2024.2449032

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Hydrogen peroxide (H_2O_2) can function as an oxidative stress elicitor through disruption of cellular ROS homoeostasis and the triggering of stress acclimation mechanisms (Smirnoff & Arnaud, 2019). Postharvest treatment with H_2O_2 has been demonstrated to retard degreening, maintain energy balance, and reduce senescent activity together with lowered ROS content in conventional broccoli heads stored at 20°C (Zhang et al., 20232023). H_2O_2 can be applied as a drench as part of hydrocooling processes, is low cost and residue free, making it an attractive source of hormetic elicitation.

Besides the use of abiotic stress to trigger adaptative hormetic responses, direct modulation of stress may also prove effective in increasing tolerance of postharvest stress. The jasmonic acid (JA) signalling pathway plays an integral role in coordinating abiotic stress (Wang et al., 2020), and external stimulation of the JA pathway promotes adaptative stress responses such as enhanced antioxidant activity (Alam et al., 2014). Methyl jasmonate (MeJA) is capable of triggering a hormetic response in that high doses promote senescence whilst low, short-term exposure enhances quality retention. MeJA fumigation reduced degreening of broccoli florets at 20°C through upregulation of antioxidant gene expression and suppression of chlorophyll catabolism (Duarte-Sierra et al., 2023; Xu et al., 2020). MeJA is attractive as an elicitor as it can be applied as a vapour and is generally recognised as safe for postharvest treatment of fresh produce. Both oxidative stress and MeJA treatments have been shown to enhance broccoli nutritive content (e.g. glucosinolates; Moreira-Rodríguez et al., 2017) and therefore these treatments may also enhance nutritional benefits in addition to postharvest quality retention.

We hypothesise that H_2O_2 and MeJA treatments can enable warmer storage of Tenderstem® broccoli through elicitation of an oxidative hormetic response, particularly through promoting antioxidant activity to reduce the effect of oxidative stress under increased storage temperature.

Materials and methods

Plant material and postharvest treatments

Tenderstem® broccoli florets cut to commercial standards (15–20 cm) were sourced from a commercial grower (Sussex, United Kingdom) and received within 24 h of harvest on 8 August 2022. Following selection for uniformity of size, colour, and maturity, florets were submerged in solutions of i) 0, 10, 100, and 1000 µmol L^{-1} MeJA with 0.1% Tween-20 (v/v) or ii) 2.5, 5, and 7.5 mmol L^{-1} H_2O_2 in deionised water, or iii) a deionised water control for 1 h, before air drying at 20°C for 3 h, adapting the approaches of Duarte-Sierra et al. (2022) and Luo et al. (2018). Florets were then stored at 5 and 10°C for 8 days in darkness at 95% relative humidity. Each replicate consisted of four florets and was assessed in triplicate. Samples of flower buds of consistent maturity were collected every 48 h and were snap frozen with liquid nitrogen. Samples for RNA analysis were maintained at −80°C until extraction, whilst samples for biochemical analysis were freeze-dried at −50°C under vacuum before powdering and storage at −40°C.

Colour analysis

Florets were imaged using a Lumenera Infinity 3-9UR high-definition digital camera with a charge-coupled device colour sensor (Lumenera Corporation, ON, Canada). Samples were photographed inside a Photo-e-Box Plus 1419 set at D65 (6500 K) (Or-tec, California, USA) under fluorescent light tubes (back and sides) to provide consistent lighting. Image analysis was conducted using ImageJ software (version 1.53t, National Institutes of Health, Bethesda, USA) according to Schneider et al. (2012). RGB values were determined for three 2 cm diameter circles per floret (Figure 1). RGB values were converted into CIELab colour space prior to determination of hue angle (°h = arctg (b^*/a^*)) and chroma ($C^* = (a^{*2}+b^{*2})^{1/2}$) according to Voss (1992).

Pigments

Chlorophyll *a* (Chl*a*), chlorophyll *b* (Chl*b*) and total carotenoids were quantified in triplicate following a modification of Wellburn (1994). Freeze-dried powder (50 mg) was extracted using 4.5 ml 80% (v/v) acetone on ice in darkness for 15 min before centrifugation at 8000 × *g* for 10 min at 4°C. Absorbance was recorded at 663 nm, 645 nm, and 470 nm using an Infinite 200 Pro plate reader (Tecan Austria GmbH, Grödig, Austria) with five reads per well. Quantification was made as follows: $Chla = 12.25A_{663} - 2.79A_{645}$; $Chlb = 21.50A_{645} -$



Figure 1. Floret colour sampling strategy. Three 2 cm diameter selections were used for capturing RGB values. Scale: 2 cm.

5.10A_{663}; Total Carotenoids = (1000A_{470} − 1.82Chl*a* − 85.02Chl*b*)/198.

Organic acids

Citric, maleic, and ascorbic acids were quantified following Crespo et al. (2010) with some modifications. Freeze-dried powder (150 mg) were extracted in 3% metaphosphoric acid for 10 min on ice before filtration (0.2 µm polypropylene filters, Millipore, UK). Extracts were analysed by High-Performance Liquid Chromatography (HPLC) fitted with diode array detector (DAD, 1200 Series, G1315B, Agilent Technology, UK) set at 210 nm. Separation was achieved using a Prevail organic acid column, 4.6 mm × 250 mm, 5 µM particle size (Hichrom, UK) using 25 mm KH_2PO_4 adjusted to pH 2.5 with a metaphosphoric acid mobile phase. Extracts were quantified using external standards (Sigma-Aldrich, UK).

Gene expression

Lipoxygenase (*BoLOX2*) and Oxophytodienoate Reductase (*BoOPR3*) were taken as candidates for activity of the JA pathway, while Vegetative Storage Protein 2 (*BoVSP2*) was used as an indicator of downstream JA activity and oxidative stress responses (Tytgat et al., 2013). Pheophytinase (*BoPPH*) was used as an indicator of vegetative senescent activity as this has been identified previously as the leading catabolic enzyme in broccoli (Aiamla-Or et al., 2012). RNA extraction from snap-frozen floret samples was performed using Rneasy Plant Mini Kit (Qiagen, UK), including on-column DNAse treatment. RNA integrity was verified using agarose gel electrophoresis and spectrophotometry (260/280 nm ratio). cDNA synthesis was performed using Superscript™ II RT (Invitrogen, UK) before RT-qPCR was performed on a CFX96™ RT-PCR system (Bio-Rad, UK) using SsoAdvanced™ Universal SYBR® Green (Bio-rad, UK) and gene-specific primers. Primers were designed using PrimerQuest™ (Integrated DNA Technologies), and specific primer sequences and targets are given in **Supplementary Information 1**. qPCR analysis was performed for triplicate biological replicates (taken from separate RNA extractions), each with triplicate technical replicates, and were normalised against β-Actin using the $^{\Delta\Delta}$Ct method.

Statistical analysis

Statistical analysis was performed using Genstat for Windows v. 22.1.0.532 (VSNI Ltd., UK) using analysis of variance (ANOVA). ANOVA assumptions were tested and found to be valid for this dataset, and analysis was carried out on treatment, storage time and temperature, and their interaction. Analysis was restricted to within treatment type (H_2O_2 or MeJA), including the water controls. Least significant difference values (LSD; $p < 0.05$) were calculated from each analysis where significant differences were identified. The LSD for the highest significant interaction was plotted in the figures.

Results

Colour

None of the florets stored at 5°C showed any visible colour change, whilst the florets stored at 10°C underwent rapid yellowing in both treatments (Figure 2). H_2O_2/5°C florets saw reductions of <1% in °h by day 8 (Figure 3(a)), whilst MeJA/5°C treatment resulted in minor reductions in h°; the largest decrease was 2.5%, found in1000 µM/5°C treatment (Figure 3(b)). H_2O_2 /10°C florets saw h° average reductions of 18.4%, whilst MeJA/10°C treated florets saw substantial reductions in h°, which increased with dosage. The greatest reduction was 24.2%, seen in 1000 µM/10°C treatment. The 0 µM/10°C treatment enhanced °h retention compared with the water/10°C control, showing a 5% greater °h on day 8.

Changes in C* were also unresponsive to H_2O_2 treatment (Figure 3(c)), with reductions of 16.1% (H_2O_2/5°C) by day 8 and increases of 57.3% (H_2O_2 /10°C); only *temperature*time* had a significant effect for H_2O_2 treatments ($p < 0.001$). MeJA treated florets stored at 5°C had an initial reduction in C* before minor increases after day 6, with the greatest recovery in 1000 µM/5°C (Figure 3(d)). MeJA/10°C treatments saw substantial increases in C*, with the greatest increased of 93.0% with 1000 µM/10°C treatment; the *treatment*temperature*time* interaction was significant ($p < 0.001$) for MeJA treatments.

Pigments

Total chlorophyll declined during storage following H_2O_2 treatment (Figure 4(a)), especially at 10°C treatment (47.4% average) compared to 5°C (29.0% average) by day 8. Following treatment with 5 mm/10°C and 7.5 mm/10°C florets showed reduced chlorophyll loss (43.9% and 36.8%, respectively, vs. 53.1% for the 0 mm/10°C Control). MeJA treatments presented similar results for chlorophyll at 5°C, with average reductions of 43.2%. However, when MeJA treated broccoli florets were stored at 10°C, more severe chlorophyll loss was seen (up to 85.1% in 1000 µM/10°C; Figure 4(b)).

Following H_2O_2 treatment, total carotenoid content initially increased until day 4, with the greatest increase seen at 2.5 mm/5°C and 2.5 mm/10°C (141% and 119% respectively) although levels declined in later storage (Figure 4(c)). MeJA treated florets showed only marginal total carotenoid

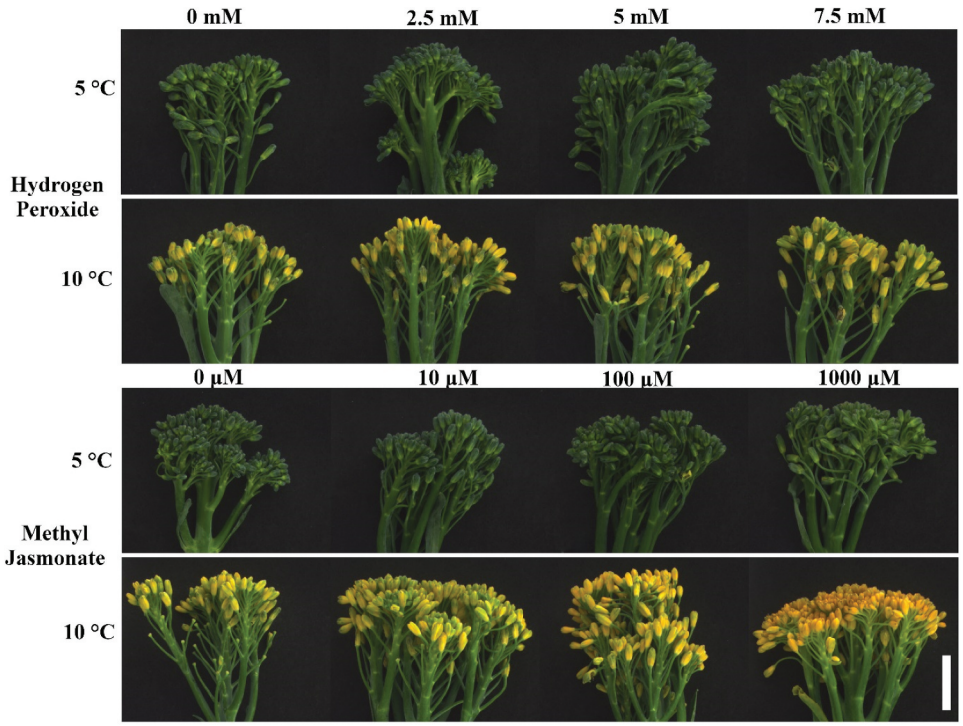


Figure 2. Representative broccoli florets after eight days of storage at either 5 or 10°C following treatment with hydrogen peroxide or methyl jasmonate. Scale = 2 cm.

increases of 9.6% and 5.8% with 1000 µM treatment at 5 and 10°C respectively (Figure 4(d)). Water controls showed greater carotenoid accumulation than MeJA-treated florets, giving 38% greater carotenoid content than the MeJA-treated florets on day 4. MeJA-treated florets also showed minor reductions in total carotenoids in later storage, although this was reduced with lower-dosed MeJA application at 5°C (20.6% with 10 µM/5°C vs. 33.7% in the control).

H_2O_2 treatment increased the floret carotenoid:chlorophyll ratio at both temperatures, although differences between storage temperatures were notable only on day 8 (Figure 4(e)) where H_2O_2/5°C treated florets showed an average increase of 92.4% compared with 178.3% for H_2O_2/10°C florets. MeJA/5°C treatment resulted in an increased carotenoid:chlorophyll ratio for 10 and 100 µM treatments of 91.% and 106.8%, respectively, compared with 15.5% in the control on day 6, although the ratio declined by day 8 (Figure 4(f)). MeJA/10°C had a more substantive effect on the carotenoid:chlorophyll ratio, with almost a three-fold increase seen in 1000 µM/10°C by day 8.

Organic acids

Ascorbate decline during storage was accelerated with temperature in both treatments (Figure 5(a,b)), especially in MeJA, which accelerated ascorbate loss, showing reductions of 90.9% by day 8 in 1000 µM/10°C. Malate increased with H_2O_2 application, and whilst increases were greater at 10°C (177% average increase compared with 37% at 5°C) there was no significant effect of treatment (Figure 5(c)). MeJA had a significant effect on malate accumulation ($p < 0.001$), particularly at 10°C, where levels increased five-fold by day 8 following 1000 µM/10°C treatment (Figure 5(d)). H_2O_2 treatment did not result in changes in citrate concentrations until day 8, when levels in florets stored at 10°C increased by an average of 32% relative to day 0 (Figure 5(e)). MeJA/5°C treatment marginally increased citrate levels with increases of 3.3% with 1000 µM/5°C treatment compared with 20.0% in the control (Figure 5(f)). This trend was absent at 10°C, where the greatest increase in citrate (112.1%) was seen with 1000 µM/5°C treatment.

Gene expression

H_2O_2 treatment triggered a rapid increase in *BoLOX2* expression, particularly in 7.5 mm/10°C treatment, although this increase was absent from florets stored at 5°C irrespective of dose (Figure 6(a)). *BoLOX2* expression declined at day 4; however, after which all H_2O_2 treatments showed comparable levels to the control. Similar reactions were seen in *BoOPR3* expression, with the greatest increase observed on day 2 following 7.5 mm/10°C treatment, which then declined by day 4 (Figure 6(b)). *BoOPR3* levels increased with later storage, particularly in H_2O_2/10°C treatments. *BoVSP2* expression followed a similar trend, with transient increases following 5 mm/10°C and 7/5 mm/10°C treatment that persisted until day 4,

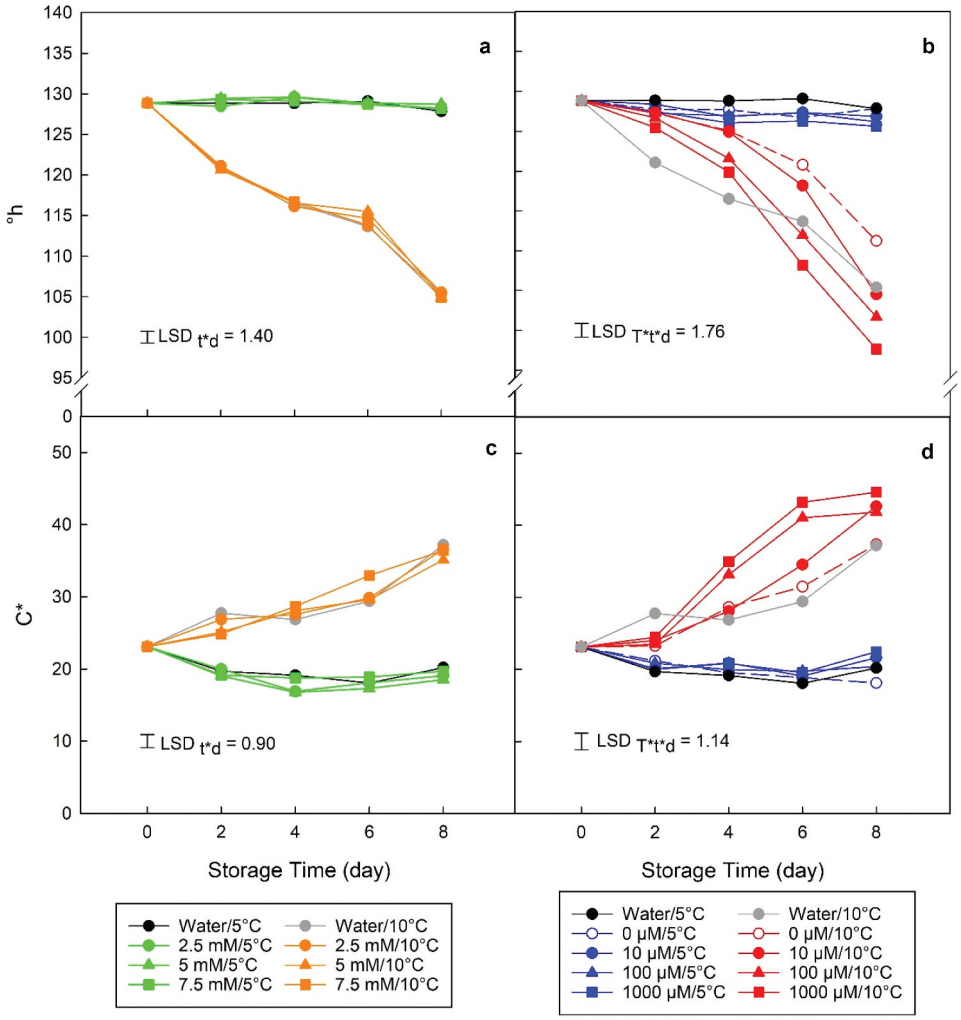


Figure 3. Changes in colour assessed through chroma (c*) or hue angle (°h) for broccoli florets treated either with hydrogen peroxide (2.5, 5 or 7.5 mm – a/c) or methyl jasmonate (0, 10, 100, or 1000 µM – b/d) and a water control. Mean values are plotted ($n = 3$), whilst vertical bars represent the least significant difference ($p = 0.05$) for the interaction between *treatment* (T), *temperature* (t) and/or *time* (d) where stated.

whilst other treatments showed no significant change (Figure 6(c)). *BoPPH* expression only saw increases in expression from day 4 in florets stored at 10°C (Figure 6(d)), whilst storage at 5°C saw only a minor increase by day 8.

MeJA treatment had a significant effect on *BoLOX2* expression, resulting in significant increases in expression in day 2 (1000 µM/5°C) and day 4 (1000 µM/10°C), although these were short-lived and declined to background levels by day 8 (Figure 7(a)). *BoOPR3* expression saw large increases in expression on day 4, with the greatest increase seen with 1000 µM/10°C treatment (Figure 7(b)). MeJA 1000 µM/5°C gave an earlier increase on day 2, although this was substantially reduced and more persistent than 1000 µM/10°C treatment. *BoVSP2* expression saw a significant increase of only under 1000 µM/5°C treatment on day 4, with increase expression occurring on day 5 before declining on day 6 (Figure 7(c)); *BoPPH* expression saw marked increases following MeJA/10°C treatment, which was absent in MeJA/5°C treated florets (Figure 7(d)). *BoPPH* expression was increased in a dose-dependent fashion on day 4 for 100 and 1000 µM/10°C treated florets before declining on day 6. *BoPPH* expression was increased in the untreated control stored at 10°C on day 6 although this wasabsent in 10 µM/10°C treated florets which remained comparable to 5°C stored florets during treatment. 0 µM MeJA/10°C increased both *BoOPR3* and *BoPPH* expression on day 6 relative to the water/10°C treatment.

Discussion

Efficacy of hydrogen peroxide as a postharvest treatment

The results of the present study demonstrated that H_2O_2 treatment has no effect on Tenderstem® broccoli floret quality. Zhang et al. (2023) reported that treatment with 2 mm H_2O_2 reduced °h declines by 57.5%

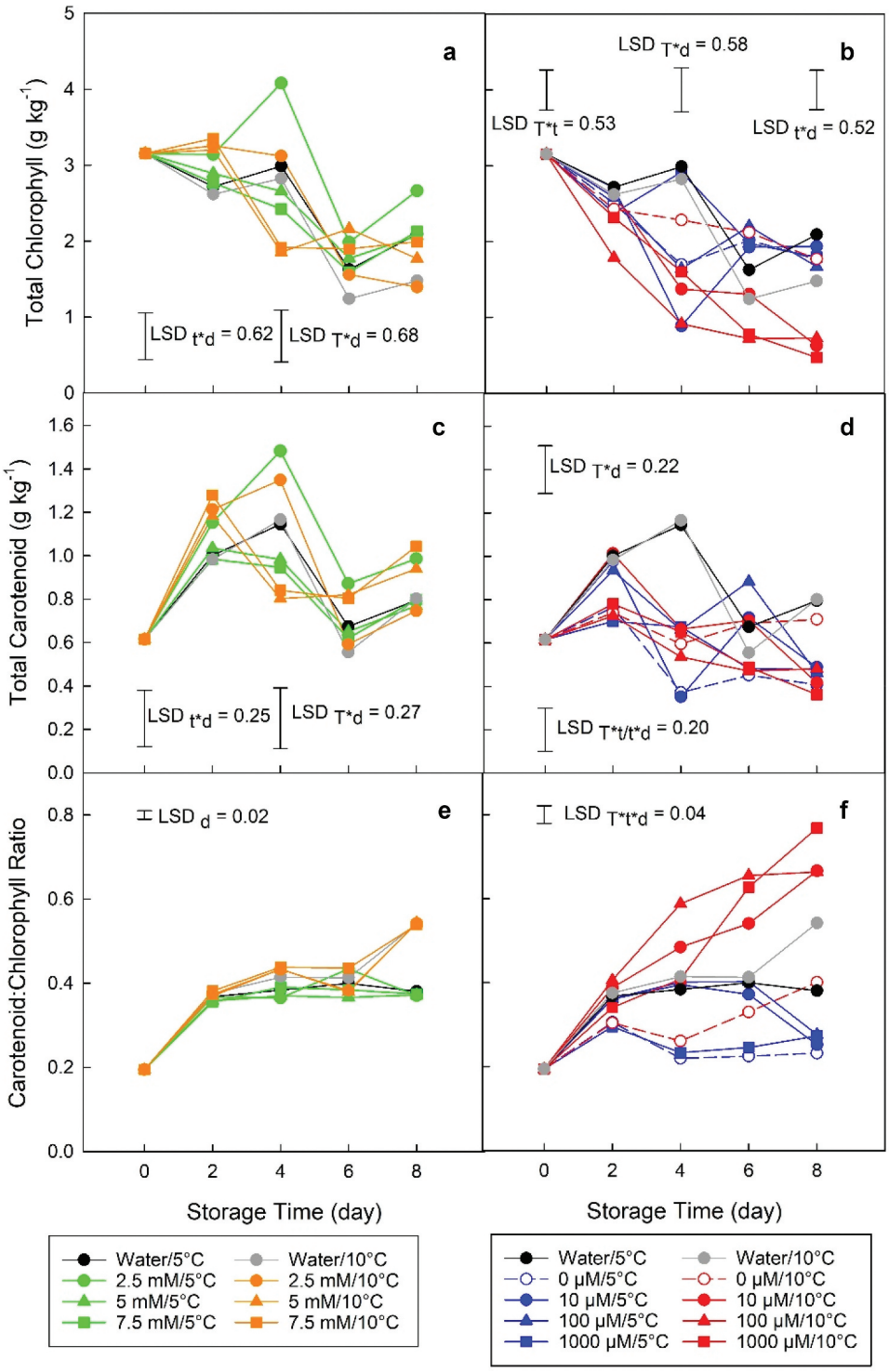


Figure 4. Changes in floret pigment content as assessed through total chlorophyll (a,b) and total carotenoid content (c,d) and the carotenoid:chlorophyll ratio (e,f) for broccoli florets treated either with hydrogen peroxide (2.5, 5 or 7.5 mm – a/c/e) or methyl jasmonate (0, 10, 100, or 1000 µM – b/d/f) and a water control. Mean values are plotted ($n = 3$), whilst vertical bars represent the least significant difference ($p = 0.05$) for the interaction between *treatment* (T), *temperature* (t) and/or *time* (d) where stated.

in broccoli stored at 20°C, together with promotion of antioxidant enzymes (e.g. catalase, superoxide dismutase) and increased ascorbate biosynthesis resulting in a significant reduction in ROS concentrations during storage. Modulation of oxidative stress defence mechanisms in broccoli through other elicitors (e.g. ultraviolet light) has been shown to increase antioxidant defence mechanisms and suppress chlorophyll catabolism (Aimala-Or et al., 2014; Costa et al., 2006; Lemoine et al., 2010). Furthermore, H_2O_2 treatment has been shown to trigger enhanced oxidative stress in other cropping systems (Gechev et al., 2002; Ishibashi et al., 2011) through enhanced ROS scavenging activity (Sonmez et al., 2023). In contrast, our results indicated that while H_2O_2 treatment of Tenderstem® broccoli resulted in minor reductions in the rate of

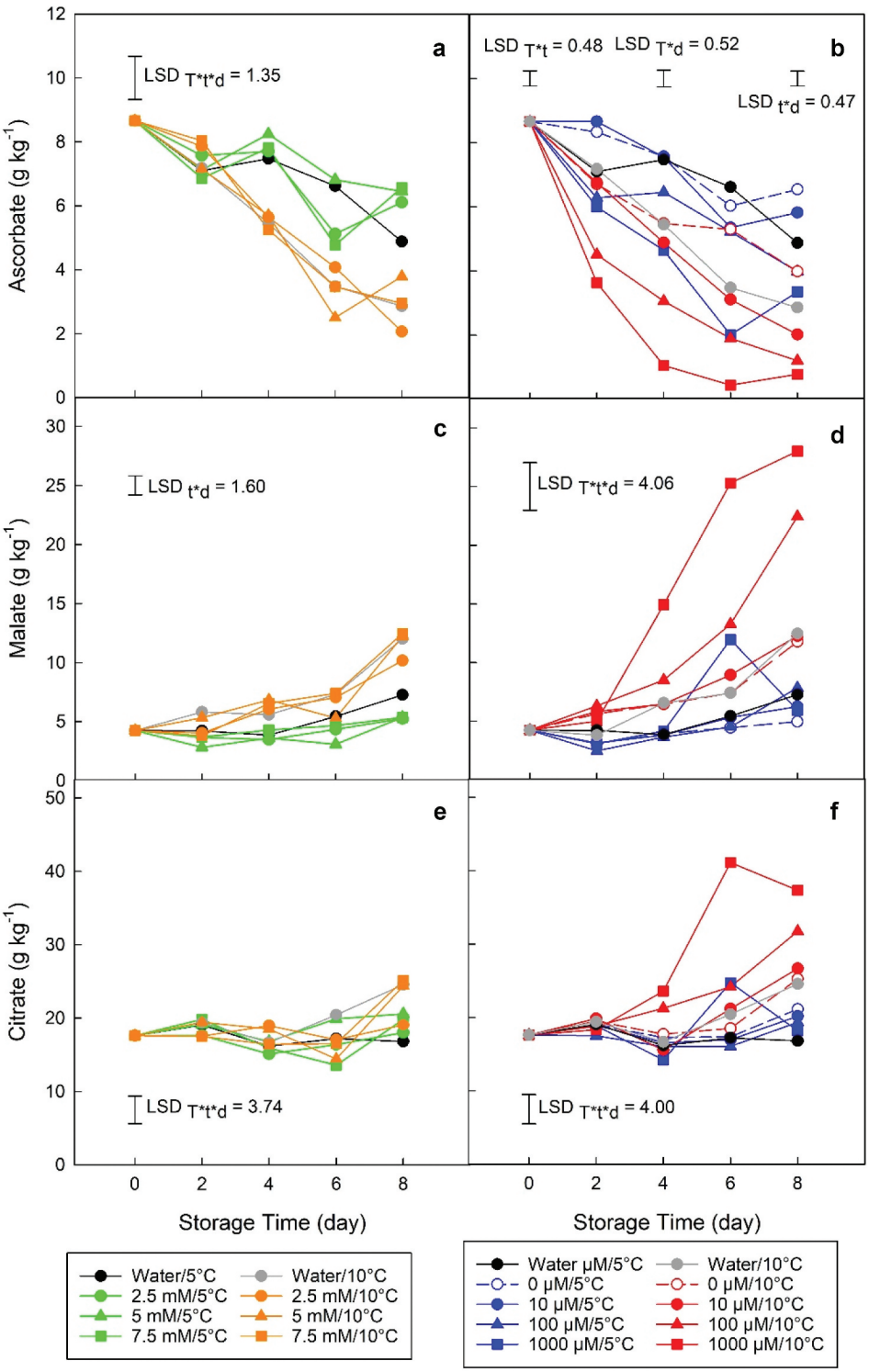


Figure 5. Changes in floret ascorbate (a,b), malate (c,d) and citrate content (e,f) for broccoli florets treated either with hydrogen peroxide (2.5, 5 or 7.5 mm – a/c/e) or methyl jasmonate (0, 10, 100, or 1000 µM – b/d/f) and a water control. Mean values are plotted ($n = 3$), whilst vertical bars represent the least significant difference ($p = 0.05$) for the interaction between *treatment* (T), *temperature* (t) and/or *time* (d) where stated.

ascorbate decline in some instances these were not significant and did not translate into improved colour retention as no difference in °h was observed at either temperature following H_2O_2 treatment.

The reduction in broccoli yellowing following oxidative stress exposure has been associated with reduced chlorophyll catabolism, with reductions in *BoPPH* expression indicating modifications at a regulatory level (Aiamla-Or et al., 2012; Büchert et al., 2011). Results in the present study demonstrate that neither the rates of chlorophyll breakdown nor the expression of *BoPPH* was impacted by H_2O_2 treatment. Therefore, the lack of response of Tenderstem® broccoli to H_2O_2 treatment may be attributed to an

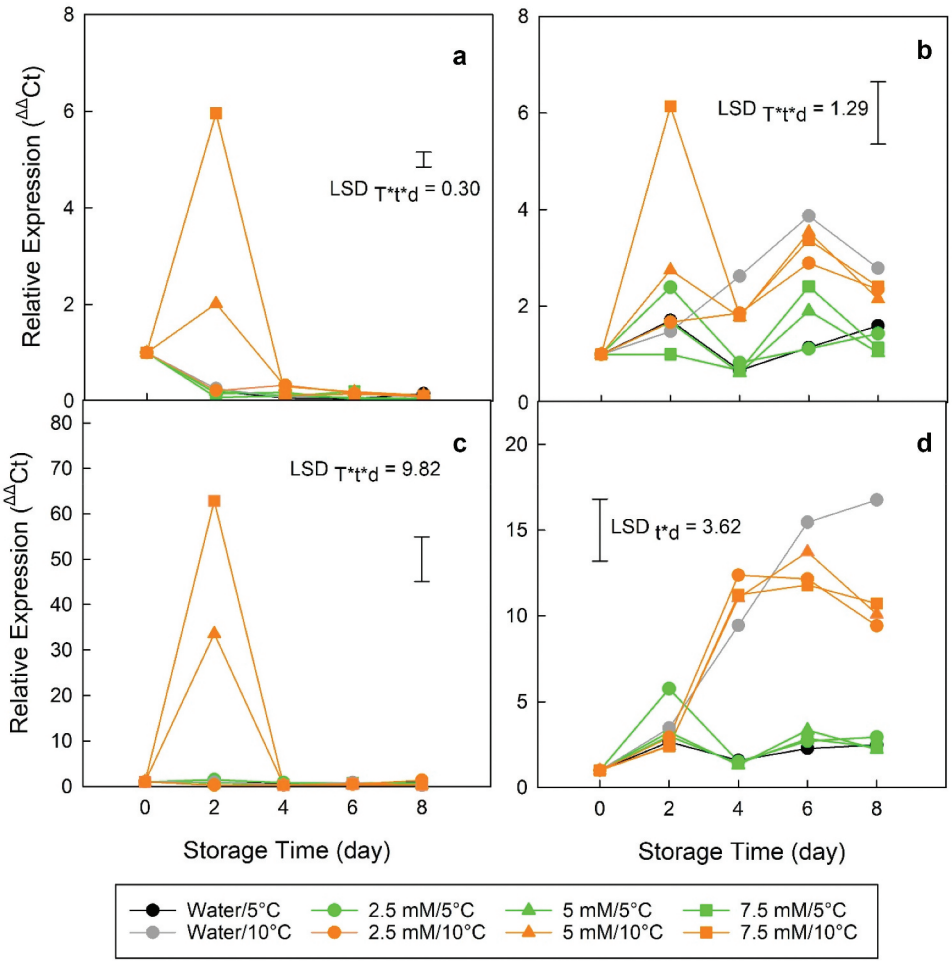


Figure 6. Gene expression changes in broccoli florets following treatment with hydrogen peroxide (0, 2.5, 5 or 7.5 mm) and a water control as quantified for *BoLOX2* (a), *BoOPR3* (b), *BoVSP2* (c) and *BoPPH* (d). Mean values are plotted ($n = 3$), whilst vertical bars represent the least significant difference ($p = 0.05$) for the interaction between *treatment* (T), *temperature* (t) and/or *time* (d) where stated.

absence of effect on either a regulatory or biochemical level, resulting in progressive colour change following chlorophyll breakdown.

Despite the absence of downstream effects, gene expression changes demonstrated that an oxidative stress signal was perceived, through the sharp rise in *BoLOX2, BoOPR3,* and *BoVSP2* following H_2O_2 treatment (particularly at 10°C). Upregulation of *VSP2* in Arabidopsis is seen during protein remobilisation following oxidative stress exposure and is induced through activity of the JA pathway (Mira et al., 2002; Tytgat et al., 2013). Lipoxygenase (*BoLOX2*) and oxophytodienoic acid reductase (*BoOPR3*) are integral to the JA signalling pathway (Santino et al., 2013) and so the correlated upregulation of these genes is also indicative of an oxidative stress response triggered following H_2O_2 treatment. However, the transient nature of this upregulation indicates that the perception of oxidative stress was limited, resulting in insufficient priming of an adaptative response to have long-term beneficial effects. The marginal increases in ascorbate seen following H_2O_2 treatment demonstrate that some upregulation of antioxidant mechanisms may have occurred, but this was insufficient to enhance quality retention.

The lack of response to H_2O_2 treatment may be due to rapid metabolism of H_2O_2 and a return to ROS homoeostasis without longer lasting effects. The clearest benefits of effective oxidative hormesis effects have been achieved with UV treatment (e.g. Costa et al., 2006), which is liable to achieve more persistent, widespread cellular disruption (Jansen et al., 1998) than H_2O_2 treatment and therefore exert a more persistent effect on adaptative responses. Alternatively, the capacity of adaptative response in Tenderstem® may be insufficient to prevent quality decline in response to postharvest stress, reflecting the increased sensitivity of this cultivar to postharvest stress compared with conventional varieties.

Efficacy of methyl jasmonate as a postharvest treatment

Similarly, MeJA treatment was not beneficial for retention of floret quality at either temperature, instead demonstrating an acceleration of senescence

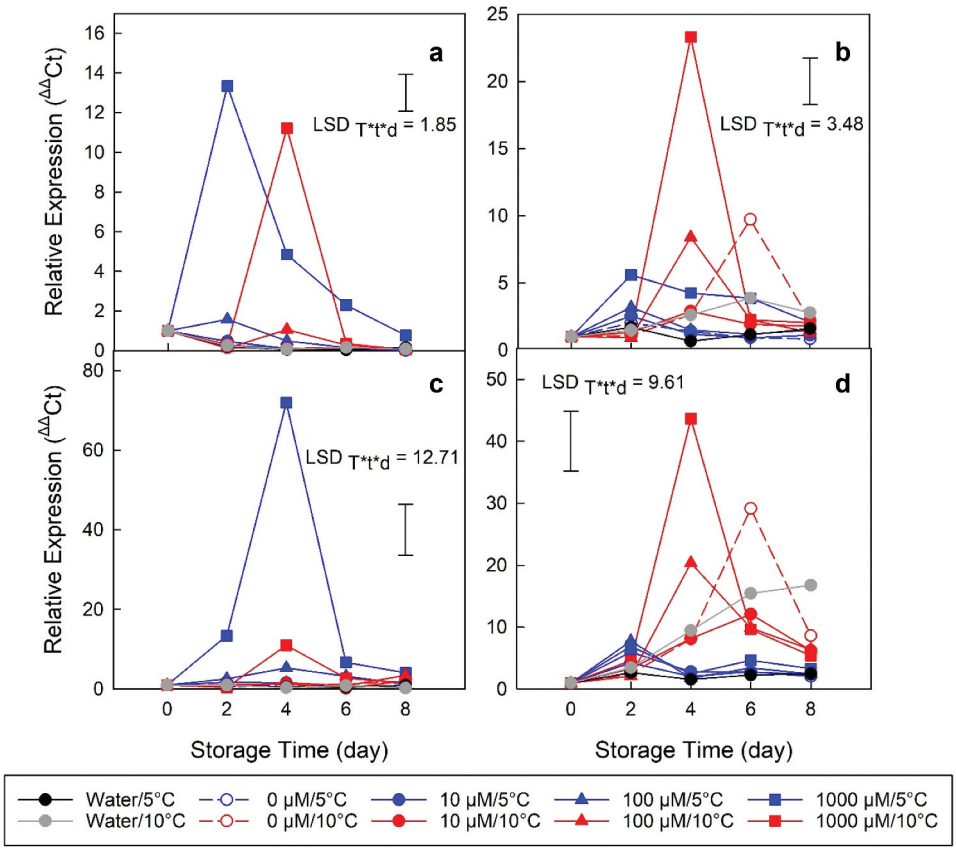


Figure 7. Gene expression changes in broccoli florets following treatment with hydrogen peroxide (10, 100 or 1000 µM) and a water control as quantified for *BoLOX2* (a), *BoOPR3* (b), *BoVSP2* (c) and *BoPPH* (d). Mean values are plotted ($n = 3$), whilst vertical bars represent the least significant difference ($p = 0.05$) for the interaction between treatment (T), temperature (t) and/or time (d) where stated.

at all dosage levels in florets stored at 10°C. Duarte-Sierra et al. (2023) reported that MeJA fumigation reduced broccoli colour change by 20.7% and reduced chlorophyll loss by 48.1% during storage at 4°C for 21 days. Xu et al. (2020) reported that 10 µM MeJA treatment reduced colour loss by 68.7% and reductions in chlorophyll and ascorbate by 68.7% and 33.9%, respectively, during 4 days of storage at 20°C. Dosage of 10 µM has also been reported as efficacious for other postharvest systems through antioxidant activity enhancement (Cao et al., 2009).

Contrary to these results, 10 µM MeJA dosage was detrimental to floret quality at 10°C due to significant reductions in °h, ascorbate content, and chlorophyll concentrations. D. Xu et al. (2020) also reported reduced expression and activity of chlorophyll catabolic enzymes following MeJA treatment, whilst our data demonstrated significant upregulation of *BoPPH*, which likely contributed to the increased rate of yellowing with greater MeJA dosage. Duarte-Sierra et al. (2023) reported that higher MeJA dosage was detrimental for quality retention, and Fang et al. (2020) reported significant chlorophyll catabolic activity in florets treated with 1 mm MeJA.

Li et al. (2021) attributed the beneficial effects of MeJA treatment to a suppression of respiration. Malate and citrate are liable to accumulate during senescence as products of catabolic metabolism and are utilised to maintain mitochondrial function, especially after energy reserve (e.g. sugars) depletion (Chrobok et al., 2016; Law et al., 2018). The increased accumulation of both organic acids is therefore indicative of increased advancement of senescence following MeJA treatment, especially with increased dosage at 10°C storage. The greater reduction of ascorbate seen in Tenderstem® may also be indicative of heightened ROS production following mitochondrial respiratory disruption as ROS production can increase under conditions of ATP depletion (Dumont & Rivoal, 2019; Launay et al., 2019). This corresponds with Duarte-Sierra et al. (2023) who reported an increased respiration rate in broccoli following MeJA treatment. Mitochondrial modification and increased ROS production are also stimulated directly by MeJA treatment, which may further contribute to respiratory dysfunction (Zhang & Xing, 2008). Under these conditions, senescent activity is liable to be stimulated, resulting in pigment breakdown and colour loss. Besides metabolic changes, MeJA may promote ethylene production that may accelerate senescent behaviour, particularly colour loss through chlorophyll catabolism (Gong & Mattheis, 2003; Zhao et al.,

2005). Surfactant use in the MeJA treatments significantly influenced floret colour through increased maintenance of °h and reduced carotenoid accumulation in the 0 µM treatment compared with water control. Disruption of epicuticular waxes with surfactant treatment (Takeno & Foy, 1974) may have altered floret water status, leading to modified stress responses to influence carotenoid accumulation. Our results showed that Tenderstem® broccoli expresses heightened sensitivity to MeJA stimulation with even low doses, triggering the onset of senescent activity including respiratory dysfunction and pigment loss feeding forward into quality declines with treatment that has been shown to be beneficial for conventional broccoli cultivars.

Causes of quality loss

Our data indicate that the origin of quality loss in Tenderstem® broccoli may occur through physiological mechanisms not targeted by oxidative hormetic action. The ability of oxidative stress to reduce head degreening has been correlated with chlorophyll catabolic enzyme suppression, preventing declines in chlorophyll content which occur during head degreening (Aiamla-Or et al., 2010; Costa et al., 2006). However, our results indicated that chlorophyll catabolism was not a leading contributor to Tenderstem® floret degreening, and this result may be responsible for the lack of observed benefit from treatment. In H_2O_2-treated florets, declines in °h in florets stored at 10°C were immediate but were asynchronous with significant declines in total chlorophyll content and upregulation of *BoPPH* that did not occur until day 8 and 6, respectively. Pheophytinase is the primary chlorophyll catabolic enzyme in broccoli (Büchert et al., 2011), and so the delayed uplifts in expression indicate that it is not a leading contributor to floret degreening in early storage.

Alternatively, substantial increases are seen in total carotenoids during early storage, with increasing carotenoid:chlorophyll ratios. Luo et al. (2019) reported that carotenoid accumulation (particularly β-cryptoxanthin and zeaxanthin) and chloroplast/chromoplast transformation preceded chlorophyll loss during broccoli storage. Therefore, we propose that the leading cause of degreening in Tenderstem® florets during early storage (e.g. up to day 4) is due to carotenoid accumulation as opposed to chlorophyll breakdown. Chlorophyll loss contributed to floret degreening in later storage (particularly following MeJA treatment) but as this occurs after unmarketable quality thresholds have been crossed this is of reduced relevance for quality preservation. It is considered that even if significant reductions of chlorophyll catabolism could have been realised through either treatment, the late stage at which chlorophyll loss becomes meaningful for floret colour would hinder overall quality retention.

Sepal carotenoid accumulation may occur as part of flower maturation (Guan et al., 2023) although Fang et al. (2020) reported that MeJA-promoted chlorophyll loss patterns did not correspond with typical maturation patterns. Carotenoids act in a protective role against oxidative damage through thermal dissipation via the xanthophyll cycle, whilst contributing to coordination of wider stress responses as precursors for abscisic acid synthesis (Duan et al., 2012). Both oxidative stress and MeJA have been shown to modify carotenoid profiles and enhance floral carotenoid content (Badmus et al., 2022; Bouvier et al., 1998; Vainstein et al., 2007). This is demonstrated in the present study by the maintenance of carotenoids following MeJA treatment despite significant declines in total chlorophyll when stored at 10°C. Therefore, by stimulating the accumulation of carotenoid pigments such treatments may promote, Tenderstem® floret yellowing during storage, rather than reducing it.

Developmental stage and hormetic effects

An additional factor which may explain the lack of a positive response to either treatment may be due to varietal differences between conventional broccoli and Tenderstem®. Hormetic responses to stress elicitation, particularly dose-dependent responses, can be highly variable between cultivars (Belz & Piepho, 2014), and so the hybrid nature of Tenderstem® broccoli may result in genotypically reduced responses to hormetic elicitation. Genotypic differences may also manifest as increased susceptibility to postharvest stress reflected in the general reduction in postharvest lifespan and increased handing requirements of Tenderstem® relative to conventional varieties. For example, Luo et al. (2019) reported that conventional broccoli varieties are colour stable at 10°C (Luo et al., 2019), whilst the present study has demonstrated that this is insufficient to prevent colour loss in Tenderstem® broccoli. Lowered tolerance of postharvest stress may reduce the ability of hormetic adaptation to mitigate postharvest stress, resulting in the lack of beneficial effects of either treatment demonstrated in the present study.

In addition to genotypic effects, the late harvesting of Tenderstem® broccoli may result in the influence of developmental differences when compared with conventional broccoli cultivars. Response to stress and effects of hormetic elicitation show considerable variation with developmental age in brassica (Ghimire et al., 2023; Jaiswal et al., 2020). The later harvest of Tenderstem® broccoli may reduce its ability to respond to hormetic elicitation or increase its sensitivity to abiotic stress. This is particularly relevant for MeJA given that JA effects vary between organs and developmental stages (Widemann et al., 2016), and JA

regulates both floral development and sepal senescence (Jibran et al., 2017; Pak et al., 2009). Therefore, mature Tenderstem® florets may either be less responsive to hormetic elicitation (e.g. H_2O_2) or promote alternative, adverse effects such as advancement of senescence (MeJA).

Temperature effects on stress and senescence

This study sought to utilise beneficial stimulation of stress responses to mitigate increases in storage temperature. However, our results revealed a complex relationship between storage temperature, stress, and postharvest physiology, which requires consideration when examining the potential for warmer storage temperatures to alleviate energy demands.

At the most fundamental level, lower storage temperatures will reduce quality loss through reduction in respiration and metabolic activity, which both conserve energy status and reduce catabolic activity. Alternative treatments that conserve energy status such as controlled atmosphere or substrate supplementation demonstrate similar effects on respiration and quality maintenance (Li et al., 2016; Xu et al., 2016). Therefore, increased respiratory dysfunction following energy reserve depletion is likely to contribute to the increased level of degreening observed at 10°C is contrast to the comparative stability of florets stored at 5°C. These effects are demonstrated in the present study by the increased citrate/malate accumulation, *BoPPH* promotion and greater declines in pigments seen in florets stored at 10°C. Warmer storage also increased *BoOPR3* expression in later storage, corresponding with the contributory role of the JA pathway in senescence coordination (Ahlawat et al., 2022; He et al., 2002). Increased storage temperature will therefore exacerbate senescence independently of stress perception/response, limiting the capacity for adaptative activity to reduce the effects of warmer storage temperature.

Our results also presented that equal stress stimuli can have varied effects under different temperature conditions. Storage temperature significantly modified abiotic stress gene expression in broccoli (Ahlawat et al., 2022) corresponding with our results which demonstrate that stress stimuli saw a greatly elevated expression at 10°C compared with reduced or absent responses at 5°C such as the H_2O_2-mediated promotion of *BoLOX2, BoOPR3,* and *BoVSP2* expression at 10°C, which was largely absent at 5°C. Exogenous application of H_2O_2 has an additive effect to endogenous ROS production (Zhang et al., 2023) which will be suppressed under cooler storage temperatures (Starzyńska et al., 2003). Increased ROS production at 10°C is liable to have worked in synergy with exogenous H_2O_2 application to promote the observed stress response, whilst suppressed endogenous production at 5°C prevented a response even with high H_2O_2 treatment.

Storage temperature also appears to influence signal transduction following stress perception. Storage at 10°C delayed the onset of MeJA-triggered upregulation in *BoLOX2* and *BoOPR3* and significantly reduced *BoVSP2* expression following stimulation with MeJA application. Chilling response has been associated with JA signalling (Hu et al., 2017) may have arisen from synergy between chilling stress and MeJA application. MeJA promotes pheophytinase activity (Fang et al., 2020) although increased expression was seen only at 10°C despite the comparable stimulation of *BoLOX2*/*BoOPR3* at both temperatures suggesting that chlorophyll catabolism is a secondary effect of MeJA treatment rather than a direct stimulus. Given that mitochondrial modification has been described as a primary effect of MeJA treatment (Zhang & Xing, 2008) the use of a lower storage temperature may reduce downstream effects of MeJA through wider respiratory suppression.

Taken together, these data indicate that temperature significantly modified stress perception and response through synergistic effects with wider physiological activities. More understanding of the interaction between separate physiological drivers at warmer storage temperatures is needed in order to facilitate management strategies that can benefit from warmer storage conditions to reduce overall energy demand. Furthermore, the beneficial effects of hormesis-derived postharvest strategies should also be examined under conditions typical of the supply chain to fully quantify their benefits. Many existing studies which reported beneficial oxidative hormesis effects in broccoli were conducted above 15°C (Aiamla-Or et al., 2012; Costa et al., 2006; Shi et al., 2016), and given the implied temperature response of stress perception it is likely that the elicitation response under these conditions will be of greater magnitude and therefore achieve enhanced, more persistent, than the effects demonstrated in the present study. However, storage at these temperatures may be rendered commercially undesirable through an inability to control quality losses unrelated to stress management (e.g. overmaturity or disease activity) or from food safety perspectives.

Conclusions

This study was undertaken to assess whether demonstratable benefits of low dosage H_2O_2 and MeJA treatment could be used to offset quality losses incurred by increasing postharvest storage temperatures of Tenderstem® broccoli. However, our results indicated that neither treatment is effective at

enhancing quality retention at either 5 or 10°C, due to reduced capacity to trigger adaptative responses (either due to reduced stress perception or lack of metabolic activity) or due to developmental/genotypic differences between Tenderstem® broccoli and conventional broccoli varieties, which have been shown to be responsive to such treatment. This highlights the need for careful optimisation of postharvest management strategies, which address production of biological behaviour in order to maximise quality retention potential. This work shows that there is an underlying interaction between temperature and stress perception/response, which needs to be further examined when optimising storage temperatures to ensure that postharvest physiology can be modulated in a predictable fashion. The lack of comparative studies on physiological responses to different temperature management and novel postharvest strategies hinders optimal management when extensive chilling is impractical. Although stress exposure can improve the nutritional quality in broccoli, such methods are commercially unfeasible if they negatively impact other quality attributes like colour. Finally, the relationship between the effects of postharvest stress, biological responses (both beneficial and counterproductive), and senescence requires further examination in order to identify priorities for controlling postharvest quality decline in fresh produce, alongside promoting exploitation of hormesis as a method of manipulating postharvest physiological responses.

Acknowledgements

Thanks are due to Neil Cairns, Monika Jodkowska, and Jade Symons for their technical support and manuscript review.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

Funding for this work was provided through the Horticulture Quality and Food Loss Network under the Biotechnology and Biological Sciences Research Council grant BB/T010819/1 and the Engineering and Physical Sciences Research Council project EP/V042548/1.

CRediT authorship contribution statement

Ewan Gage: conceptualisation, investigation, data curation, formal analysis, writing – original draft, writing – review and editing; **Leon A. Terry**: funding acquisition, writing – review and editing; **Natalia Falagán**: conceptualisation, funding acquisition, supervision, writing – review and editing.

Data availability statement

Data supporting this study is openly available from the Cranfield University research data depository at 10.57996/cran.ceres-2692

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Postharvest stress manipulation in Tenderstem® broccoli – examining the potential for stress-adaptative responses to promote sustainable quality retention

Gage, Ewan; Terry, Leon A.; Falagán, Natalia

2025-07
Taylor & Francis
https://doi.org/10.1080/14620316.2024.2449032
Gage E, Terry LA, Falagán N. (2025) Postharvest stress manipulation in Tenderstem® broccoli – examining the potential for stress-adaptative responses to promote sustainable quality retention. The Journal of Horticultural Science and Biotechnology, Volume 100, Issue 4, July 2025, pp. 484-498

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